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A preliminary multi-isotope assessment of human mobility and diet in pre-Columbian Panama

Ashley E. Sharpe [a,*], Nicole Smith-Guzmán [a], Jason Curtis [b], Ilean Isaza-Aizpurúa [c], George D. Kamenov [b], Thomas A. Wake [d], Richard G. Cooke [a]

[a] Center for Tropical Paleoecology and Archaeology, Smithsonian Tropical Research Institute, 0843-03092 Balboa, Panama
[b] Department of Geological Sciences, University of Florida, Gainesville, FL 32611, USA
[c] Coiba AIP, Edificio 205, Ciudad de Saber, Clayton, Panama
[d] The Cotsen Institute of Archaeology and Department of Anthropology, University of California, Los Angeles, CA 90095, USA

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ABSTRACT

This study uses carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), oxygen ($\delta^{18}O$), and strontium ($^{87}Sr/^{86}Sr$) isotopes to infer the diets and mobility patterns of pre-Columbian humans from seven archaeological sites in Panama: Cerro Mangote, Sitio Sierra, and Cerro Juan Díaz in central Pacific Panama; Cerro Brujo and Sitio Drago along Panama's northwest Caribbean coast; Jicarita Island in the Gulf of Chiriquí; and Pedro González Island in the Gulf of Panama. Our initial hypotheses were 1) individuals from island and coastal settlements relied more heavily on marine food than those from inland settlements, 2) dietary dependency on maize increased over time, and 3) little or no evidence exists for mobility. Generally, the results did not support these hypotheses: 1) the ecotonal community of Cerro Juan Díaz consumed large quantities of marine food, 2) maize consumption varied over time at different sites, and 3) non-local individuals appeared at multiple sites, including one possible case of an individual who had been moved after death. While this study is intended to be a preliminary analysis of human diet and mobility patterns among pre-Columbian Panamanians, it highlights the complex nature of human activities and the value of incorporating multiple lines of archaeological, osteological, geochemical, and ecological evidence for interpreting bioarchaeological data.

1. Introduction

Panama is a culturally and ecologically diverse region, uniquely situated at the junction between two continents while separating two oceans. The terrain is remarkably variable, with a broad volcanic mountain ridge extending throughout the country's central core, surrounded by lowland valleys and alternating drier and wetter regions of forests and savannas, depending on circulation and rainfall patterns across the isthmus. Many islands are scattered along both coastlines, including the Bocas del Toro archipelago in the Caribbean, the Pearl Island archipelago in the Gulf of Panama, and Coiba Island in the Gulf of Chiriquí (Fig. 1). Evidence for pre-Columbian human occupation has been found in nearly every part of the country, including the islands, and several decades of intensive excavation and artifactual analyses have revealed a long and complex history of human occupation in this geographically and climatically diverse area.

This study focuses on improving our understanding of the complex interplay between human populations and environments through stable isotope analyses of human remains from multiple archaeological sites and time periods. Previous isotope research conducted by Norr (1991) and Norr (1995) revealed dietary variation in carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes across different sites. The purpose of the present study is to re-examine some of these previously tested individuals with new strontium ($^{87}Sr/^{86}Sr$) isotope data in order to assess human mobility at these sites. Furthermore, we examine a number of humans from more recent excavations across Panama to better understand the diversity of subsistence and mobility patterns in the past.

Our study had two primary objectives. First, we sought to confirm Norr's interpretation that diet was more similar among individuals living within a single community than among individuals of different communities. To do this, we expanded Norr's original dataset with $\delta^{13}C$ and $\delta^{15}N$ data from different sites in areas that had not previously been

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* Corresponding author.

E-mail addresses: SharpeAE@si.edu (A.E. Sharpe), SmithN@si.edu (N. Smith-Guzmán), CurtisJ@ufl.edu (J. Curtis), iisaza@bu.edu (I. Isaza-Aizpurúa), kamenov@ufl.edu (G.D. Kamenov), twake@ucla.edu (T.A. Wake), CookeR@si.edu (R.G. Cooke).

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tested, including individuals recovered from the island settlements. We hypothesized that humans living near coasts likely focused their subsistence strategies on marine food more so than inland communities. Furthermore, we hypothesized that, over time, humans began to rely increasingly on maize agriculture in order to sustain expanding populations. Our second objective was to assess the degree of human mobility at the various sites by examining strontium (^{87}Sr/^{87}Sr) and oxygen (δ^{18}O) isotope values from tooth enamel. We tested 16 archaeological animal bones and shells (i.e., small mammals and land snails) to create the first terrestrial baseline strontium isotope map for Panama. With these proxy data, we compared human enamel ^{87}Sr/^{86}Sr with the expected local baselines to determine if people were born at the location where they were buried. Our base hypothesis for this test was that human enamel should generally match the ^{87}Sr/^{86}Sr and δ^{18}O of their burial location if mobility was limited during life. Overall, the results did not support our initial hypotheses, and rather revealed more variation in dietary and mobility patterns than we had anticipated.

2. Previous stable isotope research in Panama

In the last twenty years, a number of important multi-isotope investigations of pre-Columbian humans have been performed in Mesoamerica and the circum-Caribbean areas, providing valuable insights into the diets, movements, and lifestyles of the people who inhabited the American tropics (Eck et al., 2019; Krigbaum et al., 2013; Laffoon et al., 2013, 2017; Pestle and Laffoon, 2018; Price et al., 2010, 2015, 2019; Wright, 2012; Wright et al., 2010). By contrast, less research has been done in the area from eastern Honduras through Panama. Somewhat paradoxically, one of the earliest multi-isotope studies on human remains in the Americas was conducted in Panama during the late 1980s by Norr (1991) and Norr (1995). Norr compared the dietary isotope data from bone collagen among 284 individuals from 18 archaeological sites to show that the diets of individuals within communities were often more similar than when compared between communities, suggesting many sites may have had their own specific diets based on local resource availability, subsistence strategies, and sociocultural preferences. Furthermore, Norr's research showed that the populations tested from Panama consumed less maize relative to populations from Costa Rica and Maya sites in Belize. Three of the Panamanian sites that were the focus of Norr's research, Cerro Brujo (CA-3), Cerro Mangote (AG-1), and Sitio Sierra (AG-3), are included in the present study.

At the time Norr conducted her research, many sites that would redefine our view of Panama's prehistory had not yet been excavated. Foremost among these is Cerro Juan Díaz (LS-3), a large settlement in central Pacific Panama excavated from 1992 to 2001 as part of a rescue project initiated to suppress the widespread looting of pre-Columbian graves at the site (Carvajal et al., 2006; Cooke and Sánchez Herrera, 1998; Cooke et al., 1998; Sánchez Herrera, 1995). Over 400 skeletons were recovered from this site alone, spanning c. 50–1600 CE. Other important sites, such as Sitio Drago on Colón Island in the Caribbean near Costa Rica (Wake et al., 2004, 2012, 2013), and sites of occupation on the Pacific islands of Pedro González (Cooke et al., 2016; Martín et al., 2016) and Jicarita (JI-1; Isaza, 2019), reveal evidence for human settlement going back several millennia. Imported ceramic and stone artifacts from the mainland recovered at these island sites indicate that there may have been frequent communication between the islands and mainland communities in Panama.

Norr's early studies did not focus on questions of human mobility, since the isotope chemistry necessary for these studies was only beginning to be developed at that time. Strontium isotope analysis is today commonly used in bioarchaeological, forensic, and zoological studies to investigate movements of humans and animals across the landscape (Aggarwal et al., 2008; Beard and Johnson, 2000; Bentley, 2006; Sharpe et al., 2018); however, strontium research was rarely performed in the 1980s and early 1990s. As such, the present investigation includes the first terrestrial ^{87}Sr/^{86}Sr baseline isotope test for Panama.

3. Overview of the isotopes used in this study

This study uses a combination of isotopes to assess dietary variation among individuals from different communities and time periods, as well as strontium and oxygen isotopes from tooth enamel to assess human mobility. We tested strontium isotope values from 16 animal bone and terrestrial snail samples from ten archaeological sites across Panama to determine local strontium isotope values in different areas. Trace element concentrations from human enamel samples allowed us to quantify diagenesis at different sites.

Carbon and nitrogen isotope values from bone collagen, and carbon isotope values from bone hydroxyapatite, were tested to determine diet (Fig. 2). These isotopes are commonly used in bioarchaeology today, and

Fig. 1. Map of Panama and the archaeological sites referenced in this study. Map by Alexander Karnstedt (Wikimedia Commons), modified under the GNU Free Documentation License.

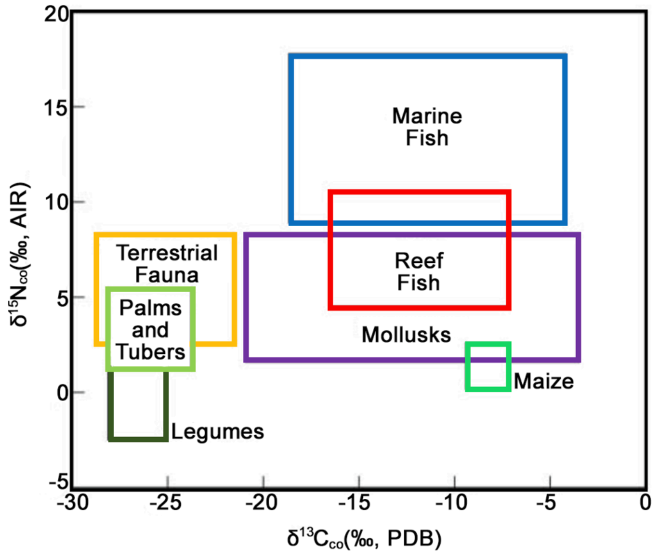

Fig. 2. Expected ranges of bone collagen $\delta^{13}C$ and $\delta^{15}N$ for different dietary components in the circum-Caribbean area. Modified from Norr (2002) and Krigbaum (2013).

there are a number of reviews of their applications (see Reitsema, 2013; Schoeninger, 2010; Schoeninger and Moore, 1992, and sources therein). Briefly, carbon isotope ratios assess the type of vegetation a human or other animal consumed during life. Many leafy plants in the American tropics, as well as fruits, gourds, squashes, and manioc, undergo C_3 photosynthesis. Consumption of these plants, or of meat from terrestrial animals that eat these plants, tends to produce human collagen $\delta^{13}C$ values below −15‰, and usually closer to −20 to −25‰ if the diet consists exclusively of C_3 sources. Many grasses, most particularly maize, have C_4 photosynthesis, and consumption of these plants tends to elevate the $\delta^{13}C_{co}$ signal relative to the quantity of C_4 plants in the diet (Schoeninger, 2009). Certain marine foods can also elevate $\delta^{13}C_{co}$, although usually not to the same extent as C_4 plants (Chisholm et al., 1982).

