Asynchronous extinction of late Quaternary sloths on continents and islands


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Unfortunately, the content of this page appears to be an incomplete or corrupted version of the original text. The text seems to be discussing the extinction of late Quaternary sloths on continents and islands, focusing on the asynchronous nature of their extinction. The paper likely explores the reasons behind this pattern and compares it to other extinctions, particularly those involving anthropogenic factors.

The text mentions the widespread distribution of sloths (Phyllophaga, Xenarthra) and discusses the near-time survival index of extinct mammals, using radiocarbon dating to infer their extinction times. The authors analyze data from sites in the West Indies and mainland South America to argue for the asynchronous extinction of sloths, contrasting it with the glacial-interglacial transition's effect on other species.

The paper likely provides a detailed analysis of the environmental factors contributing to this asynchronous extinction, including the role of climate change and human activity. The authors may compare their findings with those of other species and discuss the implications for understanding broader patterns of extinction.

This paper was submitted directly (Track II) to the PNAS office.

Abbreviations: AMS, accelerator-mass spectrometer; yr BP, radiocarbon years before present; 14C, radiocarbon; LAD, last appearance date; elev., elevation.

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200 m above the Colorado River on the southern wall of the Grand Canyon in Mojave County, AZ (8, 21–23). The $^{14}$C dates on surface sloth dung range from 10,400 ± 275 to 11,480 ± 200 radiocarbon years before present (yr BP). The oldest date is 11,764 yr BP. The 14C dates that range from 11,430 ± 60 [Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory (CAMS)-33974] to 11,710 ± 80 (CAMS-13033) yr BP (24).

South America. The South American dung-bearing sites (Table 2) vary in location from Gruta de Brejões ($\approx$11°S, $\approx$41°W, elev. ~600 m) in the tropical, arid caatinga vegetation of Bahia, Brazil (25) to Cueva del Milodón (51°35′S, 72°38′W, elev. 200 m) in the cool temperate Nothofagus forest of southern Chile (26, 27). Gruta del Indio (34°45′S, 68°22′W, elev. 660 m), Mendoza Province, Argentina, is a basalt rock-shelter surrounded by dryland shrubs resembling in their structure, height, density, and spacing those found near Rampart Cave in the Mojave Desert. Like Rampart Cave, Gruta del Indio harbors middens made by a plant-hoarding rodent, perhaps the vizchaca ($Lagidium$ sp.; Chinchillidae). Unlike Rampart Cave, Gruta del Indio is also an archaeological site, with charcoal as old as 10,530 ± 140 yr BP deposited immediately above the strata with the youngest dung balls (9, 28). No charcoal was found with or beneath the sloth dung. Gruta del Indio has yielded few remains of sloths other than dung. A single megatheriid tooth, and some dermal ossicles embedded in patches of hide (diagnostic of a mylodontid), suggest that two species of sloths had been present.

Cuchillo Curá (38°36′S, 70°18′W, elev. 1050 m) is a limestone

![Fig. 1. The Americas, showing continental fossil sites mentioned in the text.](image)

Table 1. Radiocarbon dates (yr BP and lab numbers) on dung of Shasta ground sloth ($Nothrotheriops shastense$) from North America

