



## Past and present of insular Caribbean mammals: understanding Holocene extinctions to inform modern biodiversity conservation

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Of the 116 mammal species present in the Greater Antilles at the start of the Holocene Epoch, only 56 now survive, with more extensive species losses (~80%) in native lineages of sloths, shrews, rodents, and primates than in bats (~25%). Native species occurrences and extinctions are summarized herein for Cuba, Hispaniola, Jamaica, and Puerto Rico and used to introduce this *Journal of Mammalogy* Special Feature on insular Caribbean mammals. Recent efforts to understand extinct and extant Caribbean mammal diversity highlight the utility of paleobiological perspectives for exposing the trajectory of species losses and informing how best to protect remaining biodiversity in this region.

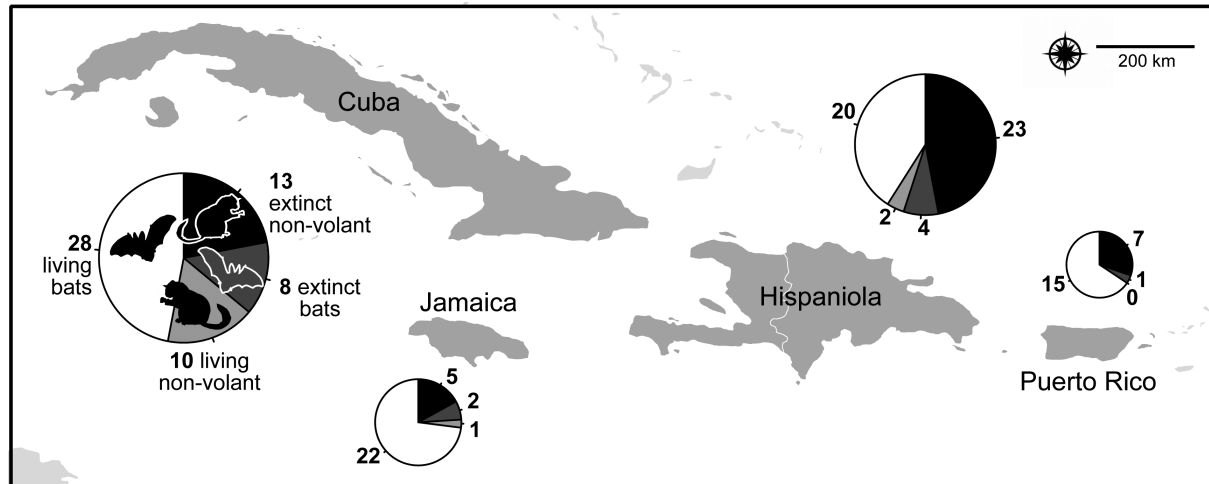
De las 116 especies de mamíferos en las Antillas Mayores al inicio de la Época Holocena, sólo 56 sobreviven ahora, con una pérdida de especies más extensa (~80%) en linajes nativos de perezosos, musarañas, roedores, y primates que en los murciélagos (~25%). Los ocurrencias de especies nativas y las extinciones se resumen aquí para Cuba, Hispaniola, Jamaica, y Puerto Rico y se utiliza para presentar esta Sección Especial de *Journal of Mammalogy* en mamíferos del Caribe. Los esfuerzos recientes para entender la diversidad de mamíferos extintos y existentes del Caribe destacan la utilidad de las perspectivas paleobiológicas para exponer la trayectoria de las pérdidas de especies e informar la mejor manera de proteger la biodiversidad remanente en esta región.

Key words: biodiversity hotspot, conservation, endemism, extinction, fossils, islands, West Indies

The insular Caribbean at the start of the Holocene Epoch (~11,700 years before present [BP]) contained a remarkable ~140 species of terrestrial mammals from 5 orders, 15 families, and 66 genera (Cooke et al. in press). Subsequent extinctions have especially impacted non-volant mammals, pruning species richness in native lineages of sloths, shrews, rodents, and primates by ~80% across the entire region, including 47 of 60 species found only on Greater Antillean islands. In contrast, 25% of endemic bats on those islands went extinct during the same time period (11 of 43 species; Fig. 1; Table 1). Now surviving are representatives of 8 families and 35 genera, most of which are present in the Greater Antilles (Table 1). The rate and extent of Caribbean mammal extinctions appears to be unparalleled among island biodiversity hotspots globally (Brooks et al. 2002), far exceeding recorded mammal extinctions in Old World archipelagos (Heaney 1986; Briggs 1999). Recent systematic efforts have refined synonymies of Caribbean paleofaunas and the species diversity of living mammals (e.g., Silva

Taboada et al. 2007; Turvey et al. this issue), but patterns of Caribbean endemism and extinction nevertheless persist in being extraordinary.

