

Late Holocene extinction of Puerto Rican native land mammals

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West Indian land mammals have suffered the most severe extinctions of any Holocene mammal faunas. However, 'last-occurrence' dates based on radiometric or robust stratigraphic data remain unavailable for most West Indian species, making it impossible to identify factors responsible for these extinctions. Here, we present new radiometric dates from archaeological and palaeontological sites on Puerto Rico, the only Greater Antillean island to have lost all native land mammals. Although it has been suggested that these species died out earlier than other West Indian mammals, we demonstrate that Puerto Rican mammal last-occurrence dates are in close agreement with those from other Antillean islands, as several species in fact persisted for millennia following Amerindian arrival. Echi-myid rodents and nesophontid 'island-shrews' were still present on Puerto Rico approximately 1000 years BP, and probably became extinct following European arrival. The large (13 kg) heptaxodontid rodent *Elasmodontomys obliquus* also appears to have survived for over 2000 years after Amerindian colonization, suggesting that at least some large West Indian mammals became extinct in protracted pre-European 'sitzkrieg'-style events rather than 'blitzkrieg'-style overkill.

Keywords: *Elasmodontomys*; *Heteropsomys*; *Nesophontes*; Quaternary extinctions; radiocarbon dating; West Indies

1. INTRODUCTION

The land mammals of the West Indies have experienced a series of severe Late Quaternary extinction events, and over 100 sloth, primate, insectivore and rodent species are known to have died out during this interval (e.g. MacPhee & Flemming 1999). The factor(s) responsible for these events remain a subject of considerable speculation, with natural or anthropogenic environmental change, introduced predators, competitors and diseases, direct human extermination or a combination of these all proposed as possible causes (Morgan & Woods 1986; MacPhee *et al.* 1989). The presence of ground sloths and megafaunal

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rodents in pre-human West Indian faunas suggests that understanding the ecology of these extinctions has the potential to clarify the dynamics of older Quaternary continental mammal extinctions, as well as informing conservation management of currently endangered island species. However, although MacPhee & Flemming (1999) could resolve 33 West Indian mammal extinctions as having occurred since AD 1500 (representing 37.5% of historical-era mammalian extinctions globally), 'last-occurrence' dates based on radiometric or robust stratigraphic data remain unavailable for most of the region's mammals, and hence few of these extinctions can be incorporated into a temporal framework necessary to identify causative drivers.

Puerto Rico is the only Greater Antillean island to have lost its entire pre-human Quaternary land mammal fauna: the megalonychid sloth *Acratocnus odontrigonus*; the 'island-shrew' *Nesophontes edithae*; the large heptaxodontid rodent *Elasmodontomys obliquus*; the echimyid rodents *Heteropsomys insulans* (?=*Homopsomys antillensis*) and *Puertoricomys corozalus* (Woods 1996); and the newly described large rodent *Tainotherium valei* (Turvey *et al.* 2006). The now-extinct capromyid rodent *Isolobodon portoricensis* was also introduced from Hispaniola by pre-Columbian Amerindians (Woods 1996). These losses form part of a larger extinction series also including the island's native iguana (which survives in the Virgin Islands) and several birds (Pregill & Olson 1981).

Radiometrically dated archaeological sites indicate that humans reached Puerto Rico by approximately 6000 cal BP (Ayes 1995), and elevated charcoal levels in sediment cores from approximately 5300 cal BP suggest that extensive anthropogenic forest burning began soon after first contact (Burney *et al.* 1994). The presence of *Elasmodontomys*, *Heteropsomys* and *Nesophontes* in a stratified bone layer at Cueva del Perro cave dated to 5410 ± 80 BP indicates that these taxa were still extant when Amerindians first settled the island (McFarlane 1999). However, although *I. portoricensis* is abundant in Amerindian middens and occupation horizons (Newsom & Wing 2004), and radiometric data show that it persisted at least until the thirteenth century AD on Puerto Rico (Flemming & MacPhee 1999), there has been no evidence indicating that any native land mammals survived beyond first Amerindian colonization. Since substantial Quaternary palaeontological fieldwork has been conducted in Puerto Rico (e.g. Anthony 1918; Choate & Birney 1968; Pregill 1981), several authors have considered that native land mammals may have become extinct much earlier than on other Antillean islands (MacPhee & Flemming 1999; MacPhee *et al.* 1999). To assess temporal survival of the island's mammal species across the Holocene, radiometric analysis was conducted on a large sample of new zooarchaeological and palaeontological material.

