The extinction of *Xenothrix mcgregori*, Jamaica's last monkey

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The Jamaican primate, *Xenothrix mcgregori*, regarded variously as either a pitheciid or a stem platyrrhine, was the terminal branch of a clade that likely entered the West Indies at least as early as the Early Miocene, although its lineage is represented by fossils of Quaternary age only. We present a new direct radiocarbon-based date of 1,477 ± 34 calibrated years before present (cal BP) for the last documented appearance of this species in the fossil record. We employed the Gaussian-resampled, inverse-weighted McInerny et al. (GRIWM) method to estimate the extinction date of *X. mcgregori*, based on the data presented here as well as 6 other dates derived from *X. mcgregori* sites. On this basis, we estimated a last occurrence ~900 BP. The cause or causes of this extinction, as well as the many others that occurred in late Quaternary of the Greater Antilles, remain a matter of debate. The likeliest inference is that these losses were largely if not completely anthropogenically driven. Although many species and populations of primates are critically threatened today, the loss of *X. mcgregori* stands as the most recent species-level extinction within Anthropoidea corroborated by radiometric evidence.

El primate de Jamaica *Xenothrix mcgregori*, considerado alternativamente como un Pitheciidae o como un Platyrrhini troncal, fue la rama terminal de un clado que probablemente ingresó a las Indias Occidentales al menos en el Mioceno Temprano, aunque su linaje está representado únicamente por fósiles del Cuaternario. Aquí presentamos una nueva datación radiocarbónica de ca. 1,477 ± 34 AP para la aparición más reciente documentada de esta especie en el registro fósil. También empleamos el método Gaussian-resampled inverse-weighted de McInerny et al. (GRIWM) para estimar el momento de extinción de *X. mcgregori*, basado tanto en datos presentados aquí, así como en otros seis fechados derivados de sitios con este primate. De otra forma, estimamos el último registro en ca. 900 AP. La causa o causas de esta extinción, así como las otras que ocurrieron en el Cuaternario tardío en las Antillas Mayores siguen siendo un tema de debate. La inferencia más probable es que estas pérdidas fueron en gran medida, si no completamente, impulsadas por la acción antrópica. Aunque muchas especies y poblaciones de primates están críticamente amenazadas hoy en día, la pérdida de *X. mcgregori* es la extinción más reciente a nivel específico dentro de Anthropoidea corroborada por evidencia radiométrica.

Key words: Caribbean, extinction, Greater Antilles, GRIWM method, Jamaica, platyrrhine evolution, radiocarbon dating, *Xenothrix mcgregori*

The fossil record of endemic Greater Antillean primates consists of 5 named species. These include *Antillothrix bernensis* and *Insulacebus toussaintiana* on Hispaniola, *Paralouatta varonai* and *Paralouatta marianae* on Cuba, and *Xenothrix mcgregori* on Jamaica. None has a settled relationship with mainland Central and South American monkey clades (Ford 1990b; MacPhee et al. 1995; Horovitz and MacPhee 1999; Rosenberger 2002; MacPhee and Horovitz 2004; Cooke et al. 2011; Kay et al. 2011; Rosenberger et al. 2011, 2013, 2015; Kay 2015), and the timing and method of their entrance onto the islands have been much debated (MacPhee et al. 1995; Iturralde-Vinent and MacPhee 1999). Despite these uncertainties concerning their

origins and relationships, Antillean primates persevered for at least 18 My (million years), from the Burdigalian (20.44–15.97 Ma—MacPhee et al. 2003) through the late Quaternary (1.0–0.5 Ma—Rímoli 1977; MacPhee 1984). One of the last, if not the very last, of these primates was the enigmatic *X. mcgregori*. Here, we present new direct radiocarbon dates, in combination with extinction modeling, to establish that the Jamaican monkey persisted longer than previously known, well into the period of human occupation of Jamaica, which began approximately 1,200 years ago (Vanderwal 1967; Fitzpatrick 2006), but potentially not into the era of European colonization, which commenced in 1503–1504 AD (Wesler 2013; see Supplementary Data SD1).

Specimens of *X. mcgregori* first were recovered through the efforts of Harold Anthony in January 1920 at Long Mile Cave in north central Jamaica (Fig. 1; Anthony n.d.; Williams and Koopman 1952). The specimens remained undescribed until Williams and Koopman (1952) designated a partial mandible preserving the left 2 molars (m1–2; AMNH 148198) as the type specimen of the new species. Although these authors briefly noted the presence of associated postcranial material in the Anthony collection, they did not assign any of it to the *X. mcgregori* hypodigm, and the description of the Long Mile Cave *X. mcgregori* femur (AMNH 259900), os coxae (AMNH 259904), and tibiae (AMNH 259902, 259903) had to wait another 40 years (MacPhee and Fleagle 1991). Though the os coxae has definitively primate morphology, the tibiae and femur are different morphologically from other known primate species and were, in part, assigned to *X. mcgregori* by MacPhee and Fleagle (1991) based on their association with the type specimen and the os coxae. That being said, the Long Mile Cave femur does possess a primate-like greater and lesser trochanter, femoral condyles consistent with a primate-like arboreal locomotor pattern, and falls within

the body-size range estimated for the partial-mandible type specimen.

From the 1920s through the 1980s, no other relevant fossils were recovered in Jamaica apart from 2 mammalian femora exhibiting characteristics implying arboreal or scansorial capabilities: 1 from Coco Ree Cave (UF 40097—Ford and Morgan 1986; Ford 1990a, 1990b) and another from Sheep Pen Cave (UF 58003—Ford and Morgan 1988; Ford 1990a, 1990b). Morphologically, these specimens differed markedly from femora associated with the type specimen, leading MacPhee and Flemming (2003) to question their status as primate (as opposed to caviomorph rodent)—a position we adopt here pending discovery of additional and more diagnostic material.

During the 1990s, several expeditions to caves on the southern coast of Jamaica conducted jointly by the American Museum of Natural History and Claremont-McKenna College resulted in the recovery of additional specimens of *X. mcgregori*. The sample comprised the 1st cranial specimens as well as additional associated postcranial material including a femur from Somerville Cave, which is dated here (AMNH 268003; see MacPhee and Horovitz 2004; MacPhee and Meldrum 2006; Fig. 2). The Somerville Cave femur and the Long Mile Cave femur share mediolaterally compressed condyles and a relatively broad and flat patellar surface, but has a somewhat more gracile shaft.