Why so many Caribbean mammals have gone extinct is a controversial but key question, since efforts to understand how Holocene events unfolded are needed to inform Anthropocene protections on remaining biodiversity. Data and methods from paleontology, zooarcheology, biogeochemistry, phylogenetics, and conservation are being marshaled to reconstruct the trajectory of extinctions so that contributing anthropogenic factors can be determined and addressed. Antique DNA techniques on enigmatic fossils are now allowing extinct biodiversity to be described and placed in needed evolutionary contexts (e.g., *Pennatomys* mice, *Nesophontes* shrews—Brace et al. 2015, 2016). So too, growing numbers and geographic extents of radiocarbon dates (e.g., Stoetzel et al. 2016) are providing per-island details of last occurrences of mammals relative to first occurrences of humans and the timing of natural climatic



**Fig. 1.**—Species extinctions and survivals for bats and non-volant mammals in the Greater Antilles since the early Holocene (~11,700 years before present). Details of the underlying data are presented in Table 1. Shading and symbols are consistent across islands, and pie charts are sized per island relative to mammal species richness at the start of the Holocene (Cuba, including offshore cays: 59 species; Hispaniola: 49; Jamaica: 30; Puerto Rico: 23). In total, 116 mammal species were present in the Greater Antilles at start of the Holocene, of which 56 species now survive (43 bats, 31 of which are endemic; 13 non-volant mammals, all are endemic). Non-volant species include native rodents, shrews, sloths, and primates, and bats represent 6 families.

fluctuations. But many Caribbean islands and species still lack radiocarbon dates, so causal determinants are elusive. Recent synthetic analyses of available dates nevertheless show that most mammalian extinctions postdate both the last glacial maximum and per-island human arrivals (Soto-Centeno and Steadman 2015; Cooke et al. in press). Those findings argue against previous suggestions that climate-only factors are sufficient to explain some Caribbean extinctions, particularly of Bahaman bats where the effect of sea-level rise was dramatic (Dávalos and Russell 2012). Instead, it appears that a potent mixture of human activities, including hunting and introductions of human commensals like dogs and rats, may actually dwarf postglacial habitat loss as a driver of Holocene extinctions (Borrito-Páez and Mancina this issue; Cooke et al. in press).

Persistent questions about the evolutionary history of native Caribbean mammals have inspired the articles in this Special Feature of the *Journal of Mammalogy*. These articles stem from a featured symposium at the 95th annual meeting of the American Society of Mammalogists, held in Jacksonville, Florida on 15 June 2015, and jointly organized by NSU, Burton K. Lim (Royal Ontario Museum), and the ASM Conservation Committee represented by Bradley J. Bergstrom (Valdosta State University). The proximity of ASM's 2015 venue to the insular Caribbean heightened the local relevance of this symposium, and allowed for invited speakers to attend from Cuba (Rafael Borrito-Páez) and the Dominican Republic (Jorge L. Brocca). The symposium titled “The Last Remaining Caribbean Mammals: Conservation Priorities and the Historical Context of Extinctions in an Island Biodiversity Hotspot” included 8 invited speakers from 5 countries, and was organized into 2 separate 2-h sessions with a joint discussion. Five of those 8 presentations led to articles in this Special Feature; 1 article by Ricardo Moratelli (Oswaldo Cruz Foundation, Brazil) and colleagues that was not part of the original program was also

included. The symposium organization is reflected in the content of this Special Feature under categories of “how we got here” (historical context) and “what to do now” (conservation priorities). Bringing together these often separate paleontological and neontological perspectives was designed to highlight the full trajectory and continued specter of biodiversity loss among Caribbean land mammals, with the chief aim of fostering realistic urgency for conservation action.