Collagen $\delta^{13}C$ is frequently reported in archaeological and biological publications, and largely comes from the protein in a human's diet (Fernandes et al., 2012; Froehle et al., 2012). Apatite $\delta^{13}C$ ($\delta^{13}C_{ap}$) represents the $\delta^{13}C$ of the entire diet, including carbohydrates. The difference between bone apatite and collagen $\delta^{13}C$ ($\Delta^{13}C_{ap-co}$) can reveal whether an individual was consuming primarily a C_3 or C_4 monoisotopic diet, or a mix of both (Ambrose and Norr, 1993; France and Owsley, 2012; Tieszen and Fragre, 1993). Comparisons of apatite-collagen spacing across multiple species occupying different trophic levels have shown that the interpretations of such spacing can vary due to physiological differences in carnivores, herbivores, and omnivores (Hedges, 2003); since humans are the focus of this study, interpretations of $\Delta^{13}C_{ap-co}$ are based only on other studies involving pre-Columbian humans in the Americas (Ambrose et al., 1997; Norr, 1995; Harrison and Katzenberg, 2003; Krigbaum et al., 2013). Working from Norr's original data (1991, 1995), we would expect to find that different communities depended on maize to varying extents. Like other regions of the Americas, we might expect to see a greater dependency on maize consumption over time, a result of increased focus on this important agricultural resource as population densities increased (Schoeninger, 2009). We might also expect to see greater dependency on maize in mainland communities as opposed to island communities, whose ability to establish extensive agricultural fields may have been limited.

Previous archaeobotanical research at Cerro Mangote, Sitio Sierra, and Cerro Juan Díaz has found evidence of maize (*Zea mays*) from macro- and microbotanical remains recovered from stone tools in kitchen middens and other house features (Dickau, 2010; Piperno, 2011; Piperno and Holst, 1998). At Sitio Sierra, there is also phytolith and pollen evidence for squash (*Cucurbita* sp.), and macrobotanical evidence for squash, legumes (Fabaceae), palms, and unidentified fruit (Dickau 2010). Other archaeological sites in the Parita Bay area that are not included in this study have provided macro- and microbotanical evidence for manioc (*Manihot esculenta*), sweet potato (*Ipomoea batatas*), arrowroot (*Maranta arundinacea*), and chili pepper (*Capsicum* sp.), as well as fruits such as nance (*Byrsonima crassifolia*; Dickau, 2010; Piperno and Holst, 1998). Thus, while maize is identified at many sites in Panama on both watersheds, the dietary products of several C_3 plants would have also been available to the ancient inhabitants of Panama.

Nitrogen from bone collagen can provide information regarding the amount and type of meat in a diet. Individuals who consume more meat tend to have higher $\delta^{15}N$ values (Schoeninger and DeNiro, 1984; Schoeninger et al., 1983). For example, studies of the hair of individuals with a strict vegan diet in modern populations have found that $\delta^{15}N$ values tend to be ∼7‰ or lower, with omnivores generally lying between ∼8–10‰ (Ellegård et al., 2019; O'Connell and Hedges, 1999). Populations who consume high proportions of meat, including seafood, usually have collagen $\delta^{15}N$ values above 10‰ (Schoeninger et al., 1983). We would therefore expect to see a greater dependency on marine food from the island and coastal communities, as opposed to individuals from inland communities who should have lower nitrogen isotope values.

Zooarchaeological evidence has inferred that some communities consumed mostly small fish (<300 g body mass) obtained primarily from estuaries on the Pacific side of the isthmus. Pre-Columbian mass-capture techniques such as tidal traps were once widespread around Panama Bay and the Gulfs of San Miguel (Darién) and Chiriquí, including the Pearl Islands (Carvajal-Contreras et al., 2008; Cooke and Jiménez, 2004; Zohar and Cooke, 1997, 2019). Small fish of species that today are trapped in tidal barriers were brought to Cueva de Los Ladrones (18–25 km inland) as early as the Monagrillo Phase (5520–3200 cal BP; Cooke, 2001). Fish consumption could therefore explain elevated nitrogen signals, if found, in inhabitants of inland communities in the region.

Since the material that constitutes bone constantly replaces itself during life, bone $\delta^{13}C$ and $\delta^{15}N$ reveal the diet of an individual during the last few years of life. Enamel, however, is stable after completing mineralization early in life. Tooth enamel formation (i.e., amelogenesis) takes place at different times in different teeth (Hillson, 2005). In this study, we tested enamel $\delta^{13}C$ and $\delta^{18}O$ (hereafter $\delta^{13}C_{en}$ and $\delta^{18}O_{en}$) from primarily molars (choosing the second molar when available and never the third molar), which would have formed within the first ten years of life (AlQahtani et al., 2010). Since we focus on second molars, it is unlikely that these values include significant proportions of $\delta^{13}C_{en}$ and $\delta^{18}O_{en}$ from the mother's diet due to nursing (Wright and Schwarcz, 1998).

Enamel $\delta^{18}O$ values are mainly dependent on the $\delta^{18}O$ in drinking water and, to a lesser extent, food. Oxygen isotopes are variable across the landscape, and $\delta^{18}O$ in drinking water catchments is primarily determined by the amount of precipitation in an area (although it can be determined by other factors as well; see Pederzani and Britton, 2019). Environmental $\delta^{18}O$ values across Panama tend to be lower along the Pacific coast than the Atlantic coast (Lachniet et al., 2007). This is a common trend throughout Central America (Lachniet and Patterson, 2009; Laffoon et al., 2013). Thus, we would expect individuals born on the Atlantic side of Panama to have higher $\delta^{18}O_{en}$ values than those born on the Pacific side. Generally, carbonate rock $\delta^{18}O$ tends to be below −4‰ on the Pacific side of the southern isthmus and around −4‰ on the Atlantic side, although due to the lack of $\delta^{18}O$ studies in the lower isthmus area, there may be some degree of variation in these values.

Due to the number of factors that can influence $\delta^{18}O_{en}$ isotopes, interpretations of $\delta^{18}O_{en}$ data are best made in conjunction with $^{87}Sr/^{86}Sr$ data. Strontium isotope ratios vary in different rock types across the landscape. Volcanic rocks tend to have lower $^{87}Sr/^{86}Sr$ (<0.7060) than sedimentary rocks such as limestone (∼0.7070–0.7090), and older rocks tend to have the highest ^{87}Sr/^{86}Sr values (>0.7090) due to the longer length of radioactive decay from rubidium-87 (Bentley, 2006; Graustein, 1989). Strontium from the soil enters water and plants, and can eventually become incorporated in human and animal tissues through consumption of plants and other animals or through drinking water. In biological organisms, strontium can behave similarly to calcium, and can substitute for calcium in bone and tooth enamel (Pors Nielsen, 2004:585). The bioavailable ^{87}Sr/^{86}Sr that humans consume depends on whether there are homogeneous or heterogenous rock types in an area; that is, regions with a single rock type may have a limited range of ^{87}Sr/^{86}Sr values, so all humans and animals eating and drinking from the area will have the same ^{87}Sr/^{86}Sr value. Areas with heterogenous rock types will have mixed ^{87}Sr/^{86}Sr values, and so humans will have a combination of the ^{87}Sr/^{86}Sr values from rocks in that area (Bataille et al., 2020). Humans who regularly drink from or consume food from rivers that traverse different geological zones may have mixed ^{87}Sr/^{86}Sr, which may differ from the ^{87}Sr/^{86}Sr where they live. Furthermore, humans and other animals who live within a few kilometers from the coast may exhibit ^{87}Sr/^{86}Sr values that range closer to 0.70917, the modern marine ^{87}Sr/^{86}Sr value, than their expected geological values due to a sea spray effect (see for example Price and Gestsdóttir, 2006; Renson et al., 2019).

In this study, we used ^{87}Sr/^{86}Sr from archaeological animal bones and terrestrial snail shells to determine the local baselines for the different sites. We focused on small mammals and snails to minimize the chance that the animals were imported or hunted from a distant area. Future ^{87}Sr/^{86}Sr studies of human and animal mobility can build upon this baseline by testing a wider array of materials in each area, including soil, bedrock, plants, and water. We tested ^{87}Sr/^{86}Sr from human tooth enamel rather than bone, since bone is more prone to diagenetic alteration, in which case non-local individuals would appear more "local" due to the absorption of ^{87}Sr/^{86}Sr from the soil over time. In order to verify the preservation of the tooth enamel, we used trace element concentrations and compared them to known values of modern human teeth (Kamenov et al., 2018).

