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Citation

Shev, G. T. (2022, December 6). *Indigenous animal management practices on the eve of Columbus' landfall: Isotopic and zooarchaeological investigations in the Dominican Republic and Jamaica*. Retrieved from https://hdl.handle.net/1887/3494380

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Published as:

Shev, G.T, Laffoon, J.E., Hofman, C.L., 2020.
Human and hutia (*Isolobodon portoricensis*) interactions in
pre-Columbian Hispaniola: The isotopic and morphological evidence
Journal of Archaeological Science: Reports 37, 102913.
https://doi.org/10.1016/j.jasrep.2021.102913

Journal of Archaeological Science: Reports 37 (2021) 102913

Contents lists available at ScienceDirect

Journal of Archaeological Science: Reports

journal homepage: www.elsevier.com/locate/jasrep

Human and hutia (*Isolobodon portoricensis*) interactions in pre-Columbian Hispaniola: The isotopic and morphological evidence

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ARTICLE INFO

Keywords:
Isotopic analysis
Osteometrics
Caribbean zooarchaeology
Garden hunting
Commensalism

ABSTRACT

There are certain animal candidates for which researchers have long speculated as having been managed, or possibly domesticated, by indigenous peoples in the pre-Columbian Caribbean, the primary candidate being some members of a group of caviomorph rodents known as hutia (Capromyinae). This study comprises an isotopic and morphological investigation of the potential management of an extinct species endemic to Hispaniola, the Puerto Rican hutia (*Isolobodon portoricensis*). For comparisons, isotopic analysis was conducted of bone collagen samples examining carbon ($\partial^{13}C_{co}$) and nitrogen ($\partial^{15}N$) values of *I. portoricensis* with two other species of endemic hutia, guinea pig (*Cavia porcellus*), Antillean slider (*Trachemys stejnegeri*), rhinoceros iguana (*Cyclura cornuta*) and edible rat (*Brotomys* sp.) from four sites in the Dominican Republic: El Flaco, El Carril, El Cabo and La Entrada. This data was compared to human and dog collagen values available from El Flaco to assess similarities between these groups. Osteometric data was recorded for hutia mandibles, allowing for body mass estimations (n = 230). The findings suggest that some *Isolobodon portoricensis* specimens possessed carbon ($\delta^{13}C_{co}$) values similar to humans and dogs at El Flaco, possibly associated with the consumption of agriculturally produced maize. This research does not indicate whether domestication or management of this species was occurring, at least not in a systematic way. Concurrence with palaeoenvironmental and zooarchaeological data from the region in which El Flaco and El Carril are located indicate that indigenous agricultural practices may have affected populations of hutia, perhaps by attracting them and supporting them within anthropogenic mosaic landscapes. The data also suggests that some degree of either purposeful feeding or scavenging from human agricultural plots was occurring and supports some degree of commensalism between humans and Puerto Rican hutia at these sites.

1. Introduction

Pre-Columbian societies in the insular Caribbean cultivated a suite of plant domesticates with only two domesticated animals purportedly utilized, dogs (*Canis familiaris*) and guinea pigs (*Cavia porcellus*) (Grouard et al., 2013; LeFebvre and deFrance, 2014; Newsom and Wing, 2004; Wing, 2001). Although hunting and fishing were the main animal-based subsistence activities throughout the region (Newsom and Wing, 2004), human-animal interactions were nuanced, as is demonstrated in canid burial practices (Grouard et al., 2013), and historical observations of sea turtle trapping and birdkeeping in Cuba (Las Casas, 1875a, 473) and the housing of hutia in corrals in Hispaniola (Las Casas, 73, 1875b; Lovén, 437-8, 2010). Researchers have suggested that some caviomorph rodents, hutias (Family: Echimyidae, Subfamily: Capromyinae; Courcelle et al., 2019), may have been managed. This proposition is supported by evidence of translocations, high proportions in zooarchaeological assemblages, size variations, and from biochemical analyses of faunal remains (Carlson and Steadman, 2009; Colten and Worthington, 2014; deFrance and Newsom, 2005; DuChemin, 2013; LeFebvre et al., 2019a, 2019b; Reynolds, 1953; Wilkins, 2001; Wing, 2008, 2012). Nonetheless no evidence in the form of animal enclosures or other material culture has been recovered, therefore requiring a combination of zooarchaeological and biochemical investigation to ascertain whether animal management was occurring (LeFebvre and DeFrance, 2018). To accomplish this, body mass estimations and isotope compositions of bone collagen from extinct Puerto Rican hutia

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https://doi.org/10.1016/j.jasrep.2021.102913
Received 7 May 2020; Received in revised form 26 February 2021; Accepted 1 March 2021

(*Isolobodon portoricensis*) were analysed from four pre-Columbian sites in the Dominican Republic (El Flaco, El Carril, El Cabo and La Entrada), and compared to other endemic fauna, domestic dogs, and humans.

This research does not seek to establish whether endemic animals were domesticated by indigenous peoples in ways that surmise animal domestication as a developmental end point, but acknowledges that domestication is just one strategy to achieve stable food production suited to particular ecologies and animal species (Smith, 2001; Zvelebil, 1995, 87). There are differing opinions as to what is meant by the term 'domestication', however the definition provided by Zeder (2006, 2012, 2015) is utilized in this paper. This defines domestication as a multigenerational relationship between human and animals which often, but not always, leads to behavioural, phenotypical and genotypical change in animals. These relationships can be viewed as mutually beneficial, however human cultural learning always tips the scale towards an "asymmetrical mutualism" squarely in favour of humans (Zeder, 2012).

Human niche construction can affect the abundancies of a broad spectrum of plants and animals that remain 'wild' in terms of an absence of morphological and genetic markers denoting domestication. Human cultures modify environments through a variety of means, such as the burning of old-growth forest, the elimination of non-economically important species of plants, and the transplanting of useful plants within altered landscapes (Boivin et al., 2016; Smith, 2005, 2007, 2011; Zeder, 2015). These activities can form mosaic environments that are advantageous to some animals. Within tropical environments, horticultural plots make available highly nutritious domestic plants, and through deforestation promote the growth of fast-growing heliophilic plant communities that attract and support animal populations, which in turn can be caught in areas close to areas of human habitation (Arce-Peña et al., 2019; Blake and Loiselle, 1991; Loiselle and Blake, 1992; Ramírez-Barajas and Calmé, 2015; Smith, 2005; Stahl, 2014; Timm, 1994). Linares (1976), in studying the faunal assemblage at Cerro Brujo, Panama, first outlined "garden hunting" to explain the practice of hunting animals attracted to horticultural plots. Ethnological studies exemplify garden hunting as a viable food production strategy in many indigenous communities, such as the Buglé people of western Panama for which 47% of their meat is derived from animals caught in agricultural areas relatively close to habitation areas (Smith, 2005). Garden hunting may have been a relatively common subsistence practice in many parts of the Neotropics in the past, as it still is in many areas today, often blurring the lines between what constitutes a wild, tame or domesticated animal (Alexander et al., 2013; Calmé et al., 2006; Jorgenson, 1995; Linares, 1976; Smith, 2005; Sugiyama et al., 2020).

1.1. The hutia: A candidate for human management

There are multiple reasons why several scholars have speculated that some species of hutia were managed by indigenous peoples, the primary candidate in Hispaniola, Puerto Rico and Virgin Islands being the Puerto Rican hutia (*Isolobodon portoricensis*) (Wing, 2012). It is important to note that 'Puerto Rican hutia' is a misnomer, as it likely evolved on Hispaniola where remains are found in early Holocene deposits (Cooke and Crowley, 2018; Morgan et al., 2018; Turvey et al., 2017). Throughout evolutionary history there existed 32 species of hutia from eight genera endemic to the Greater Antilles and the Bahamas. Hutias occupied various ecological niches and adaptive behaviours ranging from arboreal, like *Plagiodontia aedium* - the sole extant Hispaniolan species, and scansorial locomotion, such as members of the genus *Geocapromys* (Fabre et al., 2014). The oldest identified hutia, *Zazymus,* is found in Cuba and dates to the Early Miocene at approximately 16 Ma (MacPhee and Iturralde-Vinent, 1995), supporting a genetic divergence from continental Echimyidae sometime around 16.5 Ma (Courcelle et al., 2019; Woods et al., 2021). Two *Isolobodon* species once cohabited Hispaniola with humans, *I. portoricensis* and *I. montanus*. Both species went extinct alongside the majority of nonvolant mammals in Hispaniola after the arrival of Europeans in the late 15th century (MacPhee and Flemming, 1999; Turvey et al., 2017).

Puerto Rican hutia once occupied the most widespread geographic range of any Caribbean rodent, and this was likely facilitated by human translocations (Flemming and MacPhee, 1999; Reynolds, 1953; Wing, 2001: 348; Wing, 2008, 2012). Human-hutia interactions have an extensive history with 540–1400 year old coprolite evidence suggesting a transmission of zoonotic parasites from rodents (*Isolobodon portoricensis* and *Heteropsomys insulans*) to humans at the Saladoid/Huecoid site of Sorcé on Vieques island. (Wiscovitch-Russo et al., 2020). It is unknown when *I. portoricensis* was introduced into Puerto Rico but they are well attested after AD 400 (Carlson and Steadman, 2009; Narganes Storde, 1985; Wing, 1993, 2012), and are found in many pre-Columbian sites on Hispaniola and Puerto Rico in significant quantities (Carlson and Steadman, 2009; Reitz, 1985; Rimolí, 1972; Wing, 1993, 2008, 2012).

There is historic mention of hutia keeping in Hispaniola. Bartolomé de las Casas, who chronicled the physical geography and indigenous cultures of the New World in the early 16th century (Sauer, 1966, 29), informs us of the existence of hutia corrals in the Vega Real region of Hispaniola (Las Casas, 1875a, 73). 'Vega Real' was the original term which designated the montane country north of the Cordillera Central draining into the Yaque River, a region now known as the Cibao Valley (Sauer, 1966, 80). Overlooking this valley are located two of our case-study sites, El Flaco and El Carril.

1.2. Stable isotope ratio analysis of animal diets

Isotopic analysis of animal remains can establish environmental niche preferences (Cooke and Crowley, 2018; Daggers et al., 2018; Galetti et al., 2016; Roberts et al., 2017), assess mobility patterns (Giovas et al., 2016; Laffoon et al., 2015, 2017; LeFebvre et al., 2019b), and distinguish domestic from wild feeding regimes (LeFebvre et al., 2019b; Makarewicz and Tuross, 2012; Sugiyama et al., 2015, 2020). Human dietary influence often correlates to instances of domestication, such has been revealed through isotopic studies in several different contexts around the globe (De Groene et al., 2018; Grandal-d'Anglade et al., 2019; Monagle et al., 2018; Sharpe et al., 2018; Zavodny et al., 2015).

