Vertebrate community on an ice-age Caribbean island

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Contributed by Janet Franklin, September 15, 2015 (sent for review August 18, 2015; reviewed by Betsy Carlson and Ross D. E. MacPhee)

We report 95 vertebrate taxa (13 fishes, 11 reptiles, 63 birds, 8 mammals) from late Pleistocene bone deposits in Sawmill Sink, Abaco, The Bahamas. The >5,000 fossils were recovered by scuba divers on ledges at depths of 27–35 m below sea level. Of the 95 species, 39 (41%) no longer occur on Abaco (4 reptiles, 31 birds, 4 mammals). We estimate that 17 of the 39 losses (all of them birds) are linked to changes during the Pleistocene–Holocene Transition (PHT) (~15–9 ka) in climate (becoming more warm and moist), habitat (expansion of broadleaf forest at the expense of pine woodland), sea level (rising from −80 m to nearly modern levels), and island area (receding from ~17,000 km^2 to 1,214 km^2). The remaining 22 losses likely are related to the presence of humans on Abaco for the past 1,000 y. Thus, the late Holocene arrival of people probably depleted more populations than the dramatic physical and biological changes associated with the PHT.

vertebrates | fossils | island | extinction | Pleistocene

Interpreting the late Quaternary vertebrate fossil record on West Indian islands has been limited by the vague chronological resolution of most sites. Insular fossil faunas often have been assumed to be Pleistocene (rather than Holocene) in age without direct radiometric or other nonfaunal evidence such as sea level (1–3) (see *Site Setting*). This practice has been widespread with noncultural (paleontological) sites bearing extinct species of mammals, in part because extinct late Quaternary mammals from nearby North America (ground sloths, sabertooth cats, proboscideans, horses, camels, etc.) are indeed from Pleistocene contexts (4). Through direct radiocarbon (^{14}C) dating using accelerator-mass spectrometer (AMS) technology, we now know that at least some of the large, extinct West Indian mammals, such as sloths, survived well into the Holocene (5–7). Although AMS ^{14}C dates on insular sloth fossils range from the mid-Holocene to the late Pleistocene (7–9), all successful AMS ^{14}C dates done thus far on extirpated West Indian reptiles, birds, or micromammals (bats) are Holocene rather than Pleistocene (10–12).

Developing a sound chronology from cultural (archaeological) sites is often facilitated by ^{14}C dating charcoal, by stratigraphic association of the bones with temporally diagnostic ceramic or lithic artifacts, or by AMS ^{14}C dating the identified bones (e.g., refs. 13–15). In all such cases, the cultural sites on Caribbean islands are found to be mid-Holocene to late Holocene in age, not late Pleistocene. For Bahamian islands in particular, human arrival took place only about a millennium ago (~1 ka) (16, 17).

A West Indian fossil vertebrate community (38 taxa of reptiles, birds, and mammals) assigned to the Pleistocene rather than the Holocene was reported from the underwater Owl Roost deposits in Sawmill Sink, Abaco, The Bahamas (18). Our subsequent field and laboratory research at this flooded sinkhole has more than doubled the Pleistocene fauna to 95 species, by far the richest and most taxonomically diverse set of vertebrate fossils from the West Indies.

Here, we describe this mainly predator-accumulated fossil assemblage, which was deposited in glacial times when sea level was much lower than today. We focus on the late Pleistocene Owl Roost fossils rather than the younger fossils from the Sawmill Sink peat deposit, which have been AMS ^{14}C dated to the mid-Holocene to late Holocene (18, 19). The Pleistocene fossils allow us to evaluate which species were able to withstand the major changes in climate, sea level, land area, and habitat during the glacial–interglacial transition. These data thus provide long-term context for projecting how future climate change might affect West Indian biodiversity.

Site Setting

The Bahamian Archipelago consists of islands lying off southeastern Florida and north of Cuba and Hispaniola (Fig. 1). The archipelago features 23 major islands (>50 km^2) and many smaller ones that lie on shallow carbonate banks separated by deep water. All exposed bedrock is Quaternary aeolianite and shallow marine limestone; much of the build-up took place as late as Marine Isotope Substage 5e (125 ka) (20–22). The archipelago stretches 980 km from ~27° N, 79° W in the northwest to ~21° N, 71° W in the southeast; it comprises the independent Commonwealth of the Bahamas ("The Bahamas") and the Turks and Caicos Islands, a British protectorate. Our study focused on Great Abaco (hereafter, "Abaco"), the third-largest island in the group (1,214 km^2) (Fig. 1). No Bahamian island exceeds 63 m elevation, with most land below 10 m elevation. Although lying on the North American tectonic plate, no Bahamian islands ever were connected to North America, Cuba, or Hispaniola (23).

Sawmill Sink is a flooded sinkhole, or blue hole, in the pine woodlands of central Abaco. From its nearly circular water-filled entrance, the undercut walls of Sawmill Sink intersect the freshwater lens 2 m below ground level. Freshwater extends from the surface to the halocline at 9 m depth, where it also meets the

Significance

A flooded sinkhole cave on Abaco (The Bahamas) has yielded the richest (95 species) set of late Pleistocene (ice-age) vertebrates on any Caribbean island. We track changes in species composition on Abaco through time and relate those biotic changes to climate change. The warmer, wetter climate and rising sea levels from 15,000 to 9,000 years ago probably led to the disappearance on Abaco of at least 17 species of birds. Another 22 species of reptiles, birds, and mammals persisted through those environmental changes but did not survive the last 1,000 years of human activity. For the species that remain, we believe that direct human activity threatens their future more than climate change.

Author contributions: D.W.S., N.A.A., and J.F. designed research; D.W.S., B.K., and J.F. performed research; D.W.S., J.I.M., J.A.S.-C., H.M.S., and J.F. analyzed data; and D.W.S., N.A.A., J.I.M., J.A.S.-C., H.M.S., and J.F. wrote the paper.

Reviewers: B.C., Southeastern Archaeological Research, Inc.; and R.D.E.M., American Museum of Natural History.

The authors declare no conflict of interest.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1516490112/-/DCSupplemental.

