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New radiocarbon dates reveal pan-Holocene deposition of rodents at Trouing Jérémie #5, a sinkhole in the western Tiburon Peninsula, Haiti

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Abstract

We present eight new radiocarbon dates for endemic and invasive rodents from Trouing Jérémie #5, a paleontologically-rich sink hole on the Tiburon Peninsula, Haiti. This includes new dates for two species that have been previously directly dated (*Isolobodon portoricensis* and *Brotomys voratus*) as well as three endemic rodents which have no previous direct radiometric dates (*Plagiodontia velozi*, *Hexolobodon phenax*, and *Rhizoplagiodontia lemkei*). The radiocarbon date for *P. velozi*, the largest of these species, is from the very early Holocene (10,995 ± 190 calendar years before present; Cal BP). Specimens of medium-bodied species, *H. phenax* and *R. lemkei* date to the mid-Holocene, while specimens of smaller-bodied *I. portoricencis* and *B. voratus* have dates falling in the Late-Holocene. These dates confirm that several of the extinct rodent species coexisted with the first humans, who arrived on the island ca. 6000 years ago. In contrast, murid *Rattus* specimens date to the last few centuries. Rats arrived with Europeans in the late 15th or early 16th Century and a radiocarbon date of ca. 500 Cal BP for one individual suggests that they likely spread quickly across the island. Collectively, these dates establish that vertebrate accumulations at Trouing Jérémie #5 span the Holocene. Remains from this site may provide a useful time sequence for future work examining ecological change across the Holocene as well as regional extirpation patterns.

Keywords

bone collagen, Capromyidae, Caribbean, European contact, extinction, *Rattus*

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Introduction

The Caribbean experienced a catastrophic extinction of non-volant taxa during the Holocene, losing more mammalian species than any other region on the planet (Turvey, 2009). Of approximately 43 rodent species that have been described, only 10–13 are extant. Both climate (Dávalos and Russell, 2012) and anthropogenic factors, such as hunting and habitat destruction (Cooke et al., 2017a, 2017b; Hansford et al., 2012; Morgan and Woods, 1986) have been proposed as contributing to these extinctions. Last appearance dates across the Caribbean suggest that extinctions occurred in two waves, concordant with (1) initial human settlement ca. 6000 years ago (Fitzpatrick, 2006, 2015), and (2) more recent colonization by Europeans and subsequent forced relocation of enslaved African populations ca. 500 years ago (Cooke et al., 2017a). However, the data are scant. Across the Caribbean, about 150 radiometric dates exist for extinct mammal species, one-third of which are direct dates (i.e. a bone fragment from the actual species in question). The remainder are indirect dates that were obtained from other material (e.g. shell, charcoal, bone from another taxon) and used to infer ages of extinct species based on contextual evidence (Cooke et al., 2017a). For rodents, there are fewer than 20 direct dates (Cooke et al., 2017a). Disentangling competing hypotheses explaining extinction events will require a better understanding of population declines and robust last appearance dates for these now-extinct taxa.

Today, Hispaniola has one endemic rodent, *Plagiodontia aedium*, but it once harbored some 10–12 species (Table 1) that spanned a variety of body-sizes and ecological niches (Cooke and Crowley, 2018). Three direct ^{14}C dates have been published for Hispaniolan rodents (McFarlane et al., 2000; Shev et al., 2021). Two are from Cueva Nay, a paleontologically-rich cave site in the central Dominican Republic (Figure 1): One *Brotomys voratus* (340 ± 60 ^{14}C years before present; 400 ± 105 calendar years before present; Cal BP; McFarlane et al., 2000), and one *Isolobodon portoricensis* (660 ± 50 ^{14}C BP; 612.5 ± 62.5 Cal BP; McFarlane et al., 2000). An additional direct date for *I. portoricensis* exists from an archaeological site, El Flaco, in the north central region of the Dominican Republic (570 ± 30 ^{14}C BP; 585 ± 60 Cal BP; Shev et al., 2021). The vertebrate assemblage from El Flaco also included abundant specimens of *Brotomys*,

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Table 1. Phylogenetic relationships and morphological information for endemic Hispaniolan rodents.