4. Background to the archaeological sites in this study

Of the seven sites included in this study, Cerro Mangote's location vis-à-vis the active marine shore and terrestrial habitats changed considerably through time. After the Preceramic residential area was abandoned four millennia ago, the site continued as a burial ground for ceramic-using people when coastal progradation had left the site nearer terrestrial biomes but still within a low-salinity estuary. Although Cerro Mangote is about 11 km from the coast today, excavations at the site and cores taken from the surrounding area suggest that the shoreline may have been within 1.5 km of the site around 7000 BP (Clary et al., 1984; Cooke and Ranere, 1999). The two humans used for analysis in this study, excavated by McGimsey (1956), date to approximately 2476–2293 cal BCE (Table 1). These individuals were not included in Norr's isotopic tests.

By the time Sitio Sierra was occupied at the end of the first century BCE, the Parita Bay coastline would have been about 2 km closer than its present location. Zooarchaeological analyses reveal that Sitio Sierra's inhabitants consumed many fish (30% freshwater; Cooke and Ranere, 1999), avifauna, and white-tailed deer. Two discrete cemeteries were excavated between 1971 and 1975. The earlier cemetery received interments between 50 BCE–400 CE and the later one from 950 to 1150 CE. The individuals tested from Sitio Sierra were previously tested in Norr's studies (1991, 1995).

Cerro Juan Díaz is situated on the north-eastern side of the Azuero Peninsula and on both banks of the La Villa River. It is the largest community included in this study, with an estimated maximum extent of 150 ha. Initial signs of human activity date to ca. 200 BCE and occupation was continuous until the time of Spanish conquest (Isaza-Aizpurúa, 2013; Isaza, 2019). Dwellings, refuse lenses, workshops for crafting animal bone and shell, and burials were found. Human burials were recovered in nearly every area of the site, amounting to well over 400 individuals that varied in terms of demographic characteristics, burial position and type, and degree of prior disturbance (Cooke et al., 1998; Díaz, 1999; Sánchez Herrera, 1995; Smith-Guzmán et al., In Review). The earliest graves between 1 and 700 CE contained the most burial goods, including numerous marine shells and, less frequently, goldwork and whole pottery vessels. Five of the humans tested in this study dated to 200–650 CE, and the sixth is from the fourteenth century (LS-3 Op.5 Ind.9). These individuals were chosen because they had radiocarbon dates and had been previously analyzed by Smith-Guzmán.

Pedro González and Jicarita are the two Pacific island sites in this

Table 1
Archaeological human specimens used in this study. Specimen ages with calibrated dates are from skeletons that have been radiocarbon dated and calibrated with IntCal20 with 2σ ranges.

Archaeological Site	Burial Number	Burial Chronological Age	Sex	Individual Age (years)	Element Sampled
Sitio Sierra	AG3 A-4	978–1151 cal CE	male	40–50	rib and third premolar enamel
Sitio Sierra	AG3 B-6	214–401 cal CE	female	35–45	femur and second molar enamel
Sitio Sierra	AG3 B-7	50 BCE – 400 CE	male	50+	femur
Sitio Sierra	AG3 B-10	50 BCE – 400 CE	male	adult	second molar enamel
Sitio Sierra	AG3 B-13	50 BCE – 400 CE	female?	40–55	femur and second molar enamel
Sitio Sierra	AG3 B-20	50 BCE – 400 CE	male?	35–50	femur and second molar enamel
Sitio Sierra	AG3 G-2	950–1150 CE	male	35–45	rib and second molar enamel
Sitio Sierra	AG3 G-4	950–1150 CE	female?	45–55	rib and fourth premolar enamel
Cerro Juan Díaz	LS-3 Op.3 T.2P.4 Cr.1	255–433 cal CE	indeterminate	5–6	tibia and first molar enamel
Cerro Juan Díaz	LS-3 Op.3 T.2P.4 Cr.2	365–553 cal CE	male	35–45	femur and second molar enamel
Cerro Juan Díaz	LS-3 Op.3 T.2P.5	406–565 cal CE	female?	15–17	femur and second molar enamel
Cerro Juan Díaz	LS-3 Op.3 T.2P.6	418–577 cal CE	male	25–30	femur and second molar enamel
Cerro Juan Díaz	LS-3 Op.5 I.9	1263–1395 cal CE	indeterminate	5–6	rib
Cerro Juan Díaz	LS-3 Op.3 T.94 I.36	436–648 cal CE	male?	40–55	femur and second molar enamel
Cerro Mangote	CO-40 Ent. 6A	2476–2293 cal BCE	female	13–18	mandible bone and second molar enamel
Cerro Mangote	CO-40 Ent. 6C	2500 BCE – 300 CE	indeterminate	7–8	mandible bone and first molar enamel
Cerro Brujo	CA-3 6H	1267–1388 cal CE	female	14–16	rib and second molar enamel
Sitio Drago	BT-IC-1 Ent. 1	1037–1172 cal CE	male	adult	rib and second molar enamel
Sitio Drago	BT-IC-1 Ent. 4	1051–1217 cal CE	indeterminate	adult	femur
Jicarita	JI-1 U-3–09 I.1a	668–874 cal CE	male	35–50	ulna and second molar enamel
Isla Pedro González, Playa Don Bernardo	PAPG L-20 K17 N16	4200–3800 BCE	indeterminate	adult	mandible bone and second molar enamel

study. The individual from Pedro González came from a dense shell midden located on Don Bernardo Beach, which is still undergoing analysis (Cooke et al., 2016; Martín et al., 2016; Pearson et al., 2020). The Don Bernardo Beach site (PG-L-19/20), excavated under the direction of Cooke and Juan Guillermo Martín, had an occupation history going back at least 6000 years (4220 cal BCE). The human mandible and tooth tested in this study are from the mid-Holocene occupation, but could not be associated with other human skeletal remains from the beach deposit since much of the human bone material was fragmentary and scattered in the midden. The Jicarita individual (JI-1 U-3–09 I.1a) was found during excavations conducted by Isaza during a survey of Coiba Island and its surrounding smaller islands (Isaza, 2019; Isaza et al., in review). The skeleton was one of two found in a flexed position. A dentin sample dated to c. 668–874 cal CE. A neighboring excavation unit was also dated to c. 660–890 CE and exposed three levels of shell bearing middens containing numerous fish, particularly black skipjack tuna (*Euthynnus lineatus*), bullet mackerel (*Auxis thazard*), and scad mackerel (*Decapterus macarellus*), suggesting the site had been a fishing village situated on the protected eastern coast of the island. The individual tested from Jicarita was an adult male between 35 and 50 years of age, showing evidence of extreme degenerative joint disease coupled with spondylolysis of the 5th lumbar vertebra, likely due to strenuous physical activity.

The two Caribbean sites in this study are Cerro Brujo and Sitio Drago, from the Bocas del Toro Province of Panama. Cerro Brujo is a hilltop community located on Aguacate Peninsula in Almirante Bay. It was excavated in 1970 by Olga Linares and Anthony Ranere (Linares de Sapir, 1971; Linares and Ranere, 1980). The site was occupied at least twice between 600 and 1100 CE. Only one complete human skeleton was found at the site, and radiocarbon dating indicated this individual was interred almost two centuries after Cerro Brujo's abandonment (1267–1388 cal CE). Further analysis of the skeleton by Smith-Guzmán determined that it was an adolescent female with a rare primary malignant bone tumor in her right humerus, which may have contributed to the cause of her death (Smith-Guzmán et al., 2018). Her chronological age matches with the nearby settlement of Sitio Drago, located on Colón Island.

Sitio Drago was a 15 ha coastal village excavated by Wake et al. (2004, 2012, 2013), primarily occupied from 700 to 1410 CE. Artifactual analysis reveals that the Sitio Drago inhabitants had engaged in long-distance trade with mainland communities, including importing ceramic wares from the Chiriquí and Coclé regions of west-central Panama and the Diquís area of eastern Costa Rica. The vast majority of stone artifacts at the site are made of imported raw materials, not naturally present on Colón Island. Of the four sets of human remains found at the site, only one included a cranium (Wake et al., 2012); thus, although two individuals are tested in this study for bone isotopes, only one (BT-IC-1 Ind.1) could be tested for strontium and oxygen.

5. Materials and methods

A total of 21 humans were tested in this study (Table 1; Supplementary File 1), including nine previously tested for $\delta^{13}C_{co}$ and $\delta^{15}N$ by Norr from Sitio Sierra and Cerro Brujo (1991, 1995); Supplementary File 2). All human remains come from well-dated contexts, and most had been directly radiocarbon dated previously. The skeletons are currently curated at the Smithsonian Tropical Research Institute (STRI) in Panama City, Panama; a permit to conduct the experiment and transport the bones to the United States for analysis was granted by the Panama Ministry of Culture (Res. N°167-18 DNPH). All skeletons were examined by bioarchaeologist Smith-Guzmán (Smith-Guzmán and Cooke, 2018, 2019; Smith-Guzmán et al., 2018). Multiple photographs of sampled bones were taken prior to analysis. Only fragmented and broken bones were selected, so as to avoid destroying portions of complete specimens. In cases where only the cranial elements were available, or if the cranial and postcranial matches were in question (due to disturbed contexts), we selected mandibular bone near the tooth to test. In these latter instances, only broken mandibles were selected, so as not to damage a complete mandible.