This new collection of primate material confirms and further elucidates the unique morphology and adaptations of *X. mcgregori*. The 3–5 kg primate (MacPhee and Meldrum 2006; Cooke and Halenar 2012) had a robust postcranium consistent with slow arboreal quadrupedalism and climbing (MacPhee and Fleagle 1991; MacPhee and Meldrum 2006). Craniodentally, it was unique among platyrrhines in exhibiting a low-cusped, low-crowned dentition, with a dental formula convergent on that of mainland callitrichines (Rosenberger 1977; MacPhee
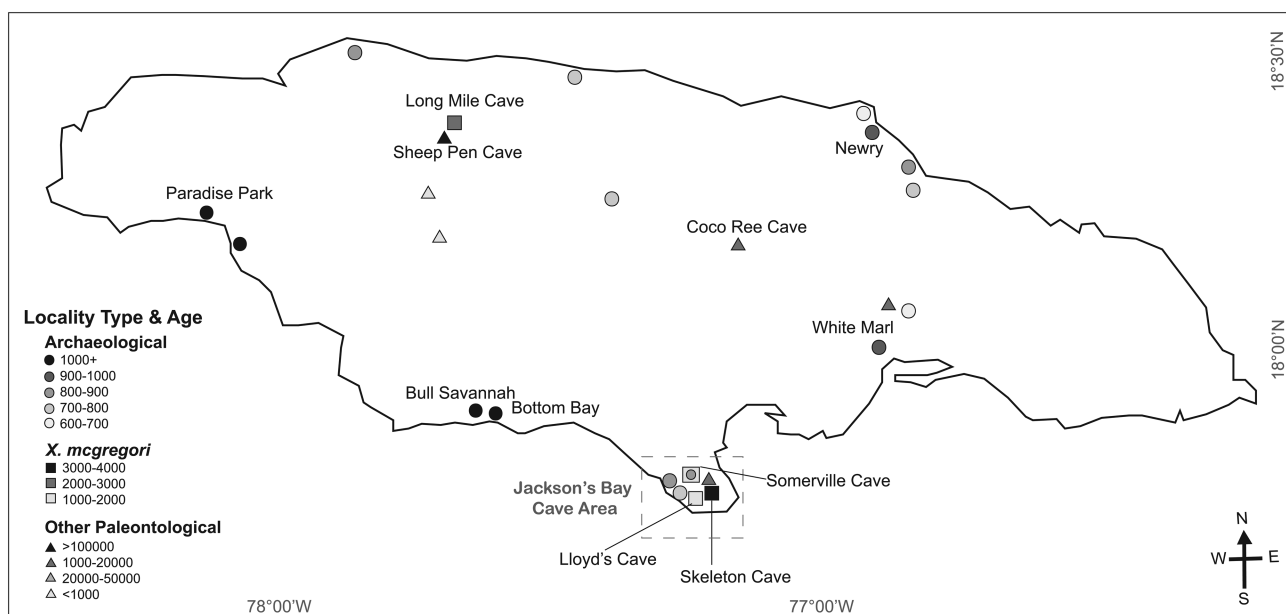

Fig. 1.—Map of Jamaica depicting archaeological, *Xenothrix mcgregori*, and paleontological sites that have radiocarbon dates available, with key sites labeled. Darker symbols indicate older dates.

Fig. 2.—*Xenothrix mcgregori* femora. AMNH 268003—the specimen dated here—shown in anterior (A) and posterior (B) views. AMNH 259900—found in Long Mile Cave, the same site from which the *X. mcgregori* type specimen (AMNH 148198) comes—shown in anterior (C) and posterior (D) views. Scale bar is 1 cm.

and Horovitz 2004). Dentitions of this character imply significant crushing and grinding abilities (Kay 1975), suggesting that *X. mcgregori* may have had a diet of fruit or hard objects (Cooke 2011).

Although the fossil evidence for this taxon is exclusively Quaternary, unlike most other Greater Antillean primates, its unusual morphology and unique adaptations do not indicate a close evolutionary relationship with any extant primate. It generally has been classified as either a pitheciid (Rosenberger 1977; Horovitz and MacPhee 1999; Rosenberger 2002; MacPhee and Horovitz 2004; Cooke 2011) or a stem platyrrhine (Kay 2015). It also shares some dental characteristics with the Miocene Patagonian genus *Soriacebus* (Cooke 2011; Cooke et al. 2011), potentially indicating morphological continuity with earlier forms.

The unusual adaptations of *X. mcgregori* evolved in the context of a depauperate, evolutionarily unique Greater Antillean mammalian fauna, which consisted of 4 orders of nonvolant mammals: Rodentia, Soricomorpha, Pilosa, and Primates. Although the Cuban and Hispaniolan faunas included all 4 orders, and each island had upwards of 20 endemic species, only 5 endemic species in 2 orders (Rodentia, Primates) have been recovered on Jamaica (Table 1). Of these species, only 1 has survived to the present: the Jamaican hutia (*Geocapromys*

brownii), a large capromyid rodent now restricted to mountain refugia and listed as Vulnerable by the IUCN (Turvey and Dávalos 2008). The largest native Jamaican species was the ?neoepiblemid rodent, *Clidomys osborni*, with an estimated body size of 20–30 kg (MacPhee 1984; Pascual et al. 1990; MacPhee 2011). Its documented fossil record is older than that of any other Jamaican mammal, with a tentative last occurrence date of 38,688 ± 3,117 calibrated years before present (cal BP; GX-9438—MacPhee 1984); however, this date is based on the apatite fraction of an associated turtle shell sample and may be substantially in error. The only other taxonomically defined rodent, the small-bodied and nominally heptaxodontid *Xaymaca fulvopulvis*, is known only from its type locality, Drum Cave, in the Jackson Bay Cave system (MacPhee and Flemming 2003; MacPhee 2011). Radiocarbon dates suggest *X. fulvopulvis* may have gone extinct prior to human occupation of the island, suggesting that anthropogenic factors were not at play in its extinction (MacPhee 1984; MacPhee and Flemming 2003), though given the scanty fossil evidence for these species, no firm conclusions can be drawn at this time. This species probably was only slightly larger than the sigmodontine rice rat, *Oryzomys antillarum* (50 g), which was common in both archaeological and paleontological sites (Morgan and Woods 1986) and was last collected in the wild in 1877 (Thomas 1898). The smaller

Table 1.—Endemic nonvolant mammals of Jamaica and their last occurrences.

