

# Changes in a West Indian bird community since the late Pleistocene

David W. Steadman<sup>1\*</sup> and Janet Franklin<sup>2</sup>

<sup>1</sup>Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA, <sup>2</sup>School of Geographical Sciences and Urban Planning, Arizona State University, Tempe, AZ 85287-5302, USA

## ABSTRACT

**Aim** To establish a chronology for late Quaternary avian extinction, extirpation and persistence in the Bahamas, thereby testing the relative roles of climate change and human impact as causes of extinction.

**Location** Great Abaco Island (Abaco), Bahamas, West Indies.

**Methods** We analysed the resident bird community as sampled by Pleistocene (> 11.7 ka) and Holocene (< 11.7 ka) fossils. Each species was classified as extinct (lost globally), extirpated (gone from Abaco but persists elsewhere), or extant (still resident on Abaco). We compared patterns of extinction, extirpation and persistence to independent estimates of climate and sea level for glacial (late Pleistocene) and interglacial (Holocene) times.

**Results** Of 45 bird species identified in Pleistocene fossils, 25 (56%) no longer occur on Abaco (21 extirpated, 4 extinct). Of 37 species recorded in Holocene deposits, 15 (14 extirpated, 1 extinct; total 41%) no longer exist on Abaco. Of the 30 extant species, 12 were recovered as both Pleistocene and Holocene fossils, as were 9 of the 30 extirpated or extinct species. Most of the extinct or extirpated species that were only recorded from Pleistocene contexts are characteristic of open habitats (pine woodlands or grasslands); several of the extirpated species are currently found only where winters are cooler than in the modern or Pleistocene Bahamas. In contrast, most of the extinct or extirpated species recorded from Holocene contexts are habitat generalists.

**Main conclusions** The fossil evidence suggests two main times of late Quaternary avian extirpation and extinction in the Bahamas. The first was during the Pleistocene–Holocene transition (PHT; 15–9 ka) and was fuelled by climate change and associated changes in sea level and island area. The second took place during the late Holocene (< 4 ka, perhaps primarily < 1 ka) and can be attributed to human impact. Although some species lost during the PHT are currently found where climates are cooler and drier than in the Bahamas today, a taxonomically and ecologically diverse set of species persisted through that major climate change but did not survive the past millennium of human presence.

## Keywords

Bahamian Archipelago, birds, extinction, extirpation, Greater Antilles, Holocene, persistence, Pleistocene, West Indies.

\*Correspondence: David W. Steadman, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA.  
E-mail: dws@flmnh.ufl.edu

## INTRODUCTION

During the late Quaternary, the most dramatic biotic phenomenon on the American continents was the extinction of most species of large terrestrial mammals (megafauna),

including both herbivores and carnivores (Martin, 1973; Johnson, 2009). These losses took place during a period of major climatic and environmental change that defines the Pleistocene–Holocene transition (PHT; 15–9 ka). Because this time interval is also roughly when people first arrived in

North and South America, the causes and consequences of continental megafaunal collapse continue to be debated (Barnosky *et al.*, 2004; Gill *et al.*, 2009).

In the West Indies, on the other hand, insular megafauna, such as sloths, monkeys and large rodents, survived until the mid-Holocene or even later, which corresponds to the first human arrival in the Greater Antilles, but was characterized by changes in climate, sea level and island area that were much less drastic than those during the PHT (Steadman *et al.*, 2005; MacPhee, 2008). On Great Abaco Island (Abaco), located in the Bahamas north of the Greater Antilles, the largest terrestrial herbivore and carnivore at first human contact were both reptiles, namely the tortoise *Chelonoidis alburyorum* and the Cuban crocodile, *Crocodylus rhombifer* (Steadman *et al.*, 2007; Franz & Franz, 2009; Morgan & Albury, 2013). Both of these species perished on Abaco shortly after human colonization c. 1000 years ago (Hastings *et al.*, 2014; Steadman *et al.*, 2014).

Birds are the most diverse group of terrestrial vertebrates in the Bahamas and across the West Indies. As with mammals and reptiles, West Indian resident birds have undergone considerable late Quaternary losses of populations (extirpation) and species (extinction). Many of these losses have been documented through bones identified in cultural (archaeological) sites (e.g. Steadman *et al.*, 1984a; Carlson & Steadman, 2009), thereby demonstrating that the population or species survived into the period of human occupation (late Holocene). Other avian losses are based on bones identified from non-cultural (palaeontological) sites, the majority of which have not been radiocarbon-dated and their ages are therefore unknown beyond being generally 'late Quaternary' (e.g. Olson & Steadman, 1977; Suárez & Olson, 2001).

This study is based on remarkably well-preserved vertebrate fossils from Abaco in the northern Bahamas. To examine the relative rates of natural and anthropogenic faunal change, we establish a chronology for avian extinction, extirpation and persistence on Abaco, an endeavour not previously pursued for any West Indian island except Hispaniola (Steadman & Takano, 2013). The chronology allows us to test the role of climate change (and associated changes in sea level and island area) by analysing the extent to which species of Bahamian birds survived the PHT. We compare PHT patterns of extinction, extirpation and persistence with independently established estimates of climate and sea level for glacial (late Pleistocene) and interglacial (Holocene) times. We then examine the fates of the species that survived the substantial changes in climate, habitat, sea level and island area during the PHT, but were subjected to human activities (habitat loss, hunting, etc.) around 1 ka.

## MATERIALS AND METHODS

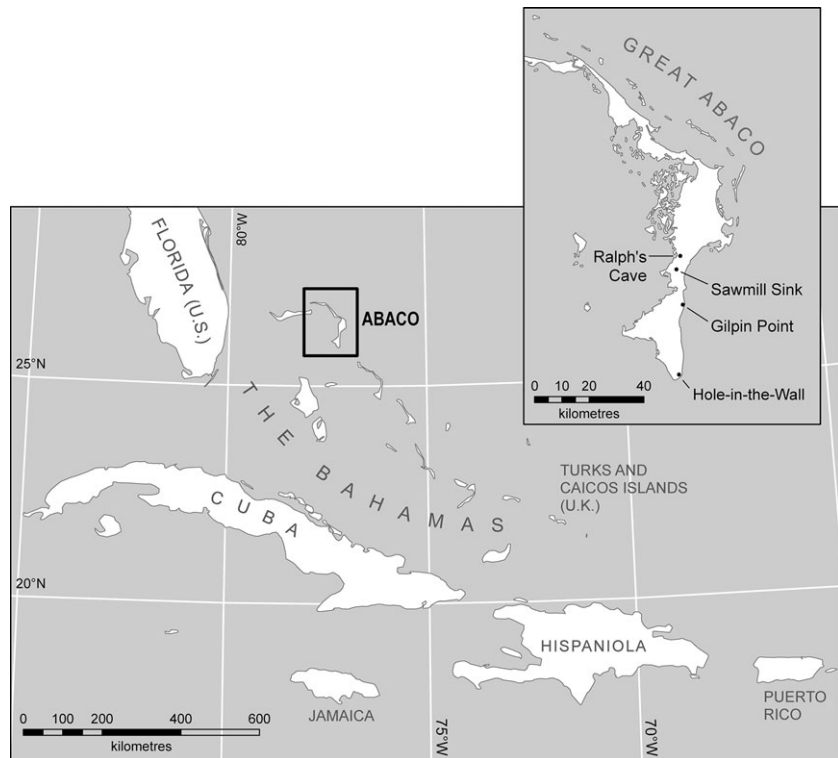
### Site setting

The Bahamian Archipelago consists of islands that lie just off the south-eastern coast of Florida and the northern coasts of

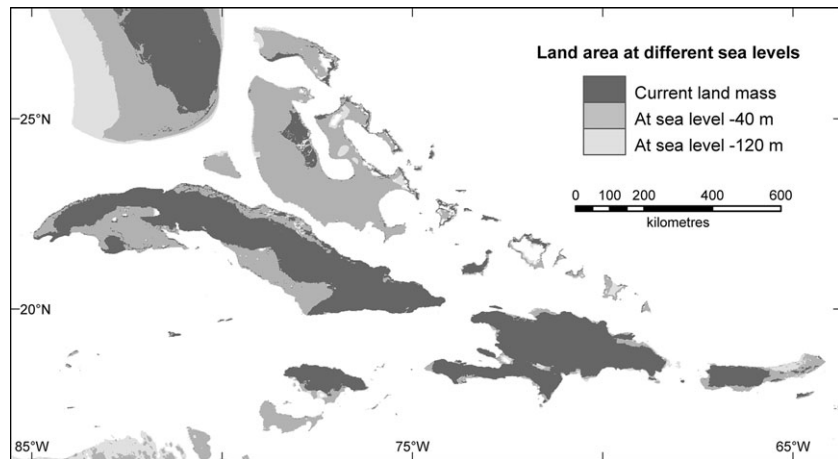
Cuba and Hispaniola (Fig. 1). The archipelago comprises 23 major islands (> 50 km<sup>2</sup>) and many smaller ones, lying on shallow carbonate banks separated by deep water. All the exposed bedrock in this tectonically stable archipelago is Quaternary aeolianite and shallow marine limestone, with the major build-up of the islands taking place as late as Marine Isotope Stage 5e, 125 ka (Carew & Mylroie, 1995; Hearty *et al.*, 1998; Hearty & Kaufman, 2000). The archipelago stretches 980 km from c. 27° N, 79° W in the north-west to c. 21° N, 71° W in the south-east. The island group comprises the independent Commonwealth of the Bahamas and the Turks and Caicos Islands, a British protectorate. Our study focuses on Great Abaco Island (hereafter, 'Abaco'), the third-largest island in the group today (1214 km<sup>2</sup>). All Bahamian islands are low-lying, with none exceeding 70 m elevation today, and most of the land is below 10 m elevation. Although lying on the North American plate, no Bahamian island was ever connected to mainland North America or any other continent.