Collagen and apatite pretreatment was performed at the STRI archaeology labs in Panama City. About 0.5 g of bone was sampled from each specimen. Surface residues were removed from bones using dental picks and mild sonication with distilled-deionized water (DI-H_2O). Clean bone fragments were individually ground with ceramic mortars and pestles. Ground bone was passed through two sieves, one to collect the collagen fraction (0.25–0.5 mm) and the second for the apatite fraction (<0.25 mm). Procedures for the collagen and apatite pretreatment followed methods by Longin (1971) and Jørkov et al. (2007). Briefly, ground bone fractions were placed in sterile 15 ml centrifuge tubes, and 12 ml of either 0.1 M or 0.2 M hydrochloric acid (HCl) was added. The weaker HCl solution was used on the specimen from Pedro González, which is about 6000 years old, as well as the Cerro Mangote specimens, which are about 4000 years old. All specimens were left to react with the HCl for 24 h, then were centrifuged and decanted and refilled with new HCl every 24 h until the samples were fully demineralized (~5 days). Afterward, the samples were rinsed to neutral pH with DI-H_2O, and 12 ml of 0.125 M sodium hydroxide (NaOH) was added. The samples were allowed to sit for ~ 20 h, shaking occasionally, and afterward were rinsed to neutral pH a second time. Next, 10 ml of $1x10^{-3}$ M HCl was added to the collagen in the tube and each was transferred to a 20 ml glass scintillation vial, then placed in an oven while loosely capped for 4–5 h at 95 °C. Thereafter, 30–40 µl of 1.0 M HCl was added to each vial, and they were returned to the oven another 4–5 h. The samples were returned to the original centrifuge tubes, centrifuged, and the solution was returned to the glass vials, with the precipitate remaining in the centrifuge tubes. The solutions in the glass vials were evaporated to ~ 2 ml at 65 °C in the oven, then placed in a freezer. Once frozen, they were placed in a freeze drier for three days, then removed and weighed to obtain the collagen yield. Specimens were brought to the Light Stable Isotope Mass Spectrometry Laboratory at the Department of Geological Sciences, University of Florida, and measured by lab director Jason Curtis on a Carlo Erba elemental analyzer connected to a Thermo Delta V isotope ratio mass spectrometer. The $\delta^{13}C_{co}$ values were compared against the standard Vienna Pee Dee Belemnite (PDB), and the $\delta^{15}N$ values were compared with atmospheric nitrogen (AIR). Precision for both $\delta^{13}C_{co}$ and $\delta^{15}N$ was 0.1‰.

Bone apatite samples were placed in sterile 15 ml centrifuge tubes. About 12 ml of 2.5% sodium hypochlorite (NaOCl) was added to each, and they were allowed to sit, with occasional agitation, for 16 h. Afterward all samples were rinsed to neutral pH with DI-H_2O. Following this, ~12 ml of 0.2 M acetic acid ($C_2H_4O_2$) was added to each sample, shaken, and allowed to sit for another 16 h. The samples were rinsed to neutral pH a second time. Samples were centrifuged one last time and excess DI-H_2O was removed. The samples were then placed in a freezer, and once frozen, placed in a freeze drier for three days. Dried samples were weighed to obtain the carbonate yield, and the samples were then brought to the Light Stable Isotope Mass Spectrometry Laboratory at the University of Florida for testing on a Kiel III carbonate prep device connected to a Finnegan MAT 252 isotope ratio mass spectrometer.

A total of 18 human teeth were tested for $\delta^{13}C_{en}$, $\delta^{18}O_{en}$, $^{87}Sr/^{86}Sr$, and trace elements. In each case, a ~0.05 g sample of enamel was removed from each tooth with a Dedeco carbide blade, and surface residues and dentin were removed with a diamond-tipped Brasseler NSK Z500 drill. Although we avoided teeth with dental calculus, in the few cases where calculus was present, we preserved the residue for future analysis. About half the sample (~0.02–0.025 g) was ground with an agate mortar and pestle, weighed, and placed in a sterile microcentrifuge tube for apatite pretreatment, similar to the preceding bone apatite steps. About 1 ml of 2.5% NaOCl was added to each sample, vortexed, and the samples were allowed to sit for ~16 h before being rinsed to neutral pH with DI-H_2O. About 1 ml of 0.2 M $C_2H_4O_2$ was then added to each sample, vortexed, and allowed to sit another ~16 h before being rinsed again to neutral pH. Afterward the excess water was removed, and samples were frozen and then placed in a freeze drier. Carbonate $\delta^{13}C_{en}$ and $\delta^{18}O_{en}$ was measured using a Kiel III carbonate prep device connected to a Finnegan MAT 252 isotope ratio mass spectrometer in the Light Stable Isotope Mass Spectrometry Laboratory at the University of Florida under direction of Curtis, and samples were measured against the PDB standard. Precision using the NBS-19 standard was ~0.01‰ for $\delta^{13}C_{en}$ and ~0.03‰ for $\delta^{18}O_{en}$.

Strontium isotope analysis was performed on both human enamel and animal bone, teeth, and terrestrial snail shells. The remaining human tooth enamel (~0.03 g) from each sample was used for this procedure, and in the case of animals, a similar quantity of clean tooth enamel, ground bone, or ground shell was used. All steps of the strontium isotope analysis were performed at the class 100 clean lab of the Department of Geological Sciences, University of Florida. Samples were placed in cleaned Teflon vials with 2 ml of 8 N nitric acid (HNO_3, Optima); small fractions of each solution were removed in order to perform the elemental concentration analyses, following methods described by Kamenov et al. (2018). The remaining solution was put on a hot plate at 100 °C, uncapped, and allowed to evaporate. Strontium was separated using ion chromatography, using strontium-selective crown ether resin (Sr-spec; Eichrom Technologies) with multiple washes of 3.5 M HNO_3 (following Pin and Bassin, 1992). Sample ratios were measured on a Nu-Plasma multiple-collector inductively coupled plasma mass spectrometer (MC-ICP-MS). The NBS 987 average was 0.710240 ($2\sigma = 0.00005$). The trace elements from human and animal teeth were analyzed on an Element2 HR-ICP-MS and are reported in Supplementary File 3.

6. Results and discussion

The majority of samples were well-preserved and provided data for $\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$, and/or $^{87}Sr/^{86}Sr$ (Table 2). Of the 20 collagen samples, only two had low carbon and nitrogen yields (C:N outside the acceptable range of 2.9–3.6): Cerro Juan Díaz sample LS-3 Op.3 T.2 P.6 and the Pedro González sample, PAPG L-20 K17 N16. The bones of the former had a darker surface coloration than the other individuals in the same context, which may indicate pre-depositional processing of the body, such as the smoke embalming described by Spanish chroniclers (Espinosa, 1994:63–64; Martyr D'Anghera, 1912:219-220). The individual from Pedro González dates to about 6000 years ago, which is the likely explanation for its poor collagen preservation. Although all human teeth experienced a low level of diagenesis based on their trace element compositions (compared with Kamenov et al., 2018), the Sr concentration in teeth was within an acceptable range (~100–700 ppm) and not enough to alter the $^{87}Sr/^{86}Sr$ values (Supplementary File 3).

6.1. *Dietary isotopes: $\delta^{13}C$, $\delta^{15}N$, and apatite-collagen spacing*

The overall results of the $\delta^{13}C$ and $\delta^{15}N$ analysis on bone collagen (Fig. 3) show a pattern that suggests that, with the exception of Cerro Juan Díaz, most individuals within a site were more similar to one another than to other sites. This pattern was discovered by Norr in her original analysis of $\delta^{13}C_{co}$ and $\delta^{15}N$ (1991, 1995; Supplementary File 2). In fact, retested samples that Norr had used for her dissertation reveal statistically similar $\delta^{13}C_{co}$ results ($t(8) = 0.52$, $p = 0.61$), with $\delta^{15}N$ appearing significantly more enriched ($t(8) = 3.31$, $p < 0.01$). This shift appears to have been the result of the analytical standard, thiourea (CH_4N_2S), that Norr had used for the mass spectrometer analysis for her studies and which might not have been correctly calibrated. Norr's samples are an average of 0.82‰ lower than the rerun samples using currently available standards (USGS40 and USGS41). Likewise, reanalysis of Norr's thiourea standard (stored in the Light Stable Isotope Lab at the University of Florida) in July 2020 indicate that it was offset 0.8‰ from the values Norr reported. Concurrent reanalysis of $\delta^{13}C$ of Norr's thiourea in July 2020 gave the same result as reported by Norr. It can be concluded that Norr's $\delta^{13}C_{co}$ values are directly comparable to the modern dataset, with the $\delta^{15}N$ values shifted ~ 0.8‰ lower than those of the current dataset.

The results show that most of the individuals from Cerro Mangote had the lowest $\delta^{13}C_{co}$ (average = -13.8‰, $\sigma = 0.5$) and $\delta^{15}N$ values (average with 0.8‰ adjustment on Norr data = 8.1‰, $\sigma = 0.4$) in the study, despite the site's close proximity to Sitio Sierra. The skeletons tested from Cerro Mangote are, however, older than those from Sitio Sierra by at least a millennium. They are also earlier than the other individuals tested in the study, with the exception of the Pedro González individual. It would appear that individuals in the Cerro Mangote community consumed far less meat, including little to no marine food, when compared with the other individuals in the study.

The Sitio Sierra humans, by comparison, appear to have consumed more meat and, generally, more maize. Samples rerun in the new study match Norr's original dataset (Supplementary File 2); differences in $\delta^{13}C_{co}$ and $\delta^{15}N$ values can be explained by the offset of Norr's original thiourea standard, and the fact that different bones from the same individuals were tested in the two studies, which could result in slightly

Table 2
Results of the carbon, nitrogen, oxygen, and strontium isotope analyses. $\delta^{18}O$ data from bone apatite is included in this chart, but not used but not used in the study due to potential diagenesis. Italics denote C:N values outside the acceptable range of 2.9–3.6, and therefore unreliably low collagen yields.