Order	Family	Species	Last occurrence
Primates	?Pitheciidae/stem platyrrhine	*Xenothrix mcgregori*	1,477 ± 34 cal BP[a]
Rodentia	Capromyidae	*Geocapromys brownii*	Extant[b]
Rodentia	Cricetidae	*Oryzomys antillarum*	1877 AD (historical)[c]
Rodentia	?Heptaxodontidae	*Xaymaca fulvopulvis*	11,994 ± 180 cal BP[d]
Rodentia	?Neoepiblemidae	*Clidomys osborni*	38,688 ± 3,117 cal BP[e]

[a]This study.
[b]Anderson et al. (1983) and Turvey and Dávalos (2008).
[c]Thomas (1898).
[d]MacPhee and Flemming (2003).
[e]MacPhee (1984).

size of *O. antillarum* likely placed it in competition with *Rattus* (Woods 1989) and predisposed it to predation by the invasive mongoose (Allen 1942; Lewis et al. 2011; see Hansford et al. 2012 for a discussion of body size and extinction), which was introduced to the island in the middle of the 19th century (Willis 1898). However, there is some evidence that it was in decline prior to the introduction of the mongoose as Gosse (1851:450) reported that at that time it was "far from numerous." Thus, at 3–5 kg, *X. mcgregori* would have been the 2nd largest species on the island in the late Quaternary and 1 of only 3 nonvolant mammal species to possibly encounter humans (Fig. 3).

The radiocarbon record of *X. mcgregori* sites was based on stratigraphically associated bat guano, terrestrial gastropod shells (McFarlane et al. 2002), or associated bone fragments of *G. brownii* (MacPhee 1984; Supplementary Data SD2). The youngest associated date is from Lloyd's Cave, which yielded an uncalibrated date of 1,750 ± 80 radiocarbon years before present (rcybp), calibrated to 1,670 ± 96 cal BP. Uncalibrated dates ranging from 6,410 ± 110 to 3,420 ± 60 rcypb were recovered at Skeleton Cave, and dates of 11,220 ± 100 to 10,250 ± 80 rcypb were recovered for specimens from Brown Dust Passage of Drum Cave (McFarlane et al. 2002; MacPhee and Meldrum 2006)—sites in close proximity to Somerville Cave, the source of the specimen dated here (Fig. 1). The older of the 2 Skeleton Cave dates, however, should be treated with caution as the cave fill containing the *Xenothrix* specimens is a flood deposit, thus this date may not reflect the actual age of *X. mcgregori*, but rather the age of the underlying sediment (MacPhee and Horovitz 2004). A date on an associated nonprimate bone fragment yielded a date of 2,151 ± 74 cal BP (2,145 ± 220 rcypb—MacPhee 1984) at the *X. mcgregori* type locality, Long Mile Cave, in northwestern Jamaica. No previous study has dated any specimen of *X. mcgregori* directly. Indeed, few published direct radiocarbon dates for Jamaican endemic non-volant mammals exist, which undermines accurate modeling of extinction dynamics on the island (Supplementary Data SD2).

The last radiocarbon date in a series of radiocarbon records is not necessarily the true last occurrence of a species, as environmental and taphonomic conditions, life-history traits, and researcher sampling biases may seriously complicate extinction estimates (Saltré et al. 2015). This is illustrated by the phenomenon of the "Lazarus effect," in which a lineage thought extinct at 1 point in time is suddenly "resurrected" by a new date recovered by additional sampling (Keith and Burgman 2004). To account for these biases, paleontological models can

take advantage of temporal gaps between known species occurrences—radiocarbon dates—to extend the temporal record a species occupies to include the most probable date of extinction (Bradshaw et al. 2012). These temporal ranges can be further corrected with methods that account for nonrandom fossilization and uncertainty in radiocarbon ages, such as the Gaussian-resampled, inverse-weighted McInerny et al. (GRIWM) method (McInerny et al. 2006; Bradshaw et al. 2012). Here, we employ the GRIWM method to better estimate the last occurrence of *X. mcgregori* in the context of potential extinction drivers including both climatic and anthropogenic factors and provide insight into mammalian extinctions across the Greater Antilles.

MATERIALS AND METHODS

Site description.—Somerville Cave is located near the coast of Jackson's Bay on the southern coast of Jamaica and is part of a large cave system on the western portion of the Portland Ridge (77°13′W, 17°44′N; for a complete description see Fincham 1997; McFarlane et al. 2002; MacPhee and Horovitz 2004). Though the processes of cave formation in this region are poorly understood, McFarlane et al. (2002) suggested that most of the caves formed in Miocene rock during the late Pliocene into the early Pleistocene; however, the earliest radiometric dates obtained using U-Th dating of flowstone indicate an age of only ~200 ka (Wadge et al. 1979; McFarlane et al. 2002). Somerville Cave is located above the current water table and is part of the "upper cave" system from which all of the fossils were recovered. The cave fill floor consists of a red paleosol-derived sediment that has yielded the fossil specimens (McFarlane et al. 2002). In some regions, a thin flowstone crust covers this fill.

In addition to its paleontological significance, the cave system also has produced archaeological remains consistently superficial to the paleontologically rich red paleosol sediment that fills the cave (McFarlane et al. 2002). Archaeological remains include pottery, cassava griddles, petroglyphs, and pictographs as well as skeletal material (Fincham and Fincham 1997; McFarlane et al. 2002; Rega 2006; Allsworth-Jones 2008).