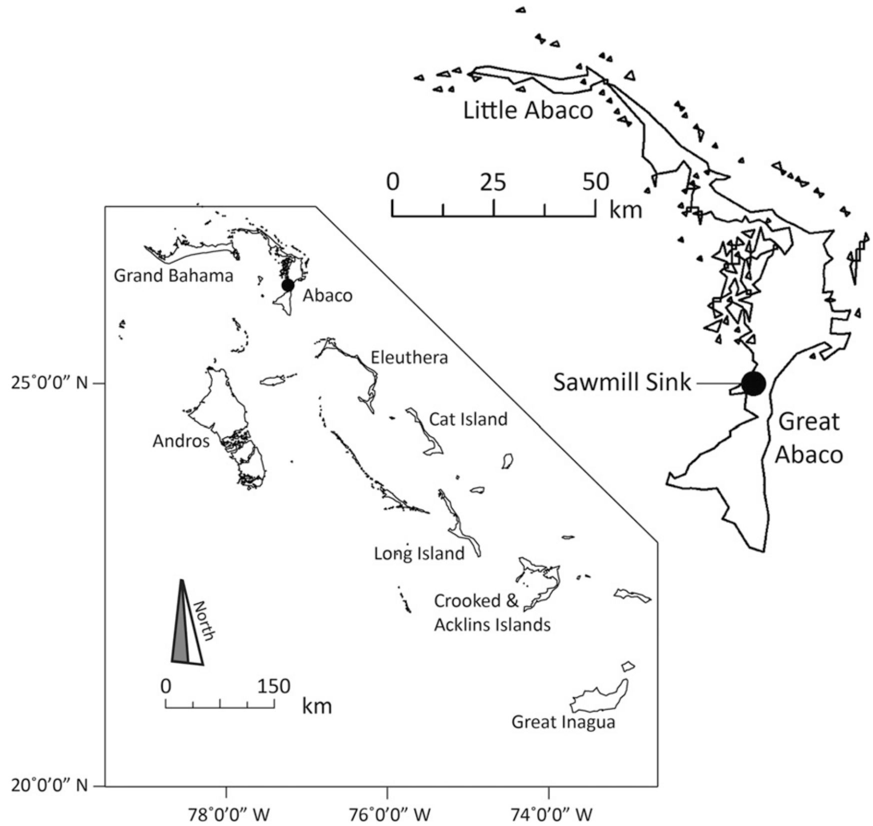

Fig. 1. The location of Sawmill Sink on Abaco (Great Abaco Island), The Bahamas.

top of a talus cone (Fig. 2). From 9 to 14 m depth, the stratified water is enriched with hydrogen sulfide from decomposing organic material, creating an opaque layer that blocks the sunlight. Clear anoxic salt water extends below 14 m to the bottom of the talus cone at 34 m depth and to a greater depth of 54 m in side passages that radiate more or less horizontally beyond the talus cone for >1,000 m.

Dark organic sediment (peat) covers the talus cone from 9 to 25 m depth but then thins with depth to inorganic fine-grained silt interspersed between boulders. Fossils in the peat are dominated by large species (tortoises, crocodiles) that accumulated through natural trap activity. No dense deposits of vertebrate microfossils occur in the peat. In the underlying anoxic salt water, three isolated deposits of bones from small vertebrates occur on ledges that we interpret as former owl roosts (R1, R2, and R3 in Figs. 2 and 3). This article is based on the fossils from these ledges, known collectively as the Owl Roost.

Results

Fish. Although often abundant in cultural contexts, no Pleistocene fish fossils have been reported before from Bahamian islands or elsewhere in the West Indies. H.M.S. identified 13 taxa (12 families) of fish from fossils in Sawmill Sink (Table 1 and Fig. 4), dominated by moray eels, blennies, and sleepers. A tooth of a rather large (1.3–2 m total length) shark (Carcharinidae) may have originated from the Pleistocene limestone surrounding the sinkhole. The remaining fishes inhabit shallow reefs, sandy shorelines and flats (including sea grass beds), coastal lagoons, tide pools, and estuaries, such as mangroves and tidal creeks (24, 25). With the exception of the large shark, the fish fossils represent very small individuals (<14 cm total length), which is compatible with their being prey remains of birds, especially the intertidal-feeding heron *Nyctanassa violacea* that once roosted and nested on ledges in Sawmill Sink. Although their preservation is excellent, the fish fossils are difficult to identify beyond the family level because of limited modern comparative material, especially for very small species or juvenile specimens.

Reptiles. J.I.M. identified 11 taxa of reptiles from Pleistocene fossils in Sawmill Sink (Table 1). Six of the genera are endemic to the West Indies (*Cyclura*, *Leiocephalus*, *Sphaerodactylus*, *Spondylurus*, *Chilabothrus*, *Cubophis*), each represented by a single species. The few small Owl Roost fossils of the extinct tortoise (*Chelonoidis alburyorum*) and crocodile (*Crocodylus rhombifer*) contrast markedly with the many associated skeletons

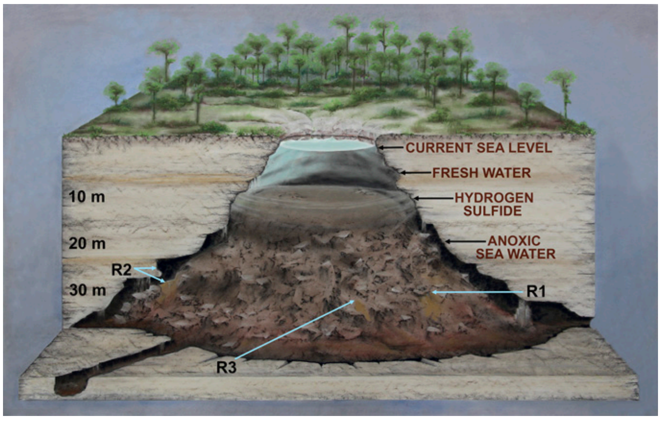

Fig. 2. Cross-section (profile) of Sawmill Sink, Abaco, The Bahamas, showing locations of the three Owl Roost Pleistocene fossil deposits (R1–R3).