Family	Species	Estimated body mass (kg)	Body mass source[e]
Echimyidae (Capromyidae)[a]	*Isolobodon montanus*	1.52–3.12	1, 2
	Isolobodon portoricensis	1.04–1.40	1, 2
	Isolobodon sp.	0.38–0.53	3
	Hexolobodon phenax	3.16–3.31	1, 2
	Hexolobodon poolei[b]		
	Plagiodontia aedium	1.56–3.85	4
	Plagiodontia velozi[c]	5.31–5.93	4
	Hyperplagiodontia araeum	2.35–5.36	4
	Rhizoplagiodontia lemkei	1.32–2.01	4
Echimyidae	*Brotomys voratus*	0.40	2
	Brotomys contractus[d]		
Debated	*Quemisia gravis*	4.17–15.00	2, 5

[a] Paleontological literature (e.g. Woods, 1989a, Woods, 1989b) uses Capromyidae as the family for *Isolobodon, Hexolobodon, Plagiodontia, Hyperplagiodontia*, and *Rhizoplagiodontia*, but recent genetic evidence indicates that *Plagiodontia*, and by extension the other taxa, are nested within Echimyidae. There is no debate about the placement of *Brotomys* within the family Echimyidae.

[b] May be synonymous with *H. phenax.*

[c] We consider *P. velozi* to be synonymous with *P. ipnaeum* (Hansford et al., 2012). A large member of the genus *Plagiodontia* lived on Hispaniola, but there is debate about which name has priority.

[d] Known only from a single edentulous palate comparable in size to *B. voratus* and possibly conspecific, though unpublished evidence may provide support for the validity of this taxon (Lazaro Vinola, 2021, personal communication; MacPhee, 2009).

[e] Body Mass Sources: 1 = Cooke et al. (2017a); 2 = Turvey and Fritz (2011); 3 = Unpublished, 4 = Hansford et al. (2012); 5 = Woods and Ottenwalder (1992).

which suggests they may have been consumed by people (Shev et al., 2021). Additional data from archaeological sites on the island (e.g. Puerto Real) provide indirect evidence of the survival of *I. portoricenis* into the colonial period (Reitz, 1986). While these data demonstrate that both *Brotomys voratus* and *I. portoricenis* survived initial human arrival and were likely still present at European contact, little is known about the extirpation of other now-extinct taxa. Here, we provide eight ^{14}C direct dates for rodents from Trouing Jérémie #5, a paleontologically-rich sinkhole in southwestern Haiti (Figure 1). This includes new dates for the two previously dated endemic species, *B. voratus* and *I. portoricensis*, three endemics that have not been dated directly previously, *Plagiodontia velozi* (here, considered synonymous with *P. ipnaeum*; Hansford et al., 2012), *Hexolobodon phenax*, and *Rhizoplagiodontia lemkei*, and invasive *Rattus.*

Regional and species overview

The Holocene climate of the Tiburon Peninsula has been reconstructed using stable oxygen isotope data from two lake cores from Lake Miragoâne (Higuera-Gundy et al., 1999), which is approximately 65 km from Trouing Jérémie #5. Climate fluctuated throughout the Holocene, but probably not extensively (summarized in Figure 2). Between ca. 12,000 and 8500 years ago, climate transitioned from relatively dry to wet, and remained mesic, and possibly warmer until ca. 3300 years ago (Figure 2). Conditions became drier again during the Late-Holocene (similar to the early Holocene), although relatively moist climate returned briefly between ca. 1700 and 1000 years ago (Higuera-Gundy et al., 1999).

In contrast, human activity varied considerably. People first arrived ca. 6000 years ago – termed the Lithic culture (Fitzpatrick, 2006, 2015; Figure 2). Little is known about the effect these people had on their surroundings; archaeological sites contain stone tools but few animal remains, and population density seems to have been low. Beginning ca. 5000 years ago, people belonging to the Archaic culture engaged in cultivation of introduced plants (Newsom and Wing, 2004). Charcoal peaks from lake cores may reflect slash and burn agriculture (Rivera-Collazo et al., 2015), though the natural occurrence of fire cannot be ruled out (Higuera-Gundy et al., 1999). Zooarchaeological remains indicate that Archaic people transported *I. portoricensis* from Hispaniola to other islands (Newsom and Wing, 2004), but there is no direct evidence for the exploitation of large-bodied mammals, including >1 kg rodents (e.g. *P. velozi*). The Ceramic culture began ca. 2500 Cal BP (Fitzpatrick, 2006), and human population expanded considerably. People cultivated over 80 types of plants (Aguilu et al., 1991), and dogs (*Canis familiaris*) and guinea pigs (*Cavia porcellus*) were introduced from mainland South America (Rick et al., 2013; Rivera-Collazo et al., 2015). Europeans, and enslaved people of African descent began arriving at the end of the 15th and beginning of the 16th Centuries CE (Heuman, 2018). Under colonial rule, deforestation accelerated with the establishment of large-scale monocultures of sugarcane, indigo, tobacco, and coffee (McClintock, 2003). Mice (*Mus musculus*), rats (*Rattus rattus* and *R. norvegicus*), domestic cats (*Felis catus*), a variety of ungulates were introduced soon after European arrival, and in the late 19th Century, mongoose (*Herpestes auropunctatus*) were also introduced (Long, 2003; Pimentel, 1955; Woods and Ottenwalder, 1992). These taxa could have impacted endemic rodents via predation, direct competition, and negative impacts on native plants (Grouard et al., 2013; Street, 1962).