The first 3 articles use paleobiological perspectives to establish the extent of Holocene mammal extinctions and endemism in the insular Caribbean. Turvey et al. (this issue) offer a state-of-the-art summary on the last surviving species of native non-volant mammals, including species accounts with revised IUCN threat assessments for living species. Updated geographic range maps and a table of 29 species considered extinct since AD 1500 (IUCN's time interval for listing species extinctions) provide a valuable overview that subsequent articles elaborate upon. Cooke et al. (this issue) document the timing of last occurrence for *Xenothrix mcgregori*, Jamaica's last living monkey, which they estimate to ~900 BP using a probabilistic analysis of available radiometric dates. This event represents the most recent species-level extinction for any monkey or ape globally, which they place in the temporal context of other Caribbean primates. Upham and Borrito-Páez (this issue) next shift the focus to native rodents in the family Capromyidae, with a phylogeographic analysis of Cuban hutias that documents a ~1 million year (Ma) genetic split from west-to-east among 15 populations of *Capromys pilorides*, the most common native hutia. Their sampling of nearly all extant hutias (9 of 11 species) and 1 recently extinct species helps to clarify the species-level context of the *Capromys* split as well as the broader evolutionary history of hutias in the Caribbean during the last 10 Ma.

The next 3 articles further document patterns of biodiversity in the context of establishing baselines and priorities for

**Table 1.**—Species occurrences (1 = present, 0 = absent) of native mammals on Cuba (C), Hispaniola (H), Jamaica (J), and Puerto Rico (P) separated into non-volant species and bats. Species also are noted as extinct (Ex.; 1 = extinct, 0 = extant) and endemic (En.; 1 = endemic to the insular Caribbean, 0 = not endemic). Per-island species occurrences compiled from recent compendia were used to construct Fig. 1 (Borroto-Páez and Mancina this issue; Cooke et al. in press; Silva Taboada et al. 2007; Dávalos and Turvey 2012). Undescribed taxa and subspecies likely to be elevated to species are included to provide a complete view of biodiversity in this region. Cuban tally includes species on offshore keys.