The fossils we studied are from three types of site on Abaco (Fig. 1) – flooded caves known as blue holes (Sawmill Sink and Ralph's Cave), inorganic sediments in dry caves (Hole-in-the-Wall Cave) and intertidal peat deposits (Gilpin Point). Of these sites (described in detail in Appendix S1 in the Supporting Information), Sawmill Sink and Hole-in-the-Wall Cave yielded the greatest number of bird fossils. Sawmill Sink (26.21767° N, 77.21052° W, WGS84 datum) is an inland blue hole with Holocene vertebrate fossils from a peat deposit, as well as late Pleistocene vertebrate fossils from inorganic sediments (Steadman *et al.*, 2007; Franz & Franz, 2009; Morgan & Albury, 2013). Ralph's Cave (26.24997° N, 77.19004° W) is an inland blue hole where vertebrate fossils occur in a peat deposit. Hole-in-the-Wall Cave (25.86021° N, 77.18369° W) yielded fossils from dry, unstratified, inorganic sediments excavated by N. A. Albury and G. S. Morgan in January 1989. The Gilpin Point site (26.10457° N, 77.17767° W) is a bone-rich intertidal peat deposit on the windward (Atlantic Ocean) coast of southern Abaco (Steadman *et al.*, 2014).

Following Cohen *et al.* (2013), we set the age of the Pleistocene–Holocene boundary at 11.7 ka. This age is near the mid-point of the PHT, when sea level rose from c. –100 m to c. –25 m (Clark & Mix, 2000; Bard *et al.*, 2010). Based on these reference points, sea level was ≥ 35 m lower than present at ≥ 11 ka. This is the minimum age for the Pleistocene 'owl roost' bone deposits in Sawmill Sink, which occur on ledges 27–35 m below modern sea level. These deposits represent prey remains of barn owls that roosted in this currently flooded sinkhole when it was above sea level and dry. We used a global topographic database that includes seafloor topography (Smith & Sandwell, 1997) to estimate that, at that time, Abaco and Grand Bahama (on the Little Bahama Bank) were joined as a single 'superisland' with an area of c. 14,250 km<sup>2</sup> (13,880–14,550 km<sup>2</sup> at –35 to –45 m sea level), which is around six times the current land area of all the islands on this bank combined (2320 km<sup>2</sup>). This latest Pleistocene land area was only slightly smaller than the largest



**Figure 1** Study region showing Bahamian Archipelago (including the Turks and Caicos Islands), Greater Antilles and Florida, USA. Inset shows Great Abaco Island, with the fossil sites mentioned in the text (Sawmill Sink, Hole-in-the-Wall Cave, Ralph's Cave and Gilpin Point).



**Figure 2** Extent of land areas in the Bahamian Archipelago and Greater Antilles (southern Florida, USA, also shown) for current sea level and sea levels  $-40$  m and  $-120$  m (lower than present).

estimated extent of land on the Little Bahama Bank ( $16,492$ – $17,004$  km<sup>2</sup>), which occurred 10 kyr earlier, during the Last Glacial Maximum (LGM: 19–23 ka; Fig. 2, Appendix S2).

### Comparative osteology

Many of the prehistoric Bahamian bones retain every detail of the birds' original anatomy, and much of their original chemical composition. There is no clear-cut criterion as to when a late Quaternary bone should be called a fossil, given that the post-mortem period extends from decades into centuries, millennia and so on, with highly variable rates of mineralization, organic preservation and physical degradation.

We therefore use 'fossil' and 'bone' interchangeably because any distinction between these two words, whether based on chronology or organic preservation, would be arbitrary.

The avian fossils from Abaco are housed in Marsh Harbour, Abaco, at the scientific collections of the National Museum of the Bahamas (NMB), and in the Florida Museum of Natural History, University of Florida (UF; Gainesville, FL, USA). Identifications were based on direct comparisons with modern skeletal specimens in the UF Ornithology Collection, which includes every species of bird that currently lives in the Bahamas. Additional comparisons were made with avian fossils from various sites in the Bahamas and Hispaniola in the UF Vertebrate Paleontology Collection.

For some species, the taxonomic resolution of our identifications is conservative because of limited fossil material and/or limited modern skeletal specimens from Cuba and Hispaniola. For this reason, we classify *Glaucidium* sp., *Colaptes* sp., *Myadestes* sp., *Xenoligea* sp. and *Loxia* sp. as extirpated rather than extinct species. In each case, an endemic congener lives today on Cuba or Hispaniola, but we cannot yet resolve whether the Bahamian fossils are conspecific or represent an extinct species that may have been endemic to the Bahamas. As fossil and modern collections grow, we hope to resolve these issues.

### Radiocarbon dating

Until now, the radiocarbon ( $^{14}\text{C}$ ) chronology for late Quaternary vertebrates from Abaco had been based on accelerator mass spectrometer (AMS)  $^{14}\text{C}$  dating of ultrapurified collagen from individual fossils of an extinct tortoise, *Chelonoidis alburyorum*, and the extirpated Cuban crocodile, *Crocodylus rhombifer* (Steadman *et al.*, 2007, 2014). AMS  $^{14}\text{C}$  dating of bird fossils is challenging because only minute amounts of purified collagen can be extracted even from well-preserved bird bones, which are typically much smaller than those of tortoises and crocodiles. To build a chronology for the prehistoric bird communities, we compiled all AMS  $^{14}\text{C}$  age determinations performed thus far on fossils from Abaco, including reptiles, birds and mammals. These datings were carried out at Beta Analytic (Miami, FL, USA; for laboratory and calibration methods, see <http://www.radiocarbon.com/>). The  $^{14}\text{C}$  dates are presented as calendar years before present (cal. yr BP). In the text, we use 'ka' (thousand years ago) for general chronological values, whether or not based on  $^{14}\text{C}$  dating (for example, 4.5 ka = 4500 cal. yr BP).

### Species climate envelopes

For six extirpated species of bird identified from Pleistocene but not Holocene deposits, and that are widely distributed today in the Western Hemisphere (not restricted to the Greater Antilles), we examined the range of climate conditions found in their current distribution (their 'climate envelope'; Hijmans & Graham, 2006) as well as their current habitat associations. We compared those ranges with the climate conditions found today and those modelled for the LGM in the Bahamas to learn whether these species are associated with different climates from those now found on Bahamian islands, but perhaps similar to those found there during the late Pleistocene. Species locality data came from the North American Breeding Bird Survey 1966–2010 annual surveys (BBS; <http://www.pwrc.usgs.gov/bbs>; accessed on 2 September 2013) (Sauer *et al.*, 2011) and, for species whose ranges extend well into Mexico and regions further south, we included data from the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org/>; accessed 10 October 2013). BBS survey routes are c. 40 km long. GBIF occurrence records are compiled from a variety of sources, primarily museum collections.

Habitat associations were from accounts in the *Birds of North America* series (<http://www.birdsofna.org/>). Climate data were from <http://www.worldclim.org/> (Hijmans *et al.*, 2005; accessed 23 October 2013). We used data with a resolution of 2.5 arcminutes (about 5 km  $\times$  5 km grid cells) for both current (averaged over 1950–2000) and LGM climate. LGM climate was reconstructed using global climate model outputs from the Paleoclimate Modelling Intercomparison Project Phase II (<http://pmip2.lsce.ipsl.fr/>) and statistically down-scaled using the WorldClim current climate data. To account for uncertainty in the modelled palaeoclimate, we used both available models of LGM climate, the Community Climate System Model (CCSM) and the Model for Interdisciplinary Research on Climate (MIROC). We examined the bioclimatic ('BIOCLIM') variables available from WorldClim, because these seasonal summaries of precipitation and temperature means and extremes are frequently used to analyse species' ranges (Beaumont *et al.*, 2005; Franklin, 2010; Booth *et al.*, 2014). Climate data interpolated at this scale are strongly spatially autocorrelated (Franklin *et al.*, 2001), which helps to obviate the effect of the coarse resolution of the BBS data and the locational uncertainty of GBIF data in our analyses, the aim of which is to broadly circumscribe the climatic conditions within each species' range.