Hispaniola's endemic rodents include the extant species, *P. aedium*, and at least nine extinct species: *P. velozi, Rhizoplagiodontia lemkei, Hyperplagiodontia araeum, Isolobodon montanus, I. portoricensis, Hexolobodon phenax, Brotomys voratus, B. contractus*, and *Quemisia gravis* (Table 1) (Hansford et al., 2012; Woods and Kilpatrick, 2005). The phylogenetic relationships of Caribbean rodents is currently under revision. Recent genetic work indicates that they are likely a monophyletic group within Echimyidae that diverged from mainland forms sometime in the early to mid-Miocene (Fabre et al., 2014, 2017; Marivaux et al., 2020; Woods et al., 2021), though to date only some extinct forms have been analyzed.

Isolobodon portoricensis was widespread and has been recovered from paleontological and archaeological sites throughout the Greater Antilles (Newsom and Wing, 2004). *Hexolobodon phenax* is present at paleontological sites across Hispaniola but rare (Rímoli, 1976). *Plagiodontia* and *Hyperplagiodontia*, appear to be most common in cave deposits in western Hispaniola (SBC personal observation), though *P. velozi* and *H. araeum* have also been recovered from northern and eastern Hispaniola. *Rhizoplagiodontia lemkei* is common at paleontological sites in SW Haiti but unknown elsewhere (Woods, 1989a). Biogeographic barriers (e.g. intermittent seaways and mountains) may have limited its

Figure 1. Maps of (a) the Caribbean, showing the location of Hispaniola and (b) Hispaniola, indicating the location of sites mentioned in the text. Trouing Jeremie #5, Cueva Nay, and El Flaco are the three localities from which endemic rodents have been dated (this paper; McFarlane et al., 2000; Shev et al., 2021). Introduced *Rattus* were dated at Monte Culo de Maco (MacPhee et al., 1999). The location of Puerto Real (Reitz, 1986), an archaeological site with abundant rodent remains is also noted.

dispersal outside of this region (Iturralde-Vinent and MacPhee, 1999; Mann et al., 1991; Maurrasse et al., 1982). Alternatively, sampling bias, regional habitat differences, or temporal variability among sites may account for its apparently limited distribution. *Brotomys* is found at sites on the Tiburon Peninsula (McFarlane et al., 2000; Rímoli, 1976; White and MacPhee, 2001) as well as in the central and eastern Dominican Republic (Miller, 1916, 1929a; SBC personal observation of unpublished collections from Altagracia Province). Differentiating the two *Brotomys* species is challenging and based only on a few cranial characters (Miller, 1929b; Rímoli, 1976); consequently, nothing is known of species range differences, should they exist.

Methods

Site description

Trouing Jérémie #5 is a sinkhole in the Massif de la Hotte, Pic Macaya National Park, near the western end of the Tiburon peninsula (Figure 1). It is 16.5 m deep, 2.5 m wide at its opening, and 12 m wide at its base (MacPhee et al., 2000). The site is located at 1275 m asl in a transitional zone between lower-elevation wet forest (850–1250 m asl) and a mosaic of higher-elevation pine and cloud forest (Upham et al., 2013). The region currently receives 1500–2500 mm of annual precipitation with no pronounced moist or dry season (www.oreworld.org/rainfall.htm; www.weather-atlas.com). Trouing