Archaeological Site	Burial Number	%N	%C	C:N	$\delta^{15}N_{co}$	$\delta^{13}C_{co}$	$\delta^{13}C_{en}$	$\delta^{13}C_{ap}$	$\delta^{18}O_{en}$	$\delta^{18}O_{ap}$	$^{87}Sr/^{86}Sr$
Sitio Sierra	AG3 A-4	13.14	36.36	3.23	10.44	−13.31	−6.76	−7.88	−6.19	−7.16	0.70520
Sitio Sierra	AG3 B-6	14.34	39.93	3.25	9.39	−10.13	−4.86	−5.76	−5.56	−7.14	0.70617
Sitio Sierra	AG3 B-7	14.55	40.51	3.25	9.78	−9.32	–	−5.58	–	−7.19	–
Sitio Sierra	AG3 B-10	–	–	–	–	–	−5.19	–	−6.29	–	0.70662
Sitio Sierra	AG3 B-13	13.99	38.99	3.25	10.20	−10.17	−7.22	−5.74	−5.91	−6.98	0.70645
Sitio Sierra	AG3 B-20	14.29	39.84	3.25	9.24	−8.98	−3.26	−4.97	−4.25	−6.48	0.70632
Sitio Sierra	AG3 G-2	14.05	38.75	3.22	9.48	−11.73	−5.86	−6.63	−5.08	−7.25	0.70524
Sitio Sierra	AG3 G-4	12.70	34.79	3.20	9.81	−13.56	−4.92	−7.65	−5.92	−7.10	0.70592
Cerro Juan Díaz	LS-3 Op.3 T.2 P.4 Cr.1	13.39	37.22	3.24	12.88	−7.89	−2.85	−5.78	−6.48	−6.75	0.70680
Cerro Juan Díaz	LS-3 Op.3 T.2 P.4 Cr.2	13.99	38.62	3.22	12.08	−10.17	−4.09	−6.46	−6.51	−7.08	0.70743
Cerro Juan Díaz	LS-3 Op.3 T.2 P.5	13.58	37.70	3.24	11.51	−9.71	−4.40	−6.29	−7.09	−7.31	0.70740
Cerro Juan Díaz	LS-3 Op.3 T.2 P.6	*4.15*	*16.89*	*4.75*	*11.18*	*−13.01*	−5.40	−6.27	−5.95	−7.15	0.70750
Cerro Juan Díaz	LS-3 Op.5 I.9	14.23	39.42	3.23	8.83	−14.38	–	−9.38	–	−7.29	–
Cerro Juan Díaz	LS-3 Op.3 T.94 I.36	14.90	41.15	3.22	10.70	−9.59	−4.02	−7.42	−6.65	−7.18	0.70792
Cerro Mangote	CO-40 Ent. 6A	11.39	34.33	3.52	8.11	−14.32	−7.56	−3.36	−6.19	−7.40	0.70623
Cerro Mangote	CO-40 Ent. 6C	7.40	22.82	3.60	7.66	−13.56	−7.37	−3.09	−6.05	−7.87	0.70698
Cerro Brujo	CA-3 6H	14.51	40.76	3.28	8.84	−12.99	−7.71	−10.43	−3.68	−4.16	0.70517
Sitio Drago	BT-IC-1 Ent. 1	14.27	39.68	3.24	10.00	−9.47	−5.02	−7.64	−4.77	−4.33	0.70877
Sitio Drago	BT-IC-1 Ent. 4	14.21	39.43	3.24	10.24	−9.20	–	−8.49	–	−3.90	–
Jicarita	JI-1 U-3–09 I.1a	14.21	39.49	3.24	12.81	−10.52	−6.40	−10.42	−5.93	−5.75	0.70795
Isla Pedro González	PAPG L-20 K17 N16	*0.27*	*1.14*	*4.93*	*2.99*	*−25.48*	−9.11	−11.67	−5.71	−7.48	0.70785

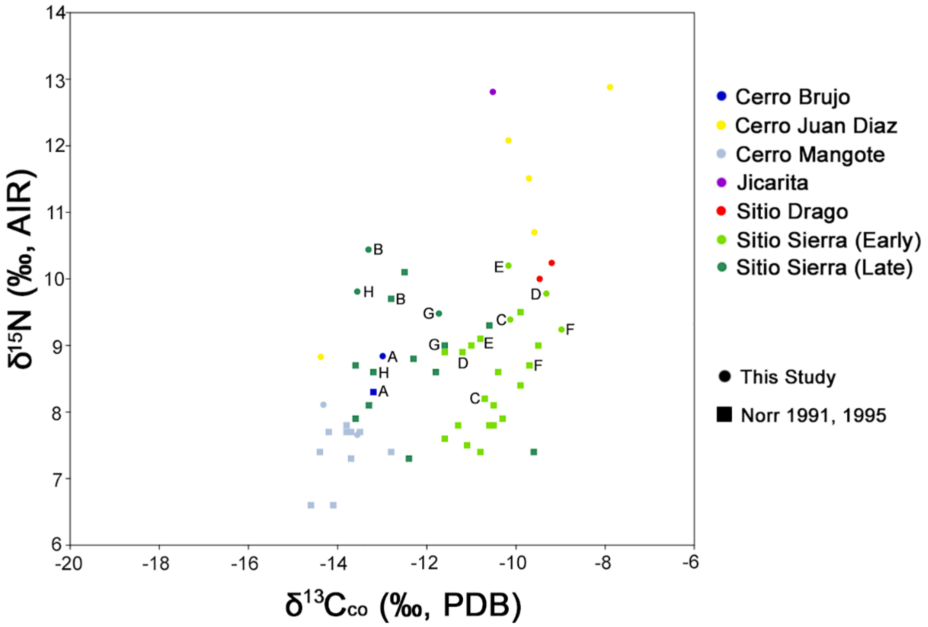

Fig. 3. δ^{13}C and δ^{15}N for archaeological human collagen samples from Panama. Letters indicate duplicate individuals tested by both Norr (1991) and Norr (1995) and retested in this study from the sites Cerro Brujo and Sitio Sierra. Nitrogen isotope values have not been adjusted in Norr's dataset.

different isotope values based on different rates of collagen development and remodeling in different bones. Individuals from Sitio Sierra's early occupation have significantly different $\delta^{13}C_{co}$ values than the later population, shifted about 1-3‰ greater, although $\delta^{15}N$ values are within the same range. This means that the early occupation may have consumed more maize, although the apatite-collagen spacing results, explained below, indicate it may in fact be due to marine food in the diet in addition to C_4 plants.

The Cerro Juan Díaz individuals exhibited the greatest dietary variation (average $\delta^{13}C_{co} = -10.3‰$, $\sigma = 2.4$; average $\delta^{15}N = 11.2‰$, $\sigma = 1.5$). Of the five individuals with preserved collagen, the four from the earlier phase of the site's history (200–650 CE) had the highest $\delta^{13}C_{co}$ and $\delta^{15}N$ values ($\delta^{13}C_{co} > -11‰$, $\delta^{15}N > 10‰$). The individual with the lowest values was an outlier ($\delta^{13}C_{co} = -14.4‰$, $\delta^{15}N = 8.8‰$), who had previously been radiocarbon dated to 1263–1395 cal CE. Notably, this child had been buried in a different area of the site (Op. 5) than the other individuals (Op. 3). The earlier individuals date to the period when Cerro Juan Díaz had been heavily involved in local and long-distance exchange, including importing a wide variety of marine fish and shellfish along the La Villa River (Cooke and Jiménez, 2004; Mayo Torné and Cooke, 2005; Martín and Sánchez Herrera, 2007). Some of the shells were used for food, but many, including the thorny oyster (*Spondylus*) shells, were used for crafting ornaments. There is evidence that some individuals from Cerro Juan Díaz went to the ocean to dive for these shells, based on apparent external auditory exostoses exhibited by four individuals from the site (Smith-Guzmán and Cooke, 2018), all dating to this same early period. The unusually low carbon and nitrogen isotope values from the single individual from the fourteenth century may be an indication that these marine excursions were discontinued by this point, and that dependency on maize agriculture had decreased. Future isotope research on a greater range of individuals from this site may provide more data to explain these trends, and whether these changes were due more to social and subsistence changes over time or to cultural or biological factors (e.g., status, age, and sex).

Individuals from the coastal and island sites showed a wide variety of dietary signals, which is somewhat surprising considering they would have all been expected to depend on marine resources. However, this does not appear to have been the case. The Pedro González sample did not produce enough collagen for the test, likely due to its age. The Jicarita sample had one of the highest $\delta^{15}N$ values in the study (12.8‰), indicating that this individual, an adult male, consumed a diet of mainly marine fish and likely some maize based on his elevated $\delta^{13}C_{co}$ value (-10.5‰). Faunal data from the Jicarita excavations near where this individual was located recovered dense middens of fish and shellfish, which were likely the diet for this individual and others living at this fishing community (Isaza, 2019).

The two Sitio Drago individuals had similar diets, consuming some marine food but apparently a significant amount of maize based on their elevated $\delta^{13}C_{co}$ values ($\delta^{13}C_{co} = -9.5‰$ and $-9.2‰$; $\delta^{15}N = 10.0‰$ and 10.2‰). The Cerro Brujo individual, however, had much lower carbon and nitrogen values ($\delta^{13}C_{co} = -13.0‰$; $\delta^{15}N = 8.8‰$), despite Cerro Brujo being located within 500 m from the shore. The $^{87}Sr/^{86}Sr$ data for the Cerro Brujo individual, discussed below, provides an explanation for this dietary discrepancy.