Collagen isotope values of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C_{co}$) indicate the types of foods that an organism has consumed. Bone collagen $\delta^{15}N$ is principally influenced by the intake of dietary nitrogen derived from proteins within consumed foods, examination of which can be used to establish the trophic level of an organism and differentiate between marine and terrestrial-based diets (DeNiro and Epstein, 1981; Schoeninger et al., 1983). Most plants $\delta^{15}N$ values derive from nitrates within soil, with a stepwise increase in $\delta^{15}N$ coinciding with the higher trophic positioning of an animal (Minigawa and Wada, 1984; Schoeninger and DeNiro, 1984). Bone collagen $\delta^{13}C$ values are influenced by the intake of dietary protein as well as by whole diet (carbohydrates, fats and protein) (Schwarcz, 2000). The $\delta^{13}C$ values within bone are influenced by the $\delta^{13}C$ values of plants, related to their photosynthetic pathways, that are consumed at the bottom of a food web (DeNiro and Epstein, 1978; Schoeninger and DeNiro, 1984). Most plants possess a C_3 pathway, exhibiting values ranging from −35 to −20‰ whilst some, mostly arid-adapted species, exhibit C_4 pathways with values ranging from −15 to 7‰. Crassulacean acid metabolism (CAM) plants demonstrate values that often overlap with that of C_4 plants (Kohn, 2010; O'Leary, 1988; Smith and Epstein, 1971). Feeding experiments have determined enrichments for $\delta^{13}C$ between 3.7 and 6.0‰, and for $\delta^{15}N$ between 1.7 and 6.9‰ from diet to collagen (Bocherens and Mariotti, 2002). Determining the exact contributions of carbohydrate and protein sources is problematic from examining collagen alone particularly when a varied diet is presumed (Froehle et al., 2010, 2012), however a diet based on C_3 plants should have a $\delta^{13}C \sim -21‰$, and a diet comprised solely of C_4 plants should be around −7‰ (Krueger and Sullivan, 1984; Lee-Thorp et al., 1989; Tykot, 2006).

In many parts of the Americas, anthropogenic influence in the diets of animals is determined by comparing relatively higher δ^{13}C values of managed animals with that of wild taxa. These disparate δ^{13}C values are associated with the prevalence of agricultural maize (*Zea mays*) in the region, a C_4 plant (Lee-Thorp et al., 1989) that animals consume due to human feeding or by scavenging from humans. A recent isotopic study by Sugiyama et al. (2020) investigated animals at four pre-Columbian sites in Panama, providing some evidence of garden hunting practices as deduced from the carbon (∂^{13}C) values of certain species. For example, white-tailed deer (*Odocoileus virginianus*) at Cerro Mangote consumed a C_3 dominated diet, but with supplementary C_4 plant consumption. The authors conclude there was a possible mixture of garden browsing, or purposeful feeding of maize to known domestics and to wild, or possibly tamed, species at these sites (Sugiyama et al., 2020).

Evidence of maize consumption is found at numerous archaeological sites throughout the Caribbean, suggesting it was one of the most common crops (Ciofalo et al., 2018; Figueredo, 2015; Pagán-Jiménez and Carlson, 2011; Mickleburgh and Pagán-Jiménez, 2012), including at one of the sites in this research, El Flaco (Ciofalo et al., 2019; Pagán-Jiménez et al., 2020). Human and dog δ^{13}C values from El Flaco have also demonstrated shared dietary regimes that indicate that C_4 plants were part of their diets (Laffoon et al., 2017; Shev et al., 2020). Isotopic analysis of archaeological hutia remains may indicate similarly shared dietary patterns between humans and hutia, however, to date this has only been conducted on Bahamian hutia (LeFebvre et al., 2019b).

1.3. Evidence of hutia management from the Caribbean

I. portoricensis is but one species of hutia speculated as having been managed. Morphometric and DNA analysis of Bahamian hutia (*Geocapromys ingrahami*) suggests a history of anthropogenic dispersals of this species after the arrival of humans in the Bahamas around AD 800–1000 (LeFebvre et al., 2019a; Oswald et al., 2020). Isotopic analysis of *G. ingrahami* bone and teeth suggests that some individuals were consuming C_4 plants, possibly due to the consumption of agricultural maize because of scavenging activities, or from the purposeful supplementation of hutia diets (LeFebvre et al., 2019b). As that study is the first in the region looking specifically at the isotopic values and morphology of a hutia species from archaeological sites it serves as a useful comparison to the findings of the present study.

In Jamaica, *Geocapromys brownii* is ubiquitous within Pre-Columbian assemblages, raising speculation as to their management (Wing, 1993). Wilkins (2001) calculated mortality ages of Jamaican hutia by measuring lower tooth row lengths (LTRL), comparing this to known-age *G. brownii* individuals to estimate mortality ages and assess if some degree of management was occurring. It was determined that there is no convincing evidence of management due to the lack of sexually mature subadults. However, subsequent applications of this method by Carlson (2012) demonstrated that most *G. brownii* from the pre-Columbian sites of Green Castle, Wentworth and Colerain may have been reproductive subadults.

Carlson and Steadman (2009) applied mortality age reconstructions to Puerto Rican hutia (n = 6) from Río Tanamá Site 2: AR-39, Puerto Rico. Following the age determinations of Jamaican hutia by Wilkins (2001), it was deduced that subadults of reproductive age may have been targeted to control populations while maximizing meat yield, reminiscent of domestication processes globally (Carlson and Steadman, 2009). However, *G. brownii* cannot safely be used as a morphological analogue for extinct *I. portoricensis*. Considering this, body mass was estimated from all *I. portoricensis* mandibles from El Flaco to assess relationships between body mass and isotopic values, with the caveat that the sexual dimorphism and ontogeny of this species are unknown.

1.4. Hutia feeding behaviour

An understanding of the feeding behavior of *I. portoricensis* is pivotal for determining human influenced or natural C_4 consumption. Feeding studies of seven extant hutias (Borroto-Páez and Woods, 2012) loosely serve as analogues here. All examined species are primarily herbivorous and will consume a wide array of plants (Eisenberg and Woods, 2012), preferring the tender parts of branch barks and petioles of trees and dicotyledons. Certain plants appear to be favorites, particularly red mangrove (*Rhizophora mangle*). Hutias will only occasionally consume monocots, which account for 80% of all C_4 plants, but there is a lack of preference for grasses (Gramineae) (Borroto-Páez and Woods, 2012, 91), which may be C_4 (Sage, 2016). The only extant hutia in Hispaniola, *P. aedium*, will readily consume maize when offered (Woods and Ottenwalder, 1992). Wild Cuban hutia (*Capromys pilorides*) have been observed scavenging mollusks and crustaceans (Borroto-Páez and Woods, 72-73, 2012; Frias and Hernandez, 1985), and within captivity, hunting insects and lizards (Manójina and Abreu, 1990). Coprophagy is a commonly observed behavior of captive hutias (Borroto-Páez and Woods, 2012, 90), potentially affecting isotopic values (Somerville et al., 2018).

Cooke and Crowley (2018) established isotopic niches for rodents recovered from two Holocene-era cave sites in the Tiburon Peninsula, Haiti, Trouing Jérémie #5, and Trou Jean Paul. Studied taxa included *I. portoricensis, Hexolobodon phenax, I. montanus, P. aedium, P. spelaeum, B. voratus, Rhizoplagiodontia lemkei*, Eurasian *Rattus* sp., and an unidentified diminutive *Isolobodon sp*. It was determined that the intermediate carbon (∂^{13}C) and low oxygen (∂^{18}O) values in *I. portoricensis* enamel samples might be due to the ‘canopy effect’ (Krigbaum et al., 2013), indicating a terrestrial lifestyle and preference for more open terrain, while low ∂^{18}O values perhaps indicate a more frugivorous diet compared to other species. The previously undescribed smaller *Isolobodon* sp. has higher ∂^{13}C values than all other taxa, likely due to a greater preference for more open habitats and some consumption of C_4 plants. Edible rat (*Brotomys voratus*) samples also possess higher carbon values than *I. portoricensis*, perhaps indicating a natural preference for open habitats or C_4 plant consumption (Cooke and Crowley, 2018).

Wild *I. portoricensis* should demonstrate isotopic values indicating a diet predominantly comprising C_3 plants, as reflected in dietary studies of extant hutias, and the isotopic niches established by Cooke and Crowley (2018). As a caveat, there is no isotopic data for most wild Hispaniolan plants so ∂^{13}C enrichment from natural sources cannot be discounted. The consumption of C_4/CAM plants such as amaranth (*Amaranthus* sp.), pineapple (*Ananas comosus*), prickly pear (*Opuntia* sp.), century plant (*Agave antillarum*), may also be possibilities (Pestle, 2010), however historical records and starch grain analysis indicate that maize was a more ubiquitously cultivated plant in pre-Columbian Hispaniola (Ciofalo et al., 2019; Figueredo, 2015; Mickleburgh and Pagán-Jiménez, 2012; Pagán-Jiménez et al., 2020).

2. Materials and methods

2.1. Overview of sites

Samples were obtained from four pre-Columbian sites throughout the Dominican Republic (Fig. 1; Table 1). These four sites, El Flaco, El Carril, La Entrada and El Cabo, date to Late Ceramic Age contexts (post AD 600–1500), although they differ in overall occupation periods. Of these four, only El Flaco has undergone qualitative zooarchaeological analysis in which approximately 50% of all faunal material was identified (Shev et al. *in prep*). Preliminary work has been done on the El Cabo assemblage, however only the sorting of faunal material into broad categories has been achieved for El Carril and La Entrada. The material for these two sites is housed at the Centro Arqueológico, Cruce de Guayacanes, Dominican Republic.