Values for all BIOCLIM variables were extracted for each location of the species' current distributions. To characterize the climate of the northern and central Bahamas, we extracted climate data at each grid point for the BIOCLIM grid cells intersecting the land area of the Little Bahama Bank and Great Bahama Bank. The frequency distributions of climatic variables were examined to compare the conditions where these species occur today with the conditions in the Bahamas today and in the Pleistocene (LGM). We expected average minimum temperature and precipitation to be the climatic factors that most limited the distributions of habitats preferred by these species. We tested for multivariate differences among climate envelopes of each species and the climate of current and LGM Bahamas using the multiresponse permutation procedure (MRPP) applied to eight largely uncorrelated ( $r < 0.7$ ) BIOCLIM variables (annual mean temperature, mean diurnal temperature range, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, annual mean precipitation, precipitation of the driest month and precipitation of the coldest quarter).

The northern Bahamian annual mean and average maximum temperatures were estimated from the WorldClim datasets to be c. 1–2 °C lower at LGM than present (Table 1), whereas the average minimum temperatures were c. 2–3 °C lower, and annual precipitation was c. 20–25% lower. Although these changes are substantial, they still reflect a subtropical climate that was likely to be frost-free. These modelled reconstructions of palaeoclimate portray the LGM Bahamas as cooler and drier than now, but did not show temperature declines as large as the 3–4 °C estimated for the southern Caribbean (Lin *et al.*, 1997; Lea *et al.*, 2003)

**Table 1** Average temperature and precipitation characteristic of the northern and central Bahamas based on WorldClim modern climate data and two models (CCSM and MIROC) for Last Glacial Maximum (LGM) climate ( $\pm$  SD). *n*, number of grid points at 5-km resolution.

| Climate period | <i>n</i> | Annual mean temperature | Average minimum temperature (°C) | Average maximum temperature (°C) | Annual mean precipitation (mm) |
|----------------|----------|-------------------------|----------------------------------|----------------------------------|--------------------------------|
| Modern         | 682      | 25.2 $\pm$ 0.6          | 18.1 $\pm$ 1.2                   | 32.0 $\pm$ 0.2                   | 1052 $\pm$ 245                 |
| LGM_CCSM       | 5428     | 23.2 $\pm$ 0.6          | 14.7 $\pm$ 1.4                   | 31.4 $\pm$ 0.4                   | 810 $\pm$ 88                   |
| LGM_MIROC      | 5428     | 23.0 $\pm$ 0.4          | 15.9 $\pm$ 0.6                   | 29.9 $\pm$ 0.4                   | 744 $\pm$ 57                   |

or the 5–6.4 °C estimated for the continental tropics (Porter, 2001). Other studies comparing these same climate reconstructions to distributions of fossil vertebrate taxa have noted that inconsistencies suggest potential inaccuracies in the modelled palaeoclimatic variables (McGuire & Davis, 2013).

## RESULTS

We submitted 11 individual avian fossils from Abaco for AMS radiocarbon ( $^{14}\text{C}$ ) dating, as well as 20 samples of associated, more readily dated, plant material (wood), reptile bones and mammal bones (Table 2). Of the seven avian fossils submitted from the owl roost deposits in Sawmill Sink (representing the extinct Small Abaco flightless rail, the extirpated burrowing owl and the extirpated eastern meadowlark; Table 3), none retained enough collagen to yield a  $^{14}\text{C}$  date. Based on independently derived sea-level data, the owl roost deposits must be older than 11 ka (see Appendix S2). From the peat deposit at Sawmill Sink, the extirpated white ibis and the extinct Creighton's caracara (Fig. 3) both have direct late Holocene AMS  $^{14}\text{C}$  dates, whereas three extirpated species (Cooper's/Gundlach's hawk, scaly-naped pigeon and burrowing owl) are associated with late Holocene AMS  $^{14}\text{C}$  dates on reptiles. From Hole-in-the-Wall Cave, a direct late Holocene AMS  $^{14}\text{C}$  date was determined on the extirpated burrowing owl, whereas a sandhill crane bone did not have enough collagen. Seven other extirpated species also occur in at Hole-in-the-Wall Cave (Audubon's shearwater, Swainson's hawk, purple gallinule, double-striped thick-knee, pygmy-owl, pearly-eyed thrasher and grasshopper sparrow). From the Gilpin Point site, the two extirpated species of birds (Bermuda petrel, Cuban crow) are associated with five late Holocene AMS  $^{14}\text{C}$  dates (on wood or reptile bones) that cluster around 920 to 900 cal. yr BP. In total, nine extinct or extirpated species from Abaco are associated with cultural deposits (Table 3), thus demonstrating their presence into the time of human occupation.

From Pleistocene contexts (the owl roost in Sawmill Sink), 25 of 45 species (21 extirpated, 4 extinct; total 56%) no longer reside on Abaco (Table 3). The 37 species of birds recorded as Holocene fossils feature 15 (14 extirpated, 1 extinct; total 41%) that are gone from Abaco. Nine of the total 30 extirpated or extinct species have been recovered in both Holocene and Pleistocene deposits, i.e. they survived the PHT only to be lost in the late Holocene. Incomplete and uneven sampling undoubtedly accounts for some of this small amount of overlap (Nowak *et al.*, 2000); our Holocene sample (280 identified

fossils) is much smaller than that from the Pleistocene (1803 identified fossils). Nevertheless, the evidence suggests two major times of avian extirpation and extinction – the Pleistocene–Holocene transition (15–9 ka) and the late Holocene (< 4 ka). From the Pleistocene sample, 96% of the individual fossils (1726 of 1803) represent extinct or extirpated species; this value for Holocene fossils is 54% (150 of 280).

Our data also document the persistence (Pleistocene fossil + Holocene fossil + extant on Abaco) of an ecologically diverse set of 12 species (Table 3) including aquatic/estuarine predators (night-herons, osprey), columbid granivores and frugivores (pigeons, doves), crepuscular/nocturnal predators (barn owl, nighthawk), and insectivorous or frugivorous songbirds (kingbird, yellowthroat, spindalis). This list will grow as more fossils are discovered and identified. Further evidence for incompleteness in the fossil data is that 12 species extant on Abaco were recorded as Pleistocene but not Holocene fossils.

For the 15 extinct or extirpated species of birds recorded only from Pleistocene contexts, the preferred habitats today for them or their nearest living relatives are pine woodlands, grasslands, or unknown (Table 3). In this group are five extirpated species, mainly continental today (brown-headed nuthatch, eastern bluebird, cliff swallow, short-eared owl and eastern meadowlark), that now occupy areas with lower average winter minimum temperatures and/or drier conditions or more open, grassy habitats than are found in the Bahamas now (Table 4, Fig. 4, Appendix S3). Their ranges may have shifted out of the Bahamas as the climate warmed and sea level rose after the last ice age, although this seems unlikely for the brown-headed nuthatch, which is still found on nearby Grand Bahama. Furthermore, the hindcast ranges of LGM minimum temperatures for the Bahamas were cooler but still more similar to those of the modern Bahamas than to those for any of these species (Fig. 4, Appendix S3). We note, however, that one of these species is a long-distance migrant today (the cliff swallow), so the minimum temperatures on its breeding grounds are irrelevant. The cave swallow is currently found in climatic conditions most similar to those found in the Bahamas today and during the LGM (Table 4, Fig. 4).

## DISCUSSION

### Biotic limitations of the Bahamas

For perspective, we note that the Bahamian islands sustain many fewer resident species of birds (and other vertebrates)

**Table 2** Accelerator mass spectrometer (AMS) radiocarbon ( $^{14}\text{C}$ ) dates from sites on Great Abaco Island (Bahamas), presented from youngest to oldest for species with multiple dates per site.