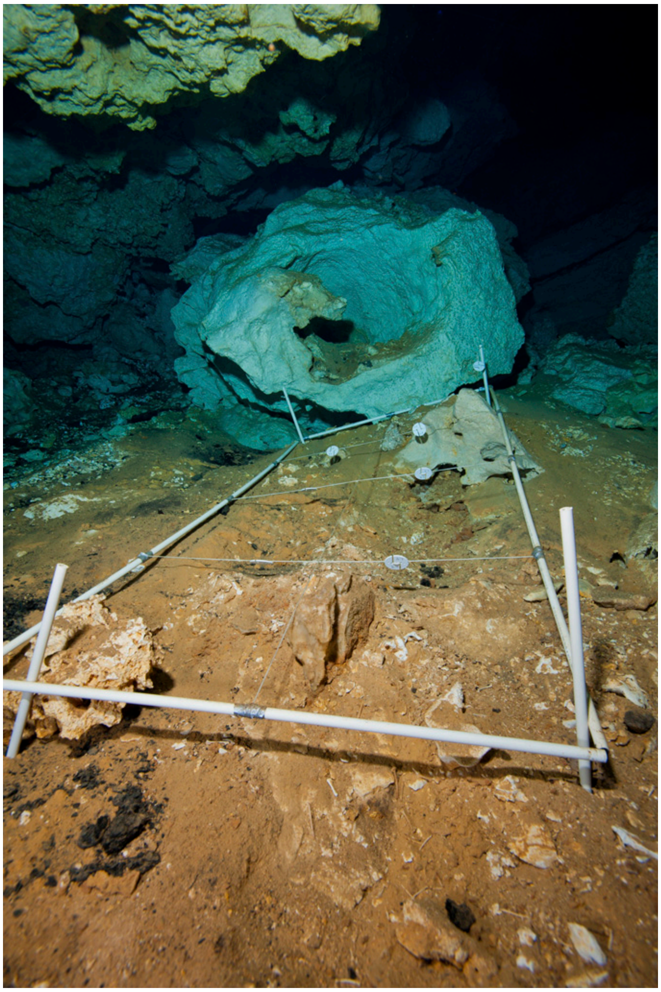

Fig. 3. Owl Roost (R1) in Sawmill Sink showing 1 × 2-m PVC grid frame.

of these large reptiles in the Holocene peat deposits of Sawmill Sink (26, 27). The iguana *Cyclura* sp. is known on the Little Bahama Bank only from fossils on Abaco (10, 18). Three species of *Cyclura* (none sympatric; all endangered) occur elsewhere in the island group (28).

Three species of *Anolis* live on Abaco today although only *Anolis sagrei* has been previously regarded as indigenous to the Little Bahama Bank (29). Late Holocene fossils of *Anolis* cf *distichus* as well as *A*. cf *sagrei* (10) provided evidence that two species of anoles are indigenous to Abaco, a proposal bolstered by the abundant Owl Roost fossils of both species.

The gecko *Sphaerodactylus* cf *notatus* is identified from characters in Hecht (30) and Pregill (31, 32). Eight species of *Sphaerodactylus* occur today in the Bahamian Archipelago, with *Sphaerodactylus notatus* the only one on Abaco (29). Two incomplete dentaries represent the skink *Spondylurus* sp. Fossil skinks are rare in the West Indies, confined to *Spondylurus* (*Mabuya*) *mabouya* on Puerto Rico (31); *S.* (*M.*) *mabouya* sensu lato occurs on Bahamian islands today only in the Turks and Caicos (28, 33, 34).

Indigenous West Indian Scolecophidia (blind snakes) include the Typhlopidae and Leptotyphlopidae (33). The fossils from Sawmill Sink are not diagnostic to family. *Typhlops lumbricalis* (Typhlopidae) inhabits Abaco today and may well be the species found as a fossil; leptotyphlopids no longer occur in the northern Bahamas (29). The boa *Chilabothrus* (= *Epicrates*) cf *exsul* is represented by more juvenile than adult vertebrae. No vertebrae from Sawmill Sink have characters of the pygmy boa *Tropidophis*, which we thus delete from the fossil record of Abaco (contra ref. 18). *Chilabothrus exsul* (on the Little Bahama Bank) has a snout-to-vent length (svl) up to 810 mm whereas *Chilabothrus striatus* (on the Great Bahama Bank) reaches an svl of 2,330 mm (31, 33, 35). The adult fossil vertebrae from Sawmill Sink suggest a midsized *Chilabothrus* (larger than modern *C. exsul*, but smaller than *C. striatus*). Our report here of *Chilabothrus* cf *exsul* is the same snake listed previously (18) as *Epicrates striatus*, which was based on *C. exsul* being regarded as a form of *C. striatus*. As with the boa *Chilabothrus*, the racer *Cubophis* cf *vudii* is recorded in Sawmill Sink by hundreds of anterior, midtrunk, and caudal vertebrae.

Birds. D.W.S. identified 63 avian taxa from Pleistocene fossils in Sawmill Sink (Table 1 and Fig. 5). All but 15 of the 3,922 bird fossils are from species that we regard as resident rather than migratory on Abaco. The 15 fossils are from four medium- or long-distance migrants (sanderling *Calidris alpina*, catbird *Dumetella carolinensis*, and warblers *Setophaga palmarum*, *Setophaga coronata*). The other 3,907 fossils reveal the late Pleistocene presence of 59 resident species, 31 of which (53%) no longer occur on Abaco. Six of these species are extinct, 20 now exist only outside of the Bahamas, and 5 still reside on Bahamian islands other than Abaco. Among the 31 species, 17 are not known from Holocene fossils on Abaco and may not have survived the glacial–interglacial transition there. These 17 species generally are characteristic of open habitats (pine woodlands and/or grasslands).

By far the three most abundant species of birds are the extirpated owl *Athene cunicularia*, extirpated meadowlark *Sturnella magna*, and extinct flightless rail *Rallus cyanocavi*. The first two species, characteristic of grasslands or open woodlands, make up 2,989 (76%) of the total 3,922 Pleistocene bird fossils (Table 1). Five of the eight Pleistocene species of raptors (osprey, hawks, kestrels, owls) no longer occur on Abaco, including open-country species such as *Buteo swainsonii*, *A. cunicularia*, and *Asio flammeus*.

Songbird (passerine) fossils are abundant in Sawmill Sink. An undescribed cowbird is the first reported large, extinct icterid in the West Indies; such species are common Pleistocene fossils on the American continents (36, 37). The five most common fossil songbirds are gone from Abaco today (in descending order, meadowlark *S. magna*, bluebird *Sialia sialis*, swallows *Petrochelidon pyrrhonota* and *Petrochelidon fulva*, and nuthatch *Sitta pusilla*). None of these species is known on Abaco from Holocene fossils, suggesting a major turnover in songbirds during the glacial–interglacial transition. *S. sialis* and *P. pyrrhonota* breed nowhere in the West Indies today; the other three species have modern breeding distributions that are mostly continental.