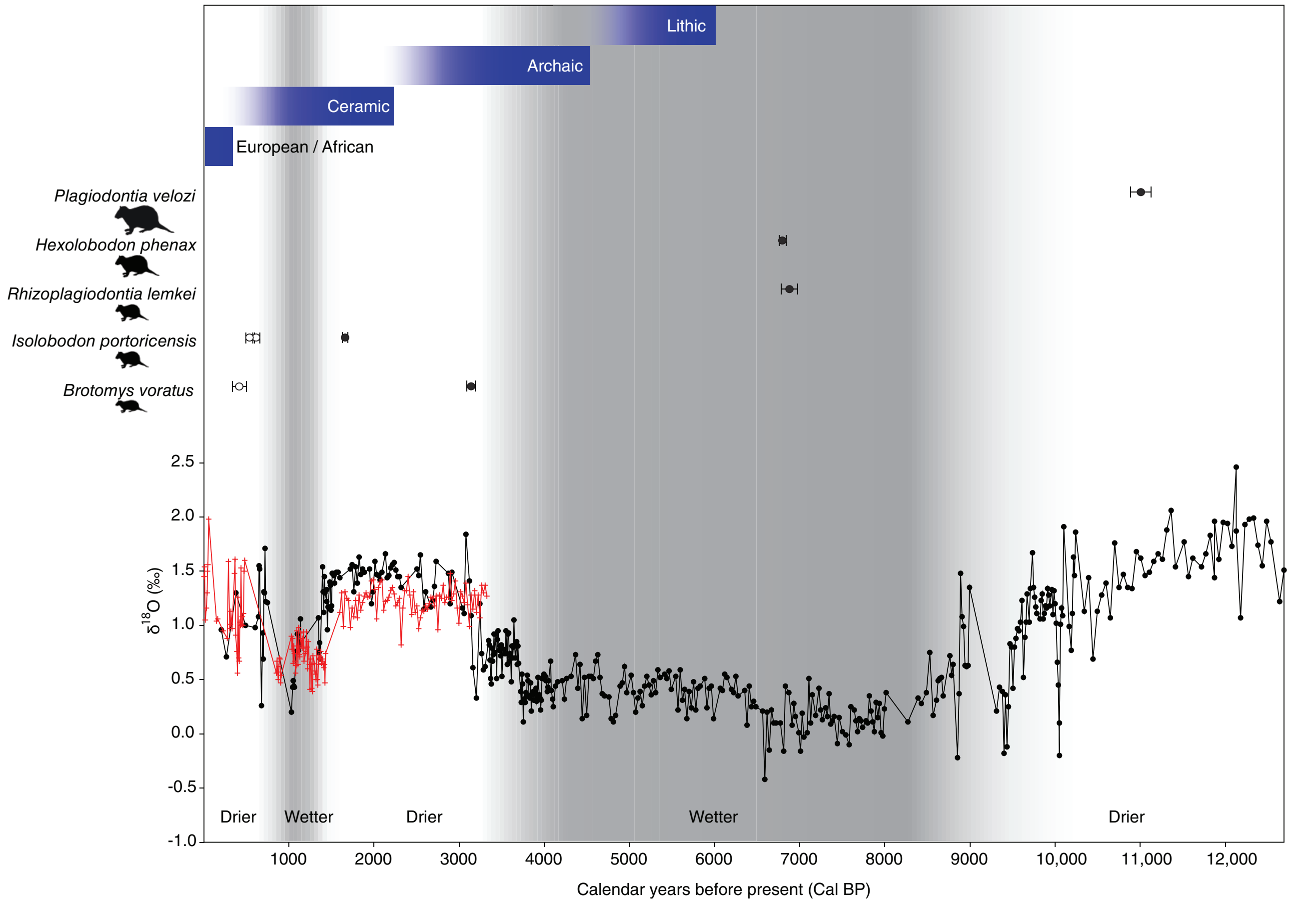

Figure 2. Plot showing calibrated ^{14}C dates for endemic Hispaniolan rodents (mean ± 1σ), along with human settlement patterns (Fitzpatrick, 2006, 2015), and major climatic wet and dry periods based on stable oxygen isotope values from two lake cores (red crosses and small black circles) taken at Lake Miragoâne, Haiti (Hodell et al., 1991; data available from NOAA and can be accessed here: https://www.ncei.noaa.gov/access/paleo-search/study/23092). Dates from this study are solid black; published dates from McFarlane et al. (2000) and Shev et al. (2021) are white outlined in black. Error bars for some dates are smaller than the symbol size and are therefore not easily visible. Relative rodent body sizes are represented by outlines (see Table 1).