| Species                         | Material dated  | Sample number | $\delta^{13}\text{C}$ (‰) | Conventional $^{14}\text{C}$ age (yr BP) | $^{14}\text{C}$ age (cal. yr BP, $2\sigma$ ) |
|---------------------------------|-----------------|---------------|---------------------------|--|--|
| Sawmill Sink: peat              |                 |               |                           |  |  |
| * <i>Eudocimus albus</i>        | Ulna            | Beta-366019   | -16.6                     | 1780 ± 30                                | 1810–1690, 1680–1620                         |
| † <i>Caracara creightoni</i>    | Femur           | Beta-362616   | -19.0                     | 2390 ± 30                                | 2650–2650, 2490–2480, 2470–2350              |
| # <i>Crocodylus rhombifer</i>   | Radius          | Beta-298217   | -17.0                     | 2750 ± 30                                | 2920–2900, 2890–2770                         |
| # <i>Crocodylus rhombifer</i>   | Humerus         | Beta-230221   | -19.3                     | 2990 ± 50                                | 3340–3000                                    |
| # <i>Crocodylus rhombifer</i>   | Radius          | Beta-298218   | -16.5                     | 3580 ± 30                                | 3970–3830                                    |
| # <i>Crocodylus rhombifer</i>   | Vertebra        | Beta-230223   | -19.0                     | 3780 ± 50                                | 4340–4340, 4290–4060, 4050–3990              |
| # <i>Crocodylus rhombifer</i>   | Femur           | Beta-230222   | -16.4                     | 3820 ± 50                                | 4410–4080                                    |
| # <i>Chelonoidis alburyorum</i> | Humerus         | Beta-298219   | -20.3                     | 1020 ± 30                                | 970–920                                      |
| # <i>Chelonoidis alburyorum</i> | Scapula         | Beta-225509   | -21.1                     | 2580 ± 50                                | 2770–2690, 2640–2610, 2590–2500              |
| # <i>Chelonoidis alburyorum</i> | Vertebra        | Beta-225508   | -21.2                     | 2720 ± 40                                | 2880–2750                                    |
| # <i>Homo sapiens</i>           | Tibia           | Beta-228852   | -14.7                     | 1040 ± 40                                | 1050–1030, 1000–920                          |
| Sawmill Sink: owl roost         |                 |               |                           |  |  |
| † <i>Rallus cyanocavi</i>       | Humerus         | Beta-229508   | —                         | —  | Not enough collagen                          |
| † <i>Rallus cyanocavi</i>       | Humerus         | Beta-362618   | —                         | —  | Not enough collagen                          |
| † <i>Rallus cyanocavi</i>       | Tibiotarsus     | Beta-366021   | —                         | —  | Not enough collagen                          |
| * <i>Athene cunicularia</i>     | Tibiotarsus     | Beta-366020   | —                         | —  | Not enough collagen                          |
| * <i>Sturnella magna</i>        | Tarsometatarsus | Beta-229507   | —                         | —  | Not enough collagen                          |
| * <i>Sturnella magna</i>        | Tibiotarsus     | Beta-362617   | —                         | —  | Not enough collagen                          |
| * <i>Sturnella magna</i>        | Tibiotarsus     | Beta-366022   | —                         | —  | Not enough collagen                          |
| Hole-in-the-Wall Cave           |                 |               |                           |  |  |
| * <i>Grus canadensis</i>        | Pedal phalanx   | Beta-362619   | —                         | —  | Not enough collagen                          |
| * <i>Athene cunicularia</i>     | Scapula         | Beta-362620   | -18.3                     | 3580 ± 30                                | 3970–3940, 3930–3830                         |
| Ralph's Cave                    |                 |               |                           |  |  |
| # <i>Lasiurus minor</i>         | Humerus         | Beta-360273   | -19.3                     | 3580 ± 30                                | 3690–3560                                    |
| # <i>Myotis austroriparius</i>  | Humerus         | Beta-358784   | -18.5                     | 3740 ± 30                                | 4220–4210, 4160–4060, 4050–3990              |
| # <i>Natalus primus</i>         | Humerus         | Beta-358785   | -18.4                     | 3390 ± 30                                | 3700–3570                                    |
| # <i>Monophyllus redmani</i>    | Humerus         | Beta-358786   | -17.6                     | 1810 ± 30                                | 1820–1690, 1650–1630                         |
| # <i>Pteronotus parnellii</i>   | Humerus         | Beta-345516   | -18.0                     | 3310 ± 30                                | 3630–3460                                    |
| # <i>Pteronotus parnellii</i>   | Humerus         | Beta-345515   | -18.6                     | 3490 ± 30                                | 3840–3690                                    |
| Gilpin Point                    |                 |               |                           |  |  |
| # <i>Sabal palmetto</i>         | Wood            | Beta-345519   | -28.0                     | 990 ± 30                                 | 960–900, 860–830, 810–800                    |
| # <i>Conocarpus erectus</i>     | Wood            | Beta-345518   | -28.4                     | 900 ± 30                                 | 920–740                                      |
| # <i>Crocodylus rhombifer</i>   | Postorbital     | Beta-345510   | -19.8                     | 1020 ± 30                                | 970–920                                      |
| # <i>Chelonoidis alburyorum</i> | First costal    | Beta-345511   | -21.6                     | 1010 ± 30                                | 960–910, 840–840                             |
| # <i>Chelonia mydas</i>         | First costal    | Beta-345512   | -9.6                      | 990 ± 30                                 | 950–910, 850–840                             |

\*Extirpated species of bird.

†Extinct species of bird.

#Associated non-bird species (plants, reptiles and mammals).

today than the larger, nearby islands of Cuba and Hispaniola. At least four related causes underlie this phenomenon:

1. Much less time has elapsed for the evolution of endemic Bahamian forms because of the much younger subaerial geological age of the Bahamas (c. 500 ka; Hearty & Kaufman, 2000) than those of Cuba and Hispaniola ( $\geq 20$  million years; MacPhee, 2005).

2. Quaternary fluctuations in sea level led to much greater expansions and contractions in Bahamian land area than on Cuba or Hispaniola, neither of which lost more than 6% of land area from the LGM to today (compared to 80–90% losses in the Bahamas; Appendix S2). A lowered water table during glacial times probably reduced soil moisture in the karstic Bahamian soils even beyond the effects of reduced rainfall. On the other hand, the land areas of Bahamian islands would have been much smaller than even today

during the high sea-level stands at c. 125 and 400 ka (Hearty & Kaufman, 2000). We note, nevertheless, that small oceanic islands can have considerable potential to sustain substantial bird communities, including islands two to three orders of magnitude smaller than Abaco (Franklin & Steadman, 2008). Perhaps a factor in the current faunal impoverishment of small Bahamian islands is their greater vulnerability to human-caused losses (see 4, below).

3. The lower elevations and minimal topographic relief of Bahamian islands, even during glacial intervals, means that these islands have had much less diversity in climate and habitats than large, high islands such as Cuba or Hispaniola.

4. The Bahamian islands may have undergone more drastic human impact in the late Holocene than the larger, higher and more rugged Greater Antillean islands because of the relative ease of access to all parts of the islands by people, a

**Table 3** Numbers of Holocene and late Pleistocene bird fossils identified from Great Abaco Island, Bahamas. Values are numbers of identified specimens (NISP). Holocene sites are Gilpin Point, Hole-in-the-Wall Cave, Ralph’s Cave and the peat deposit at Sawmill Sink (see text). The owl roost deposit at Sawmill Sink is the only late Pleistocene site. Habitat categories: AE, aquatic/estuarine; CC, cave- or cliff-nester; CO, coppice (broad-leaved forest); GE, generalist; GR, grassland; MA, marine; PW, pine woodland. For the Holocene, NISP values in bold designate species that have been recovered from cultural (archaeological) sites in the West Indies.