The distal femur of *X. mcgregori* (AMNH 268003) was recovered on the surface of an exposed ledge near the entrance of Somerville Cave in August 1993 (Fig. 1). The specimen may have fallen from a notch in the cave wall, which MacPhee and Meldrum (2006) tentatively suggested may have once been an owl roost. No other primate bones were found with it, though
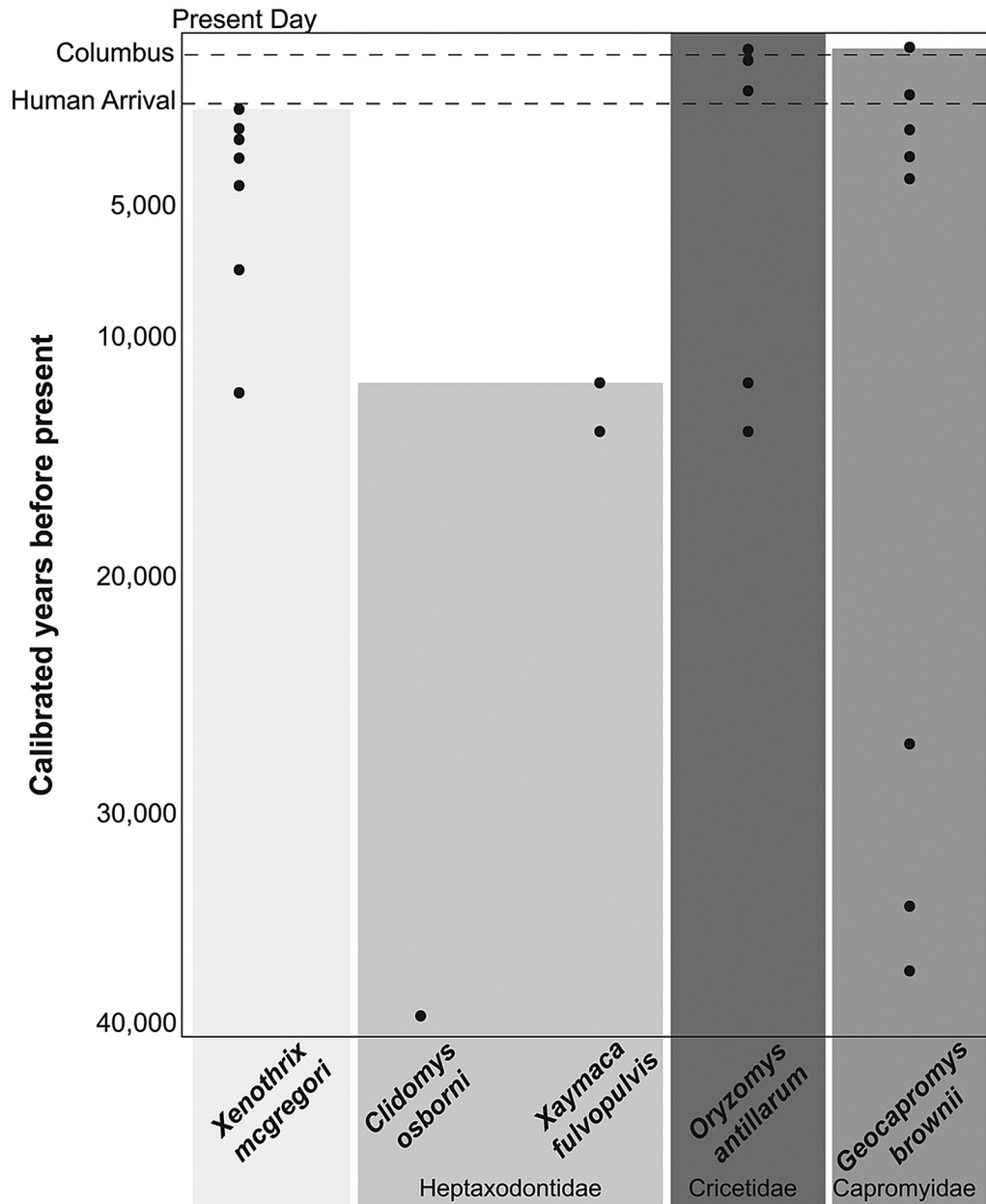
Fig. 3.—Radiocarbon chronology of mammal species endemic to Jamaica, where each black circle represents a calibrated radiocarbon date associated with a species. Not all dates are direct (see Supplementary Data SD2).

Geocapromys bones were found in the vicinity. The location is therefore best classified as a surface find, with no clear relationship to the red palesol comprising the cave fill.

Today, dry scrub forest with xerophyllic vegetation covers the area. There is a lengthy dry season of 6–10 months. Historically, the region may have had a more mesic environment as evidenced by copious quantities of subfossil bat guano in some of the caves where no substantial modern chiropteran populations exist (Mizutani et al. 1992; McFarlane et al. 2002).

Sample processing and calibration.—The sample was processed at the W.W. Keck Carbon Cycle Accelerator Mass Spectrometer Center at the University of California, Irvine in 2014. The femur originally was preserved using a solution of the consolidant Butvar (polyvinyl butyral or PVB) in acetone.

As Butvar is itself derived from fossil fuel materials, it could potentially bias radiocarbon dates toward a date older than its true geological age.

We employed several processing strategies, including 2 removal treatments and ultrafiltration, to determine the impact of resin contamination, if any, on the bone. Aliquots of powdered bone were sonicated in acetone or methanol (known effective Butvar solvents) and then in water prior to decalcification and gelatinization. Ultrafiltration allowed for the selection of molecular weight fractions of > 30 kilodaltons (kDa) and 3–30 kDa. For comparison, samples of modern and radiocarbon-dead bone were soaked overnight in a 7% solution of Butvar in acetone, rinsed in an acetone rinse, then air-dried for 48 h. These comparative samples and standards were processed

with the *X. mcgregori* femur. All radiocarbon dates were background-corrected and corrected for isotopic fractionation of ^{13}C using conventions from Stuvier and Polach (1977).

All ^{14}C dates from the AMNH 268003 femur, and all other ^{14}C dates included in this paper, were calibrated using the program OxCal 4.2 (Bronk Ramsey 2009) and the IntCal13 atmospheric Northern Hemisphere calibration curve (Reimer et al. 2013). The Marine13 modeled ocean average curve was applied to ^{14}C dates from the literature derived from shells and fish bones (Reimer et al. 2013). Additionally, we reviewed the literature to compile a data set of verifiable radiocarbon dates associated with archaeological sites from Jamaica and calibrated these dates using OxCal. Dates were excluded if the type of material dated was not listed or could not be identified, if lab identifications were missing, or other vital information was not included in the publication.

Calculating extinction timing.—We applied the GRIWM method to estimate the timing of *X. mcgregori*'s extinction (McInerny et al. 2006; Bradshaw et al. 2012), using an R script produced by Saltré et al. (2015) and executed in R version 3.2.2 (R Development Core Team 2015). This method inversely weighs observations (radiocarbon dates) according to the temporal distance from the last observation of the species; thus, the model emphasizes the weight of the most recent occurrences (Bradshaw et al. 2012). As this method incorporates uncertainty of temporal records and down-weighting intervals, it has been found to both provide model accuracy and avoid misclassification errors at a better rate relative to other procedures available in the field (Bradshaw et al. 2012; Saltré et al. 2015).

The GRIWM method is most appropriately applied to a sample size of 5 or more calibrated radiocarbon dates, but the authors caution that both date uncertainty (e.g., large radiometric dating errors, > 150 cal BP [Prevosti et al. 2015]) and a small number of occurrences can yield large confidence intervals in extinction timing estimates (Bradshaw et al. 2012). The full radiocarbon record of *X. mcgregori* has 7 dates available, including our newly reported Somerville Cave date (UCIAMS-14165X), with only 1 date exceeding > 150 cal BP error (Long Mile Cave, GX-9436). Taking into account these caveats, we assessed the sensitivity of the GRIWM method to our data set by calculating a range of extinction estimates using different subsets of the data as well as a mean of multiple subsets. The use of subsets allows a better understanding of the relative influence of each available radiocarbon date and highlights the importance of the newest date in constraining the uncertainty and temporal gaps associated with the GRIWM model. This approach addresses the fact that some dates may be inherently less reliable than others and their inclusion in analyses may create more rather than less uncertainty. The use of subsets allows us to address how each date contributes to uncertainty and temporal gap estimation (see Prevosti et al. 2015).