El Flaco is located at the southern end of the Paso de Los Hidalgos that runs through the Cordillera Septentrional to the Cibao Valley, and is characterized by levelled occupation areas encircled by artificial earthworks used for refuse, burials and agricultural activities (Hofman

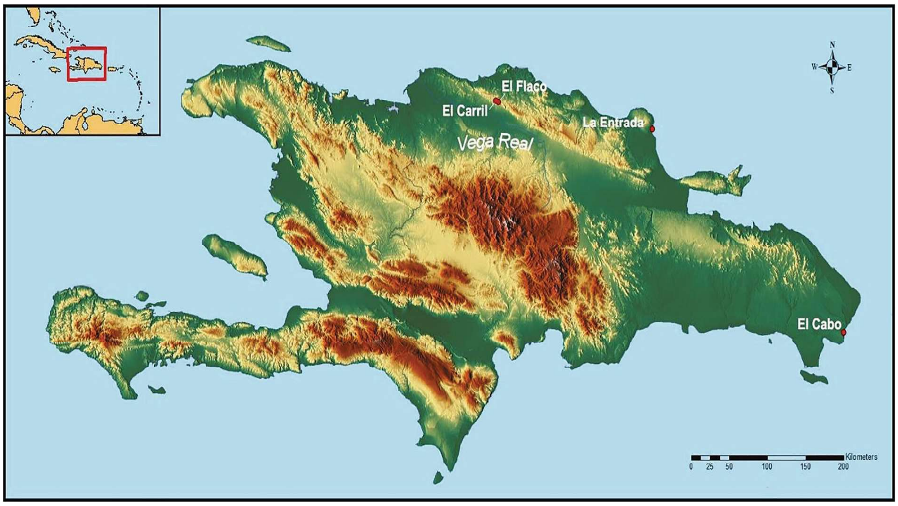

Fig. 1. Map of pre-Columbian sites in the Dominican Republic from which samples were acquired: El Flaco, El Carril, El Cabo, La Entrada, as well as the location of the region formerly known as the 'Vega Real' where Las Casas (vol. 64, 210) mentioned the presence of hutia corrals.

and Hoogland, 2015; Hofman et al., 2020; Keegan and Hofman, 128, 2017). Excavated as part of the NEXUS-1492 project (ERC-Synergy ID: 319209), El Flaco encompasses 2680 m^2 and was occupied between cal. AD 990 – 1452 (Hofman et al., 2018; Hofman and Hoogland, 2015). Zooarchaeological analysis of three archaeological units (Units 69, 71, 72) indicate *I. portoricensis*, accounts for 29.8% (MNI = 234) of terrestrial vertebrates (Shev et al. *in prep*) (Online Supplement 1). Edible rat (*Brotomys* sp.) also forms a significant proportion (MNI = 131) of the faunal assemblage.

El Carril is likewise situated at the southern end of a narrow pass through the Cordillera Septentrional, approximately 3 km west of El Flaco, and encompasses an area of 43,000 m^2 containing more than 100 artificial mounds (Hofman and Hoogland, 2015; Hofman et al., 2020; Sonnemann et al., 2016; van Dijk, 2019; Pagán-Jiménez et al., 2020). It was occupied intermittently between cal. CE 1030–1262, and more intensively between cal. CE 1200–1520 (Hofman, 2017; Hofman et al., 2018). Sorting of faunal material into broad categories was conducted, with Echimyidae (edible rats and hutia) comprising approximately 41.8% (NISP = 12,502) of identifiable terrestrial vertebrates (Online Supplement 1). All samples from El Carril were taken from Unit 56.

Palaeoenvironmental studies provide insight into the ecological conditions of the region containing these two sites. Sediment coring from Laguna Biajaca in the Cibao Valley, located approximately 10–12 km southwest of the sites, indicated a diminishment of diverse palm-dominated hardwood communities before CE 1250 (700 cal. BP). An increase in deforestation and evidence of the human use of fire between CE 1150–1450 (800 to 350 cal. BP) suggests an intensification of slash-and-burn agricultural practices during this period. Maize (*Zea mays*) pollen grains are present between cal. AD 950–1450 (Castilla-Beltrán et al., 2018, 2020). There was evidently a decrease in fire usage and the expansion of arboreal forests between CE 1500–1800, likely the result of the abandonment of managed agricultural landscapes (Castilla-Beltrán et al., 2020).

The use of fire in the landscape is well attested in the work of Las Casas. Importantly, about hutia in what was likely the Cibao Valley, he declared:

> "…en esta isla especialmente, como por este tiempo hace seca, y los indios eran inclinados, y se holgaban, de poner fuego á los herbazales, que eran grandísimos por las innumerables campiñas llanas y rasas que había… lo uno, porque tanta es y tanto crece la hierba, que tapa ó ocupa los caminos, y como andan desnudos, la hierba grande les lastima, lo otro, porque entre la hierba se criaban los conejos desta isla, que nombraban hutias… y eran sin número, y, con quemar las çabanas, mataban todos los que querian, por esto tenian de costumbre de quemarlas." (Las Casas, 1875c, 384), redactions by the author/s.

From this entry it can be ascertained that hutia inhabited these grasslands in great numbers and fire was regularly utilized to clear vegetation.

El Cabo de San Rafael, Altagracia, occupies a limestone cliff in southeastern Hispaniola and was occupied between cal. AD 604–1504 (Hofman et al., 2020; Keegan and Hofman:123, 2017; Samson, 2010; Samson and Hoogland, 2007). Occupational intensity increased over time and between the 9th and early 16th centuries AD El Cabo likely supported a population of around 250 inhabitants (Samson, 2010). Analysis is ongoing, however within Units 50 and 51, fish accounts for 88.2% (NISP = 4213) of all identifiable remains, while 140 Capromyinae remains were identified. *I. portoricensis* mandibles are represented by 14 specimens.

La Entrada is coastally situated in the northern María Trinidad Sánchez province. A small excavation (2 × 1 m) was conducted at the site in July 2019 by Leiden University, led by Prof. dr. Corinne L. Hofman and Dr. Menno L.P. Hoogland upon invitation and in collaboration with Arq. Juan I. Tineo and Clenis Tavarez Maria from the Museo del Hombre Dominicano. Radiocarbon dating revealed a range of cal. AD 840–900. No qualitative analysis has been conducted on the La Entrada faunal material to this moment, though the material appears to be dominated by reef and inshore fish species, shellfish, sea turtle (Chelonidae), and rhinoceros iguana (*Cyclura cornuta*).

2.2. Sample selection

A selection of bone samples from seven species was chosen from the four sites (Fig. 2; Table 1). To prevent repeated testing of the same individual only hemimandibles of one side were selected, otherwise samples were taken from varied depths and excavation units. Only cranial bones with dentition of hutia were positively identified, as postcrania of Capromyinae are exceedingly difficult to identify to species (Hermanson and Woods, 2012, 187). The choice of mandibles containing dentition allowed the sampling of bone collagen and enamel

Table 1

Carbon and nitrogen values from all bone collagen samples from the four sites. Table includes the values of previously analysed *Canis familiaris*, *Homo sapiens* and *Cyclura cornuta* samples from El Flaco.