| Taxon   | Common name                   | Habitat      | Holocene  | Late Pleistocene |
|---|-------------------------------|--------------|-----------|------------------|
| * <i>Puffinus lherminieri</i>                   | Audubon’s shearwater          | MA           | <b>4</b>  | 7                |
| * <i>Pterodroma cahow</i>                       | Bermuda petrel                | MA           | <b>3</b>  | —                |
| <i>Nyctanassa violacea</i>                      | Yellow-crowned night-heron    | AE           | <b>32</b> | 20               |
| <i>Nycticorax nycticorax</i>                    | Black-crowned night-heron     | AE           | <b>4</b>  | 2                |
| * <i>Eudocimus albus</i>                        | White ibis                    | AE           | <b>6</b>  | 2                |
| <i>Cathartes aura</i>                           | Turkey vulture                | GE           | 3         | —                |
| <i>Pandion haliaetus</i>                        | Osprey                        | AE           | <b>1</b>  | 1                |
| * <i>Accipiter cooperii/Accipiter gundlachi</i> | Cooper’s hawk/Gundlach’s hawk | CO           | 1         | 1                |
| * <i>Buteo swainsonii</i>                       | Swainson’s hawk               | GR           | 3         | 1                |
| <i>Falco sparverius</i>                         | American kestrel              | GR / PW      | —         | 4                |
| † <i>Caracara creightoni</i>                    | Creighton’s caracara          | GE?          | 64        | —                |
| * <i>Grus canadensis</i>                        | Sandhill crane                | GR           | 4         | —                |
| <i>Porzana carolina</i> (m)                     | Sora                          | AE           | 1         | —                |
| <i>Rallus longirostris</i>                      | Clapper rail                  | AE           | <b>1</b>  | —                |
| <i>Rallus limicola</i> (m)                      | Virginia rail                 | AE           | 4         | —                |
| † <i>Rallus cyanocavi</i>                       | Small Abaco flightless rail   | ?            | —         | 277              |
| † <i>Rallus new sp.</i>                         | Large Abaco flightless rail   | ?            | —         | 17               |
| * <i>Porphyrio martinicus</i>                   | Purple gallinule              | AE           | <b>1</b>  | —                |
| * <i>Burhinus bistriatus nanus</i>              | Double-striped thick-knee     | GR / PW      | <b>9</b>  | 2                |
| † <i>Gallinago new sp.</i>                      | Bahama snipe                  | ?            | —         | 3                |
| <i>Patagioenas leucocephala</i>                 | White-crowned pigeon          | CO           | <b>15</b> | 2                |
| * <i>Patagioenas squamosa</i>                   | Scaly-naped pigeon            | CO           | <b>11</b> | 4                |
| <i>Zenaida aurita</i>                           | Zenaida dove                  | CO           | <b>8</b>  | 3                |
| <i>Geotrygon chrysis</i>                        | Bridled quail-dove            | CO           | 3         | 1                |
| <i>Columbina passerina</i>                      | Common ground-dove            | CO / PW      | <b>4</b>  | 3                |
| † <i>Forpus new sp.</i>                         | Bahama parrotlet              | ?            | —         | 1                |
| <i>Amazona leucocephala</i>                     | Rose-throated parrot          | CO / PW      | —         | 2                |
| <i>Coccyzus minor</i>                           | Mangrove cuckoo               | CO           | <b>4</b>  | —                |
| <i>Tyto alba</i>                                | Common barn-owl               | CO / PW      | <b>6</b>  | 2                |
| * <i>Athene cucularia</i>                       | Burrowing owl                 | GR / PW      | <b>16</b> | 866              |
| * <i>Glaucidium sp.</i>                         | Pygmy-owl                     | CO / PW      | 1         | —                |
| * <i>Asio flammeus</i>                          | Short-eared owl               | GR / PW      | —         | 1                |
| <i>Chordeiles gundlachi</i>                     | Antillean nighthawk           | CO / GR / PW | <b>1</b>  | 2                |
| * <i>Caprimulgus cf. cubanensis</i>             | Greater Antillean nightjar    | CO / PW      | —         | 1                |
| <i>Chlorostilbon ricardii</i>                   | Cuban emerald                 | CO / PW      | 4         | —                |
| <i>Calliphlox evelynae</i>                      | Bahama woodstar               | CO           | 3         | —                |
| * <i>Colaptes sp.</i>                           | Flicker                       | PW           | —         | 1                |
| <i>Melanerpes superciliaris</i>                 | West Indian woodpecker        | CO / PW      | 2         | —                |
| <i>Sphyrapicus varius</i> (m)                   | Yellow-bellied sapsucker      | CO           | 2         | —                |
| <i>Contopus caribaeus</i>                       | Cuban pewee                   | PW           | —         | 3                |
| <i>Tyrannus dominicensis</i>                    | Gray kingbird                 | GR / PW      | —         | 3                |
| <i>Tyrannus caudifasciatus</i>                  | Loggerhead kingbird           | PW           | 1         | 2                |
| * <i>Corvus nasicus</i>                         | Cuban crow                    | CO / PW      | <b>22</b> | 1                |
| <i>Tachycineta cyaneoviridis</i>                | Bahama swallow                | PW           | —         | 3                |
| * <i>Petrochelidon pyrrhonota</i>               | Cliff swallow                 | CC           | —         | 5                |
| * <i>Petrochelidon fulva</i>                    | Cave swallow                  | CC           | —         | 14               |
| * <i>Sitta pusilla</i>                          | Brown-headed nuthatch         | PW           | —         | 5                |
| <i>Dumetella carolina</i> (m)                   | Gray catbird                  | CO           | —         | 3                |
| <i>Mimus gundlachi</i>                          | Bahama mockingbird            | CO / PW      | 6         | —                |
| <i>Mimus polyglottos</i>                        | Northern mockingbird          | PW           | 1         | —                |
| * <i>Margarops fuscatus</i>                     | Pearly-eyed thrasher          | CO           | <b>4</b>  | 1                |
| * <i>Myadestes sp.</i>                          | Solitaire                     | PW           | —         | 7                |
| * <i>Sialia sialis</i>                          | Eastern bluebird              | GR / PW      | —         | 18               |
| <i>Turdus plumbeus</i>                          | Red-legged thrush             | CO           | 11        | —                |
| <i>Dendroica pinus</i>                          | Pine warbler                  | PW           | —         | 5                |

**Table 3** Continued

| Taxon   | Common name                 | Habitat      | Holocene  | Late Pleistocene |
|---|-----------------------------|--------------|-----------|------------------|
| <i>Dendroica dominica</i>                                   | Yellow-throated warbler     | PW           | —         | 1                |
| <i>Dendroica palmarum</i> (m)                               | Palm warbler                | PW           | —         | 1                |
| <i>Dendroica coronata</i> (m)                               | Yellow-rumped warbler       | PW           | —         | 4                |
| <i>Seiurus aurocapillus</i> (m)                             | Ovenbird                    | CO           | 1         | —                |
| <i>Geothlypis rostrata</i>                                  | Bahama yellowthroat         | CO / PW      | 1         | 6                |
| * <i>Xenoligea</i> sp.                                      | 'highland-tanager'          | PW           | —         | 3                |
| <i>Spindalis zena</i>                                       | Western spindalis           | CO / PW      | 6         | 1                |
| <i>Pheucticus ludovicianus</i> (m)                          | Rose-breasted grosbeak      | CO           | 1         | —                |
| <i>Spizella passerina</i> (m?)                              | Chipping sparrow            | GR / PW      | —         | 2                |
| <i>Ammodramus sandwichensis</i> (m?)                        | Savannah sparrow            | GR / PW      | —         | 1                |
| * <i>Ammodramus savannarum</i>                              | Grasshopper sparrow         | GR           | 1         | —                |
| <i>Tiaris bicolor</i>                                       | Black-faced grassquit       | CO / GR / PW | —         | 2                |
| <i>Loxigilla violacea</i>                                   | Greater Antillean bullfinch | CO           | 4         | —                |
| * <i>Sturnella magna</i>                                    | Eastern meadowlark          | GR / PW      | —         | 480              |
| * <i>Icterus cf. dominicensis</i>                           | Greater Antillean oriole    | PW           | —         | 3                |
| * <i>Loxia</i> sp.  | Crossbill                   | PW           | —         | 3                |
| Total NISP (all species vs. */† species)                    |                             | —            | 280 / 150 | 1803 / 1726      |
| Total species (all species vs. */† species; residents only) |                             | —            | 37 / 15   | 45 / 25          |

\*Extant species but no longer on Abaco (= extirpated).

†extinct species; (m) migrant (included for completeness; not analysed with resident species).

trend seen on oceanic islands worldwide (Steadman, 2006, pp. 466–469).

### Chronology of extinction

Without chronological data, we have no basis for understanding when species became extinct or extirpated. Across the West Indies, we are still in the early stages of developing precise chronologies for fossil sites, most of which remain undated. Even at the Banana Hole site (New Providence Island), a dry cave site that had yielded the largest sample of Bahamian bird fossils until our work on Abaco, scientists assumed that the fossils dated to the Pleistocene (Brodkorb, 1959; Olson & Hilgartner, 1982) although no radiocarbon dates had been determined. Having a chronology for the sites on Abaco, we can interpret the fossil assemblages in terms of independent estimates of climate, sea level and island area for glacial (late Pleistocene) versus interglacial (Holocene) times. Within the Holocene, we can also evaluate the fossil assemblages by whether they pre-date or post-date human arrival.

Most of the extinct or extirpated species recorded on Abaco only from Pleistocene contexts are characteristic of open habitats, such as pine woodlands or grasslands. Furthermore, some of the extirpated species are found today where winters are cooler than in the modern or Pleistocene Bahamas. By contrast, the extinct or extirpated species recorded from Holocene contexts, regardless of their presence or absence as a Pleistocene fossil, are characteristic of a number of habitats, with no clear trend toward any one type. Because we have a much larger sample of fossils from Pleistocene than Holocene deposits on Abaco (1803 vs. 280 identified specimens as of 21 December 2013), a future priority will be to excavate more Holocene sites. We suspect that some of

the Holocene absences will prove to be sampling artefacts; further work is likely to increase the number of documented Holocene losses.

None of the Bahamian or Cuban sites with fossils of Creighton's caracara (Brodkorb, 1959; Suárez & Olson, 2001, 2003) had been <sup>14</sup>C dated until now. The dated Sawmill Sink specimen shows that this extinct carrion-feeder lived until the late Holocene, and is likely to have died out when the Bahamas and Cuba lost their large reptiles and mammals. This is comparable to the losses of avian scavengers in North America when most large mammals went extinct at the end of the Pleistocene (Steadman & Martin, 1984). With large species, whether reptiles, birds or mammals, it is intuitively easier to propose that direct human impact accounts for their extinction. Smaller species tend to have larger populations, to be less conspicuous, and to provide less meat and other raw materials, making it less likely that direct human exploitation caused their extirpation or extinction. Our results show, however, that even small species on West Indian islands can be vulnerable to extirpation and extinction following human arrival, regardless of the precise cause. Among the many examples of this phenomenon are lizards from the Lesser Antilles (Pregill *et al.*, 1994) and bats on Abaco (J. A. Soto-Centeno, American Museum of Natural History, New York, unpublished data).