Four of these species (all but *P. fulva*) currently occupy climates that are cooler and in some cases drier than the modern Bahamas (38). The two swallows are cliff nesters; the other three species are characteristic of grassland or pine woodland. Five of the six species of birds we examined here by species distribution models (SDMs) were predicted to have had more climatically suitable habitat available in the Bahamas under Last Glacial Maximum (LGM) conditions (Table 2 and *SI Appendix*, Tables S1 and S2 and Figs. S1–S3). For the three species with purely continental modern distributions (hawk *Buteo lineatus*, sparrows *Spizella passerina*, and *Passerculus sandwichensis*), the predicted median habitat suitability in the Bahamas under the present climate ranges from 0.13 to 0.25 (on a scale of 0–1), compared with 0.37–0.62 at the LGM. The land area of the Bahamian Archipelago now is ~13,000 km^2, compared with ~125,000 km^2 at the LGM; for Abaco/Little Bahama Bank, the values are 1,214 km^2 and 16,750 km^2 (38) (*SI Appendix*, Fig. S4).

For the three modeled species with modern Greater Antillean distributions (Table 2), habitat suitability was predicted to have been much higher in the Bahamas during the LGM for the

Table 1. Summary of late Quaternary vertebrate fossils from Abaco, The Bahamas

Taxon	Common name	Habitat	Late Pleistocene fossils	Holocene fossil
Fish				
Carcharinidae	Shark	MA	1	—
Rhizoprionodon sp.	Sharpnose shark	MA	1	—
Muraenidae	Moray eel	MA	20	—
Serranidae (Epinephelinae)	Grouper	MA	1	—
Haemulidae	Grunt	MA	1	—
Gerreidae	Mojarra	MA/ES	1	—
Labridae	Wrass	MA	4	—
Scaridae	Parrotfish	MA	2	—
Labrisomidae	Scaled blenny	MA	25	—
Blenniidae	Combtooth blenny	MA	25	—
Eleotridae	Sleeper	AQ/MA/ES	44	—
Eleotridae/Gobiidae	Sleeper/goby	AQ/MA/ES	4	—
Diodontidae	Porcupinefish	MA/ES	3	—
Reptiles				
*Chelonoidis alburyorum**	Albury's tortoise	CO/PW	8	X
Crocodylus rhombifer†	Cuban crocodile	CO/PW	4	X
Cyclura sp.†	Rock iguana	CO/PW	5	X
Leiocephalus cf *carinata*	Bahama curly-tailed lizard	CO/PW	62	X
Anolis cf *sagrei*	Cuban anole	CO/PW	212	X
Anolis cf *distichus*	Bahama bark anole	CO	76	X
Sphaerodactylus cf *notatus*	Gecko	CO/PW	3	X
Spondylurus cf *mabouya*†	Skink	CO/PW	2	—
Scolecophidia (*Typhlops lumbricalis*?)	Blind snake	CO/PW	223	X
Chilabothrus cf *exsul*	Bahama boa	CO/PW	>300	X
Cubophis cf *vudii*	Bahama racer	CO/PW	>300	X
Birds				
Puffinus lherminieri†	Audubon's shearwater	MA	16	X
Pterodroma cahow†	Bermuda petrel	MA	—	X
Nyctanassa violacea	Yellow-crowned night-heron	AQ/ES	34	X
Nycticorax nycticorax	Black-crowned night-heron	AQ/ES	2	X
Eudocimus albus†	White ibis	AQ/ES	2	X
Cathartes aura	Turkey vulture	GE	1	X
Pandion haliaetus	Osprey	ES	1	X
Accipiter cooperii/Accipiter gundlachii†	Cooper's hawk/Gundlach's hawk	CO	1	X
Buteo aff. *lineatus**	"Red-shouldered" hawk	CO/PW?	1	—
Buteo swainsonii†	Swainson's hawk	GR	1	X
Falco sparverius	American kestrel	GR/PW	18	—
*Caracara creightoni**	Creighton's caracara	GE?	—	X
Grus canadensis†	Sandhill crane	GR	—	X
Porzana carolina (m)	Sora	AQ/ES	—	X
Rallus longirostris	Clapper rail	ES	—	X
Rallus limicola (m)	Virginia rail	AQ/ES	—	X
*Rallus cyanocavi**	Small Abaco flightless rail	?	545	—
Rallus new sp.*	Large Abaco flightless rail	?	19	—
Porphyrio martinicus†	Purple gallinule	AQ	—	X
Burhinus bistriatus nanus†	Double-striped thick-knee	GR/PW	4	X
Calidris alpina (m)	Dunlin	SH	1	—
Gallinago new sp.*	Bahama snipe	?	4	—
Patagioenas leucocephala	White-crowned pigeon	CO	2	X
Patagioenas squamosa†	Scaly-naped pigeon	CO	9	X
Zenaida aurita	Zenaida dove	CO	3	X
Zenaida asiatica	White-winged dove	CO/PW	1	—
Geotrygon chrysia	Bridled quail-dove	CO	6	X
Columbina passerina	Common ground-dove	CO/PW	5	X
Forpus new sp.*	Bahama parrotlet	?	1	—
Amazona leucocephala	Rose-throated parrot	CO/PW	2	—
Coccyzus minor	Mangrove cuckoo	CO	—	X
Tyto alba	Common barn-owl	CO/PW	2	X
Athene cunicularia†	Burrowing owl	GR/PW	1,914	X
Glaucidium sp.†	Pygmy-owl	CO/PW	—	X
Asio flammeus†	Short-eared Owl	GR/PW	1	—
Chordeiles gundlachii	Antillean nighthawk	CO/GR/PW	3	X
Antrostomus cf *cubanensis*†	Greater Antillean nightjar	CO/PW	1	—

Table 1. Cont.