2. MATERIAL AND METHODS

A hemimandible of *N. edithae* and mandibular fragment of *H. insulans* bearing the second lower molar (figure 1) were recovered in 1997–1998 from a primary burial tomb fill at the Cag-3 archaeological site (figure 2), a ritual-ceremonial funerary site situated in Cueva de Juan Miguel containing Ostiones period (AD 1050–1300) ceramic assemblages. Palaeontological fieldwork in 2005 collected subfossil mammal material from surficial deposits

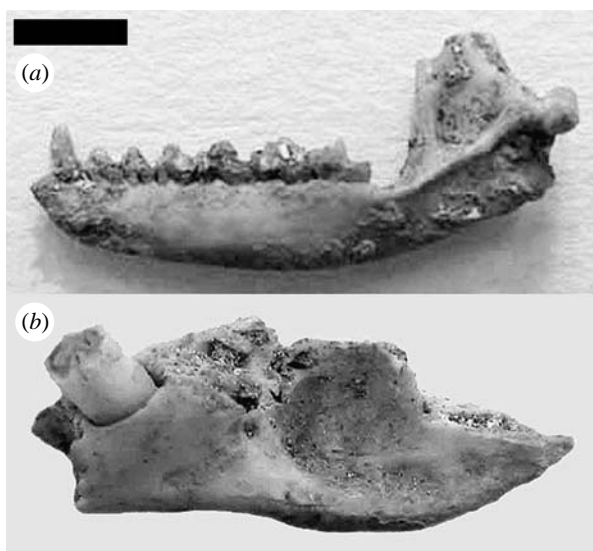


Figure 1. Cag-3 mammal subfossils. (a) *Nesophontes edithae* mandible; (b) *Heteropsomys insulans* mandibular fragment. Scale bar, 5 mm.

in 19 non-archaeological Puerto Rican cave sites (electronic supplementary material). Fieldwork focused on Cueva del Perro (figure 2), as sparse vertebrate remains had previously been reported in an approximately 18 cm layer ('Layer A') above the stratified bone layer ('Layer B') described by McFarlane (1999). An *in situ* *E. obliquus* molar toothplate was retrieved from the uppermost 2 cm of compacted sediment in Layer A at Cueva del Perro, and material representing all native Puerto Rican land mammals except *P. corozalus* was recovered from different palaeontological sites.

Ninety-five representative palaeontological samples and the zooarchaeological samples from Cag-3 were submitted for accelerator mass spectrometer (AMS) ^{14}C dating at the Oxford Radiocarbon Accelerator Unit (ORAU; electronic supplementary material).

3. RESULTS

The relatively recent survival of *N. edithae* and *H. insulans*, suggested by their presence in an Ostiones period tomb fill, is confirmed by AMS ^{14}C dates for both Cag-3 specimens (table 1). However, despite attempts to collect young surficial material at non-archaeological sites, pre-screening at ORAU revealed that palaeontological samples had experienced almost complete diagenetic loss of collagen, and no direct AMS ^{14}C dates were obtained from any native mammal subfossils. This probably reflects geologically recent sample degradation under subtropical conditions, also reported for other Puerto Rican palaeontological material (MacPhee & Flemming 1999; McFarlane 1999; Steadman *et al.* 2005), rather than subfossil antiquity. However, two associated radiometric dates were obtained from non-anthropogenic charcoal from the same stratigraphic interval as the Cueva del Perro *E. obliquus* toothplate at different positions in the sampling quadrat (table 1).