RESULTS

Radiocarbon dating.—We recovered 4 ^{14}C dates from our analyses (UCIAMS 141651, 141653, 141656, 141659; Table 2). The femur yielded atomic C:N ratios of 3.2–3.3, well within the normal C:N range of 2.9–3.6 for well-preserved modern bone collagen (Ambrose 1990; Bocherens et al. 1997). Ratios higher than 3.6 suggest the presence of contaminants in the form of either humic and fulvic acids produced through organic degradation in associated sediments or externally applied consolidants.

The ^{14}C dates from *X. mcgregori* samples > 30 kDa produced slightly older age estimates than those from the 3–30 kDa fraction (Table 2), and 1 of the 2 > 30 kDa samples from the Butvar-treated modern test bone yielded an anomalously radiocarbon-depleted result, whereas both aliquots of the 3–30 kDa fraction gave results consistent with the known age. These data suggest that trace amounts of Butvar contamination may have survived the solvent treatments, but were effectively removed from the 3–30 kDa fraction by ultrafiltration, as Butvar has a molecular weight of 40–250 kDa. We therefore conclude that the age estimates for the 3–30 kDa *X. mcgregori* samples (UCIAMS 141656, 141659) are likely more accurate than the dates recovered from the larger-size fractions.

Radiocarbon dates taken from the same object should be combined prior to calibration, which can be performed using the function R_Combine in OxCal (Bronk Ramsey 2009). We tested the accuracy of several date combinations using chi-squared tests as implemented in OxCal (Shennan 1988; Bronk Ramsey 2009), a method that was first described mathematically by Ward and Wilson (1978). This method tests whether the 2 radiocarbon dates resulting from 2 subsamples of the same bone are consistent with these subsamples having the same content of ^{14}C; this depends greatly on the variation in ^{14}C on the calibration curve, which varies through time.

The oldest date, UCIAMS 14153 (^{14}C age of 1655 ± 20), was discarded from further analyses due to consistent failure in chi-squared tests, due to its distant placement along the calibration curve (Table 3; Supplementary Data SD3 and SD4) as well

Table 2.—^{14}C ages obtained from a distal femur of *Xenothrix mcgregori* (AMNH 268003) using varying molecular weights of recovered "bone collagen" and preservative removal treatments. Values are reported following the conventions of Stuvier and Polach (1977).

UCIAMS #	Collagen yield	Molecular weight	Atomic C:N ratio	^{14}C age ± σ	Median cal BP ± σ
141653	8.3%	> 30[a]	3.31	1,655 ± 20	1,555 ± 25
141651	10.1%	> 30[b]	3.27	1,585 ± 15	1,460 ± 35
141656	2.3%	3–30[b]	3.23	1,540 ± 15	1,464 ± 44
141659	2.0%	3–30[a]	3.25	1,545 ± 15	1,469 ± 41

[a]Methanol.
[b]Acetone.

Table 3.—Combined ^{14}C ages for *Xenothrix mcgregori* (AMNH 268003) at 95.4% *CI*. We retained the combined calibrated date of 1,477 cal BP as 14165X (row shaded gray).

Samples included UCIAMS # 1416-	Combined ^{14}C age ± σ	Median cal BP ± σ	Chi-squared result
All dates	1,572 ± 8	1,472 ± 33	Fail
51, 53	1,610 ± 13	1,508 ± 45	Fail
51, 56, 59	1,557 ± 9	1,477 ± 34	Pass
56, 59	1,543 ± 11	1,469 ± 42	Pass

as its likely contamination with Butvar. The remaining 3 dates (UCIAMS 14151, 14156, 14159) can be accurately combined, and we denote this composite result as UCIAMS 1415X. This selection includes UCIAMS 14151, which is a > 30 kDa sample that is slightly older than the 3–30 kDa samples, but falls within the same calibration curve range as the 3–30 kDa samples. By including this slightly older date, we remove the bias of using only the younger 2 samples that support human-monkey coexistence, hence this represents a conservative choice. Calibrated, this result suggests the persistence of *X. mcgregori* until 1,477 ± 34 cal BP, providing a new last occurrence date for Jamaican primates and endemic primates of the Caribbean as a whole.

GRIWM analyses.—The GRIWM method provides support for human-monkey overlap on Jamaica. Including all 7 dates, the median extinction time is 887 cal BP—overlapping with the earliest calibrated date of human arrival (Fig. 4). Of 5 subsets with a minimum sample size of 5 dates (Table 4; Supplementary Data SD5), median extinction estimate values ranged from 782 to 990 cal BP, with a mean extinction estimate of 919.6 cal BP. The lower confidence intervals (97.5%) overlap with the occurrence of our calibrated composite (UCIAMS-14165X) radiocarbon date.

Two of our 6 subsets excluded this new result: our conservative estimate lacked the 2 most recent dates and a subset that included all dates except the UCIAMS-14165X data. Our conservative estimate yielded a median estimate of 988 cal BP, which is within the range of other estimates. However, excluding the UCIAMS-14165X data results in a median estimate of 329 cal BP, with the upper confidence interval (2.5%) extending 531 years into the future, suggesting the current persistence of the species. This clear overestimation of occurrence likely results from an overestimation of the gap size between occurrences, which UCIAMS-14165X helps constrain with its small error and close temporal position relative to other recent occurrences (Beta-67572, GX-9436). For example, the range of extinction estimates for all 7 dates (887 cal BP) has a range of 944 years, whereas the range of the anomalous 329 cal BP date is 2,086 years—clearly showing the increased certainty with the inclusion of UCIAMS-14165X. Indeed, the authors of the GRIWM method hypothesized that the most recent radiocarbon records in a series would be the most influential for extinction timing inferences (McInerny et al. 2006; Bradshaw et al. 2012); consequently, if additional recent dates become available, the hypothesized date of extinction may change and will become more secure.

The weighted emphasis on the most recent dates as indicators of extinction timing highlights the significance of our newest

and only direct date for *X. mcgregori*. Given the similarities of multiple data subsets, including our most conservative estimate containing the 5 oldest dates (Supplementary Data SD4), we retain the extinction estimate of 887 cal BP from our largest sample of 7 dates.