Taxon	Common name	Habitat	Late Pleistocene fossils	Holocene fossil
Chlorostilbon ricordii	Cuban emerald	CO/PW	—	X
Calliphlox evelynae	Bahama woodstar	CO	—	X
Colaptes sp.[†]	Flicker	PW	2	—
Melanerpes superciliaris	West Indian woodpecker	CO/PW	1	X
Picoides villosus	Hairy woodpecker	CO/PW	3	—
Sphyrapicus varius (m)	Yellow-bellied sapsucker	CO	—	X
Contopus caribaeus	Cuban pewee	PW	4	—
Tyrannus dominicensis	Gray kingbird	GR/PW	3	—
Tyrannus caudifasciatus	Loggerhead kingbird	PW	6	X
Tyrannus cubensis[†]	Giant kingbird	CO/PW	2	—
Corvus nasicus[†]	Cuban crow	CO/PW	2	X
Tachycineta cyaneoviridis	Bahama swallow	PW	5	—
Petrochelidon pyrrhonota[†]	Cliff swallow	CC	30	—
Petrochelidon fulva[†]	Cave swallow	CC	29	—
Sitta pusilla[†]	Brown-headed nuthatch	PW	20	—
Dumetella carolinensis (m)	Gray catbird	CO	4	—
Mimus gundlachii	Bahama mockingbird	CO/PW	—	X
Mimus polyglottos	Northern mockingbird	PW	—	X
Margarops fuscatus[†]	Pearly-eyed thrasher	CO	1	X
Myadestes sp.[†]	Solitaire	PW	7	—
Sialia sialis[†]	Eastern bluebird	GR/PW	35	—
Turdus plumbeus	Red-legged thrush	CO	3	X
Dendroica pinus	Pine warbler	PW	10	—
Dendroica dominica	Yellow-throated warbler	PW	3	—
Dendroica palmarum (m)	Palm warbler	PW	5	—
Dendroica coronata (m)	Yellow-rumped warbler	PW	5	—
Seiurus aurocapillus (m)	Ovenbird	CO	—	X
Geothlypis rostrata	Bahama yellowthroat	CO/PW	12	X
Xenoligea sp.[†]	"Highland-tanager"	PW	5	—
Coereba flaveola	Bananaquit	CO	1	—
Spindalis zena	Western spindalis	CO/PW	1	X
Pheucticus ludovicianus (m)	Rose-breasted grosbeak	CO	—	X
Spizella passerina[‡]	Chipping sparrow	GR/PW	12	—
Passerculus sandwichensis[‡]	Savannah sparrow	GR/PW	2	—
Ammodramus savannarum[†]	Grasshopper sparrow	GR	1	X
Tiaris bicolor	Black-faced grassquit	CO/GR/PW	6	—
Loxigilla violacea	Greater Antillean bullfinch	CO	5	X
Sturnella magna[†]	Eastern meadowlark	GR/PW	1,075	—
Agelaius phoeniceus	Red-winged blackbird	AQ/GR	4	—
Icterid, genus uncertain[†]	Large cowbird	?	5	—
Icterus cf *dominicensis*[†]	Greater Antillean oriole	PW	4	—
Loxia megaplaga[†]	Hispaniolan crossbill	PW	7	—
Mammals				
Eptesicus fuscus	Big brown bat	CC	27	X
Myotis austroriparius[†]	Southeastern myotis	CC	27	X
Lasiurus minor[†]	Minor red bat	CC	1	X
Tadarida brasiliensis	Mexican free-tailed bat	CC	18	—
Macrotus waterhousii	Waterhouse's leaf-nosed bat	CC	22	X
Erophylla sezekorni	Buffy flower bat	CC	1	X
Mormoops blainvillii[†]	Antillean ghost-faced bat	CC	1	—
Geocapromys ingrahami[†]	Bahaman hutia	GE	1	X
Fish totals				
NISP			132	—
Species (all)			13	—
Species (*/† only)			0	—
Reptile totals				
NISP			>1,195	—
Species (all)			11	10
Species (*/† only)			4	3
Bird totals				
NISP (all species)			3,922	—
NISP (residents only)			3,907	—
NISP (*/† species only)			3,773	—

Table 1. Cont.

Taxon	Common name	Habitat	Late Pleistocene fossils	Holocene fossil
Species (all)			63	42
Species (residents only)			59	37
Species (*/† only)			31	14
Mammal totals				
NISP (all species)			98	—
NISP (*/† species only)			30	—
Species (all)			8	6
Species (*/† only)			4	4

Values are numbers of identified specimens (NISP). Late Pleistocene, the Owl Roost deposit at Sawmill Sink. The Holocene sites are Gilpin Point, Hole-in-the-Wall Cave, Ralph's Cave, and the peat deposit at Sawmill Sink (10, 12, 38). Habitat categories: AQ, aquatic (freshwater); CC, cave- or cliff-nester; CO, coppice (broadleaf forest); ES, estuarine; GE, generalist; GR, grassland; MA, marine; PW, pine woodland; SH, shoreline. m, migrant species (birds only). —, not present.
*Extinct species.
†Extant species but no longer occurring on Abaco (= extirpated).
‡Species exists on Abaco today only as a migrant, not a resident.

nightjar *Antrostomus cubanensis*, and higher but still very low for the crossbill *Loxia megaplaga*. For the kingbird *Tyrannus cubensis*, the LGM was predicted to have been less climatically suitable than the Bahamas today. This rare species now occurs only in a few regions of Cuba (39). Its historic distribution may not be well characterized by the data used for modeling, given the old records of *T. cubensis* in the southern Bahamas (40). *L. megaplaga* also has a small, fragmented, and declining range; its climatically suitable habitat may also be poorly represented in our SDM.

Mammals. We identified a single fossil of the extirpated rodent *Geocapromys ingrahami* from Sawmill Sink. J.A.S.-C. identified 98 bat fossils from maxillae, dentaries, humeri, and radii (Table 1 and Fig. 6). These fossils include seven species of bats in four families. Four of the seven species of bats still are common and widespread on Abaco (*Eptesicus fuscus*, *Tadarida brasiliensis*, *Macrotus waterhousii*, and *Erophylla sezekorni*). *Lasiurus minor* is rare across the Bahamas and in need of current population assessment. The other two species (*Myotis austroriparius* and *Mormoops blainvillii*) certainly have been extirpated from Abaco. The surviving group of bats includes both insectivores and nectarivores/frugivores whereas all extirpated species are insectivores.

The two most abundant species in Sawmill Sink are the insectivorous *E. fuscus* and *M. austroriparius* (Table 1). *E. fuscus* occurs across the Americas and the Caribbean and is widely distributed in the Bahamas (41, 42). Although widespread in the southeastern United States (43), Sawmill Sink is the only locality where *M. austroriparius* has been found in the Caribbean. The third and fourth most abundant species (*M. waterhousii* and *T. brasiliensis*) are insectivorous bats found throughout the Bahamas (41, 42). Only one of the extirpated species, *M. blainvillii*, was found on Abaco as a Pleistocene but not Holocene fossil (12).