4. DISCUSSION

The new last-occurrence dates show that both *H. insulans* and *N. edithae* were still present on Puerto Rico approximately 1000 years ago. There is no archaeological evidence for increased anthropogenic pressures on Antillean terrestrial environments between this period and European arrival around AD

1500, as the island's major pre-Columbian socio-economic changes had already occurred; low-density Archaic hunter–fisher–gatherer communities practising incipient cultivation were invaded by fully agricultural Saladoid–Huecoid populations around 200 BC, and their Ostionoid descendants reached higher densities and spread into the interior highlands around AD 700 (Curet 2005). It is therefore likely that both *H. insulans* and *N. edithae* survived until the European historical period. Other radiometric studies indicate that small echimyids and island-shrews also survived on Cuba and Hispaniola until European arrival (MacPhee *et al.* 1999; McFarlane *et al.* 2000), so, although both Puerto Rican species are markedly larger than related taxa (electronic supplementary material), these two groups appear to have experienced contemporaneous extinction events across the Caribbean. Of the primary post-Columbian extinction drivers operating in Puerto Rico, massive-scale deforestation for sugarcane did not commence until the late 1700s, and mongoose were only introduced in 1877 (Watts 1987; Woods 1996). It is probable that both extinctions were driven by interactions (predation/competition) with *Rattus rattus*, which reached the Caribbean by the early 1500s and has been implicated in large numbers of other insular vertebrate extinctions (e.g. MacPhee *et al.* 1999).

Large-bodied vertebrates are typically the first species to become extinct following human arrival on islands, either through selective targeting by hunters (Duncan *et al.* 2002) or because size-dependent scaling of ecological and life-history traits increases their vulnerability to anthropogenic disturbance (Cardillo *et al.* 2005). However, associated dates for the large rodent (approx. 13 kg; McFarlane 1999) *E. obliquus* are both more than 2000 years younger than earliest human occupation of the island, suggesting that at least one large-bodied (more than 10 kg) member of Puerto Rico's mammal fauna also persisted for millennia after Amerindian arrival. This contrasts markedly with rapid extinctions of large-bodied insular taxa known to have been overexploited by early hunters (e.g. New Zealand moa; Holdaway & Jacomb 2000), but matches protracted Late Holocene declines of large-bodied mammals on Madagascar (Burney *et al.* 2004). It is also comparable with direct radiometric last-occurrence dates for megalonychid sloths on Hispaniola, where *Neocnus comes* survived until at least approximately 5000 cal BP (Steadman *et al.* 2005) and other sloth material has been dated to 3755 ± 175 BP (MacPhee *et al.* 1999).

Our limited new radiometric data therefore suggest that Puerto Rico's mammals experienced two waves of extinction, with small-bodied species probably surviving until European arrival, and at least some large-bodied species becoming extinct in protracted pre-Columbian 'sitzkrieg'-style events rather than 'blitzkrieg'-style overkill following initial Amerindian colonization (cf. Diamond 1989). The current general lack of understanding of pre-human ecology or pre-Ceramic environmental interactions precludes meaningful speculation over these apparently delayed 'megafaunal' extinctions. Pre-Ceramic sites typically consist of coastal shell middens, indicating substantial