Sample no.	Find no.	Site	Genus	Species	Element	Collagen %	∂^{15}N (‰ vs N $_{air}$)	∂^{13}C (‰ vs VPDB)	C/N (mol/ mol)	Reference
CA10	3722	El Carril	*Brotomys*	*sp.*	mandible	4.87%	9.29	−20.00	3.17	
CA13	3689	El Carril	*Isolobodon*	*portoricensis*	mandible	2.65%	3.28	−21.45	3.21	
CA14	3849	El Carril	*Isolobodon*	*portoricensis*	mandible	8.90%	4.04	−20.38	3.43	
CA15	3849	El Carril	*Isolobodon*	*portoricensis*	mandible	4.83%	6.83	−17.17	3.14	
CA17	3892	El Carril	*Isolobodon*	*portoricensis*	mandible	2.76%	5.50	−20.79	3.41	
CA21	3718	El Carril	*Isolobodon*	*portoricensis*	mandible	2.71%	4.46	−20.85	3.19	
CA23	3713	El Carril	*Isolobodon*	*portoricensis*	mandible	4.85%	2.86	−19.57	3.17	
CA24	3713	El Carril	*Brotomys*	*sp.*	mandible	9.29%	6.09	−20.54	3.19	
CA27	3699	El Carril	*Isolobodon*	*portoricensis*	mandible	4.09%	4.27	−21.18	3.29	
CA30	3775	El Carril	*Isolobodon*	*portoricensis*	mandible	1.90%	7.81	−18.70	3.32	
CA31	3775	El Carril	*Isolobodon*	*portoricensis*	mandible	1.80%	8.07	−20.38	3.37	
CA32	3715	El Carril	*Isolobodon*	*portoricensis*	mandible	7.28%	6.88	−20.18	3.24	
CA4	3876	El Carril	*Trachemys*	*stejnegeri*	carapace	1.26%	6.20	−23.39	3.38	
CA5	3789	El Carril	*Trachemys*	*stejnegeri*	hyoplastron	1.20%	6.18	−23.26	3.21	
CA8	3891	El Carril	*Brotomys*	*sp.*	mandible	4.49%	11.26	−21.28	3.10	
CB 1229	3090	El Cabo	*Isolobodon*	*portoricensis*	mandible	3.62%	8.65	−18.44	2.99	
CB 1326	1521	El Cabo	*Isolobodon*	*portoricensis*	mandible	4.24%	2.83	−20.76	3.18	
CB 1454	1959	El Cabo	*Isolobodon*	*portoricensis*	mandible	5.92%	5.88	−19.05	2.92	
CB 2527	1608	El Cabo	*Isolobodon*	*portoricensis*	mandible	11.72%	8.95	−20.77	2.97	
CB 3835	1957	El Cabo	*Isolobodon*	*portoricensis*	mandible	2.39%	3.96	−19.70	3.40	
CB 4000	1610	El Cabo	*Isolobodon*	*portoricensis*	mandible	1.36%	10.12	−20.91	3.33	
CB 4001	259	El Cabo	*Isolobodon*	*portoricensis*	mandible	5.05%	6.58	−21.14	3.33	
CB 4002	3681	El Cabo	*Isolobodon*	*portoricensis*	mandible	7.85%	4.74	−20.15	3.03	
CB 4003	3681	El Cabo	*Isolobodon*	*portoricensis*	mandible	3.27%	4.45	−20.62	3.35	
CB 457	1605	El Cabo	*Isolobodon*	*portoricensis*	mandible	2.91%	6.87	−20.50	3.18	
CB 920	3685	El Cabo	*Isolobodon*	*portoricensis*	mandible	3.51%	5.93	−20.65	3.11	
EN1	BAG15	La Entrada	*Isolobodon*	*portoricensis*	mandible	4.01%	6.30	−21.59	3.36	
EN2	BAG15	La Entrada	*Isolobodon*	*portoricensis*	mandible	9.58%	4.09	−20.42	3.60	
EN3	–	La Entrada	*Brotomys*	*sp.*	mandible	1.63%	4.59	−21.68	3.22	
EN4	BAG15	La Entrada	*Isolobodon*	*portoricensis*	mandible	9.21%	5.10	−20.68	3.47	
EN5	–	La Entrada	*Plagiodontia*	*aedium*	maxilla	1.30%	3.75	−15.69	3.13	
EN6	–	La Entrada	*Isolobodon*	*portoricensis*	mandible	1.12%	3.86	−21.82	3.21	
EN7	–	La Entrada	*Isolobodon*	*portoricensis*	mandible	2.28%	8.74	−20.15	3.18	
FL1097	3246	El Flaco	*Isolobodon*	*portoricensis*	mandible	5.18%	2.95	−18.30	3.27	
FL1099	3246	El Flaco	*Isolobodon*	*portoricensis*	mandible	10.33%	6.74	−17.79	2.96	
FL1264	3434	El Flaco	*Isolobodon*	*portoricensis*	mandible	5.59%	6.36	−21.37	3.25	
FL1421	2963	El Flaco	*Isolobodon*	*portoricensis*	mandible	1.06%	12.90	−18.56	3.22	
FL1543	2956	El Flaco	*Isolobodon*	*portoricensis*	mandible	2.64%	9.82	−20.45	3.33	
FL1664	3078	El Flaco	*Cavia*	*porcellus*	mandible	3.18%	8.25	−17.18	3.35	
FL1774	2759	El Flaco	*Brotomys*	*sp.*	mandible	5.18%	4.49	−21.29	3.10	
FL1952	2873	El Flaco	*Isolobodon*	*portoricensis*	mandible	10.09%	2.69	−14.45	3.36	
FL1976	2712	El Flaco	*Isolobodon*	*portoricensis*	mandible	8.22%	2.50	−19.86	3.27	
FL2009	3032	El Flaco	*Isolobodon*	*portoricensis*	mandible	13.10%	5.59	−19.72	3.25	
FL2017	3026	El Flaco	*Brotomys*	*sp.*	mandible	6.89%	6.86	−21.34	3.02	
FL2413	3057	El Flaco	*Isolobodon*	*portoricensis*	mandible	4.70%	14.10	−11.88	3.12	
FL2482	3009	El Flaco	*Isolobodon*	*portoricensis*	mandible	7.65%	3.82	−20.60	3.00	
FL2542	2776	El Flaco	*Isolobodon*	*portoricensis*	mandible	6.67%	5.19	−19.34	3.23	
FL26	3218	El Flaco	*Isolobodon*	*portoricensis*	mandible	3.00%	4.83	−19.10	3.50	
FL2703	2703	El Flaco	*Trachemys*	*stejnegeri*	plastron	3.67%	5.65	−23.34	3.32	
FL3072	2750	El Flaco	*Trachemys*	*stejnegeri*	plastron	2.10%	7.46	−22.13	3.20	
FL3329	2815	El Flaco	*Trachemys*	*stejnegeri*	plastron	3.53%	5.51	−18.62	3.29	
FL3504	2757	El Flaco	*Isolobodon*	*montanus*	mandible	6.10%	7.62	−21.32	3.22	
FL4025	3212	El Flaco	*Brotomys*	*sp.*	mandible	8.36%	6.29	−21.09	3.17	
FL4075	2816	El Flaco	*Isolobodon*	*portoricensis*	mandible	8.06%	6.16	−21.85	3.21	
FL438	3269	El Flaco	*Isolobodon*	*portoricensis*	mandible	3.11%	8.62	−18.36	3.32	
FL86	3167	El Flaco	*Isolobodon*	*portoricensis*	mandible	5.55%	1.68	−20.44	3.12	
FL901	2778	El Flaco	*Plagiodontia*	*aedium*	maxilla	2.51%	8.63	−22.10	3.21	
#8	3170	El Flaco	*Canis*	*familiaris*	vertebra	–	8.9	−18.6	–	Shev, 2018
#10	2801	El Flaco	*Canis*	*familiaris*	metacarpal	–	8.7	−18.5	–	Shev, 2018
#11	2821	El Flaco	*Canis*	*familiaris*	metacarpal	–	8.4	−18.4	–	Shev, 2018
#19	3261	El Flaco	*Canis*	*familiaris*	mandible	–	13.1	−18.7	–	Shev, 2018
#21	N/A	El Flaco	*Canis*	*familiaris*	ulna	–	8.2	−16.5	–	Shev, 2018
#23	2828	El Flaco	*Canis*	*familiaris*	maxilla	–	9.9	−19.5	–	Shev, 2018
#27	3050	El Flaco	*Canis*	*familiaris*	vertebra	–	11.1	−16.9	–	Shev, 2018
#29	2270	El Flaco	*Canis*	*familiaris*	cranial	–	10.8	−18.5	–	Shev, 2018
#32	2649	El Flaco	*Canis*	*familiaris*	femur	–	8.2	−16.5	–	Shev, 2018
#44	2812	El Flaco	*Canis*	*familiaris*	radius	–	9.7	−18.5	–	Shev, 2018
–	F45-15	El Flaco	*Homo*	*sapiens*	–	–	10.89	−18.40	–	
–	F45-18	El Flaco	*Homo*	*sapiens*	–	–	10.19	−18.19	–	
–	F45-22	El Flaco	*Homo*	*sapiens*	–	–	9.75	−17.32	–	
–	F47-223	El Flaco	*Homo*	*sapiens*	–	–	10.92	−18.31	–	
–	F56-19	El Flaco	*Homo*	*sapiens*	–	–	10.02	−18.92	–	

(*continued on next page*)

Table 1 (*continued*)

Sample no.	Find no.	Site	Genus	Species	Element	Collagen %	∂^{15}N (‰ vs N $_{air}$)	∂^{13}C (‰ vs VPDB)	C/N (mol/mol)	Reference
–	F67-08	El Flaco	*Homo*	*sapiens*	–	–	11.87	−18.48	–	
–	F45-20	El Flaco	*Homo*	*sapiens*	–	–	8.83	−18.45	–	
–	F45-27	El Flaco	*Homo*	*sapiens*	–	–	9.63	−18.07	–	
–	F44-04	El Flaco	*Homo*	*sapiens*	–	–	10.45	−18.13	–	
–	F54-66	El Flaco	*Homo*	*sapiens*	–	–	9.18	−17.85	–	
–	F55-141	El Flaco	*Homo*	*sapiens*	–	–	9.86	−19.13	–	
–	F45-31	El Flaco	*Homo*	*sapiens*	–	–	9.88	−19.03	–	
–	F55-128	El Flaco	*Homo*	*sapiens*	–	–	9.31	−18.93	–	
–	F45-29	El Flaco	*Homo*	*sapiens*	–	–	10.67	−19.01	–	
–	F63-73–38	El Flaco	*Homo*	*sapiens*	–	–	10.38	−18.61	–	
#17	1400	El Carril	*Cyclura*	*cornuta*	dentary	18.34%	7.36	−21.34	3.34	
#5	952	El Carril	*Cyclura*	*cornuta*	dentary	4.71%	8.96	−20.77	3.26	
#6	953	El Carril	*Cyclura*	*cornuta*	dentary	8.73%	11.29	−20.85	3.21	
#7	996	El Carril	*Cyclura*	*cornuta*	vertebra	5.80%	8.17	−20.35	3.31	
#1	11	El Carril	*Cyclura*	*cornuta*	vertebra	1.69%	7.12	−21.05	3.32	
#14	1284	El Carril	*Cyclura*	*cornuta*	maxilla	5.22%	14.26	−20.57	3.27	
#18	1498	El Carril	*Cyclura*	*cornuta*	mandible	1.50%	7.08	−21.25	3.23	

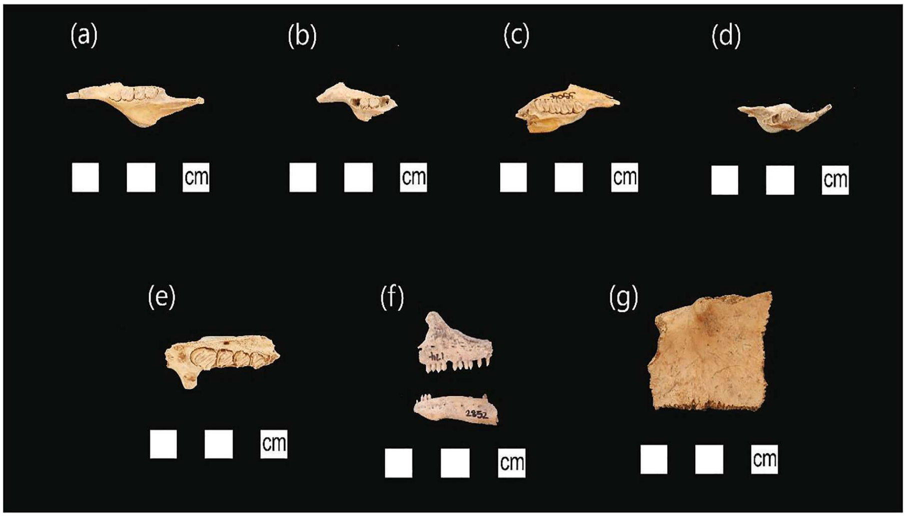

Fig. 2. A selection of bone samples from the case study sites demonstrating all the species that underwent isotopic analysis; (a) *Isolobodon portoricensis*, left hemimandible, occlusal view, FL1976, El Flaco; (b) *Cavia porcellus*, left hemimandible, occlusal view, FL1664, El Flaco; (c) *Isolobodon montanus*, right hemimandible, occlusal view, FL3504, El Flaco; (d) *Brotomys* sp., left hemimandible, occlusal view, FL1738, El Flaco; (e) *Plagiodontia aedium*, left maxilla, occlusal view, Bag 15, La Entrada; (f) *Cyclura cornuta*, top- right maxilla, lateral view; bottom – left dentary, lateral view, FL174, FL2852, El Flaco; (g) *Trachemys stejnegeri*, plastron fragment, dorsal view, FL3978, El Flaco.

from the same individuals. Examination of enamel carbon ($\partial^{13}C_{en}$), oxygen ($\partial^{18}O$) and strontium ($^{87}Sr/^{86}Sr$) values is ongoing, and will serve as a the focus of a future study applying dietary mixing models to animal isotopic values to examine nutrition partitioning (Pestle and Laffoon, 2018; Shev et al., 2020), hutia mobility, and possibly mortality season based on $\partial^{18}O$ fluctuations (Pederzani and Britton, 2019).