That a number of extirpated or extinct species of birds survived on Abaco into the late Holocene is supported by the remains of such birds in Amerindian middens elsewhere in the archipelago, such as sites MC-6 (Jones O'Day, 2002) and MC-37 (Indian Cave; D.W.S., unpublished data) on Middle Caicos, and site GT-2 (Coralie) on Grand Turk (Carlson & Keegan, 2004). Late Holocene bones of extirpated or extinct birds also occur in prehistoric Amerindian middens elsewhere in the West Indies, such as Puerto Rico and





**Figure 3** Example of a fossil used for radiocarbon dating. Femur of Creighton's caracara (*Caracara creightoni*) from Great Abaco Island (Bahamas) in (a) posterior and (b) anterior aspects.

the Virgin Islands (Wetmore, 1918; Carlson & Steadman, 2009), Antigua (Steadman *et al.*, 1984b), and Montserrat (Steadman *et al.*, 1984a). These species form a taxonomically diverse group of water birds and land birds.

Large and sudden increases in rates of sedimentation, charcoal concentration, and pine pollen (pine woodland is a pyrogenic vegetation community; O'Brien *et al.*, 2008) took place 1.2–0.8 ka in the Bahamas (Kjellmark, 1996; Slayton, 2010). This is when people arrived in the northern Bahamas (Steadman *et al.*, 2007) and strongly suggests an increase in fire from human burning of the landscape. Similarly pronounced increases in charcoal have also been reported for earlier Holocene time intervals corresponding to human arrival in the Greater Antilles (Burney *et al.*, 1994; Horn *et al.*, 2000).

Other late Holocene changes in pollen spectra, charcoal influx or other sedimentary features from wetland cores in the Caribbean have been attributed to fluctuating wetter or drier conditions (Hodell *et al.*, 1991; Higuera-Gundy *et al.*, 1999; Lane *et al.*, 2014). Although these changes are not nearly as dramatic as the increase in charcoal when people arrived, non-anthropogenic late Holocene changes in wetlands could account for the loss on Abaco of at least one species, the white ibis, which is known to have nomadic breeding colonies that are affected by weather patterns and wetland conditions (Frederick *et al.*, 1996; Kushlan, 2010).

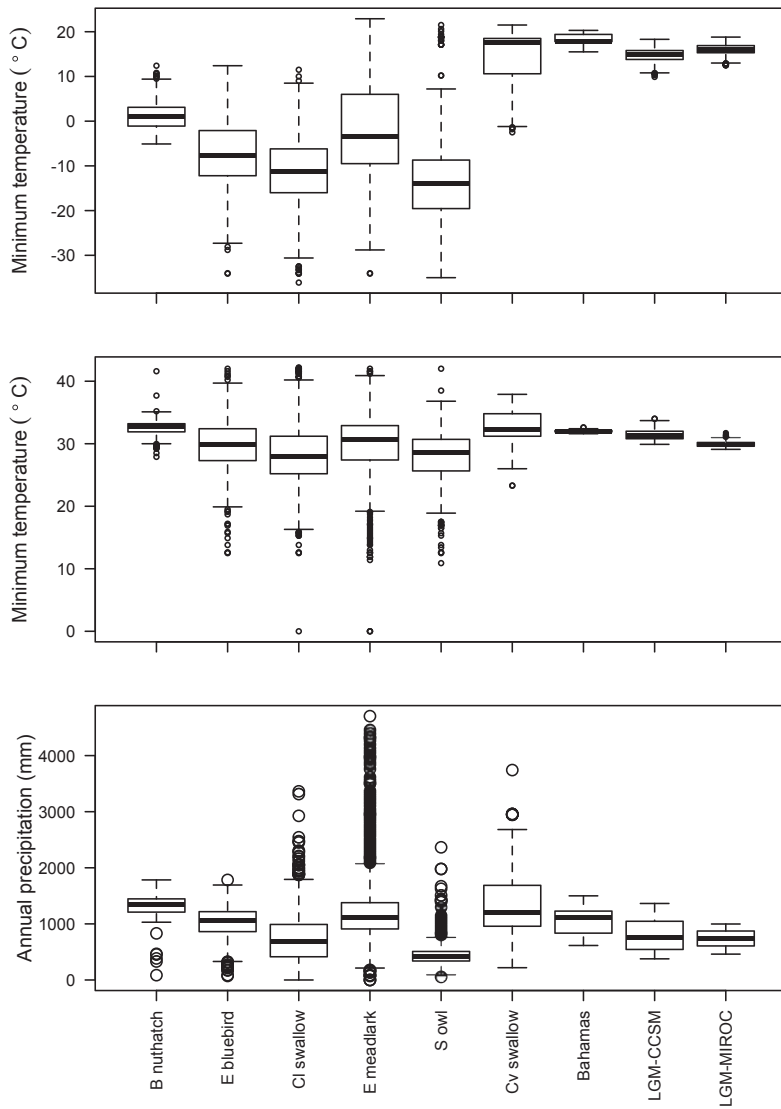
### The long view

When sea level was  $-40$  m, c. 10–12 ka, the two superislands of the Little Bahama Bank and Great Bahama Bank were separated by less than 34 km of ocean (Appendix S2). (The closest major islands on these separate banks are now c. 90 km apart.) In addition, the Great Bahama Bank super-island was only 20 km from Cuba at that time (now c. 180 km) and had a land area of 102,231–103,670 km<sup>2</sup>, nearly the same size as the largest West Indian island today

**Table 4** Extant bird species found as late Pleistocene fossils on Great Abaco Island but not occurring in the Bahamas today. *n*, number of occurrences [from the North American Breeding Bird Survey 1966–2010 annual surveys (BBS) and the Global Biodiversity Information Facility (GBIF); see text] used in the climate envelope analysis. The *A*-statistic from the multiresponse permutation procedure (MRPP) indicates the degree of dissimilarity between bioclimates of each species to modern and LGM climates in the Bahamas (1 = maximum dissimilarity;  $A < 0.3$  considered not very dissimilar). Species are listed in order of least to most similar climates. Although all values of *A* are  $P < 0.001$  based on 999 permutations, this level of significance is due to a very large sample size where even a very small effect size can be statistically significant. We therefore focus on the differences in *A* between species. Means and standard deviations of average minimum temperature of the coldest period ( $T_{\min}$ ), average maximum temperature of the warmest period ( $T_{\max}$ ) and annual mean precipitation (MAP) are from WorldClim data for species localities.

| Species                           |                       | <i>n</i> | <i>A</i> | $T_{\min}$ (°C) | $T_{\max}$ (°C) | MAP (mm)   |
|-----------------------------------|-----------------------|----------|----------|-----------------|-----------------|------------|
| <i>Sitta pusilla</i>              | Brown-headed nuthatch | 449      | 0.606    | 1.1 (3.0)       | 32.6 (1.2)      | 1326 (181) |
| <i>Sialia sialis</i>              | Eastern bluebird      | 2355     | 0.449    | -7.4 (7.3)      | 29.7 (3.4)      | 1036 (277) |
| * <i>Petrochelidon pyrrhonota</i> | Cliff swallow         | 2661     | 0.349    | -10.8 (7.7)     | 28.2 (4.5)      | 727 (379)  |
| <i>Sturnella magna</i>            | Eastern meadowlark    | 3234     | 0.280    | -1.2 (11.3)     | 29.9 (4.1)      | 1233 (614) |
| <i>Asio flammeus</i>              | Short-eared owl       | 468      | 0.263    | -12.8 (9.8)     | 27.8 (4.4)      | 477 (269)  |
| <i>Petrochelidon fulva</i>        | Cave swallow          | 257      | 0.125    | 14.3 (6.5)      | 32.6 (2.7)      | 1320 (616) |

\*Long-distance migrant today.



**Figure 4** Box-and-whisker plots showing the distributions (median heavy line, 25%/75% quartiles edges of box, 5%/95% whiskers, and outliers as points) of average minimum temperature of the coldest period, average maximum temperature of the warmest period and annual mean precipitation based on modern climate for modern localities [from the North American Breeding Bird Survey 1966–2010 annual surveys (BBS) and the Global Biodiversity Information Facility (GBIF); see text] for six extant bird species identified on Great Abaco Island (Bahamas) from Pleistocene but not Holocene deposits and that no longer occur in the Bahamas (Table 4): brown-headed nuthatch (*Sitta pusilla*), eastern bluebird (*Sialia sialis*), cliff swallow (*Petrochelidon pyrrhonota*), eastern meadowlark (*Sturnella magna*), short-eared owl (*Asio flammeus*) and cave swallow (*Petrochelidon fulva*). The distributions of those climate variables over the land area of the Little Bahama Bank and Great Bahama Bank are from modern climate data (Bahamas) and from two modelled Last Glacial Maximum climates (LGM-CCSM and LGM-MIROC; see text).