Discussion

Extinction. Our research helps to assess the abilities of species to withstand changes in climate, land area, and habitat associated with the Pleistocene–Holocene Transition (PHT) (∼15–9 ka), as well as the late Holocene phenomena associated with human occupation. Climate models have the West Indies being cooler and drier in the late Pleistocene than today (44, 45). By analogy with the habitat preferences of extant conspecific or congeneric taxa, the bird evidence suggests that pine woodlands or pine grasslands (savannas) dominated the large island formed by the Little Bahama Bank during the late Pleistocene (38).

Among fishes, all 13 identified Pleistocene taxa are widespread in the Caribbean today; even if species-level identifications were possible, they probably would be found to exist in estuarine or shallow marine habitats on Abaco. As the first Pleistocene fish fossils from a Bahamian island, the Sawmill Sink specimens are a starting point for understanding the biogeographic history of shallow-water marine vertebrates in the region.

The terrestrial vertebrates (reptiles, birds, and mammals) tell a different story. Four of the 11 reptilian taxa recorded in the Pleistocene (36%) no longer occur on Abaco, with three large species (*Chelonoidis alburyorum*, *Crocodylus rhombifer*, and *Cyclura* sp.) surviving the PHT but not human presence. The skink *Spondylurus* sp. is the only reptile known exclusively (thus far) from Pleistocene fossils; whether it survived the PHT cannot be gauged until more Holocene small reptile fossils are available from Abaco. It is noteworthy that the tortoise, crocodile, and rock iguana all existed on Abaco during the cooler and drier late Pleistocene. Although ectothermic, these reptiles (and the ones that still survive) must have had expanded habitat/climate tolerances compared with where they are found today or during the late Holocene.

Among resident birds, 31 of the 59 Pleistocene species (53%) are gone from Abaco, with 17 of them unrecorded after the PHT (Table 1). These losses cover most feeding guilds (raptors, insectivores, omnivores, frugivores, and granivores) but are united by a general preference for open habitats (grasslands and pine

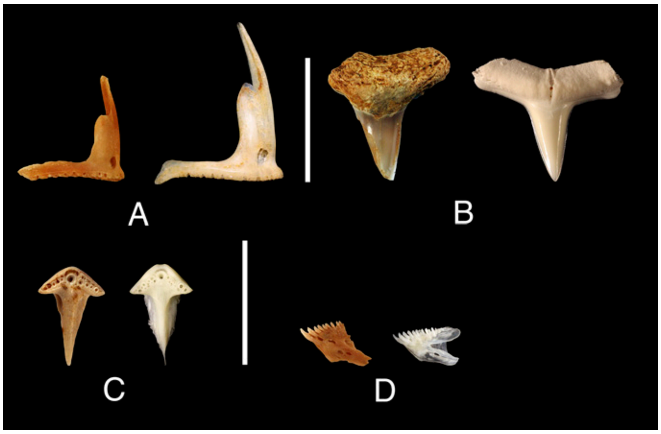

Fig. 4. (*A*) Maxilla of grunts in lateral aspect. (*Left*) Fossil, Haemulidae. (*Right*) Modern, *Orthopristis chalceus*. (*B*) Tooth of sharks in labial aspect. (*Left*) Fossil, Carcharhinidae. (*Right*) Modern, *Carcharhinus limbatus*. (*C*) Vomer of scaled blennies in ventral aspect. (*Left*) Fossil, Labrisomidae. (*Right*) Modern, *Labrisomus nuchipinnis*. (*D*) Dentary of wrasses in lateral aspect. (*Left*) Fossil, Labridae. (*Right*) Modern, *Thalassoma bifasciatum*. All fossils are from Sawmill Sink, Abaco, The Bahamas. (Scale bars: 10 mm.)

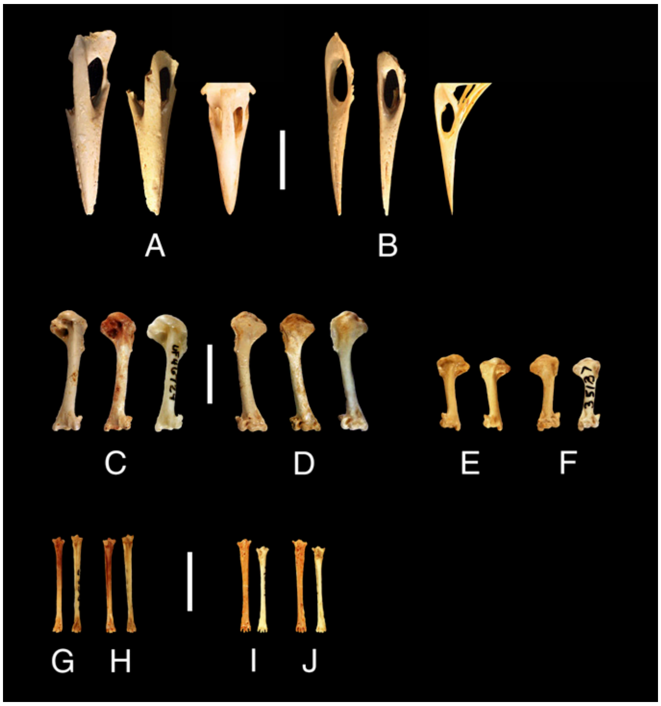

Fig. 5. (*A* and *B*) Rostrum of Eastern meadowlark *S. magna* in dorsal (*A*) and lateral (*B*) aspects. (*Left* and *Center*) Fossils. (*Right*) Modern, UF 31012 (PB 17171). (*C* and *D*) Humerus of Eastern bluebird *S. sialis* in anconal (*C*) and palmar (*D*) aspects. (*Left* and *Center*) Fossils. (*Right*) Modern, UF 46724. (*E* and *F*) Humerus of cave swallow *P. fulva* in anconal (*E*) and palmar (*F*) aspects. (*Left*) Fossil. (*Right*) Modern, UF 33972 (PB 35137). (*G* and *H*) Tarsometatarsus of chipping sparrow *S. passerina* in acrotarsial (*G*) and plantar (*H*) aspects. (*Left*) Fossil. (*Right*) Modern, UF 28905 (PB 20060). (*I* and *J*) Tarsometatarsus of brown-headed nuthatch *S. pusilla* in acrotarsial (*I*) and plantar (*J*) aspects. (*Left*) Fossil. (*Right*) Modern, UF 28653 (PB 17024). All fossils are from Sawmill Sink, Abaco, The Bahamas. (Scale bars: 10 mm.) PB, formerly in collection of Pierce Brodkorb.

woodlands). Species distribution modeling of bioclimatic niches suggests that climate/habitat changes account for the Holocene absence of several species, with distributions now centered at more northerly latitudes. The subsequent losses of 14 bird species that had persisted to the mid/late Holocene coincided with the arrival of humans on Abaco.