Other samples include humans and dogs from El Flaco (Shev et al., 2020), montane hutia (*Isolobodon montanus*) (n = 1), edible rat (*Brotomys* sp.) (n = 7), rhinoceros iguana (*Cyclura cornuta*) (n = 7), Central Antillean slider (*Trachemys stejnegeri stejnegeri*) (n = 5), Dominican hutia (*Plagiodontia aedium hylaeum*) (n = 2), and one guinea pig recovered from El Flaco which is one of only four examples recovered from pre-Columbian contexts in Hispaniola (LeFebvre and deFrance, 2014). These taxa serve as control groups of mostly herbivorous wild animals native to Hispaniola. The inclusion of guinea pig also serves to demonstrate what the isotopic values of a domesticated caviomorph rodent might resemble.

2.3. Sample extraction and isotopic analyses

Chemical treatment of bone samples follows a modified version of the procedure by Müldner and Richards (2005). Bones samples were crushed and inserted into Elkay Ezee filter tubes and 7 mL of 0.6 M HCl was added and samples were refrigerated at 4 °C. Every 48–72 h the HCl was replaced, this step repeated until bone was demineralized. Samples were washed three times in deionized water to remove traces of HCl. To remove unwanted humic contaminants, 7 mL of 0.125 M NaOH was added and left at room temperature for 20 h, after which samples were washed in deionized water. To gelatinize the samples, 9 mL of 0.001 M HCl (pH 3) was added and samples were placed in an oven set at 80 °C for 48 h. Ezee filters were then used to purify the collagen solution, samples were then frozen overnight before being lyophilized for 48 h. Collagen stable isotopes were analyzsed by a ThermoQuest IRMS Delta XP plus interfaced with a Flash elemental analyzer at the Earth Science Stable Isotope Lab, Vrije Universiteit Amsterdam.

2.4. Body mass estimations

Measurements of LTRL were made on complete *I. portoricensis* mandibles recovered from El Flaco in Units 69, 71, 72 ($n = 230$), allowing body mass estimations following formulae outlined by Hopkins (2008). Measurements were taken of the mandibular molar row from the most anterior point of the premolar to the most posterior point of the third molar.

Body mass was calculated using the following formula:

In (body mass) = a + b ln (LTRL)

The regression intercept values for all species of rodents under 5 kg was used ($a = -0.5992$, $b = 2.7283$).

2.5. Statistical analysis

To assess possible similarities in the average carbon values, statistical tests were conducted comparing different species according to sites. Using Past (version 4.04), a Kruskal-Wallis test for equal medians, and a one-way ANOVA test for equal means were conducted on all taxa and sites to assess significant similarities between population groups. Post-hoc non-parametric Mann-Whitney pairwise and Dunn tests were conducted to further assess similarities between populations. When comparing two isotopic sample populations a simple *t*-test was conducted. To examine if the body mass of El Flaco Puerto Rican hutia ($n = 230$) is normally distributed a Shapiro Wilk test for normality was conducted. All statistical tests employed an α-value of 0.05. The results, including relevant statistical values are listed in the results section and in the Online Supplement 2.

3. Results

Sixty-four samples yielded collagen above 1% of the original sample weight. Three samples had C:N ratios outside the accepted range of 2.9–3.6 (Ambrose, 1990), so are not discussed further. *I. portoricensis* ($n = 41$) samples demonstrated a mean ∂^{13}C value of −19.76‰. El Flaco contains the highest mean and median values ($\mu = -18.8$‰, Mdn = −19.34‰, $\sigma = 2.52$) for this species compared to El Carril ($\mu = -20.07$‰, Mdn = −20.38‰, $\sigma = 1.23$), El Cabo ($\mu = -20.25$‰, Mdn = −20.62‰, $\sigma = 0.81$) and La Entrada ($\mu = -20.93$‰, Mdn = −20.68‰, $\sigma = 0.66$). The average carbon isotope values for *I. portoricensis* are higher than other endemic species, such as *Trachemys stejnegeri* ($n = 5$, $\mu = -22.15$‰, Mdn = −23.26‰, $\sigma = 1.83$) and *Brotomys* sp. ($n = 7$, $\mu = -21.03$‰, Mdn = −21.28‰, $\sigma = 0.53$). Overall, *I. portoricensis* carbon values have the widest range (−21.85 to −11.88‰). Nitrogen values vary considerably within each species and site, however *I. portoricensis* samples had the widest range (1.68 to 14.1‰) but the lowest mean and median values ($\mu = 5.98$‰, Mdn = 5.59‰, $\sigma = 2.7$) compared to the averages of other species. One *I. portoricensis* possessed the highest ∂^{13}C (−11.88‰) and second highest ∂^{15}N (14.1‰) values, however as all collagen quality control guidelines are acceptable this has not been excluded as an outlier.

3.1. Statistical analyses of carbon values

A Kruskal-Wallis test for equal medians determined significant differences when all populations were tested together (p (same) = 1.221E-06). An ANOVA test was conducted on all taxa, with the exclusion of populations with only one sample. It was determined that there are significant differences in the means between populations ($df = 10$, $F = 6.381$, p (same) = 5.699), but both Mann-Whitney pairwise and Dunn's posthoc tests revealed that there is no significant difference ($p > 0.05$) between *I. portoricensis*, dogs and humans from El Flaco. All other taxa shared p values < 0.05 indicating differences between them against humans and dogs from El Flaco (Online Supplement 2).

Further one-way ANOVA testing was done comparing El Flaco samples of Puerto Rican hutia, humans and dogs, demonstrating that there is no significant difference in means between these three groups ($df = 2$, $F = 0.5716$, $p = 0.5695$). A simple *t*-test between humans and *I. portoricensis* from El Flaco demonstrated no significant difference in mean values (critical t value = 2.0484, $p = 0.6145$), whereas all other hutia populations have significant differences with humans. These statistics do not indicate that there was no commensalism occurring at other sites and might be associated with the lack of human collagen data from those sites. These results do however suggest significant similarities in the isotopic values between Puerto Rican hutia, humans, and dogs at El Flaco, while humans and dogs are both dissimilar to other examined taxa from all sites.

The mean ∂^{13}C values of humans, dogs, and *I. portoricensis* at El Flaco are similar albeit with considerable variation in the diets of hutias. *I. portoricensis* ∂^{13}C values ($\mu = -18.8$‰, range = 9.97, $\sigma^2 = 6.35$) from El Flaco vary considerably compared to humans ($\mu = -18.46$‰, range = 1.81, $\sigma^2 = 0.49$) and dogs ($\mu = -18.04$‰, range = 3.02, $\sigma^2 = 0.99$). The high variance in *I. portoricensis* isotopic values indicates that there was likely no systemised management strategy that would lend to a uniform diet for hutia at El Flaco or may suggest the opportunistic scavenging of garden plots by hutia.

3.2. Carbon values

The findings show that some *I. portoricensis* individuals possessed carbon isotope values similar to that of humans and dogs from El Flaco (Laffoon et al., 2017; Shev et al., 2020), and in some instances exceeded these species in both carbon and nitrogen (Fig. 3; Fig. 4). The two highest ∂^{13}C values within this study (−11.88‰; −14.45‰) were *I. portoricensis* from El Flaco (Table 1). El Flaco hutia also demonstrate the widest range in values (9.97‰) and highest degree of variance ($\sigma^2 = 6.8$) of all sampled populations.

Due to a high degree of commensalism with humans, dogs can be a viable isotopic surrogate for humans in pre-modern contexts globally (Guiry, 2012). The value ranges of dogs from El Flaco (∂^{13}C = −19.47 to −16.45‰, ∂^{15}N = 8.15 to 13.08‰, Shev, 2018) serve as a proxy denoting commensality with humans, but allows for greater variation in protein and carbohydrate sources as animals may not eat the same parts of plants or animals as humans. Bone can possess higher carbon values than muscle (Schoeninger and DeNiro, 1984) and different plant organs also express variations in isotopic values (Badeck et al., 2005). Dog isotopic values, although largely correlative, can vary as much as 2–3‰ from humans (Guiry, 2012).

The only other known domesticate from the region, the guinea pig, demonstrates values (∂^{13}C −17.18‰, ∂^{15}N 8.25‰) that cluster within the range of dogs, and are similar to that of humans from El Flaco (∂^{13}C −19.13 to −17.32‰, ∂^{15}N 8.83 to 11.87‰). One Puerto Rican hutia from El Flaco (∂^{13}C −18.36‰, ∂^{15}N 8.62‰) and another from El Cabo (∂^{13}C −18.44‰, ∂^{15}N 8.65‰), also fit within the isotopic value range of humans, whilst another El Flaco *I. portoricensis* (^{13}C −18.56‰, ∂^{15}N 12.9‰) fits within the human ∂^{13}C range (Fig. 4) but exceeds humans in ∂^{15}N (Table 1).

Overall, almost a third (29.3%, $n = 12$) of *I. portoricensis* exceeded the lowest ∂^{13}C of dogs. This trend differs across sites, with 53.3% ($n = 8$) of hutia from El Flaco, 20% ($n = 2$) at El Carril, and 18.2% ($n = 2$) of individuals at El Cabo exceeding this minimum. No *I. portoricensis* from La Entrada have values that would indicate regular C_4 consumption.

The potential ingestion of native C_4 plants by hutia cannot be completely discounted, however most isotopic values of the other tested herbivores support an inference of C_3 plant-based diets. Edible rat (*Brotomys* sp.) across all sites demonstrates ∂^{13}C values consistent with this ($n = 7$, $\mu = -21.24$‰), as does Hispaniolan slider (*Trachemys stejgnegeri*) ($n = 5$, $\mu = -21.36$‰) with the exception of one slider from El Flaco that had higher ∂^{13}C values (−18.62‰). Another exception was one *P. aedium* from La Entrada that is relatively high (−15.69‰) compared to the same species from El Flaco (−22.1‰). The La Entrada *P. aedium* also possesses a relatively low ∂^{15}N value (3.75‰).