(Cuba, 111,463 km<sup>2</sup>) and exceeding that of the next largest island (Hispaniola, 76,193 km<sup>2</sup>). Thus, we must entertain the fact that the Bahamian Archipelago, although never higher than 200 m elevation even at the lowest late-Pleistocene sea levels, was essentially Greater Antillean in its land area, location and proximity to other islands during glacial times.

Climate fluctuations on Hispaniola were small in the Holocene compared to those of the PHT (Hodell *et al.*, 1991). Given the 20 or more glacial–interglacial cycles of the past 2 million years, perhaps it should not be surprising that most species of West Indian birds persisted on high islands during these drastic shifts in climate, sea level and land area. Nevertheless, extinctions and extirpations could have occurred on Bahamian banks, because the PHT’s rising sea levels caused the superislands to be replaced by smaller and more isolated islands, or as a result of the associated change in climate and habitat (becoming somewhat warmer and wetter; Pregill & Olson, 1981). For any of the 16 species of bird that lack evidence of persistence into the Holocene on Abaco, we must entertain this possibility, although we have

no real understanding of the lapse time to extinction from island shrinkage during the glacial-to-interglacial sea-level rise. Our analysis of climates and habitats associated with five of these species supports the notion that they would have found climatic conditions in the Bahamas somewhat more suitable in the LGM Pleistocene than currently, and/or that they prefer open habitats that probably were more widespread. The climate-based models do not consider plasticity in habitat preferences, or species interactions, which can be important in shaping distributions independent of climate (Cole, 1995; Stafford *et al.*, 1999; Semken *et al.*, 2010). Based on the evidence presented here, we can demonstrate that a taxonomically and ecologically diverse set of species did persist through the PHT, but did not survive the past millennium of human activities.

**ACKNOWLEDGEMENTS**

For help in the field or laboratory, we thank Nancy Albury, Bray Béltran, Richard Franz, Richard Hulbert, Brian Kakuk,

Kenney Krysko, Perry Maillis, Jim Mead, Gary Morgan, Julie Ripplinger, Hayley Singleton and Angel Soto-Centeno. Barbara Trapido-Lurie prepared Figs 1 and 2. This research was supported by the National Science Foundation (grant BCS-1118340 to J.F., grant BCS-1118369 to D.W.S.), National Geographic Society (grant EC0372-08) and the UF Ornithology Endowment. Research permits and other important logistical assistance were kindly provided by the Bahamas National Trust (Eric Carey, Markus Davis, Lynn Gape and David Knowles), Abaco Friends of the Environment (Michael Albury, Ruth Albury, Olivia Patterson and Kristin Williams), the National Museum of the Bahamas (Antiquities, Monuments and Museums Corporation) (Nancy Albury, Michael Pateman and Keith Tinker) and the Bahamas Caves Research Foundation (Brian Kakuk). We are especially grateful to Brian Kakuk and Nancy Albury for carrying out or coordinating the scuba-diving to collect fossils in flooded caves. For comments that improved the manuscript, we thank Jessica Oswald, Julie Ripplinger, Scott Robinson, Trevor Worthly and two referees.

## REFERENCES

- Bard, E., Hamelin, B. & Delanghe-Sabatier, D. (2010) Deglacial meltwater pulse 1B and Younger Dryas sea levels revisited with boreholes at Tahiti. *Science*, **327**, 1235–1237.
- Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L. & Shabel, A.B. (2004) Assessing the causes of late Pleistocene extinctions on the continents. *Science*, **306**, 70–75.
- Beaumont, L.J., Hughes, L. & Poulsen, M. (2005) Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecological Modelling*, **186**, 250–269.
- Booth, T.H., Nix, H.A., Busby, J.R. & Hutchinson, M.F. (2014) BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MAXENT studies. *Diversity and Distributions*, **20**, 1–9.
- Brodkorb, P. (1959) Pleistocene birds from New Providence Island, Bahamas. *Bulletin of the Florida State Museum, Biological Sciences*, **4**, 349–371.
- Burney, D.A., Burney, L.P. & MacPhee, R.D.E. (1994) Holocene charcoal stratigraphy from Laguna Tortuguero, Puerto Rico, and the timing of human arrival on the island. *Journal of Archaeological Science*, **21**, 273–281.
- Carew, J.L. & Mylroie, J.E. (1995) Quaternary tectonic stability of the Bahamian Archipelago: evidence from fossil coral reefs and flank margin caves. *Quaternary Science Reviews*, **14**, 145–153.
- Carlson, L.A. & Keegan, W.F. (2004) Resource depletion in the prehistoric northern West Indies. *Voyages of discovery: the archaeology of islands* (ed. by S. Fitzpatrick), pp. 85–107. Praeger, Westport, CT.
- Carlson, L.A. & Steadman, D.W. (2009) Examining temporal differences in faunal exploitation at two ceramic age sites in Puerto Rico. *Journal of Island and Coastal Archaeology*, **4**, 207–222.
- Clark, P.U. & Mix, A.C. (2000) Ice sheets by volume. *Nature*, **406**, 689–690.
- Cohen, K.M., Finney, S.C., Gibbard, P.L. & Fan, J.-X. (2013) The ICS International Chronostratigraphic Chart. *Episodes*, **36**, 199–204.
- Cole, K.L. (1995) Equable climates, mixed assemblages, and the regression fallacy. *Late Quaternary environments and deep history: a tribute to Paul S. Martin* (ed. by D.W. Steadman and J.I. Mead), pp. 131–138. The Mammoth Site of Hot Springs, Hot Springs, SD.
- Franklin, J. (2010) *Mapping species distributions: spatial inference and prediction*. Cambridge University Press, Cambridge, UK.
- Franklin, J. & Steadman, D.W. (2008) Prehistoric species richness of birds on oceanic islands. *Oikos*, **117**, 1885–1891.
- Franklin, J., Keeler-Wolf, T., Thomas, K., Shaari, D.A., Stine, P., Michaelsen, J. & Miller, J. (2001) Stratified sampling for field survey of environmental gradients in the Mojave Desert Ecoregion. *GIS and remote sensing applications in biogeography and ecology* (ed. by A. Millington, S. Walsh and P. Osborne), pp. 229–253. Kluwer Academic Publishers, Dordrecht.
- Franz, R. & Franz, S.E. (2009) A new fossil land tortoise in the *Chelonoidis* (Testudines: Testudinidae) from the northern Bahamas, with an osteological assessment of other Neotropical tortoises. *Bulletin of the Florida Museum of Natural History*, **49**, 1–44.
- Frederick, P.C., Bildstein, K.L., Fleury, B. & Ogden, J. (1996) Conservation of large, nomadic populations of White Ibises (*Eudocimus albus*) in the United States. *Conservation Biology*, **10**, 203–216.
- Gill, J.L., Williams, J.W., Jackson, S.T., Lininger, K.B. & Robinson, G.S. (2009) Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science*, **326**, 1100–1103.
- Hastings, A.K., Krigbaum, J., Steadman, D.W. & Albury, N.A. (2014) Domination by reptiles in a terrestrial food web of the Bahamas prior to human occupation. *Journal of Herpetology*, **48**, 380–388.
- Hearty, P.J. & Kaufman, D.S. (2000) Whole-rock aminostratigraphy and Quaternary sea-level history of the Bahamas. *Quaternary Research*, **54**, 163–173.
- Hearty, P.J., Neumann, A.C. & Kaufman, D.S. (1998) Chevron ridges and runup deposits in the Bahamas from storms late in oxygen-isotope substage 5e. *Quaternary Research*, **50**, 309–322.
- Higuera-Gundy, A., Brenner, M., Hodell, D.A., Curtis, J.H., Leyden, B.W. & Binford, M.W. (1999) A 10,300 <sup>14</sup>C yr record of climate and vegetation change from Haiti. *Quaternary Research*, **52**, 159–170.
- Hijmans, R.J. & Graham, C.H. (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, **12**, 2272–2281.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate sur-