Jérémie #5 is one of the paleontologically-richest sites on the Tiburon Peninsula. It was excavated and mapped in June and July 1984 by Dan Cordier and colleagues, who removed numerous bags of sediment for later sorting. Seven endemic rodents, as well as invasive murid rats (*Rattus* sp.) and mice (*Mus musculus*) have been recovered from the top 5 cm of sediment, and some of these taxa are extremely abundant (See MacPhee et al., 2000 for a description of faunal abundance in Trouing Jérémie #5). It serves as the type locality for the rodent *Rhizoplagiodontia lemkei* (Woods, 1989a), the primate *Insulacebus toussaintiana* (Cooke et al., 2011), and the sloth *Neocnus toupiti* (MacPhee et al., 2000). Several published radiocarbon dates exist for Trouing Jérémie #5: Extinct sloths (*Neocnus comes*) range in age from 6875 ± 47 to 8326 ± 57 ^{14}C BP (7702.5 ± 92.5 and 9335 ± 140 Cal BP; Steadman et al., 2005), while a specimen of the extant bat, *Macrotus waterhousii*, dates to 2030 ± 30 ^{14}C BP (1617.5 ± 437.5 Cal BP; Soto-Centeno and Steadman, 2015).

Specimen selection and analysis

We selected mandibles from the collections at the Florida Museum of Natural History (FLMNH) that appeared to be well-preserved (robust with little flaking or discoloration; Crowley, 2012). Bone collagen was isolated following Sparks and Crowley (2018). At the University of Cincinnati, we removed ca. 150 mg of bone from each mandible, demineralized samples in 0.5 N HCl, removed humic acids with 0.001 N NaOH, gelatinized collagenous residue in ~0.001 N HCl, filtered samples through 1.5 µm glass-fiber filters, and lyophilized them. We confirmed specimen preservation via collagen yield and atomic C:N (Ambrose, 1990; Van Klinken, 1999). Samples were then sent to the W.M. Keck Carbon Cycle Accelerator Mass Spectrometer Facility at the University of California, Irvine for radiocarbon dating. Conventional ^{14}C dates were calibrated to calendar years before present (Cal BP) using the IntCal20 curve (Reimer et al., 2020) in Calib 8.2 (Stuiver et al., 2021).

Results and discussion

Dates for endemic and introduced rodents at Trouing Jérémie #5 span the Holocene (Table 2; Figure 2), which is consistent with previously-published radiocarbon dates for the site (Soto-Centeno and Steadman, 2015; Steadman et al., 2005). The earliest date, 10,995 ± 190 Cal BP, is for *Plagiodontia velozi*; this date confirms that this large-bodied (5–6 kg) species was present until at least the beginning of the Holocene and consequently survived the climatic change and sea level rise of the terminal Pleistocene (Curtis et al., 2001; Dávalos and Russell, 2012; Lisiecki and Raymo, 2005). Dates for the medium-bodied species, *Rhizoplagiodontia lemkei* (1.3–2.0 kg) and *Hexolobodon phenax* (3.2–3.3 kg), all fall within a relatively short temporal window between ca. 6700 and 7050 Cal BP (Table 2), coinciding with, or immediately preceding the arrival of the first people on Hispaniola (Fitzpatrick, 2006, 2015).

Dates for *Brotomys voratus* and *Isolobodon portoricensis* are more recent (3135 ± 75 and 1655 ± 50 Cal BP, respectively). These are older than the dates previously reported by McFarlane et al. (2000) for these two species but help confirm that both of

Table 2. New radiocarbon dates for extinct endemic rodents and invasive *Rattus* at Trouing Jérémie #5.

Species	Specimen ID	^{14}C lab #	Atomic C:N	^{14}C year BP ± 1σ	2σ CAL BP range	Mean ± 1σ Cal BP[a]	Median Cal BP
Brotomys voratus	UF 293811	UCIAMS 191024	3.4	2960 ± 20	3061–3210	3135 ± 75	3122
Hexolobodon phenax	UF 293817	UCIAMS 191026	3.6	5955 ± 25	6726–6856	6790 ± 65	6779
Isolobodon portoricensis	UF 293821	UCIAMS 191027	3.3	1760 ± 15	1605–1707	1655 ± 50	1659
Plagiodontia velozi	UF 293822	UCIAMS 191025	3.5	9650 ± 25	10,806–11,184	10,995 ± 190	11,091
Rhizoplagiodontia lemkei	UF 74968	UCIAMS 191021	3.5	6145 ± 20	6951–7157	7052.5 ± 102.5	7050
Rhizoplagiodontia lemkei	UF 74978	UCIAMS 191022	3.4	5865 ± 20	6641–6741	6690 ± 50	6696
Rattus sp.	UF 293844	UCIAMS 191028	3.4	435 ± 15	490–515	502.5 ± 12.5	502
Rattus sp.	UF 293847	UCIAMS 191029	3.4	280 ± 20	289–429	360 ± 70	377