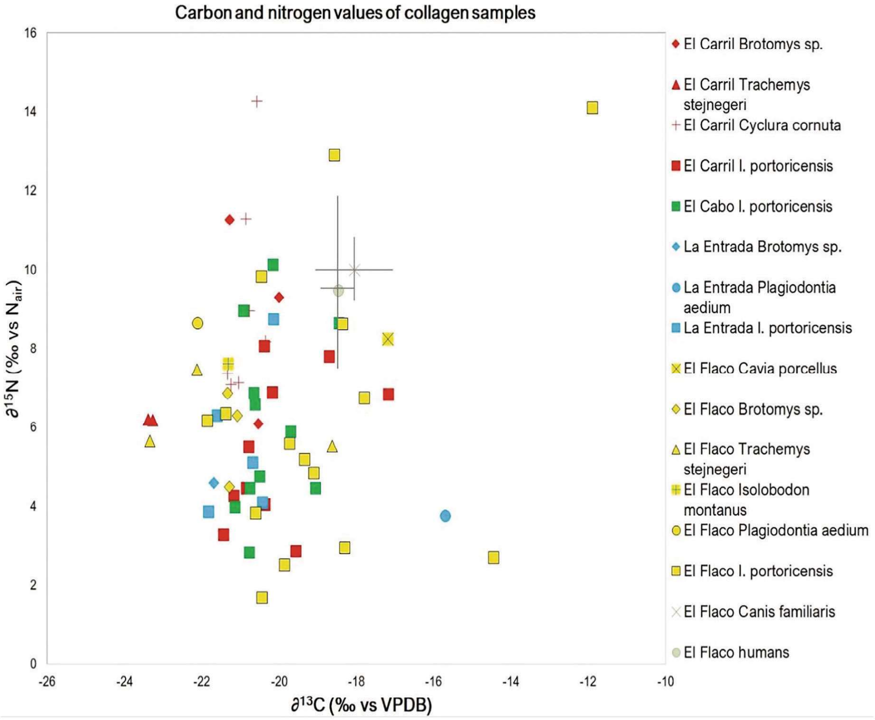

Fig. 3. Scatterplot representing the isotopic values of all collagen samples according to site and species investigated. Only the mean values of human and dogs from El Flaco have been included, bars indicate one standard deviation from the mean.

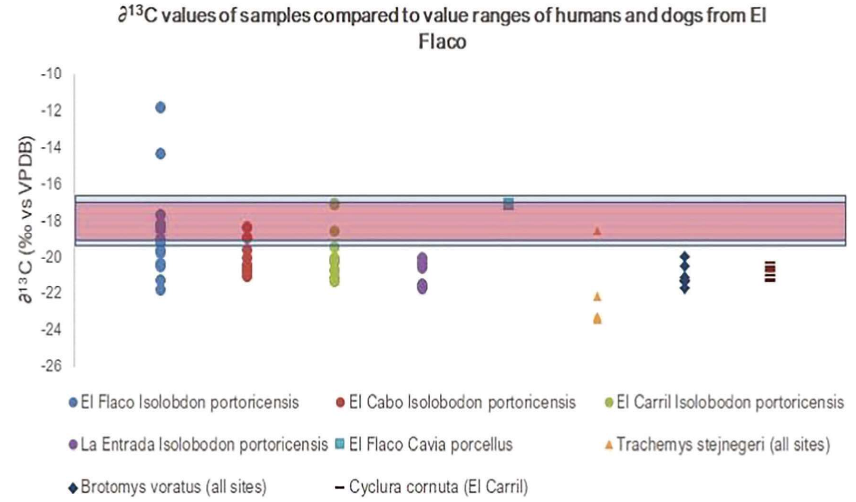

Fig. 4. Carbon values of all taxa with *Isolobodon portoricensis* listed per site. The blue box indicates the value range of dogs from El Flaco, the red box symbolises the value range of humans from El Flaco. Note the values overlapping with human and dog ranges for some *I. portoricensis*, the *Cavia porcellus* and one *Trachemys stejnegeri.*

Unlike LeFebvre's (2019b) study of Bahamian hutia only collagen isotope values are available for this study, however several comparisons can be made. Eight *I. portoricensis* exceeded the highest ∂^{13}C value (Palmetto Junction BCL#3851, −18.7‰) of any ancient Bahamian hutia, with one third (n = 5) of El Flacco hutia demonstrating higher ∂^{13}C values. Overall, the results from both studies suggest that some hutia were consuming a mixed diet of mainly C_3 supplemented with C_4 plants. Starch grain evidence suggests that maize was consumed at both

El Flaco and Palmetto Junction, however with the latter site possibly seeing more C_3 manioc (*Manihot esculenta*) production (Ciofalo et al., 2019). These disparities in carbon isotope enrichment may be associated with differences in agricultural practices. Unlike with Puerto Rican hutia and humans at El Flaco, no Bahamian hutia fit into the $\partial^{13}C_{co}$ value ranges of Bahamian humans, although Bahamian humans likely had a more seafood-heavy diet compared to El Flaco humans (Keegan and DeNiro, 1988; Laffoon et al., 2017).

3.3. *Nitrogen values*

Some individual hutias possess ∂^{15}N values much higher than should be expected for an herbivorous animal. Two *I. portoricensis* from El Flaco (12.9‰ and 14.1‰) far exceed other animals except for one rhinoceros iguana (14.26‰), a species that is opportunistically omnivorous (Capula, 1989). Many taxa exhibit low ∂^{13}C but fluctuate in nitrogen values, one possible explanation may be that these animals regularly consumed detritivorous invertebrates, for example earthworms, which can demonstrate ∂^{15}N value enrichment of up to 10‰ (Hyodo, 2015). There are several other possible explanations for high nitrogen values in Puerto Rican Hutia: suckling, coprophagy, foddering or malnutrition. Suckling in mammals is known to potentially raise ∂^{15}N between 1.5 and 3‰ (Beaumont et al., 2013; de Luca et al., 2012; Fuller et al., 2006). Feces becomes higher in ∂^{15}N compared to the original food source within the digestive tracts of small-bodied herbivores (Hwang et al., 2007; Montanari, 2017), and three genera of hutia, *Capromys, Geocapromys* and *Plagiodontia*, have been observed re-ingesting feces within captivity (Eisenberg and Woods, 2012, 150). High nitrogen values may also be associated with foddering if animals are fed plants which have been fertilized with their own manure (Fraser et al., 2011). Another possible explanation is catabolism from nutritional stress in which the body breaks down tissues, expending lighter ∂^{14}N over heavier isotopes (Fuller et al., 2005; Nicholls et al., 2020). Consuming detritivorous invertebrates, suckling, foddering, coprophagy, or nutritional stress are all feasible explanations for these high ∂^{15}N values.

3.4. *Body mass*

Lower tooth row lengths (LTRL) were measured for all *I. portoricensis* mandibles from El Flaco Units 69, 71 and 72 (n = 230), and some specimens from La Entrada (n = 2) and El Carril (n = 8). From these measurements body mass was estimated (Fig. 5; Table 2), with the caveat that no conclusions can be drawn about mortality ages from body mass. The results indicate that hutia at El Flaco ranged from 493.12 g to 1541.68 g (μ= 1014.18 g; Mdn = 1003.26 g; Sd = 225.25). A Shapiro Wilk statistical test was run to check for normality of El Flaco hutia determining a normal distribution of values ($p = 0.1560$, $W = 0.9908$) (Online Supplement 2). Plotted in a histogram (Fig. 5), the distribution of values clusters towards the centre as half of hutias (n = 125) weighed between 843 and 1,192 g. Two individuals from La Entrada were notably larger (1642.2 g and 1541.7 g) than all others, perhaps representative of selective hunting practices targeting larger individuals at this site, or reflecting differences in environment that may have affected a larger body size as has been speculated for Bahamian hutia (Jordan, 2012; LeFebvre et al., 2019a).

There is seemingly no correlation between isotopic variation and body mass of Puerto Rican hutias. The individual with the highest carbon and nitrogen values amongst hutia (∂^{13}C −11.9‰, ∂^{15}N 14.1‰) likely weighed around 967.9 g, and far exceeded the mean carbon (μ =−19.76‰,) and nitrogen (μ= 6.03‰) values for this species. The size of this animal may rule out weaning as the cause of such high values, however this is unclear as the ontogeny and sexual dimorphism of this species is unknown.

4. Conclusion

Suggesting that Puerto Rican hutia were systematically kept in captivity is not possible from the data presented here, let alone if nascent processes of domestication were occurring. There are currently no diachronic studies of morphological or genetic change to qualify this species as being domesticated. Additionally, in the Neotropics, human-animal interactions can take forms that blur the dichotomy between 'wild' and 'domestic' (Smith, 2005; Sugiyama et al., 2020). Some *I. portoricensis* are demonstrably commensal with humans and dogs recovered from El Flaco, which may or may not be associated with their direct management or captivity. Variation within isotopic values rules out dietary uniformity and indicate that Puerto Rican hutia may have been dietary generalists, despite the isotopic study by Cooke and Crowley (2018) suggesting otherwise. Although generalists exhibit wider variations in carbon intake (Bearhop et al., 2004), perhaps this variation can be explained as the result of human actions. The prevalence of this species at El Flaco might be a by-product of agricultural

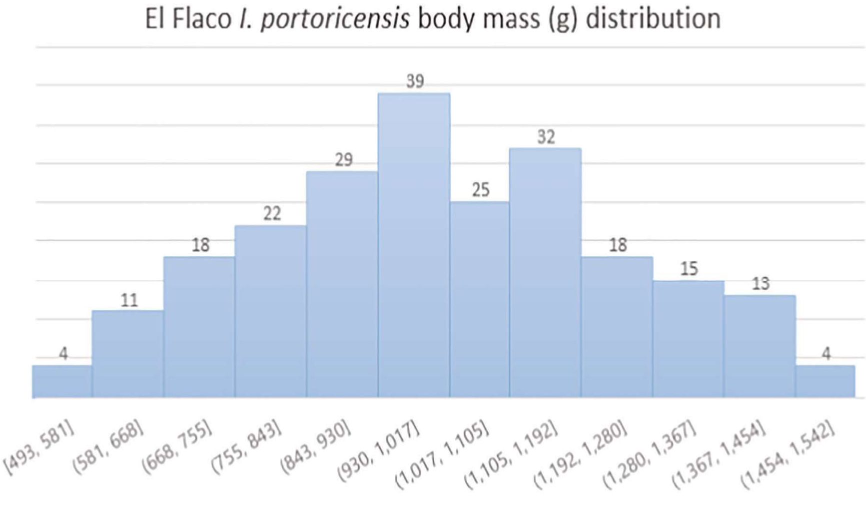

Fig. 5. Histogram demonstrating the distribution of Puerto Rican hutias according to body mass (g) at El Flaco. Numbers above columns indicate the MNI within each weight range.

Table 2
Body mass of *Isolobodon portoricensis* from El Flaco estimated from lower tooth row length (LRTL). Body mass (g) is calculated using the formula for all rodents under 5 kg by Hopkins (2008). Samples that underwent isotopic analysis have these bone collagen carbon and nitrogen values listed.