The results of the apatite-collagen spacing (Fig. 4) provide evidence concerning how much each individual's dietary $\delta^{13}C$ was affected by terrestrial meat and C_3 plant consumption, C_4 plant consumption, and marine food, the latter of which has been known to elevate $\delta^{13}C$ values (Chisholm et al., 1982; Schoeninger et al., 1983). Based on previous experiments using laboratory rodents consuming different quantities of carbohydrates and proteins from C_3 and C_4 sources (Ambrose and Norr, 1993; Tieszen and Fragre, 1993), studies have found that individuals consuming a primarily monoisotopic diet (strictly C_3 or C_4 foods) can be distinguished from those eating mixed C_3 proteins and C_4 carbohydrates (terrestrial meat and maize) and individuals eating mixed C_3 carbohydrates and C_4 proteins (C_3 plants and seafood, with a possible C_4 plant component). We would therefore expect individuals living near the coast to have $\Delta^{13}C_{ap\text{-}co}$ values that are indicative of mixed C_3 carbohydrates/C_4 proteins, whereas individuals living far from the coast to have either monoisotopic or mixed C_3 protein/C_4 carbohydrate diets.

Recent isotope investigations of fauna from archaeological sites in the Panama Bay area, including those in the present study, found that deer had generally low $\delta^{13}C_{co}$ values (-20.9‰, $\sigma = 2.3$; Sugiyama et al. 2020). These animals perhaps contributed to the terrestrial C_3 signature in human diets. Waterfowl and other birds (excluding parrots) had higher $\delta^{13}C_{co}$ values (-13.1‰, $\sigma = 3.7$ and $-11.9‰$, $\sigma = 4.4$, respectively), indicating that consumption of birds in this area may increase the $\delta^{13}C$ values of humans. In particular, protein from birds with higher

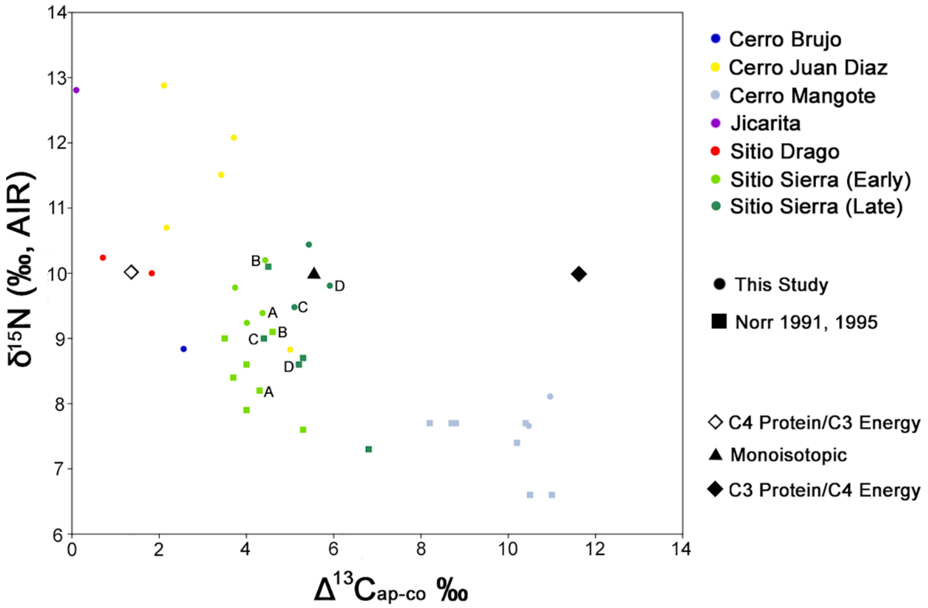

Fig. 4. $\Delta^{13}C_{ap\text{-}co}$ and $\delta^{15}N$ for archaeological human bone samples from Panama. Letters indicate duplicate individuals from Sitio Sierra tested by both Norr (1995) and this study. Dietary estimates for C_3 and C_4 energy/protein sources from Ambrose and Norr (1993), following Norr (1995). Nitrogen isotope values have not been adjusted in Norr's dataset.

$\delta^{13}C_{co}$ values may resemble C_4 protein when comparing human apatite and collagen values through $\Delta^{13}C_{ap\text{-}co}$ (see Ambrose et al., 1997 for a similar Pacific island example).

All of the human individuals from Cerro Mangote appear to have consumed more C_3 proteins and C_4 carbohydrates compared to the other humans in this study, based on their elevated $\Delta^{13}C_{ap\text{-}co}$ values (~5.5–11.5‰). This indicates that these individuals were consuming primarily terrestrial meat and maize, although they likely consumed some amount of C_3 plant foodstuffs as well (tubers, fruit, squash, etc). In contrast, the isotopic values of the individuals from Sitio Sierra's early and late occupations contain more C_4 protein and C_3 carbohydrates ($\Delta^{13}C_{ap\text{-}co}$ = 3.5–6.8‰). Both early and late occupations overlap, although individuals from the later occupation tend to have slightly higher $\Delta^{13}C_{ap\text{-}co}$ values. Norr (1995) found this result as well in her dataset, and suggested it meant a mixed diet with a reliance on maize. Sitio Sierra's early occupation is shifted slightly more toward the direction of C_3 carbohydrates/C_4 proteins, indicating they likely consumed some amount of marine food. Interestingly, of these early individuals, AG3 B-7 has one of the lowest $\Delta^{13}C_{ap\text{-}co}$ values (3.7‰). This older adult male was found to have external auditory exostosis in the right ear, resulting from cold-water diving (Smith-Guzmán and Cooke, 2019), and was the only individual found from the site with this condition. This individual may have spent more time near the ocean than others in the community, perhaps diving for *Spondylus* shells and other mollusks for shell crafting, and thus consumed more marine food.

The three individuals from the Bocas del Toro Province lean further toward the range of C_3 carbohydrates/C_4 proteins, particularly the two individuals from Sitio Drago. These individuals also have higher $\delta^{15}N$ in their diets (10.0‰ and 10.2‰), and so their low $\Delta^{13}C_{ap\text{-}co}$ values (<2‰) are likely due to seafood that exhibits a C_4 signature (Ambrose et al., 1997; Harrison and Katzenberg, 2003). The source of this C_4 signature could be identified with a closer examination of the marine faunal species found at the site (e.g., Wake et al., 2013), and an assessment of the isotope compositions of these taxa, since not all marine food elevates the $\delta^{13}C$ in consumers to the same extent. The individual from Cerro Brujo has a higher $\Delta^{13}C_{ap\text{-}co}$ value, indicating she may have consumed some seafood, but not has much as the individuals from Sitio Drago. This is reaffirmed by the Cerro Brujo individual's lower $\delta^{15}N$ value (8.8‰).

The four individuals from Cerro Juan Díaz's early phase and the single individual from Jicarita have diets shifted toward the C_3 carbohydrates/C_4 proteins range. The individuals from Cerro Juan Díaz lie between those from Sitio Drago and Sitio Sierra; based on their elevated $\delta^{15}N$ values, they regularly consumed seafood, and likely maize as well. The fifth individual and latest individual in the study (LS-3 Op.5 I.9) had a higher $\Delta^{13}C_{ap\text{-}co}$ value of 5.0‰, and likely did not consume any marine food. As was mentioned, this individual postdates the others by almost 1000 years, and is an indication that subsistence practices may have significantly changed at Cerro Juan Díaz over the centuries. The individual from Jicarita has a $\Delta^{13}C_{ap\text{-}co}$ value of 0.1‰, the lowest in the study. This is likely due to this individual's primarily marine diet. Part of the C_4 component in their diet likely included maize and was not exclusively due to seafood, and ground stone tools such as *manos* and *metates* found near the location of the burial support this conclusion.

6.2. *Mobility isotopes: $^{87}Sr/^{86}Sr$ and $\delta^{18}O$*

The results of the $^{87}Sr/^{86}Sr$ and $\delta^{18}O_{en}$ data (Table 2) reveal variable degrees of mobility among individuals across Panama, which is best understood on a site-by-site basis. The results of the faunal $^{87}Sr/^{86}Sr$ data (Table 3; Fig. 5) reveal values that closely align with what would be expected for each location, based on the local geology of each site. Fauna from inland sites located near volcanic terrain, including Ladrones Cave, the Aguadulce Rockshelter, and Sitio Sierra, have low $^{87}Sr/^{86}Sr$ values (0.70427–0.70592). Since Cerro Mangote is located near Sitio Sierra and the Aguadulce Rockshelter, it would be expected to have a similar $^{87}Sr/^{86}Sr$ value to these sites. These values resemble a previous $^{87}Sr/^{86}Sr$ water sample reported from the Santa María River (0.70391; Harmon et al., 2016). The agoutis (*Dasyprocta punctata*) tested from Pedro González Island also had low $^{87}Sr/^{86}Sr$ (0.70559 and 0.70607), likely due to the volcanic terrain on that island. It should be noted that these rodents were uncovered from the archaeological midden near the modern beach, but it is likely that they were hunted from the interior of the island based on their $^{87}Sr/^{86}Sr$, and did not live in close enough proximity to the ocean to have experienced a strong sea spray effect on their strontium isotope values. Furthermore, the sea level around Pedro González Island was lower by ~1.5–3 m when the midden was created, meaning that it was likely originally located further from the coast (Redwood, 2020). Sampling bedrock, soil, and vegetation across the

Table 3
Archaeological fauna specimens used in this study for developing a preliminary $^{87}Sr/^{86}Sr$ baseline.