Non-volant species	Ex.	En.	C	H	J	P	Bat species	Ex.	En.	C	H	J	P
PILOSA							CHIROPTERA						
Megalonychidae							Molossidae						
† <i>Acratocnus antillensis</i>	1	1	1	0	0	0	<i>Eumops auripendulus</i>	0	0	0	0	1	0
† <i>Acratocnus odontrionus</i>	1	1	0	0	0	1	<i>Eumops glaucinus</i>	0	0	1	0	1	0
† <i>Acratocnus simorhynchus</i>	1	1	0	1	0	0	<i>Eumops perotis</i>	0	0	1	0	0	0
† <i>Acratocnus ye</i>	1	1	0	1	0	0	<i>Molossus molossus</i>	0	0	1	1	1	1
† <i>Megalocnus rodens</i>	1	1	1	0	0	0	<i>Mormopterus minutus</i>	0	1	1	0	0	0
† <i>Megalocnus zile</i>	1	1	0	1	0	0	<i>Nyctinomops laticaudatus</i>	0	0	1	0	0	0
† <i>Neocnus comes</i>	1	1	0	1	0	0	<i>Nyctinomops macrotis</i>	0	0	1	1	1	0
† <i>Neocnus dousman</i>	1	1	0	1	0	0	<i>Tadarida brasiliensis</i>	0	0	1	1	1	1
† <i>Neocnus glirifomis</i>	1	1	1	0	0	0	† <i>Tadarida</i> sp.	1	1	0	1	0	0
† <i>Neocnus toupiti</i>	1	1	0	1	0	0	Mormoopidae						
† <i>Parocnus browni</i>	1	1	1	0	0	0	<i>Mormoops blainvillei</i>	0	1	1	1	1	1
† <i>Parocnus serus</i>	1	1	0	1	0	0	<i>Pteronotus macleayii</i>	0	1	1	1	1	0
PRIMATES							<i>Pteronotus parnellii parnellii</i>	0	1	1	0	1	0
?Aotidae							<i>Pteronotus parnellii portoricensis</i>	0	1	0	0	0	1
† <i>Insulacebus toussaintiana</i>	1	1	0	1	0	0	<i>Pteronotus parnellii pusillus</i>	0	1	0	1	0	0
† <i>Xenothrix mcgregori</i>	1	1	0	0	1	0	<i>Pteronotus quadridens</i>	0	1	1	1	1	1
?Cebidae							† <i>Mormoops magna</i>	1	1	1	1	0	0
† <i>Antillothrix bernensis</i>	1	1	0	1	0	0	† <i>Mormoops megalophylla</i>	1	1	1	1	1	0
Pitheciidae							† <i>Pteronotus pristinus</i>	1	1	1	0	0	0
† <i>Paralouatta varonai</i>	1	1	1	0	0	0	† <i>Pteronotus</i> sp. nov.	1	1	0	1	0	0
RODENTIA							Natalidae						
Capromyidae							<i>Chilonatalus micropus macer</i>	0	1	1	0	0	0
<i>Capromys garridoi</i>	0	1	1	0	0	0	<i>Chilonatalus micropus micropus</i>	0	1	0	1	1	0
<i>Capromys pilorides</i>	0	1	1	0	0	0	<i>Natalus jamaicensis</i>	0	1	0	0	1	0
<i>Capromys</i> sp. nov. (eastern clade)	0	1	1	0	0	0	<i>Natalus major</i>	0	1	0	1	0	0
<i>Geocapromys brownii</i>	0	1	0	0	1	0	<i>Natalus primus</i>	0	1	1	0	0	0
<i>Mesocapromys angelcabrerai</i>	0	1	1	0	0	0	<i>Nyctiellus lepidus</i>	0	1	1	0	0	0
<i>Mesocapromys auritus</i>	0	1	1	0	0	0	Noctilionidae						
<i>Mesocapromys melanurus</i>	0	1	1	0	0	0	<i>Noctilio leporinus</i>	0	0	1	1	1	1
<i>Mesocapromys nanus</i>	0	1	1	0	0	0	Phyllostomidae						
<i>Mesocapromys sanfelipensis</i>	0	1	1	0	0	0	<i>Artibeus flavescens</i>	0	1	0	0	1	0
<i>Mysateles prehensilis</i>	0	1	1	0	0	0	<i>Artibeus jamaicensis</i>	0	0	1	1	1	1
<i>Plagiodontia aedium</i>	0	1	0	1	0	0	<i>Brachyphylla cavernarum</i>	0	1	0	0	0	1
†gen. nov.? (aff. <i>Hexolobodon</i> ) sp. nov.	1	1	0	1	0	0	<i>Brachyphylla nana nana</i>	0	1	1	0	0	0
† <i>Geocapromys columbianus</i>	1	1	1	0	0	0	<i>Brachyphylla nana pumila</i>	0	1	0	1	1	0
† <i>Hexolobodon phenax</i>	1	1	0	1	0	0	<i>Erophylla bombifrons</i>	0	1	0	1	0	1
† <i>Isolobodon montanus</i>	1	1	0	1	0	0	<i>Erophylla sezekorni</i>	0	1	1	0	1	0
† <i>Isolobodon portoricensis</i>	1	1	0	1	0	1	<i>Glossophaga soricina</i>	0	0	0	0	1	0
† <i>Macrocapromys acevedo</i>	1	1	1	0	0	0	<i>Macrotus waterhousii</i>	0	1	1	1	1	1
† <i>Macrocapromys latus</i>	1	1	1	0	0	0	<i>Monophyllus plethodon</i>	0	1	0	0	0	1
† <i>Mesocapromys kraglievichi</i>	1	1	1	0	0	0	<i>Monophyllus redmani</i>	0	1	1	1	1	1
† <i>Plagiodontia araeum</i>	1	1	0	1	0	0	<i>Phyllonycteris aphylla</i>	0	1	0	0	1	0
† <i>Plagiodontia ipnaeum</i>	1	1	0	1	0	0	† <i>Phyllonycteris poeyi</i>	0	1	1	1	0	0
† <i>Rhizoplagiodontia lemkei</i>	1	1	0	1	0	0	<i>Phyllops falcatus</i>	0	1	1	1	0	0
Cricetidae							<i>Stenoderma rufum</i>	0	1	0	0	0	1
† <i>Oryzomys antillarum</i>	1	1	0	0	1	0	† <i>Artibeus anthonyi</i>	1	1	1	0	0	0
Echimyidae							† <i>Cubanycyteris silvai</i>	1	1	1	0	0	0
† <i>Boromys offella</i>	1	1	1	0	0	0	† <i>Desmodus puntajudensis</i>	1	1	1	0	0	0
† <i>Boromys torrei</i>	1	1	1	0	0	0	† <i>Phyllonycteris major</i>	1	1	0	0	0	1
† <i>Brotomys contractus</i>	1	1	0	1	0	0	† <i>Phyllops silvai</i>	1	1	1	0	0	0
† <i>Brotomys voratus</i>	1	1	0	1	0	0	† <i>Phyllops vetus</i>	1	1	1	0	0	0
† <i>Heteropsomys insulans</i>	1	1	0	0	0	1	† <i>Tonatia saurophila</i>	1	0	0	0	1	0
† <i>Puertoricomys corozalus</i>	1	1	0	0	0	1	Vespertilionidae						
Heptaxodontidae							<i>Antrozous pallidus</i>	0	0	1	0	0	0
† <i>Clidomys osborni</i>	1	1	0	0	1	0	<i>Eptesicus fuscus</i>	0	0	1	1	1	1
† <i>Elasmodontomys obliquus</i>	1	1	0	0	0	1	<i>Lasiurus degelidus</i>	0	1	0	0	1	0
† <i>Quemisia gravis</i>	1	1	0	1	0	0	<i>Lasiurus insularis</i>	0	1	1	1	0	0