Sample no.	Find no.	Site	Unit	Layer	Feature	LTRL (mm)	Body Mass (g)
CA14	3849	El Carril	56	11	25–41	14.03	740.1
CA15	3849	El Carril	56	11	25–41	16.52	1155.76
CA17	3892	El Carril	56	13	25–42	16.65	1180.74
CA21	3718	El Carril	56	5	–	16.89	1227.76
CA23	3713	El Carril	56	5	25–38	15.51	973.01
CA27	3699	El Carril	56	3	25–37	15.91	1043.01
CA30	3775	El Carril	56	8	25–38	16.39	1131.11
CA32	3715	El Carril	56	4	–	16.08	1073.7
CA12	3941	El Carril	56	16	25–42	16.73	1196.3
CA18	3888	El Carril	56	12	25–41	16.58	1167.2
CA19	3911	El Carril	56	14	25–45	17.22	1294.3
CA26	3699	El Carril	56	3	25–37	16.36	1125.5
CA22	3578	El Carril	56	2	25–35	14.94	878.5
EN1	BAG15	La Entrada	–	–	–	18.79	1642.2
EN2	BAG15	La Entrada	–	–	–	18.36	1541.68
FL1097	3246	El Flaco	69	4	–	13.9	721.54
FL1099	3246	El Flaco	69	4	–	17.66	1386.55
FL1264	3434	El Flaco	69	5	–	17.22	1294.32
FL1421	2963	El Flaco	71	10	–	15.09	902.79
FL1543	2956	El Flaco	71	9	–	16.35	1123.6
FL1952	2873	El Flaco	71	7	–	13.52	668.98
FL1976	2712	El Flaco	72	4	–	15.67	1000.64
FL2009	3032	El Flaco	72	9	–	16.01	1060.99
FL2413	3057	El Flaco	72	11	–	15.48	967.88
FL2482	3009	El Flaco	72	6	–	16.18	1092.01
FL2542	2776	El Flaco	69	1	–	16.63	1176.88
FL26	3218	El Flaco	69	3	–	13.94	727.21
FL4075	2816	El Flaco	69	2	–	18.36	1541.68
FL438	3269	El Flaco	69	4	–	15.44	961.07
FL86	3167	El Flaco	69	1	–	15.05	896.28
FL21	3218	El Flaco	69	3	–	15.61	990.22
FL22	3218	El Flaco	69	3	–	17.34	1319.07
FL25	3218	El Flaco	69	3	–	13.91	722.95
FL32	3218	El Flaco	69	3	–	16.53	1157.67
FL34	3218	El Flaco	69	3	–	16.45	1142.45
FL36	3218	El Flaco	69	3	–	15.92	1044.80
FL37	3218	El Flaco	69	3	–	14.94	878.52
FL38	3218	El Flaco	69	3	–	15.62	991.95
FL97	3167	El Flaco	69	1	–	15.04	894.66
FL98	3167	El Flaco	69	1	–	15.2	920.86
FL126	3135	El Flaco	69	2	–	15.33	942.51
FL149	3452	El Flaco	69	4	–	18.11	1485.08
FL180	3443	El Flaco	69	4	–	16.46	1144.34
FL193	3482	El Flaco	69	6	–	15.47	966.18
FL200	3482	El Flaco	69	6	–	15.92	1044.80
FL240	3445	El Flaco	69	4	–	15.59	986.76
FL241	3445	El Flaco	69	4	–	17.7	1395.13
FL244	3445	El Flaco	69	4	–	16.18	1092.01
FL270	3290	El Flaco	69	3	–	16.55	1161.49
FL291	3212	El Flaco	69	3	–	17.8	1416.74
FL334	3465	El Flaco	69	4	–	16.07	1071.87
FL343	3465	El Flaco	69	4	–	14.06	744.42
FL390	3304	El Flaco	69	2	–	17.02	1253.71
FL428	3269	El Flaco	69	4	–	15.78	1019.92
FL431	3269	El Flaco	69	4	–	15.83	1028.76
FL436	3269	El Flaco	69	4	–	16.91	1231.73
FL442	3269	El Flaco	69	4	–	13.94	727.21
FL443	3269	El Flaco	69	4	–	14.51	811.24
FL452	3454	El Flaco	69	4	–	14.48	806.67
FL465	3276	El Flaco	69	3	–	14.72	843.67
FL542	3484	El Flaco	69	6	–	16.37	1127.35
FL573	3273	El Flaco	69	3	–	17.18	1286.13
FL626	3262	El Flaco	69	3	–	15.75	1014.64
FL680	3525	El Flaco	69	7	–	17.72	1399.44
FL702	3302	El Flaco	69	4	–	13.59	678.47
FL713	3302	El Flaco	69	4	–	15.72	1009.37
FL716	3302	El Flaco	69	4	–	15.71	1007.62
FL719	3302	El Flaco	69	4	–	14.69	838.99
FL800	3532	El Flaco	69	8	–	15.31	939.16
FL809	3177	El Flaco	69	2	–	15.27	932.48
FL857	3224	El Flaco	69	3	–	16.77	1204.11
FL871	3224	El Flaco	69	3	–	15.64	995.42
FL912	3446	El Flaco	69	4	–	12.87	584.84

(continued on next page)

Table 2 (*continued*)

Sample no.	Find no.	Site	Unit	Layer	Feature	LTRL (mm)	Body Mass (g)
FL918	3528	El Flaco	69	6	–	14.11	751.67
FL954	3488	El Flaco	69	5	–	17.49	1350.44
FL955	3488	El Flaco	69	5	–	17.51	1354.65
FL986	3228	El Flaco	69	3	–	13.22	629.25
FL992	3228	El Flaco	69	3	–	17.12	1273.91
FL1020	3503	El Flaco	69	8	–	16.66	1182.68
FL1072	3246	El Flaco	69	4	–	13.57	675.75
FL1078	3246	El Flaco	69	4	–	14.04	741.54
FL1084	3246	El Flaco	69	4	–	15.61	990.22
FL1087	3246	El Flaco	69	4	–	15.33	942.51
FL1096	3246	El Flaco	69	4	–	16.1	1077.34
FL1098	3246	El Flaco	69	4	–	17.61	1375.87
FL1104	3246	El Flaco	69	4	–	14.93	876.92
FL1113	3246	El Flaco	69	4	–	13.77	703.27
FL1116	3246	El Flaco	69	4	–	16.37	1127.35
FL1118	3246	El Flaco	69	4	–	13.65	686.68
FL1119	3246	El Flaco	69	4	–	16.67	1184.62
FL1120	3246	El Flaco	69	4	–	15.1	904.43
FL1137	3246	El Flaco	69	4	–	14.62	828.13
FL1140	3246	El Flaco	69	4	–	14.57	820.42
FL1168	3293	El Flaco	69	3	–	15.4	954.30
FL1186	2624	El Flaco	69	2	–	16.54	1159.58
FL1207	2820	El Flaco	69	2	–	13.05	607.42
FL1210	2820	El Flaco	69	2	–	14.91	873.71
FL1214	2820	El Flaco	69	2	–	13.36	647.60
FL1267	3434	El Flaco	69	5	–	15.39	952.61
FL1299	3501	El Flaco	69	7	–	15.16	914.27
FL1301	3390	El Flaco	69	3	–	14.51	811.24
FL1302	3390	El Flaco	69	3	–	16.55	1161.49
FL1330	3128	El Flaco	69	2	–	13.86	715.89
FL1340	3128	El Flaco	69	2	–	15.77	1018.16
FL1351	3128	El Flaco	69	2	–	15.16	914.27
FL1383	2415	El Flaco	71	2	–	15.88	1037.65
FL1386	2882	El Flaco	71	7	74–10	16.12	1081.00
FL1437	2946	El Flaco	71	9	–	14.86	865.74
FL1446	2946	El Flaco	71	9	–	17.27	1304.59
FL1528	2436	El Flaco	71	2	–	16.07	1071.87
FL1530	2436	El Flaco	71	2	–	16.21	1097.54
FL1544	2956	El Flaco	71	9	–	17.87	1432.00
FL1546	2956	El Flaco	71	9	–	12.58	549.58
FL1559	2956	El Flaco	71	9	–	14.51	811.24
FL1596	2736	El Flaco	71	5	–	14.49	808.19
FL1611	2726	El Flaco	71	4	–	14.41	796.07
FL1613	2726	El Flaco	71	4	–	15.89	1039.43
FL1615	2726	El Flaco	71	4	–	13.37	648.93
FL1643	3099	El Flaco	71	11	–	14.77	851.51
FL1674	2876	El Flaco	71	7	–	15.72	1009.37
FL1686	2725	El Flaco	71	4	–	16.64	1178.81
FL1710	2439	El Flaco	71	2	–	16.74	1198.24
FL1712	2439	El Flaco	71	2	–	16.27	1108.66
FL1724	3092	El Flaco	71	11	–	15.39	952.61
FL1736	2952	El Flaco	71	9	–	15.65	997.16
FL1743	2952	El Flaco	71	9	–	15.21	922.52
FL1776	2759	El Flaco	71	5	–	14.47	805.15
FL1798	2930	El Flaco	71	8	–	17.52	1356.77
FL1799	2930	El Flaco	71	8	–	16.12	1081.00
FL1871	2830	El Flaco	71	6	–	15.74	1012.88
FL1876	2830	El Flaco	71	6	–	16.67	1184.62
FL1877	2830	El Flaco	71	6	–	15.24	927.49
FL1909	2926	El Flaco	71	8	–	16.46	1144.34
FL1977	2712	El Flaco	72	4	–	13.21	627.96
FL2008	3032	El Flaco	72	9	–	16.46	1144.34
FL2057	3030	El Flaco	72	8	–	15.36	947.55
FL2058	3030	El Flaco	72	8	–	15.21	922.52
FL2072	3024	El Flaco	72	7	–	12.88	586.08
FL2081	3037	El Flaco	72	9	–	16.85	1219.84
FL2167	3059	El Flaco	72	11	–	14.53	814.29
FL2171	2714	El Flaco	72	4	–	16.37	1127.35
FL2200	2703	El Flaco	72	3	–	17.9	1438.57
FL2202	2703	El Flaco	72	3	–	16.73	1196.28
FL2216	2973	El Flaco	72	5	–	12.46	535.39
FL2340	2985	El Flaco	72	6	–	15.7	1005.87
FL2343	2985	El Flaco	72	6	–	17.54	1361.00
FL2352	3069	El Flaco	72	13	–	17.33	1317.00
FL2382	3023	El Flaco	72	7	–	15.13	909.34
FL2443	3031	El Flaco	72	8	–	16.62	1174.95

(continued on next page)