Open-habitat species of birds that now occur in the Bahamas only as nonbreeding migrants may have had resident populations during the late Pleistocene. Two examples are the sparrows *Spizella passerina* and *Passerculus sandwichensis*, which winter uncommonly but do not breed in the Bahamas today (40). A distinctive subspecies of the former (*S. passerina pinetorum*) now resides in Caribbean pine savannas on the Neotropical mainland from Belize to Nicaragua (46) whereas *P. sandwichensis* breeds locally in grasslands (1,200–2,500 m elevation) from the northern to central Mexican interior, but no farther south than New Jersey along the Atlantic coast (47, 48).

The endemic *Chilonatalus tumidifrons*, identified in late Holocene sediments of Ralph's Cave (12), is Abaco's only extant bat that was not identified at Sawmill Sink. Four of the eight species of mammals (50%) from Sawmill Sink no longer occur on Abaco (Table 1). Two of the bats (*Myotis austroriparius* and *Lasiurus minor*) existed on Abaco until the late Holocene (<4 ka) (12). The presence of 27 and 173 fossils of *M. austroriparius* in Sawmill Sink (late Pleistocene; herein) and Ralph's Cave (late Holocene) (12), respectively, suggest that it was once abundant.

Among endemic Caribbean bats, fossils of *Mormoops blainvillii* in Sawmill Sink represent an extirpated population although the age of other *M. blainvillii* fossils in the Bahamas (2) is unknown and may be Holocene. *M. blainvillii* is now restricted to the Greater Antilles (49). This species roosts primarily in "hot caves," where temperatures range from 28 °C to 40 °C and humidity exceeds 90% (50, 51). Although aeolianite karst in the Bahamas does not have the geomorphological features needed to create hot caves, this bat could have subsisted in the Bahamas in small populations by behaviorally creating warm temperatures in cave bell holes. Small populations are highly susceptible to disturbance, and this trait, in combination with the scarcity of suitable roost sites, could have led to the loss of *M. blainvillii*.

Increased interisland distances, from sea level rise after the PHT (*SI Appendix*, Fig. S4), likely affected interisland gene flow of bats among Bahamian islands. In two widespread lineages, *Erophylla sezekorni* and *Macrotus waterhousii*, past population connectivity is congruent with the late Pleistocene exposure of large carbonate banks (52). Although untested, it is possible that restricted gene flow from increased interisland distance contributed to the extirpation of other Sawmill Sink bat species.

Which Predator(s) Deposited the Fossils? Fossils of adult and nestling night-herons (*Nyctanassa violacea*) are common in Sawmill Sink; this species probably accounts for most of the fish fossils. The great majority of nonfish fossils probably were accumulated by the barn-owl *Tyto alba*, the only species of tytonid owl recovered from Sawmill Sink. As with living and extinct congeneric species, *T. alba* deposits bones from regurgitated prey items in caves and sinkholes (53). From Cuba and the Bahamas eastward to Barbuda in the Lesser Antilles, the West Indian islands once hosted a considerable radiation of barn-owls, most of which were larger than extant congeners (54, 55). In the Bahamas, the large, extinct *Tyto pollens* has been found as a fossil only on Little Exuma, New Providence, and Andros (all on the Great Bahama Bank) (1, 56) (D.W.S., personal observation). On the Little

Table 2. Median (and first–third quartile range) of habitat suitability values (range 0–1) for The Bahamas

Common name	Species	Modern	LGM (MIROC-ESM)	LGM (CCSM4)
Continental				
Savannah sparrow	*Passerculus sandwichensis*	0.241 (0.194–0.250)	0.549 (0.365–0.596)	0.553 (0.311–0.652)
Chipping sparrow	*Spizella passerina*	0.167 (0.135–0.186)	0.356 (0.256–0.446)	0.363 (0.260–0.446)
Red-shouldered hawk	*Buteo lineatus*	0.156 (0.101–0.296)	0.615 (0.561–0.645)	0.596 (0.511–0.631)
Antillean				
Giant kingbird	*Tyrannus cubensis*	0.191 (0.148–0.238)	0.030 (0.003–0.203)	0.047 (0.033–0.197)
Greater Antillean nightjar	*Antrostomus cubanensis*	0.145 (0.090–0.202)	0.682 (0.479–0.795)	0.680 (0.497–0.752)
Hispaniolan crossbill	*Loxia megaplaga*	0.0003 (0.0001–0.0051)	0.0006 (0.0000–0.0436)	0.0007 (0.0002–0.0037)

Predicted by MaxEnt Species Distribution Models, calibrated with modern distribution and climate data, and projected to modern climate and two paleoclimate datasets for Last Glacial Maximum (LGM), the Model for Interdisciplinary Research on Climate, Earth System Model (MIROC-ESM), and the Community Climate System Model, version 4 (CCSM4). The six species include three with modern distributions in North and Central America (Continental) and three endemic to the Greater Antilles (Antillean).

Fig. 6. (*A*) Humerus of Antillean ghost-faced bat *Mormoops blainvillii* in anconal aspect. (*Left*) Fossil. (*Right*) Modern, AMNH 275504. (*B*) Humerus of Southeastern myotis *Myotis austroriparius* in anconal aspect. (*Left*) Fossil. (*Right*) Modern, UF 19003. (*C*) Dentary of *M. austroriparius* in medial (*Left*, fossil), lateral (*Center*, different fossil), and lateral (*Right*, modern, UF 19003) aspects. All fossils are from Sawmill Sink, Abaco, The Bahamas. (Scale bars: 10 mm.)

Bahama Bank (Abaco, Grand Bahama), the only tytonid owl known, whether today or as a fossil, is *T. alba*.