Table 1.—Continued

Non-volant species	Ex.	En.	C	H	J	P	Bat species	Ex.	En.	C	H	J	P
† <i>Xaymaca fulvopulvis</i>	1	1	0	0	1	0	<i>Lasiurus intermedius</i>	0	1	1	0	0	0
Incertae sedis							<i>Lasiurus minor</i>	0	1	0	1	0	1
†gen. nov. sp. nov.	1	1	0	0	1	0	<i>Lasiurus pfeifferi</i>	0	1	1	0	0	0
† <i>Tainotherium valei</i>	1	1	0	0	0	1	<i>Nycticeius cubanus</i>	0	1	1	0	0	0
EULIPOTYPHILA							Bat total	12	43	36	24	24	16
Nesophontidae													
† <i>Nesophontes edithae</i>	1	1	0	0	0	1							
† <i>Nesophontes hypomicrus</i>	1	1	0	1	0	0							
† <i>Nesophontes micrus</i>	1	1	1	0	0	0							
† <i>Nesophontes paramicrus</i>	1	1	0	1	0	0							
† <i>Nesophontes zamicros</i>	1	1	0	1	0	0							
Solenodontidae													
<i>Solenodon cubanus</i>	0	1	1	0	0	0							
<i>Solenodon paradoxus</i>	0	1	0	1	0	0							
† <i>Solenodon arredondo</i>	1	1	1	0	0	0							
† <i>Solenodon marcano</i>	1	1	0	1	0	0							
Non-volant total	47	60	23	25	6	7							

conservation. Borroto-Páez and Mancina (this issue) continue the focus on Cuban mammals, with a wide-ranging review of current extinction threats to non-volant species as well as the highly diverse assemblages of bats in Cuba. They highlight the deleterious effect of Cuba's 44 invasive species on native mammals, including a full compendium of their island and protected area occurrences, date of first introduction, and estimated level of impact. Lim et al. (this issue) next focus on phylogeographic diversity among chiropterans of the Dominican Republic. Using cytochrome oxidase I barcodes sampled from 132 bats at 11 different localities, they find evidence for north-south phylogeographic splits in 3 species, which are consistent with intraspecific splits recovered in the Hispaniolan hutia and other tetrapods (Brace et al. 2012). Lastly, Moratelli et al. (this issue) expand the known biodiversity of Caribbean bats with the description of a new species of *Myotis* from coastal Tobago Island in the Republic of Trinidad and Tobago. They join morphological analyses and cytochrome-*b* genetic data to delimit this lineage as related to *Myotis* from Venezuela, Peru, and Ecuador, and in an apt homage they name the new species for a renowned British naturalist and educator (the suspense!).

Reconstructing abiotic and biotic (including human-mediated) events leading to mammal extinctions in the Caribbean archipelago is a work in progress that this Special Feature advances by improving the taxonomic, temporal, and geographic resolution of living and fossil diversity. The hypothesis that extinction pressures were greater here than elsewhere is intriguing, but will require similarly detailed efforts in island biodiversity hotspots globally to understand the extent of contingent versus deterministic factors in the extinctions of island mammals. Factors such as the distribution of karstic rocks and caves suitable for fossil preservation (Plotnick et al. 2014), the antiquity of regional human diasporas (Karmin et al. 2015), and the extent of systematic revisions for respective faunas will be key for evening out spatial biases in insular patterns of extinction and endemism globally. New techniques based on mass spectrometry of bone collagen now allow both temporal and

phylogenetic information to be gathered from even fragmentary fossils (ZooMS—Harvey et al. 2016), an exciting approach that should further aid faunal reconstructions. Phylogenetic approaches that consider the distribution of species-level traits relative to extinction timing are promising, particularly for risk factors associated with slower life histories (Turvey 2009). Integration among fossil, molecular, and ecological trait data will continue to open doors of perception about the differential persistence and demise of mammals in the Caribbean Biodiversity Hotspot, informing how we got here and what to do next.

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