<table>
<thead>
<tr>
<th>Gypsum Cave, NV</th>
<th>Rampart Cave, AZ</th>
<th>Muav Caves, AZ</th>
<th>Shelter Cave, NM</th>
<th>Aden Crater, NM</th>
<th>Upper Sloth Caves, TX</th>
<th>Williams Cave, TX</th>
</tr>
</thead>
<tbody>
<tr>
<td>(610 m)</td>
<td>(535 m)</td>
<td>(400 m)</td>
<td>(1475 m)</td>
<td>(1200 m)</td>
<td>(2000 m)</td>
<td>(1500 m)</td>
</tr>
<tr>
<td>11,360 ± 260</td>
<td>10,400 ± 275</td>
<td>11,140 ± 160</td>
<td>11,330 ± 370</td>
<td>11,080 ± 200</td>
<td>10,750 ± 140</td>
<td>11,140 ± 320</td>
</tr>
<tr>
<td>11,690 ± 250</td>
<td>10,780 ± 200</td>
<td>11,290 ± 170</td>
<td>12,330 ± 190</td>
<td>12,430 ± 250</td>
<td>10,780 ± 140</td>
<td>11,930 ± 170</td>
</tr>
<tr>
<td></td>
<td>10,940 ± 60</td>
<td></td>
<td></td>
<td></td>
<td>11,060 ± 180</td>
<td>12,100 ± 210</td>
</tr>
<tr>
<td></td>
<td>CAMS-19997</td>
<td></td>
<td></td>
<td></td>
<td>A-1584</td>
<td>A-1563</td>
</tr>
<tr>
<td>11,000 ± 140</td>
<td>11,020 ± 200</td>
<td>11,140 ± 160</td>
<td>11,330 ± 370</td>
<td>12,440 ± 300</td>
<td>11,590 ± 230</td>
<td>11,590 ± 230</td>
</tr>
<tr>
<td>11,140 ± 250</td>
<td>11,370 ± 300</td>
<td>A-1453</td>
<td>A-1392</td>
<td>12,050 ± 400</td>
<td>A-1070</td>
<td></td>
</tr>
<tr>
<td>A-1054</td>
<td>11,480 ± 200</td>
<td>A-1392</td>
<td></td>
<td>L-437C</td>
<td></td>
<td></td>
</tr>
<tr>
<td>11,020 ± 200</td>
<td>A-1041</td>
<td>A-1392</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12,050 ± 400</td>
<td>L-437C</td>
<td>A-1392</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12,440 ± 300</td>
<td>A-1070</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Elevations are given for each site. For Rampart Cave, only the 10 youngest dates are given. Data are compiled from refs. 8, 22, 55, 58, 65, and 66, where additional details can be found. A, University of Arizona Radiocarbon Laboratory; CAMS, Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory; I, Isotopes, Inc.; L, Lamont Geological Observatory; LJ, La Jolla Radiocarbon Laboratory; Y, Yale Radiocarbon Laboratory.
cave at the foot of the Andes in Neuquén Province, Argentina. An AMS $^{14}$C date on the dung of an unknown species of sloth, preserved in a late glacial vischachama midden, is $14,665 \pm 150$ yr BP (29). Cueva del Milodón, a large cave in quartz conglomerate bedrock in southern Chile (26, 27), has yielded six $^{14}$C dates on dung of Mylodon darwini who are <11,000 yr BP at their 2σ low range; three of these $^{14}$C dates are <10,000 yr BP at their 2σ low range. Two of these three dates are not older than 11,100 yr BP at their 2σ high range, just as at Gruta del Indio.

The other extinct South American sloth with a direct age determination is Ereitherium laurillardi from the Itatuba Quarry alluvial site on the lower Rio Tapajos, Pará State, Brazil, a humid tropical lowland setting (30). The single AMS $^{14}$C date available for purified collagen of E. laurillardi bone is $11,340 \pm 50$ yr BP.

To summarize the South American chronology, the youngest reliable dates on dung or tissue of extinct sloths have means of $\approx 10,600$ to 10,200 yr BP (Table 2). They are slightly younger than the surface dates on Shasta sloth dung from North America. Based on this chronology, if the first Americans triggered sloth extinctions, then these people must have spread rapidly from North America through South America. Some archaeologists (e.g., ref. 31) question whether the archaeological evidence supports such a rapid human colonization and believe that both American continents sustained people earlier than 11,000 yr BP. We are at a loss to explain why these hypothesized earlier Americans would be so cryptic archaeologically, especially in well-explored North America.

**Last Appearance Radiocarbon Dates on Extinct West Indian Sloths**

The late Quaternary sloths of the West Indies feature five endemic genera and at least 13 species (5), with five species in Cuba and Isla de Pinos (Acratocnus antillensis, Megalocnus rodens, Neocnus gliriformis, N. major, and Parocnus brownii), six in Hispaniola and its nearby small islands of Gonâve and Ile de la Tortue (Acratocnus ye, Megalocnus zile, Neocnus comes, N. douman, N. toupiti, and Parocnus serus), one in Puerto Rico (Acratocnus odontirigonus), and one in Curacao (Paulocnus petrifactus). In the absence of $^{14}$C dates it is not certain that Paulocnus persisted into the late Quaternary (see Supporting Text), although we regard this hypothesis as more probable than not. Associated K/Ar dates for the unnamed Grenadian sloth place this taxon in the late Pliocene (32); in the absence of late Quaternary dates, there is no basis for including it in this survey.