DISCUSSION

Our direct radiocarbon date is the youngest yet recorded for an extinct Caribbean primate. In combination with a quantitative approach to better estimate a last occurrence date for *X. mcgregori*, it allows us to reevaluate the relative role of humans and climate change in Jamaican mammalian extinctions and helps to place *X. mcgregori* in the broader context of Greater Antillean primates. Across the Greater Antilles, dates derived from endemic mammalian remains are sparse. None of the other 4 Caribbean primate species have been directly dated, but several dates from associated charcoal, bone, shell, or speleothem are available (Table 5). On Hispaniola, 3 specimens have associated dates. In the eastern Dominican Republic, charcoal associated with the type specimen of *A. bernensis* (CENDIA 1) yielded an estimate of 4,262 ± 196 cal BP (3,850 ± 135 rcybp—Rímoli 1977). In a nearby flooded cave, U-Th dating of speleothem encrusting a tibia (MHD 12) of *A. bernensis* yielded a much greater age of 1.3 ± 0.11 Ma (mega annum, millions of years—Rosenberger et al. 2015), indicating that this Hispaniolan species may have had a long tenure on the island. In Haiti, a bone fragment associated with a partial primate mandible (UF 29038) yielded a date of 10,875 ± 210 cal BP (9,550 ± 150 rcybp—MacPhee and Woods 1982). The other Hispaniolan primate, *I. toussaintiana*, currently does not have a radiometric date. While it was collected from a richly fossiliferous sinkhole where *Rattus* was recovered in upper layers (Cooke et al. 2011), this does not necessarily indicate that *I. toussaintiana* survived into the historic period, and its temporal range remains largely uncertain.

On Cuba, 2 species, *P. varonai* and *P. marianae*, have been described (Rivero and Arredondo 1991; MacPhee et al. 2003). *P. varonai* remains poorly dated, but is likely Quaternary in age (Rivero and Arredondo 1991; Horovitz and MacPhee 1999). An astragalus of a much older primate, *P. marianae*—the earliest primate yet recorded in the Caribbean—was recovered at Domo de Zaza. Domo de Zaza is considered to fall within Burdigalian time (17.5–18.5 Ma) on the basis of stratigraphic correlations (MacPhee et al. 2003). A ^{87}Sr/^{86}Sr date on oyster shell found at the level of the astragalus returned a date of 14.68 Ma; however, MacPhee et al. (2003) cautioned this should be considered a minimum age due to probable diagenesis of the shell.
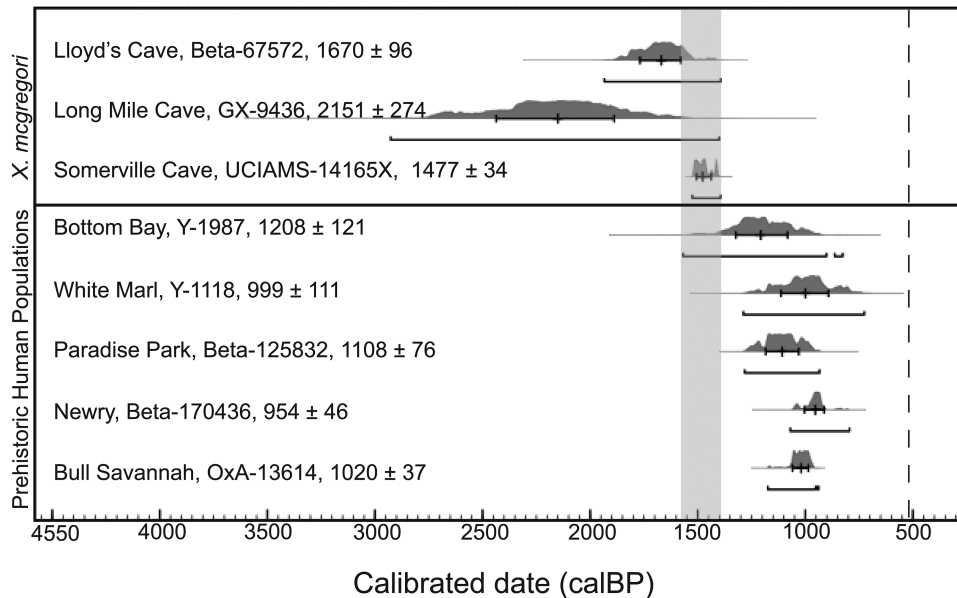
Fig. 4.—Calibrated radiocarbon dates of latest *Xenothrix mcgregori* occurrences in the fossil record and earliest occurrences of non-European human populations from the archaeological record. For each individual date (denoted by laboratory ID), black brackets represent the 95.4% probability range of a given date; black underlines represent the *SD*; black cross represents the median calibrated age. The dashed line indicates the timing of European arrival (1494 AD). Light gray shading indicates potential overlap of *X. mcgregori* and indigenous human populations from the 95.4% probability range of their radiocarbon dates.

Table 4.—Results of Gaussian-resampled, inverse-weighted McInerny et al. (2006; GRIWM) method of inferring extinction timing, including the number of dates analyzed (*N*), the upper boundary of the *CI* (2.5%), median extinction time, and lower boundary of the *CI* (97.5%).

Description of dates included	N	Upper *CI* (2.5%)	Median	Lower *CI* (97.5%)
All dates	7	471	887	1,415
Mean GRIWM results[a] (5 results)	5–7	493.6	919.6	1,420.2
Excluding UCIAMS-14165X	6	−531	329	1,556

[a]See Supplementary Data SD5 for more information. Excludes median 329 cal BP.

Table 5.—Distribution and last occurrence of native primate species in the Caribbean. No native primates have been recovered from Puerto Rico. Current data suggest plausible temporal overlap between humans and monkeys in Jamaica and Hispaniola; however, radiometric dates of archaeological material should be treated with caution.

Island	Island area (km²)[a]	Earliest human arrival	Native primate species	Last occurrence
Puerto Rico	8,761	3,192 ± 102 cal BP[b]	NA	NA
Cuba	105,805	6,059 ± 67 cal BP[c]	*Paralouatta marianae*	17.5–18.5 Ma[d]
			Paralouatta varonai	Late Quaternary[e]
Jamaica	11,026	1,208 ± 121 cal BP[f]	*Xenothrix mcgregori*	1,477 ± 34 cal BP[g]
Hispaniola	74,546	5,985 ± 100 cal BP[h]	*Antillothrix bernensis*	4,262 ± 196 cal BP[i]

[a]Giovas and Fitzpatrick (2014).
[b]Rouse (1993).
[c]Pino and Castellanos (1985).
[d]MacPhee et al. (2003).
[e]Rivero and Arredondo (1991).
[f]Vanderwal (1967).
[g]This study.
[h]Moore (1991).
[i]Rímoli (1977).

The only other relevant Caribbean taxon for which a direct radiocarbon date exists is the alleged "Cuban spider monkey," *Ateles* (= *Montaneia*) *anthropomorphus*. This nominal species was based on a series of teeth found in 1888 AD in a cave in central Cuba, in a possibly pre-Columbian setting (Montané 1908; Ameghino 1910; MacPhee and Rivero de Calle 1996). A canine root from this material yielded an uncalibrated age of 0 ± 70 rcybp, calibrated to 295 cal BP, i.e., "present" (MacPhee and Rivero de Calle 1996). This result suggests that the age of this specimen is indistinguishable from modern. As Miller (1916)

originally indicated, the teeth of *A. anthropomorphus* closely resemble those of extant *Ateles fusciceps*, a species common in Central and northern South America but never naturally resident in Cuba. Although the true circumstances surrounding the discovery of these monkey teeth probably will never be known, it may be plausibly concluded that these remains pertain to a recent introduction, purposeful or otherwise.