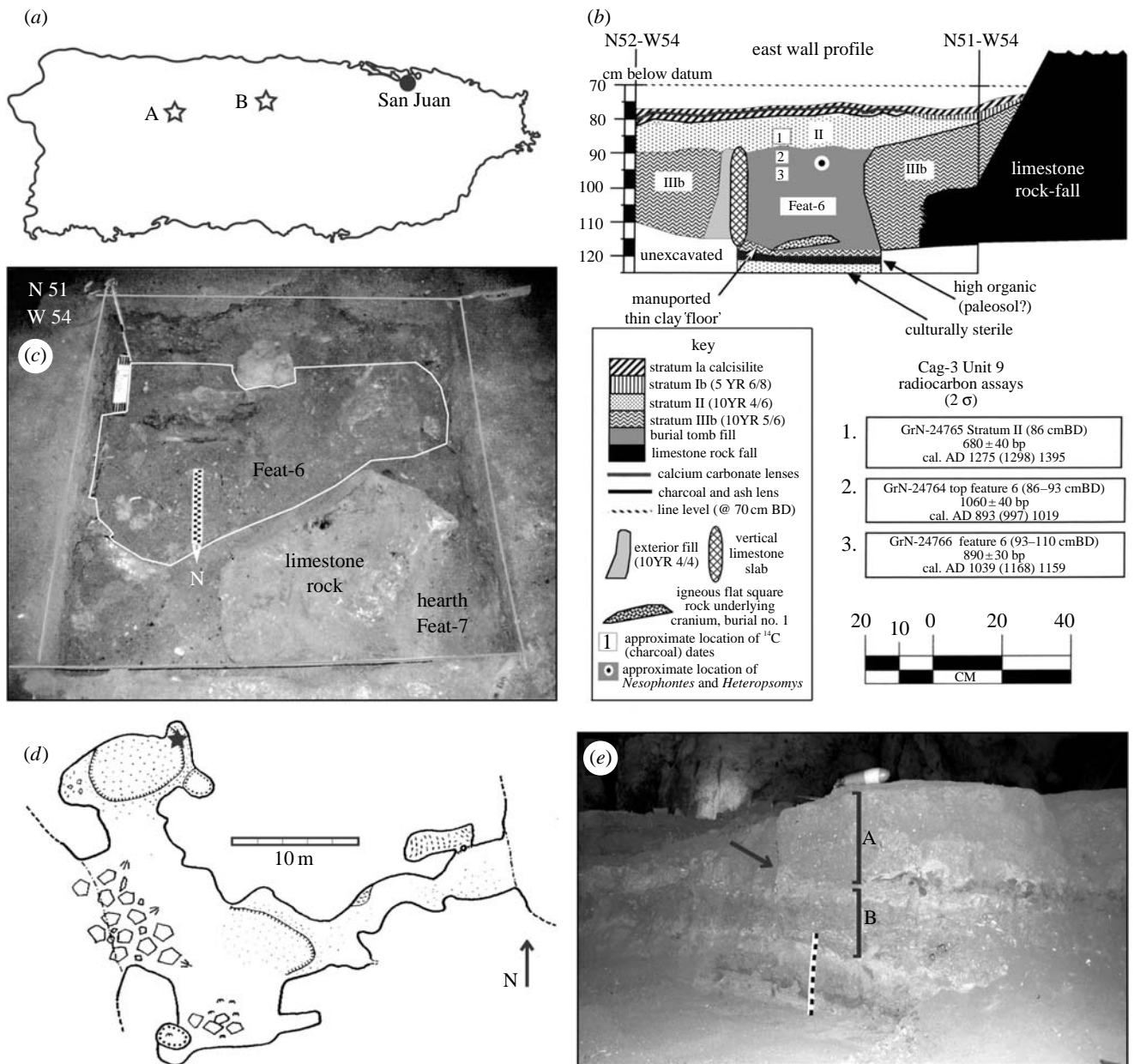


Figure 2. (a) Map of Puerto Rico, showing locations of Cag-3 (A) and Cueva del Perro (B). (b) Cag-3 tomb fill stratigraphic profile, showing locations of dated samples and charcoal dates. (c) Cag-3 tomb fill. (d) Cueva del Perro plan view. Quadrat location indicated by star. (e) Cueva del Perro section, showing stratigraphic layers and quadrat location. (b) and (c) after Oliver & Narganes Storde (2005); (d) after McFarlane (1999).

Table 1. AMS dates for extinct Puerto Rican mammals.

species	lab. no.	material	site	$^{13}\text{C}/^{12}\text{C}$	age $\pm 1\sigma$	calibrated date, 68.2% probability	calibrated date, 95.5% probability
<i>Heteropsomys insulans</i>	OxA-15142	mandibular fragment	grave infill, Cag-3	-19.6	1219 \pm 26	772-870 AD	694-887 AD
<i>Nesophontes edithae</i>	OxA-15141	mandible	grave infill, Cag-3	-19.3	990 \pm 24	1015-1147 AD	991-1153 AD
<i>Elasmodontomys obliquus</i>	OxA-15129	charcoal, 0-2 cm interval	Cueva del Perro	-27.3	3512 \pm 28	1887-1775 BC	1913-1751 BC
<i>Elasmodontomys obliquus</i>	OxA-15132	charcoal, combined 0-4 cm interval	Cueva del Perro	-26.8	2407 \pm 28	511-407 BC	732-399 BC

exploitation of marine resources (Newsom & Wing 2004), which may have limited the potential for massive overexploitation and resultant rapid

extinction of terrestrial vertebrate faunas on larger West Indian islands. However, this contrasts with the archaeological record of New Zealand, the only

insular region for which extensive data are available on prehistoric human hunting of extinct megafauna; moa were heavily exploited immediately after colonization, with marine resources instead increasingly utilized in later occupation horizons (Holdaway & Jacomb 2000).

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