Before the radiometric chronology of West Indian fossil sites began to be determined, it was often assumed that humans and sloths overlapped in time because some cave localities had evidence of human occupation in addition to the remains of the extinct fauna (33, 34). As is often the case on tropical islands (35, 36), these assumed stratigraphic associations have not been, and probably cannot be, verified because of inadequate field notes and subsequent damage to the sites. Nevertheless, the larger question of the timing and significance of the West Indian losses in relation to the extinction chronology on the American continents now can be reexamined, thanks to a previously unreported series of AMS $^{14}$C dates for sloth bones from Cuba and Hispaniola.

**Cuba.** Sloths survived into the Holocene in Cuba, as evidenced by an AMS $^{14}$C date of 6,250 ± 50 yr (Table 3) on a humerus of the largest West Indian sloth, Megalocnus rodens, from a limestone cave (Cueva Beruvides) in Matanzas Province (37). An even younger date (4,960 ± 280 yr BP) is available for a smaller species, Parocnus brownii, from Las Breas de San Felipe, a small tar pit in Matanzas Province (38, 39). The associated fauna at Cueva Beruvides has not yet been pub-

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**Table 2. Radiocarbon dates (yr BP and lab numbers) on sloth dung from South America**

<table>
<thead>
<tr>
<th>Species</th>
<th>Gruta del Indio, Argentina (660 m)</th>
<th>Cueva del Milodón, Chile (200 m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nothrotherium maquinense</td>
<td>$12,200 \pm 120$ (NZA-6984)</td>
<td>$10,200 \pm 400$ (SA-49)</td>
</tr>
</tbody>
</table>

For Gruta del Indio and Cueva del Milodón, only the 10 youngest dates are given. Data are compiled from refs. 9, 22, 25–29, where additional details can be found. A, University of Arizona Radiocarbon Laboratory; BM, British Museum Radiocarbon Laboratory; GrN, Groningen Radiocarbon Laboratory; GX, Geochronology Laboratories, Inc.; LP, Tritium and Radiocarbon Laboratory, Universidad de la Plata; NZA, Rafter Radiocarbon Laboratory; SA, Gif sur Yvette, Saclay; Ua, Uppsala Accelerator.

*Body tissue rather than dung.*
lished by its discoverers but is known to include several species of sloths as well as endemic rodents and insectivores. Las Breas de San Felipe has yielded a great variety of fossils in addition to vertebrates, including plants, insects, decapods, and mollusks. The oldest reliable 14C date for a cultural site on Cuba is 5,270 ± 20 yr BP (39).

**Hispaniola.** Although several Holocene “whole bone” 14C dates have been reported for Haitian cave sites (40–42), these dates were not necessarily tied to individual taxa. For sloths, this task would have been difficult in do in any event, because Hispaniolan sloths were not revised systematically until recently (5). Nevertheless, a single “whole-bone” date (8,120 ± 216 yr BP) on an assortment of sloth bones (42) provided the first evidence that phyllophagans had persisted into the Holocene, which may have survived even later (42).

**Puerto Rico.** No bones of *Acratocnus odontorhagus*, Puerto Rico’s only species of sloth, have been successfully 14C dated, apparently because available samples have suffered total diagenetic loss of collagen (R.D.E.M., unpublished observations). Charcoal from a dated sediment sequence in Laguna Tortuguero indicates a major shift in the Puerto Rican fire regime at ~5,000 yr BP, which may indicate the arrival of people (14). If organically well-preserved bones of *A. odontorhagus* can be found, we suspect that at least some of the resulting 14C dates would fall within the Holocene.

**Discussion and Conclusions**

When examined critically, the youngest sloth dung deposits in South America are only centuries later than the youngest from North America. Although younger age estimates appear from time to time (see Supporting Text), no remains of megafaunal sloths or any other large, extinct mammal in either North or South America have been reliably dated to within the last 10,000 14C years (~11,600 cal BP). Sloth remains are absent from...
abundant Holocene fossil deposits on both continents. The entire pattern is in step with conventional views of human colonization in the Americas, with Clovis arrival in western North America no more than 1,000 yr before people arrived in South America (43).