Table 2 (*continued*)

Sample no.	Find no.	Site	Unit	Layer	Feature	LTRL (mm)	Body Mass (g)
FL2445	3031	El Flaco	72	8	–	16.73	1196.28
FL2463	2704	El Flaco	72	3	–	16.91	1231.73
FL2478	3068	El Flaco	72	13	–	17.52	1356.77
FL2520	2773	El Flaco	69	1	–	17.33	1317.00
FL2534	3132	El Flaco	69	2	–	15.24	927.49
FL2610	2764	El Flaco	69	2	–	12.46	535.39
FL2612	2764	El Flaco	69	2	–	15.22	924.17
FL2672	3143	El Flaco	69	2	–	16.73	1196.28
FL2677	3143	El Flaco	69	2	–	15.51	973.01
FL2679	3143	El Flaco	69	2	–	14.57	820.42
FL2680	3143	El Flaco	69	2	–	14.31	781.09
FL2726	2779	El Flaco	69	2	–	16.8	1209.99
FL2728	2779	El Flaco	69	2	–	13.38	650.25
FL2729	2779	El Flaco	69	2	–	17.85	1427.63
FL2740	2779	El Flaco	69	2	–	15.55	979.87
FL2741	2779	El Flaco	69	2	–	16.27	1108.66
FL2742	2779	El Flaco	69	2	–	15.73	1011.13
FL2751	2779	El Flaco	69	2	–	15.12	907.70
FL2823	3259	El Flaco	69	4	–	15.83	1028.76
FL2829	3259	El Flaco	69	4	–	13.4	652.91
FL2836	3161	El Flaco	69	2	–	15.38	950.92
FL2837	3161	El Flaco	69	2	–	14.6	825.04
FL2857	2790	El Flaco	69	1	–	17.41	1333.65
FL2886	2401	El Flaco	69	1	–	16.94	1237.70
FL2915	2751	El Flaco	69	2	–	14.85	864.16
FL2937	2740	El Flaco	69	1	–	16.21	1097.54
FL2989	2778	El Flaco	69	2	–	16.27	1108.66
FL2990	2778	El Flaco	69	2	–	15.37	949.23
FL2991	2778	El Flaco	69	2	–	17.34	1319.07
FL2997	2778	El Flaco	69	2	–	14.71	842.11
FL3080	3279	El Flaco	69	2	55–105	14.53	814.29
FL3086	3279	El Flaco	69	2	55–105	14.64	831.22
FL3103	2839	El Flaco	69	2	–	15.76	1016.40
FL3128	3259	El Flaco	69	4	–	15.64	995.42
FL3133	3259	El Flaco	69	4	–	13.01	602.36
FL3138	3259	El Flaco	69	4	–	15.77	1018.16
FL3172	2732	El Flaco	69	3	45–27	15.33	942.51
FL3218	2838	El Flaco	69	2	–	15.51	973.01
FL3234	3281	El Flaco	69	3	–	18.28	1523.42
FL3238	3281	El Flaco	69	3	–	14	735.79
FL3270	2438	El Flaco	69	2	–	16.98	1245.69
FL3281	2729	El Flaco	77	6	–	16.55	1161.49
FL3282	2729	El Flaco	77	6	–	15.19	919.21
FL3402	3294	El Flaco	69	3	–	14.19	763.51
FL3409	3294	El Flaco	69	3	–	15.91	1043.01
FL3434	3294	El Flaco	69	3	–	14.09	748.76
FL3468	2476	El Flaco	69	2	45–26	17.63	1380.13
FL3470	2761	El Flaco	69	2	–	16.65	1180.74
FL3504	2757	El Flaco	69	1	–	15.97	1053.77
FL3522	2787	El Flaco	69	1	–	16.6	1171.09
FL3614	2827	El Flaco	69	2	–	14.69	838.99
FL3629	2800	El Flaco	69	2	–	18.03	1467.25
FL3662	2803	El Flaco	69	3	–	17.21	1292.27
FL3722	2623	El Flaco	69	2	45–30	17.58	1369.48
FL3723	2623	El Flaco	69	2	45–30	17.58	1369.48
FL3724	2623	El Flaco	69	2	45–30	16.83	1215.90
FL3729	2623	El Flaco	69	2	45–30	13.66	688.05
FL3730	2623	El Flaco	69	2	45–30	14.04	741.54
FL3759	2623	El Flaco	69	2	45–30	13.77	703.27
FL3772	2623	El Flaco	69	2	45–30	12.92	591.06
FL3779	3225	El Flaco	69	3	–	15.16	914.27
FL3799	2791	El Flaco	69	3	–	14.23	769.24
FL3801	2791	El Flaco	69	3	–	14.96	881.73
FL3813	2810	El Flaco	69	1	–	16.17	1090.17
FL3882	3246	El Flaco	69	4	–	16.66	1182.68
FL3885	3246	El Flaco	69	4	–	16.08	1073.69
FL3908	2801	El Flaco	69	1	–	15.81	1025.22
FL3913	2808	El Flaco	69	1	–	15.59	986.76
FL3949	3216	El Flaco	69	3	–	16.63	1176.88
FL3951	3216	El Flaco	69	3	–	16.51	1153.85
FL3955	3216	El Flaco	69	3	–	14.61	826.58
FL3956	3216	El Flaco	69	3	–	15.42	957.68
FL4007	3212	El Flaco	69	3	–	16.51	1153.85
FL4009	3212	El Flaco	69	3	–	12.09	493.12
FL4011	3212	El Flaco	69	3	–	14.91	873.71
FL4021	3212	El Flaco	69	3	–	14.75	848.37

(*continued on next page*)

Table 2 (*continued*)

Sample no.	Find no.	Site	Unit	Layer	Feature	LTRL (mm)	Body Mass (g)
FL4023	3212	El Flaco	69	3	–	16.77	1204.11
FL4027	3212	El Flaco	69	3	–	16.58	1167.25
FL4047	3128	El Flaco	69	2	–	15.41	955.99
FL4087	2816	El Flaco	69	2	–	17.79	1414.57
FL4093	2812	El Flaco	69	1	–	17.62	1378.00
FL4102	3222	El Flaco	69	3	–	15.2	920.86
FL4143	2826	El Flaco	69	2	44–4	15.91	1043.01
FL4156	2821	El Flaco	69	3	–	16.65	1180.74
FL4192	3223	El Flaco	69	3	–	14.15	757.49
FL4225	3250	El Flaco	69	4	–	16.71	1192.39
FL4231	3250	El Flaco	69	4	–	14.83	860.98
FL4237	3250	El Flaco	69	4	–	16.62	1174.95
FL4272	2621	El Flaco	69	2	–	17.12	1273.91
FL4280	2621	El Flaco	69	2	–	16.89	1227.76
FL4281	2621	El Flaco	69	2	–	15.15	912.62
FL4295	2785	El Flaco	69	1	–	15.34	944.19
FL4313	2524	El Flaco	69	2	45–28	15.45	962.77
FL4319	2602	El Flaco	69	1	–	16.61	1173.02
FL4324	2795	El Flaco	69	1	–	17.55	1363.11
FL4332	2500	El Flaco	69	3	–	15.63	993.69

practices that attracted and benefited this animal. It has been proposed that one of the reasons that *I. portoricensis* went extinct, whereas *P, aedium* did not, is due to the latter's more generalist behaviour and arboreal nature (Cooke and Crowley, 2018; Hansford et al., 2012). If *I. portoricensis* was a more ground-dwelling species, then the clearing of forest may have served to attract and support populations.

This study does not discount some hutia may have been kept within captivity to ensure a steady supply, as mentioned by Las Casas, or alternatively as pets. Another possibility, as discussed by LeFebvre et al. (2019a) and LeFebvre et al. (2019b) for Bahamian hutia, is that indigenous people may have also purposefully supplemented the diets of non-captive hutia, suggesting a degree of tameness associated with prolonged human-hutia interaction. However, there is no evidence to suggest that there was a systemised method of management affecting the diets of all hutia. Predation upon hutia was possibly part of the active management of garden plots or agricultural areas, which if they were opportunistically scavenging may explain their dietary variation.

In terms of the scope of future research examining the translocation and potential management of Puerto Rican hutia, ancient DNA studies, morphometric studies, as well as more in-depth isotopic niche studies of this species both from palaeontological and archaeological contexts, would be greatly beneficial. This study highlights the need for varied interpretations of human-animal interactions in the humid Neotropics, and calls for greater synthesis between zooarchaeology, isotopic analyses and palaeoenvironmental studies to gain more holistic insights into indigenous environmental practices.

CRediT authorship contribution statement

Gene T. Shev: Conceptualization, Data curation, Methodology, Formal analysis, Visualization, Funding acquisition, Investigation, Writing - original draft. **Jason E. Laffoon:** Conceptualization, Methodology, Supervision, Writing - review & editing. **Corinne L. Hofman:** Project administration, Resources, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

There are no conflicts of interest regarding the financing of this research or in the authoring of this paper. This results of this research form part of the project entitled “Human-animal entanglements on the eve of Columbus’ landfall: a study of indigenous animal husbandry practices in the island of Hispaniola” funded by the NWO PhDs in the Humanities grant (2018–2022). The final form of this paper would not have been possible without the helpful and constructive comments from the anonymous reviewers, so we are graciously indebted to them. Special thanks go to Sr. Juan Almonte and the Museo de Historía Natural, Santo Domingo for assistance in identifying endemic Hispaniolan fauna, to the Museo del Hombre Dominicano and the Ministerio de Cultura, República Dominicana for allowing access to sites and materials. Simone Casale is acknowledged for assistance in the generation of figures. Samples were provided as part of the ERC-Synergy NEXUS1492 project (gr, agreement Nr. 319209), which carried out the excavations at El Flaco and El Carril and which received funding from the European Research Council under the European Union’s Seventh Framework Programme. The El Cabo samples were collected as part of the NWO project Houses for the Living and the Dead (gr. Nr. 360-62-030). Thanks goes to Arq. Juan I. Tineo and the Museo del Hombre Dominicano for inviting the NEXUS team to collaborate in the La Entrada salvage study. All collagen extraction was conducted at the Leiden University Faculty of Archaeology. Thanks goes to Suzan Verdegaal-Warmerdam and the Faculty of Science, Vrije Universiteit Amsterdam, for providing access to their lab facilities.

Funding

This work was supported by the Netherlands Organisation for Scientific Research (NWO) (PhD in the Humanities project PGW.18.015), and the European Research Council (NEXUS1492 project, ERC-Synergy grant: 319209).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2021.102913.

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