Archaeological Site	Specimen Number	Common Name	Scientific Name	Tested Elements	$^{87}Sr/^{86}Sr$
Abrigo de Aguadulce	AG13-522b	gray fox	*Urocyon cinereoargenteus*	bone of mandible (right, central area)	0.705589
Cerro Juan Díaz	CC94; Op 31–95; 65S17E	common opossum	*Didelphis marsupialis*	innominate (left ilium)	0.707029
Cerro Juan Díaz	14–1	lowland paca	*Cuniculus paca*	mandibular left third molar (M3) enamel	0.707122
Cueva de los Ladrones	CL-90-L	Central American agouti	*Dasyprocta punctata*	incisor enamel	0.704268
Cueva de los Vampiros	AG-145–162	rat (cane mouse?)	Rodentia (*Zygodontomys* sp.?)	femur (right)	0.708954
Jicarita	J1-1; NWE4, 30–40 cm	cane mouse	*Zygodontomys* sp.	femur (right)	0.708799
Jicarita	J1-1; E2NE, 25–30 cm	hispid cotton rat	*Sigmodon hispidus*	femur (right)	0.708701
Panamá Viejo	Pma-Viejo CC. B3, N. 9, B.11	common opossum	*Didelphis marsupialis*	bone of mandible (right, central area)	0.708475
Isla Pedro González, Playa Don Bernardo	Corte I, J17N28E7, 10–1982	Central American agouti	*Dasyprocta punctata*	mandibular (right) molar enamel	0.706071
Isla Pedro González, Playa Don Bernardo	PAPGL19-20, C'17 Corte 2, N17-E5	Central American agouti	*Dasyprocta punctata*	mandibular (right) molar enamel	0.705591
Sitio Sierra	AG3-A-1–1	lowland paca	*Cuniculus paca*	tibia (left, central diaphysis)	0.705922
Sitio Sierra	181 A/1–1	lowland paca	*Cuniculus paca*	thoracic vertebra	0.705475
Zapotal	PR32-11–6	lowland paca	*Cuniculus paca*	bone of mandible (left, central diastema area)	0.707219
Sitio Drago	Drago Snail U1	terrestrial snail	Gastropoda, terrestrial	shell	0.708779
Sitio Drago	Drago Snail U22	terrestrial snail	Gastropoda, terrestrial	shell	0.708852
Sitio Drago	Drago Snail U60	terrestrial snail	Gastropoda, terrestrial	shell	0.708901

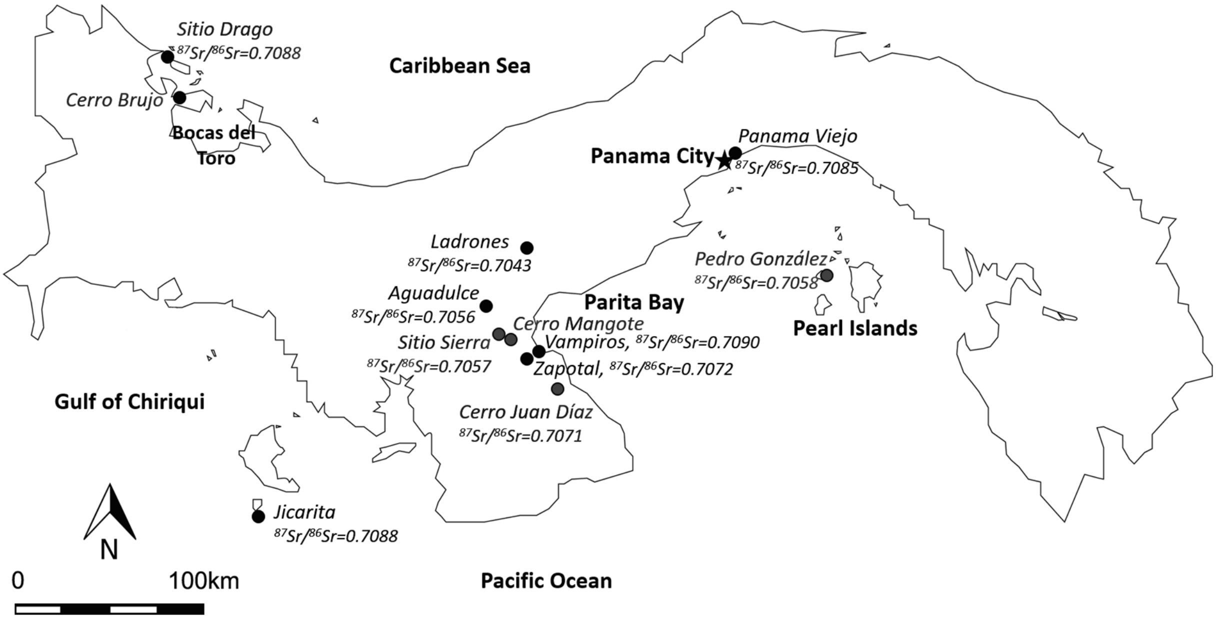

Fig. 5. Map of $^{87}Sr/^{86}Sr$ derived from archaeological fauna for various regions of Panama.

island may provide a more accurate assessment of its bioavailable $^{87}Sr/^{86}Sr$.

Two sites located in areas of mixed sedimentary/volcanic rock in the eastern Azuero, Cerro Juan Díaz and Zapotal, had $^{87}Sr/^{86}Sr$ that was higher than volcanic terrain but lower than would be expected from coastal values (0.70703–0.70722), indicating that movement to the interior or coast from these locations might be observable in human enamel $^{87}Sr/^{86}Sr$. A previous $^{87}Sr/^{86}Sr$ value reported from a water sample taken from the La Villa River, near Cerro Juan Díaz's location, was reported to be 0.70462 (Harmon et al., 2016). This value indicates the river water may have lower $^{87}Sr/^{86}Sr$ values from the weathering of silicate rock in the region. The coastal sites, including Jicarita, Sitio Drago, Panama Viejo, and Vampiros Cave, all had elevated $^{87}Sr/^{86}Sr$ that would be expected from coastal areas (0.70848–0.70895). Since Cerro Brujo is located <1 km from the coast, it would be expected that humans or animals from that site would have $^{87}Sr/^{86}Sr$ values in this range.

The individuals from the sites of Sitio Sierra and Cerro Mangote, who would be expected to have $^{87}Sr/^{86}Sr$ around the range of ~0.70548–0.70592, vary about this local range by 0.70520–0.70698 (Fig. 6). It is unclear why this may be, although individuals from the earlier occupation at Sitio Sierra, and the two Cerro Mangote humans who are four millennia old, are higher than the expected $^{87}Sr/^{86}Sr$ value, whereas the late Sitio Sierra occupation is below the baseline average. One possibility is that some of these individuals may not have been born in this area, despite being buried at these sites. In the case of Cerro Mangote, it has been proposed that early occupation at the site was seasonal or temporary (Norr, 1995). A second possibility may be due to environmental changes that occurred along the Santa María River where these two sites are located: about 7000 years ago, the coastline of the Parita Bay had extended further inland, possibly to within 1.5 km of Cerro Mangote, where evidence for ancient mangrove habitats has been

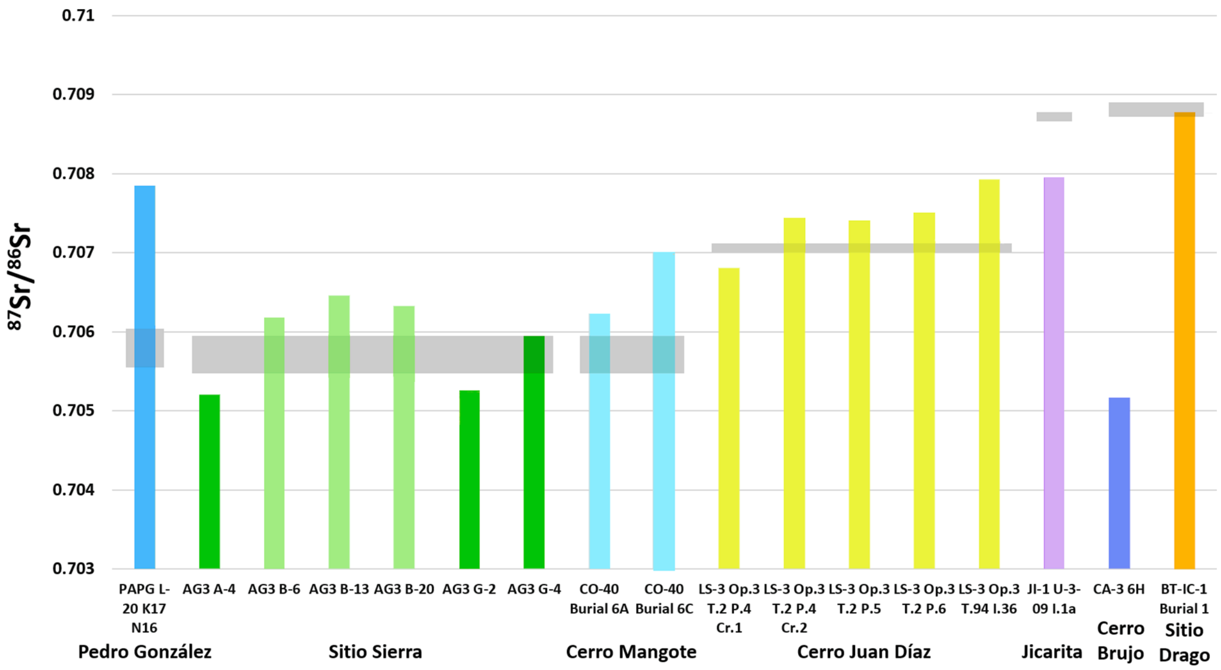

Fig. 6. Comparison of archaeological human tooth enamel ^{87}Sr/^{86}Sr with ^{87}Sr/^{86}Sr ranges from fauna at each site, marked as shaded boxes. Fauna were not tested from Cerro Mangote or Cerro Brujo, so their shaded regions represent expected bioavailable ^{87}Sr/^{86}Sr based on data from nearby locations. Sitio Sierra's two occupations are distinguished by light (early) and dark (late) green.

identified (Clary et al., 1984; Cooke and Ranere, 1999). This may explain the elevated ^{87}Sr/^{86}Sr in the earlier populations. A third possibility could be that the early Sitio Sierra occupation had been regularly consuming greater quantities of marine food than the later population, and this may have slightly elevated their ^{87}Sr/^{86}Sr. The faunal evidence from the site, combined with the data from the $\Delta^{13}C_{ap\text{-}co}$ and $\delta^{15}N$ results, suggest this may have been the case.