Patterns of human settlement and resource exploitation on Jamaica.—Given these last occurrence dates, it is of great interest that the earliest accepted date for prehistoric humans in Jamaica is 1,208 ± 121 cal BP (charcoal; lab ID Y-1897 [Fig. 4]; Vanderwal 1967; Fitzpatrick 2006), found at the Bottom Bay-Alligator Pond site in the southwestern portion of the island with the 2nd earliest date of 1,108 ± 76 cal BP (shell; lab ID Beta-125832) following closely at Paradise Park (Keegan et al. 2003). This stands in stark contrast with other islands in the Greater Antilles, where the 1st evidence of humans dates back to 6,059 ± 67 cal BP on Cuba (Pino and Castellanos 1985), 3,192 ± 102 cal BP on Puerto Rico (Rouse 1993; but see Burney et al. 1994), and 5,985 ± 100 cal BP on Hispaniola (Moore 1991; see Fitzpatrick 2006 and Giovas and Fitzpatrick 2014 for a discussion of archaeological dates; Table 5).

This apparently delayed colonization of Jamaica can be explained by 2 mechanisms: either Jamaica truly was more difficult to reach, perhaps due to unfavorable sea current patterns (Callaghan 2008), or the archaeological sampling of Jamaica is incomplete and earlier sites exist but have not yet been documented. Although the Jamaican archaeological record is poorly published, Allsworth-Jones (2008) has consolidated available knowledge on sites and radiocarbon dates. There are roughly 300 archaeological sites of varying excavation and documentation quality on Jamaica (Allsworth-Jones 2008). We have documented 47 verifiable radiocarbon dates at 16 sites from this literature. Coastal sites far exceed the number of well-excavated inland sites in keeping with expected early Jamaican Amerindian settlement patterns. The majority of dated sites are within 500–800 cal BP (Allsworth-Jones 2008; Supplementary Data SD1).

At these early archaeological sites, middens reveal significant exploitation of marine resources, resulting in declining populations of fish, turtles, and marine mammals (Little River-Redware age site of Bluefields Bay—Azevedo 2015). Terrestrial fauna including native rice rats (*O. antillarum*), hutias (*G. brownii*), and native reptiles also are found in middens. Additionally, humans had a significant impact on the island's flora through horticulture and cultivation of both native and introduced plants (Allsworth-Jones 2008). In general, the earliest human populations on Jamaica mainly were foragers and used available local resources depending on their environment, whether it was inland or coastal.

The historical record can provide additional information from eye-witness accounts of Native Caribbean people's interactions with endemic fauna, human population densities, and also may signal the arrival of new selective forces such as invasive species. Columbus saw Jamaica in 1494 AD, but there was no European settlement there until 1503–1504 AD, at St. Ann's Bay on the north coast (Wesler 2013). Columbus was greeted by an estimated 60,000 people at the harbor, based on a letter from Michele de Cuneo in 1495 AD (de Cuneo 1495). However, after the spread of disease and forced labor in European large-scale agricultural pursuits, the large indigenous population was reduced to 74 individuals, as recorded by the Abbot of Jamaica in 1611 AD (Cundall 1919). These major demographic upheavals undoubtedly produced significant challenges for endemic fauna and flora. For example, although the Jamaican rice rat, *O. antillarum*, persisted into historical times, its extinction likely is linked to both the invasive species that accompanied Europeans and the expansion of agriculture (Morgan and Woods 1986; MacPhee and Flemming 1999; MacPhee 2009).

Spanish sources documented Amerindian Taino use of dogs to catch hutias on Hispaniola. Oviedo's 1546 AD account refers to the local people hunting "an animal called hutia, four-footed, and resembling a rabbit, but smaller sized, smaller ears and rat tailed" (Miller 1929:12), but no direct mention of a native monkey is made at the time of initial contact, though, circumstantial evidence may exist. The Drake Manuscript, *Histoire Naturelle des Indies* (about 1586), documents 3 primates in the circum-Caribbean region, 2 of which are mainland forms. The third, however, is described as, "…a very agile beast. The Indians cannot tame it or feed it for they die of grief and do not eat in captivity. They have a face like a human and are very mischievous and rebellious and throw themselves against people mainly at their faces and eyes" (*Histoire Naturelle des Indies, folio 69*). Whether these few lines refer to an island endemic primate is unclear. On the basis of accounts by Sloane (1707–1725), MacPhee and Fleagle (1991; MacPhee 1996) speculated that *X. mcgregori* might have survived into colonial times, citing Sloane's description of "monkeys" being resident on the island. All that can be said is that, if Sloane actually was describing monkeys rather than hutias—a point that cannot be resolved from his inadequate descriptions—they may have been species introduced from either South America or the Old World. Finally, an engraving by Buffon in 1776 AD of "Le Potot ou Kinajou potot" depicts a kinkajou-like creature supposedly native to the "mountains" of Jamaica (Buffon 1776; MacPhee and Fleagle 1991). Given that the importation of exotic species for entertainment and pest control was popular among plantation owners in the 18th century, the "potot" could simply be an introduced escapee, not *X. mcgregori* whose authentic dates are firmly within the prehistoric period.

Pleistocene climatic conditions and change.—Several climate proxies exist for the Greater Antilles during the late Quaternary when humans would have come to colonize the islands—most notably the 12,000-year ostracod shell record of Lake Miragoane, Hispaniola (Hodell et al. 1991; Higuera-Gundy et al. 1999). Oxygen isotope ratios ($^{18}O/^{16}O$) suggest that the climate was dry during the Younger Dryas (12.9–11.7 ka) until 10,000 years BP, when more moist conditions of the early Holocene caused water levels of the lake to rise. Drier conditions returned again in the late Holocene ~3,200 BP. Lagoon records from Punta de Cartas and Playa Balien, Cuba, provide further insight into the late Holocene, with arid conditions and

increased drying occurring over the last 1,200 years (Gregory et al. 2015).

Pollen records from Lake Miragoane, Hispaniola, also provide insight into vegetation changes in the Greater Antilles, potentially allowing for a better understanding of ecological mechanisms affecting mammals experiencing changing conditions. Forest growth occurred from 8,200 to 5,400 BP after mostly xeric conditions of the Younger Dryas, followed by expanding and maturing mesic forests (Hodell et al. 1991; Higuera-Gundy et al. 1999). These mesic forests began to decline ~2,500 BP, leading to landscapes dominated by dry forest species. Given that the Taino extensively used this area, Hodell et al. (1991) indicate that interruptions in vegetation structure during the last 2,000 years could be linked to early agricultural practices rather than climatic perturbations. Thus, disruptive vegetation changes that may have had an impact on native mammals relying on forests were decoupled from natural climatic changes and instead resulted from prehistoric human activities.