[a] Two-sigma (2σ) calibrated date ranges were rounded to the nearest 5-year intervals to obtain mean ± 1σ calibrated dates, as well as median dates (Table 2).

these geographically widespread taxa persisted well-beyond the initial settlement of Hispaniola by humans. These dates span the time periods of the Archaic culture, beginning ca. 5000 Cal BP, and the Ceramic culture, beginning ca. 2500 Cal BP (Fitzpatrick, 2006).

Finally, dates for two *Rattus* specimens are 502.5 ± 12.5 and 360 ± 70 Cal BP, contemporaneous with the colonization of Hispaniola by European and African populations. Columbus first landed on the northern coast of Hispaniola on December 6, 1492 CE, and permission was granted to import enslaved people of African descent in 1501 CE. Initial colonial outposts were on the central northern and southern coasts, including where Santo Domingo is still present today (Heuman, 2018). These are far from the highlands of the Tiburon Peninsula. Murid rats at Trouing Jérémie #5 likely got there on their own through dispersal and population expansion. Our date of ca. 500 Cal BP for one individual suggests that rats experienced very rapid colonization and population expansion on Hispaniola. Indeed, MacPhee et al. (2000) found that *Rattus* is one of the most common taxa in the top 5 cm of sediment at Trouing Jérémie #5; it accounts for ca. 13.9% of the rodent fauna and is second only to the extant *Plagiodontia aedium* (20.1%). *Rattus* has also been found comingled with extinct endemic species at other caves across Hispaniola. Few of these *Rattus* specimens have been directly dated, but three individuals from Monte Culo de Maco in the Dominican Republic (Figure 1) ranged from 220 ± 40 to 440 ± 60 ^{14}C BP (157.5 ± 157.5 to 432.5 ± 117.5 Cal BP; MacPhee et al., 1999). These dates are very similar to those that we obtained, and together support a rapid expansion of *Rattus* once introduced on Hispaniola.

The degree to which endemic rodents survived into the European period is an open question. Certainly some persisted, as Oviedo Y Valdés (1535) noted several endemic rodents were hunted and consumed. However, which species were present, and their population sizes, are unknown. Moreover, temporal overlap of most extinct species with any human groups, or even their persistence past the Pleistocene was previously unconfirmed. Indirect evidence for the persistence of extinct rodents into the Holocene previously existed from dates for other taxa that were found in association with rodents (MacPhee et al., 2000; Steadman et al., 2005). However, the uncertain stratigraphy of many caves and the age of dates obtained for some rodent-rich sites (e.g. ca. 25,000 Cal BP for an unidentified sloth bone from Trou Woch Dadier; MacPhee et al., 2000) have limited our understanding of when extinct rodent species disappeared. Here, we have provided the first direct evidence for three taxa that are not frequently found in archaeological deposits (*P. velozi*, *R. lemkei*, and *H. phenax*) as well as additional dates for *I. portoricensis* and *B. voratus.* These dates confirm survivorship of these species into the Holocene (and potentially into the period of human occupation) and help to set a baseline for understanding their disappearance.

Conclusions

New ^{14}C dates for Trouing Jérémie #5 in the Tiburon Peninsula indicate that bones have been accumulating at this site for at least 10,000 years. The dates build on an existing dataset for Trouing Jérémie #5, which includes radiometric dates for sloth species (Steadman et al., 2005), an analysis of faunal abundance (MacPhee et al., 2000), and several species descriptions (Cooke et al., 2011; MacPhee et al., 2000; Woods, 1989a). While scant, these dates do suggest possible temporal differences in regional species persistence and extirpation related to body size. This site may have excellent potential for exploring regional patterns of extirpation and persistence of endemic rodents (and other vertebrates more broadly) in response to both climate and anthropogenic factors.

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