The presence of *T. alba* in Sawmill Sink helps to explain the scarcity of fossils of *Geocapromys ingrahami*, a large rodent that is abundant in fossil sites with *T. pollens* (on the Great Bahamas Bank). *T. alba* is too small to prey on adult *G. ingrahami*. The most abundant fossil species in Sawmill Sink is the owl *A. cunicularia* (Table 1), which seems to have been consumed preferentially by the larger *T. alba*. On islands, *T. alba* (as well as *Tyto glaucops*) feed on a large variety of bats, birds, lizards, snakes, and frogs as available (57–60). Thus, the absence of anuran fossils in Sawmill Sink would argue that frogs were not present on Abaco in the late Pleistocene. The frog *Osteopilus septentrionalis* occurs on Abaco today (29) and is common as a late Holocene fossil in Ralph's Cave, associated with AMS ^{14}C dates from ∼3.8–1.8 ka (12). This age predates human arrival, suggesting that *O. septentrionalis* colonized Abaco during the Holocene without human assistance.

Conclusions and Future Prospects

Sawmill Sink is unique for yielding a rich vertebrate fauna (95 species documented thus far) from submerged owl roosts that were active in late glacial times. As skilled divers continue to explore blue holes elsewhere in the West Indies, we expect similarly rich Pleistocene sites to yield a much improved picture of Caribbean vertebrate communities during the last Ice Age. We are beginning a new era in West Indian biogeography where we can track changes in species composition through time with unprecedented precision, thereby corroborating a previously proposed model of vertebrates preferring dry habitats being more widespread during glacial intervals (61).

The changes in climate, habitat, and island area that took place from 15,000–9,000 y ago probably led to the loss of Bahamian populations in at least 17 species of birds, including several that today are continental rather than insular in their breeding range. The larger, cooler, drier ice-age islands in the Bahamas had a much richer avifauna with more open-habitat species than the smaller, forested interglacial islands that exist today. A diverse group of 23 reptiles, birds, and mammals persisted through the dramatic environmental changes associated with the PHT but did not survive the last millennium of human presence on Abaco. These losses included species that would have played key roles in terrestrial food webs (19). For the indigenous species of terrestrial vertebrates that remain, we fear that direct human activities, such as habitat alteration and introduction of invasive species, threaten their future more than climate change.

Materials and Methods

Diving and collections in Sawmill Sink have continued since the project began in 2005 under the direction of B.K. and N.A.A. Guidelines established for dive safety and collecting procedures are now standard protocol for research in blue holes. Using an open circuit sidemount scuba configuration, the fossil deposits (Fig. 3) were identified, tagged, photographed, and selectively excavated. A 1 × 2-m PVC grid divided into eight equal 0.5-m sections was labeled with nondirectional markers and secured over the collecting areas for excavation. Each collection was made in 10-cm levels, placed in one-gallon plastic zipper bags, and labeled for grid location, sediment level, and depth within the blue hole.

All bags of sediment from Sawmill Sink were transported to N.A.A.'s laboratory on Abaco for screenwashing. After being picked from the sediment, the fossils were sorted by D.W.S. into broad taxonomic categories and then dispersed to the appropriate specialists for identification: namely, H.M.S. (fish), J.I.M. (reptiles), D.W.S. (birds), and J.A.S.-C. (bats). The fossils were identified by direct comparison with modern and fossil specimens in the collections of the Florida Museum of Natural History, University of Florida (UF) and the American Museum of Natural History (AMNH). For fish, reptiles, and mammals, all data herein are new (*SI Appendix*, Table S3). The data for birds are based on 3,922 identified fossils (*SI Appendix*, Table S3), which is 2,119 more than reported previously (38).

We developed species distribution models (SDMs) for all extant terrestrial birds (excluding aquatic, marine, and shorebirds) that were identified to species from Pleistocene but not Holocene fossils, that are now extirpated from Abaco, and for which we had not previously developed climate envelope models (38). These models included six species, three with large modern ranges in North and Central America and three now found mainly or only in the Greater Antilles. We restricted the modeling to birds, the only group with multiple taxa fitting these criteria. SDMs were based on occurrence data from the Global Biodiversity Information Facility (www.gbif.org/). All available research-grade observations were used for the Antillean species, and a random sample of 15,000 points was selected for the continental species, further limited to one per climate grid cell (*SI Appendix*, Table S1). Predictors included a subset (62) of six uncorrelated bioclimatic variables (63) expected to limit species distributions (38), extracted from WorldClim (www.worldclim.org/) at 2.5 minute resolution: annual temperature, temperature seasonality, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, and precipitation seasonality (*SI Appendix*, Table S2).

SDMs were developed with MaxEnt software, widely used when only species presence data are available (64). Because models were used to extrapolate to a different climate state, regularization was set to 2.5 (65). Models were applied to downscaled climate reconstructions (from WorldClim) for the Last Glacial Maximum (LGM, ∼22 ka), based on two general circulation models available from Coupled Model Intercomparison Project Phase 5, the Community Climate System Model, version 4 (CCSM4), and the Model for Interdisciplinary Research on Climate, Earth System Model (MIROC-ESM), to hindcast the paleodistributions of climatically suitable habitat. We used two models of LGM climate to circumscribe uncertainty in climate models. Hindcasting to LGM allowed us to determine whether climate change during the PHT is a plausible explanation for the Holocene absence of these species on Abaco and elsewhere in the Bahamas. We averaged (and summed) predicted suitability from SDMs hindcast to the climate maps for LGM Bahamas (including for land areas exposed by lower sea level) to measure whether the Pleistocene climate was more suitable for these species than the current climate in the Bahamas. Averaging avoided the use of arbitrary thresholds to distinguish suitable from unsuitable habitat. This approach assumes that species distributions are in equilibrium with, and determined by, climate or by other factors for which climate is a good proxy: e.g., vegetation (66).

ACKNOWLEDGMENTS. For permission to conduct the research or other courtesies, we thank M. Albury, R. Albury, E. Carey, R. Franz, D. Knowles,

G. Morgan, M. Pateman, O. Patterson, K. Tinker, and K. Williams. For comments that improved the manuscript, we thank G. Stull. V. Perez identified the two shark fossils. J. Ripplinger and A. Sakrison helped to prepare data and figures. We acknowledge funding from National Science Foundation Grants BCS-1118340, BCS-1118369, and GSS-1461496, National Geographic Society Grant EC0372-08, and the University of Florida Ornithology Endowment. J.A.S.-C. was supported by Theodore Roosevelt and Gerstner Scholar Postdoctoral Fellowships at the American Museum of Natural History.

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