- faces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Hodell, D.A., Curtis, J.H., Jones, G.A., Higuera-Gundy, A., Brenner, M., Binford, M.W. & Dorsey, K.T. (1991) Reconstruction of Caribbean climate change over the past 10,500 years. *Nature*, **352**, 790–793.
- Horn, S.P., Orvis, K.H., Kennedy, L.M. & Clark, G.M. (2000) Prehistoric fires in the highlands of the Dominican Republic: evidence from charcoal in soils and sediments. *Caribbean Journal of Science*, **36**, 10–18.
- Johnson, C.N. (2009) Ecological consequences of Late Quaternary extinctions of megafauna. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 2509–2519.
- Jones O'Day, S. (2002) Late prehistoric Lucayan occupation and subsistence on Middle Caicos Island, northern West Indies. *Caribbean Journal of Science*, **38**, 1–10.
- Kjellmark, E. (1996) Late Holocene climate change and human disturbance on Andros Island, Bahamas. *Journal of Paleolimnology*, **15**, 133–145.
- Kushlan, J.A. (2010) White Ibis (*Eudocimus albus*) nesting in the Bahamas. *Florida Field Naturalist*, **38**, 68–70.
- Lane, C.S., Horn, S.P. & Kerr, M.T. (2014) Beyond the Mayan Lowlands: impacts of the Terminal Classic Drought in the Caribbean Antilles. *Quaternary Science Reviews*, **86**, 89–98.
- Lea, D.W., Pak, D.K., Peterson, L.C. & Hughen, K.A. (2003) Synchronicity of tropical and high-latitude Atlantic temperatures over the last glacial termination. *Science*, **301**, 1361–1364.
- Lin, H.-L., Peterson, L.C., Overpeck, J.T., Trumbore, S.E. & Murray, D.W. (1997) Late Quaternary climate change from  $\delta^{18}\text{O}$  records of multiple species of planktonic foraminifera: high-resolution records from the anoxic Cariaco Basin, Venezuela. *Paleoceanography*, **12**, 415–427.
- MacPhee, R.D.E. (2005) 'First' appearances in the Cenozoic land-mammal record of the Greater Antilles: significance and comparison with South American and Antarctic records. *Journal of Biogeography*, **32**, 551–564.
- MacPhee, R.D.E. (2008) *Insulae infortunatae*: establishing the chronology of late Quaternary mammal extinctions in the West Indies. *American megafaunal extinctions at the end of the Pleistocene* (ed. by G. Haynes), pp. 169–193. Springer, Dordrecht.
- Martin, P.S. (1973) The discovery of America. *Science*, **179**, 969–974.
- McGuire, J.L. & Davis, E.B. (2013) Using the palaeontological record of *Microtus* to test species distribution models and reveal responses to climate change. *Journal of Biogeography*, **40**, 1490–1500.
- Morgan, G.S. & Albury, N.A. (2013) The Cuban crocodile (*Crocodylus rhombifer*) from late Quaternary fossil deposits in the Bahamas and Cayman Islands. *Florida Museum of Natural History Bulletin*, **52**, 161–236.
- Nowak, R.S., Nowak, C.L. & Tausch, R.J. (2000) Probability that a fossil absent from a sample is also absent from the paleolandscape. *Quaternary Research*, **54**, 144–154.
- O'Brien, J.J., Hiers, J.K., Callahan, M.A., Mitchell, R.J. & Jack, S.B. (2008) Interactions among overstory structure, seedling life-history traits, and fire in frequently burned Neotropical pine forests. *Ambio*, **37**, 542–547.
- Olson, S.L. & Hilgartner, W.B. (1982) Fossil and subfossil birds from the Bahamas. *Smithsonian Contributions to Paleobiology*, **48**, 22–56.
- Olson, S.L. & Steadman, D.W. (1977) A new genus of flightless ibis (Threskiornithidae) and other fossil birds from cave deposits in Jamaica. *Proceedings of the Biological Society of Washington*, **90**, 447–457.
- Porter, S.C. (2001) Snowline depression in the tropics during the Last Glaciation. *Quaternary Science Reviews*, **20**, 1067–1091.
- Pregill, G.K. & Olson, S.L. (1981) Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles. *Annual Review of Ecology and Systematics*, **12**, 75–z98.
- Pregill, G.K., Steadman, D.W. & Watters, D.R. (1994) Late Quaternary vertebrate faunas of the Lesser Antilles: historical components of Caribbean biogeography. *Bulletin of the Carnegie Museum of Natural History*, **30**, 1–51.
- Sauer, J.R., Hines, J.E., Fallon, J.E., Pardieck, K.L., Ziolkowski, D.J., Jr & Link, W.A. (2011) *The North American Breeding Bird Survey, results and analysis 1966–2010*. Version 12.07.2011. USGS Patuxent Wildlife Research Center, Laurel, MD. Available at: <http://www.mbr-pwrc.usgs.gov/bbs/> (accessed 2 September 2013)
- Semken, H.A., Graham, R.W. & Stafford, T.W. (2010) AMS  $^{14}\text{C}$  analysis of Late Pleistocene non-analog faunal components from 21 cave deposits in southeastern North America. *Quaternary International*, **217**, 240–255.
- Slayton, I.A. (2010) *A vegetation history from Emerald Pond, Great Abaco Island, the Bahamas, based on pollen analysis*. MS Thesis, University of Tennessee, Knoxville, TN.
- Smith, W.H.F. & Sandwell, D.T. (1997) Global sea floor topography from satellite altimetry and ship depth soundings. *Science*, **277**, 1956–1962.
- Stafford, T.W., Semken, H.A., Graham, R.W., Klippel, W.F., Markova, A., Smirnov, N.G. & Southon, J. (1999) First accelerator mass spectrometry  $^{14}\text{C}$  dates documenting contemporaneity of nonanalog species in late Pleistocene mammal communities. *Geology*, **27**, 903–906.
- Steadman, D.W. (2006) *Extinction and biogeography of tropical Pacific birds*. University of Chicago Press, Chicago.
- Steadman, D.W. & Martin, P.S. (1984) Extinction of birds in the late Pleistocene of North America. *Quaternary extinctions* (ed. by P.S. Martin and R.G. Klein), pp. 466–477. University of Arizona Press, Tucson, AZ.
- Steadman, D.W. & Takano, O.M. (2013) A late-Holocene bird community from Hispaniola: refining the chronology of vertebrate extinction in the West Indies. *The Holocene*, **23**, 936–944.
- Steadman, D.W., Watters, D.R., Reitz, E.J. & Pregill, G.K. (1984a) Vertebrates from archaeological sites on Montserrat, West Indies. *Annals of the Carnegie Museum*, **53**, 1–29.

- Steadman, D.W., Pregill, G.K. & Olson, S.L. (1984b) Fossil vertebrates from Antigua, Lesser Antilles: evidence for late Holocene human-caused extinctions in the West Indies. *Proceedings of the National Academy of Sciences USA*, **81**, 4448–4451.
- Steadman, D.W., Martin, P.S., MacPhee, R.D.E., Jull, A.J.T., McDonald, H.G., Woods, C.A., Iturralde-Vinent, M. & Hodgins, G.W.L. (2005) Asynchronous extinction of late Quaternary sloths on continents and islands. *Proceedings of the National Academy of Sciences USA*, **102**, 11763–11768.
- Steadman, D.W., Franz, R., Morgan, G.S., Albury, N.A., Kakuk, B., Broad, K., Franz, S.E., Tinker, K., Pateman, M.P., Lott, T.A., Jarzen, D.M. & Dilcher, D.L. (2007) Exceptionally well preserved late Quaternary plant and vertebrate fossils from a blue hole on Abaco, The Bahamas. *Proceedings of the National Academy of Sciences USA*, **104**, 19897–19902.
- Steadman, D.W., Albury, N.A., Maillis, P., Mead, J.I., Slapcinsky, J.D., Krysko, K.L., Singleton, H.M. & Franklin, J. (2014) Late Holocene faunal and landscape change in the Bahamas. *The Holocene*, **24**, 220–223.
- Suárez, W. & Olson, S.L. (2001) Further characterization of *Caracara creightoni* Brodkorb based on fossils from the Quaternary of Cuba (Aves: Falconidae). *Proceedings of the Biological Society of Washington*, **114**, 501–508.
- Suárez, W. & Olson, S.L. (2003) A new species of caracara (*Milvago*) from Quaternary asphalt deposits in Cuba, with notes on new material of *Caracara creightoni* Brodkorb (Aves: Falconidae). *Proceedings of the Biological Society of Washington*, **116**, 301–307.
- Wetmore, A. (1918) Bones of birds collected by Theodoor de Booy from kitchen midden deposits in the islands of St.

Thomas and St. Croix. *Proceedings of the U.S. National Museum*, **54**, 513–522.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Detailed descriptions of fossil sites and excavation methods.

**Appendix S2** Island areas and interisland distances estimated for sea levels from the Last Glacial Maximum to early Holocene.

**Appendix S3** Climate scatter-plots for six species of birds identified on Great Abaco Island from Pleistocene contexts.

## BIOSKETCHES

**David W. Steadman** is the Curator of Ornithology at the Florida Museum of Natural History, University of Florida. A biologist and palaeontologist interested in the modern and late Quaternary vertebrate communities on tropical islands, Steadman's current research focuses on the chronology of faunal change.

**Janet Franklin** is a professor in the School of Geographical Sciences and Urban Planning at Arizona State University. She is a biogeographer and landscape ecologist who is interested in understanding the long-term impacts of human and natural disturbance on the distribution of species and communities, particularly on Caribbean and Pacific islands.

---

Editor: John Stewart