In Cuba and Haiti, conversely, eight of the 13 AMS $^{14}$C dates are Holocene rather than Pleistocene, with two of them <5,000 yr BP. The early (>2,000 yr BP) archaeology of these islands has not been studied intensively, although several sites have produced lithic artifacts (especially large chert blades) in probable association with $^{14}$C dates as old as ~5,500 yr BP (15, 16, 44–46). Sloth bones have not been found with certainty in any West Indian archaeological locality. Nevertheless, as on the continents, the extinction of West Indian sloths followed the peopling of these islands, which took place in the Holocene rather than the Pleistocene.

If the extinction of West Indian sloths was forced by the Upper Dryas or some other late Quaternary cold stage, it is hard to understand how final loss could have been delayed into the mid-Holocene. That insular sloths persisted 5,000–6,000 yr longer than their continental relatives agrees with the global pattern of late Quaternary vertebrate extinction following human dispersal, whether on continents or islands (12, 47, 48). Deferred extinction of insular sloths resembles the situation with mammoths (Mammuthus), where isolated populations survived on Wrangel Island (Chukchi Sea, northeastern Asia) and St. Paul Island (Bering Sea) into the early to mid-Holocene, which is several millennia later than on the Eurasian or American continents (49, 50).

By themselves, the AMS $^{14}$C dates do not demonstrate that people caused the extinction of N. comes. In yielding $^{14}$C ages ranging from ~27,000 to 4,500 yr BP, however, the seven dated bones of Neocnus comes do show that this sloth survived the glacial-interglacial (Pleistocene–Holocene) transition when the West Indian climate in general and the Hispaniolan climate in particular became warmer and wetter (~11,000 to 8,000 yr BP) (51), only to perish in the mid-Holocene, during a period of relatively stable local climate (Fig. 3). There is both archaeological and environmental evidence of considerable mid-Holocene human activity in the West Indies, including burning (14, 52, 53). From sediments in Lake Miragoâne in Haiti, for example, charcoal influx increases dramatically and pollen of forest taxa (such as Palmae and Podocarpus) decline to near absence at ~5,730 yr BP, accompanied by a major increase in pollen of Ambrosia, a disturbance indicator (52).

All extinct continental species of Quaternary sloths were exclusively ground-dwelling, but those of the West Indies were more varied. Morphometric analyses suggest that the largest (Megalocnus, Parocnus) were entirely terrestrial or nearly so, whereas the small ones such as Neocnus comes had skeletal features consistent with arboreality (4). It is easy to conceive unsustainable levels of direct predation by skilled human hunters on any species of ground-dwelling sloth, which moved slowly and had not been exposed previously to human predators, whether on islands or continents. The survival of small tree-dwelling sloths on continents is probably because they are so cryptic (live high in trees, are silent, relatively immobile, and have algal camouflage; see ref. 54). The extent to which N. comes had these characteristics is unknown, although spending time on the ground would be safer for a small sloth on an island lacking placental carnivores (such as any of the West Indies) than on the continents, where felids and canids patrol. The arrival of people may have rendered the small insular sloths more vulnerable than their arboreal counterparts on continents.

Should further work on the chronology of sloth extinction support what has been learned so far, it will be difficult to explain how a change in climate or habitat could have eliminated this durable group from North and South America thousands of years before they became extinct on Caribbean islands. Because all surviving species of sloths and other xenarthrans are tropical or subtropical, we see no reason why the glacial-interglacial global warming that took place at the Pleistocene–Holocene

![Fig. 2. AMS $^{14}$C-dated bones of Neocnus comes, an extinct sloth from Haiti.](image-url)
transition should have had a negative effect on sloths or their relatives, whether on islands or continents. The plants identified in the ancient sloth dung in North or South America are dominated by species still found near the fossil sites (refs. 23, 26, and 55–59; see also Supporting Text). If they were alive today, megafaunal sloths could eat the same kind of plants that they ingested at the end of their existence. This finding argues further against a climate-driven change in habitat as causing the extinction of sloths by affecting their food supply.

Many other endemic West Indian mammals became extinct in the late Quaternary along with the sloths, namely 75% of the species of insectivores, 80% of the rodents, and 100% of the primates (39, 59–64). A fruitful topic for new research would be to compare the extinction chronology of insular sloths with that of the other endemic mammals (e.g., 37). With a more intensive program of AMS 14C dating on islands, we predict that more species of West Indian sloths will be found to have existed during the period of human occupation. We also encourage a renewed effort to locate and study early archaeological sites across the West Indies.

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