Unfortunately, few climatic proxies as extensive as those at Lake Miragoane have been examined for Jamaica. The island lacks natural lakes and to date there have been no published efforts to extract palynologial information from speleothems. However, carbon stable isotope ($^{13}C/^{12}C$) analysis of bat guano in the Jackson Bay Cave system is in agreement with the Hispaniolan record (McFarlane et al. 2002). McFarlane et al. (2002) found that Jamaica experienced a xerophyllic period 16,500–10,000 years before present. As compared with the present in which bats show more use of xerophyllic CAM and C4 plants, late Holocene bat populations had more C3 plant species in their diet, leading McFarlane et al. (2002) to tentatively suggest a paleoclimate that alternated between dry and wet periods, with the last 2,000 years bringing a change from a wet humid climate to a dry one.

Reconciling anthropogenic and climatic factors in the extinction of X. mcgregori.—Examining the co-occurrence of archaeological sites and *X. mcgregori* localities, direct spatial (but not confirmed temporal) overlap occurs in the Jackson Bay Cave area. Potoo Hole and Water Jar Cave are both close to the *X. mcgregori* localities of Skeleton Cave and Lloyd's Cave, and the *X. mcgregori* locality Somerville Cave also is known to have been used by humans around 852 cal BP (McFarlane et al. 2002; Rega 2006; Allsworth-Jones 2008). On the northern coast, Long Mile Cave has evidence of human activity in the sediment above the *X. mcgregori* layer, though, again, there is no definitive confirmation of temporal overlap (Anthony n.d.; Williams and Koopman 1952; MacPhee 1984).

Cultural records in the form of petroglyphs and zoomorphic artifacts suggest that the 1st people on Jamaica were very aware of the endemic fauna (Hayward et al. 2009). Pottery found at Little River-Redware sites on Jamaica consistently features zoomorphic handles depicting fish, birds, snakes, lizards, and crocodiles (Bercht et al. 1997), though the relatively common rodent, *G. brownii*, is not frequently shown. The petroglyphs of Jamaica have not been as thoroughly documented as they have on other islands, where depictions of birds, iguanas, and bats have been found, though, they are also not particularly common (Hayward et al. 2009). The 1 piece of archaeological evidence of Taino and primate interaction that does exist comes not from Jamaica but from Hispaniola, in the form of a ceremonial ax decorated with an apparent monkey and deposited in the collections of the Museo del Hombre Dominicano (Santo Domingo, Dominican Republic—Guerrero 2012). No information exists concerning the age of the object, and it remains possible that the decoration depicts not an endemic Caribbean primate but a mainland import.

Despite the fact that native Jamaican rodents are well known from Taino middens and even consumed today in the case of *G. brownii* (Wilkins 2001; Allsworth-Jones 2008), no obviously butchered *X. mcgregori* bones have been found in any midden context. This simply may be due to the ease of catching and storing abundant social rodents as compared with comparatively rare arboreal primates, even within the same geographic area. Elsewhere in the Caribbean evidence of primate exploitation also is, for the most part, absent. On Hispaniola, Miller (1929) supposedly found the endemic *A. bernensis* in a midden context, but this has not been verified since his initial report. On Cuba, there is no evidence for human exploitation of *Paralouatta*. Thus, direct evidence for consumption of endemic primates is minimal and based on limited evidence.

While the new date for *X. mcgregori* indicates a likely overlap in time between Jamaican monkeys and humans, it does not imply sustained coexistence. For example, if we use the mean extinction estimate from our GRIWM analysis (919.6 cal BP) and the earliest secure date for human occupation of the island (1,208 ± 121 cal BP), a temporal overlap for humans and X. mcgregori exisits for 168–409 years. A similar pattern of extinction subsequent to human arrival appears to be present on other Greater Antillean islands (e.g., sloths—Steadman et al. 2005; rodents—Turvey et al. 2007; Hansford et al. 2012). Hansford et al. (2012) have argued that body size may play a role in survivorship in the Caribbean, with organisms about 1 kg (e.g., *G. brownii*) being more likely to survive overexploitation through hunting by humans, while simultaneously being less likely to be the prey of introduced carnivores. *X. mcgregori* falls above the hypothesized "Goldilocks" zone potentially predisposing it to exploitation by humans. Comparatively large-bodied sloths like *Megalocnus* and *Acratocnus* did not survive appreciably longer than their smaller-bodied relatives like *Neocnus* on either Cuba or Hispaniola (Steadman et al. 2005), and at least some sloth species survived for millennia after presumed initial human arrival. An additional factor was probably at play in the case of *X. mcgregori*. One possibility is that it was indeed rare in the environment, increasing the chances for catastrophic loss soon after the arrival of humans.

SUPPLEMENTARY DATA

Supplementary Data SD1.—Further text discussion of Jamaican archaeological evidence.
Supplementary Data SD2.—Radiocarbon dates pertinent to endemic nonvolant Jamaican mammals. Direct dates are

highlighted in gray; dates not highlighted are from material associated with the specimen.

Supplementary Data SD3.—All dates calibrated individually (smaller gray histograms) along the IntCal13 calibration curve (large gray vertical curve). Black brackets represent 95.4% range for each date. UCIAMS-141653 falls outside a cluster formed by the other 3 obtained dates.

Supplementary Data SD4.—Radiocarbon date combinations that pass chi-squared tests. The large light gray vertical curve represents the IntCal13 calibration curve. The small light gray curve along the *y*-axis is the radiocarbon concentration of the samples. The dark gray histograms along the horizontal axis are the calibrated probability density functions indicating the calibrated age. Black underlines are the standard deviation; black cross in the center represents the median age. (A) The combination of 141656 and 141659, which has 1 *d.f.* and $T = 0.1$ (5% 3.8). (B) The combination of 141651, 141656, and 141659, which we adopt as a conservative estimate, has 2 *d.f.* and $T = 5.4$ (5% 6.0).

Supplementary Data SD5.—Results of Gaussian-resampled, inverse-weighted McInerny et al. (GRIWM) method of inferring extinction timing, including the number of dates analyzed (*N*), the upper boundary of the confidence interval (2.5%), median extinction time, and lower boundary of the confidence interval (97.5%). Shaded gray indicates estimates that exclude the most recent Somerville Cave date published here (UCIAMS-14165X). Negative dates indicate that the confidence interval extends into the future as both the GRIWM model and radiocarbon dating in general assume 1950 AD as the present.

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