Despite the wide variety of $\delta^{13}C$ and $\delta^{15}N$ values at Cerro Juan Díaz over time, most of the individuals were likely born in or around the site. With the exception of individual LS-3 Op.3 T.94 I.36, there is a small amount of variation from the local baseline (+/- 0.00035); due to the size of the site and the fact that it was used as an intentional burial ground for people living in the area, this variation is to be expected. Individual LS-3 Op.3 T.94 I.36, a probable male between 40 and 55 years of age, has a more elevated ^{87}Sr/^{86}Sr value than would be expected (0.70792), especially considering that the river water has lower ^{87}Sr/^{86}Sr than the local fauna (Harmon et al., 2016), and drinking regularly from it would lower one's strontium isotope value. This individual was the central occupant of a tomb containing shell, ground stone, and ceramic offerings (Cooke et al., 1998; Smith-Guzmán et al., in review). None of the individuals from this study show Sr values typical for seawater (0.70917), indicating that they were not born near the coast, despite Cerro Juan Díaz's close trade ties with that area. A possible reason some of the individuals from this site had elevated ^{87}Sr/^{86}Sr values may be due to the fact that they consumed a large quantity of seafood early in life during tooth enamel formation.

The two individuals from the Pacific islands of Pedro González and Jicarita did not match their expected baselines. The Pedro González individual has an elevated ^{87}Sr/^{86}Sr value of 0.70785, which is much higher than volcanic rock, but lower than a marine signature. A possible explanation is that this individual was consuming food and water from both the marine environment and from the interior of the island during enamel formation, and so they had a mixed ^{87}Sr/^{86}Sr value. Jicarita, however, is only ~1 km in diameter, and is unlikely to have been the birthplace for the individual recovered at JI-1, who had a much lower value (0.70795) than the local ^{87}Sr/^{86}Sr. The nearest islands of Jicarón and Coiba, as well as the western side of the Azuero Peninsula, have variable rock types ranging from sedimentary to volcanic, and it is possible that this person was born in one of these areas and consumed a mix of terrestrial and marine food during enamel formation. It is therefore unclear where exactly this person was born, except that it was likely not Jicarita, nor immediately near the coast.

The most variation was found when comparing the individuals from Sitio Drago and Cerro Brujo, who, theoretically, should both have had marine ^{87}Sr/^{86}Sr values. The individual from Sitio Drago had a ^{87}Sr/^{86}Sr value that exactly matched the local ^{87}Sr/^{86}Sr value (0.70877), which would be expected from someone born near the coast. This individual was likely born at Sitio Drago or in a neighboring coastal settlement. The individual from Cerro Brujo, however, diverged more than any other individual in this study from their expected ^{87}Sr/^{86}Sr value. As noted above, this adolescent female was recovered from an intrusive burial that was found to post-date the midden at the site by almost two centuries, making her contemporaneous with the habitation at Sitio Drago. However, it appears she did not come from Sitio Drago, but rather an inland community with a volcanic ^{87}Sr/^{86}Sr value (0.70517).

The Cerro Brujo individual is particularly unique due to the presence of a primary malignant bone tumor on her right humerus (Smith-Guzmán et al., 2018). This is one of the earliest known cases of cancer in the lower circum-Caribbean region. The tumor would have been noticeable during life, and the fact that the young individual survived as long as she did infers that she had been cared for during life. Her $\delta^{13}C_{co}$ and $\delta^{15}N$ values show that she had a low nitrogen diet comparable to someone who did not regularly consume marine food, meaning she probably lived most of her life in an inland location. Since she postdates Cerro Brujo's occupation by two centuries and was the only complete burial found at the site, conspicuously located at the top of the hill in a midden from the site's previous occupants, it is possible she had been brought to Cerro Brujo after her death. If this was the case, it suggests that inland inhabitants living near the Bocas del Toro area may have held this ancient site as a sacred location in their social memory, and may have even had ancestral ties to the coast. It is also possible that interments near the coast itself were a practice performed at this time by societies living in the area.

When comparing the $\delta^{18}O_{en}$ data in relation with the ^{87}Sr/^{86}Sr results, we find that the oxygen isotope values generally conform to previous environmental $\delta^{18}O$ data (Lachniet et al., 2007). Individuals living on the Pacific side of Panama's central mountain range have $\delta^{18}O$ values below −5‰. This matches the $\delta^{18}O$ of environmental data from both Panama and other areas along the Pacific slope throughout Central America (Lachniet and Patterson, 2009; Laffoon et al., 2013). The only two individuals tested from the Caribbean side of the Cordillera were individuals BT-IC-1 Ent. 1 from Sitio Drago and CA-3 6H from Cerro Brujo, who had $\delta^{18}O_{en}$ values of −4.77‰ and −3.68‰, respectively. These values match those of previously reported Caribbean $\delta^{18}O$ values, which are generally above −4‰. The fact that the adolescent from Cerro Brujo has a higher $\delta^{18}O_{en}$ value that matches what would be expected from the Caribbean side of the Cordillera Central means she likely came from the inland northern slope of the volcanic range, rather than the Pacific side.

The only individual in this study whose enamel $\delta^{18}O$ cannot be readily explained is AG-3B-20, with an intermediary value of −4.25‰. This individual's $^{87}Sr/^{86}Sr$ value is similar to others recovered from Sitio Sierra's early occupation. Lachniet and colleagues (2007) found that environmental $\delta^{18}O$ in speleothems from the central part of Panama were between Caribbean and Pacific values, and so it may be that this individual was born in a more inland location, although not in an area with a low volcanic $^{87}Sr/^{86}Sr$ value like Ladrones Cave. This adult male, 35–50 years of age, had numerous indicators for anemia during life, including healed bilateral cribra orbitalia and porotic hyperostosis on the superior occipital, and also had lytic lesions on multiple vertebrae. It may be that this individual's unusual oxygen isotope value was a result of dietary or metabolic stress (Reitsema, 2013), although this would need to be examined in more detail in the future with a broader sample of enamel $\delta^{18}O$ from other individuals.

7. Conclusions

The results of this isotope analysis provide a glimpse into the remarkable variability in human diet and mobility patterns throughout Panama's history. Dietary evidence from $\delta^{13}C$ and $\delta^{15}N$ shows that communities had their own dietary practices, with varying degrees of dependency on maize agriculture supplemented by different amounts of terrestrial meat and marine food. Maize dependency did not necessarily increase over time, especially since the most recent skeleton in the study (Cerro Juan Díaz individual LS-3 Op.5 I.9) had one of the lowest $\delta^{13}C_{co}$ values. The degree of dependence on maize agriculture likely resulted from the social history of local subsistence practices at each site. For example, it appears that some of the island inhabitants, such as the individuals living at Sitio Drago and Jicarita, were consuming maize in higher quantities than some of the mainland sites (Cerro Mangote; late occupation Cerro Juan Díaz); while they may have been able to grow small quantities of maize near their communities, more likely they obtained most of this maize from the mainland, perhaps dried. This coincides with other lines of artifactual evidence at these sites, including imported ceramic wares and grinding stones.

Based on the high $\delta^{15}N$ values found in the earlier burials at Cerro Juan Díaz, it would appear the individuals at this site were regularly importing large quantities of marine food from the coast, elevating their nitrogen values even more than individuals living at coastal sites like Sitio Drago. This coincides with the large quantity of marine fish and shellfish recovered at Cerro Juan Díaz. The individuals recovered from the earlier mortuary context at Sitio Sierra also appear to have been consuming marine food to some extent, correlating in time to the earlier mortuary horizon at Cerro Juan Díaz, and suggesting that the exchange of marine food may have been a common practice at this time throughout the Parita Bay area. This has already been suggested by zooarchaeological analyses of marine fauna at the two sites; the human isotope data reveals the degree of dependency on these resources by members in the community, in that marine food was consumed consistently rather than occasionally.

The strontium and oxygen results show that, while many individuals were born near the place where they were buried, some may have been born much further away. Among the latter, the individual from Jicarita was likely not born on that island, but either on a larger island such as Coiba or Jicarón, or on the mainland, perhaps the Azuero peninsula. The individual found at Cerro Brujo was likely born and lived most of her life in an inland location based on her $^{87}Sr/^{86}Sr$ and low $\delta^{15}N$ values, perhaps the modern Bocas del Toro Province or Ngäbe-Buglé Comarca, and was moved near to or after the time of her death to be buried at the long-abandoned hilltop location. More regional $^{87}Sr/^{86}Sr$ baseline data is needed to explain the variation in the individuals from Cerro Mangote, Sitio Sierra, and Cerro Juan Díaz, because it would appear there is a relative degree of movement exhibited among some of these individuals. A possible explanation is that these locations were used as burial grounds for people living near, but not necessarily at, these sites, but there may be other social (e.g., imported marine food) or even environmental (e.g., coastal progradation) factors to explain this variation as well.

Interpreting the life histories of individuals from regions that lacked written records is a difficult process, but by combining archaeological, osteological, geochemical, and ecological data, we can begin to piece together clues to explain what occurred at these ancient settlements. When Norr began her dietary isotope research in the 1980s, strontium isotope analysis was only beginning to be developed for sourcing archaeological remains. Today, strontium isotopes are commonly used to track the ancient movements of humans and animals, and it is possible that other novel geochemical methods could be applied in the future to further enhance our ability to track human diet, movement, or even health patterns in the past. For regions of the world and periods of time where written records are lacking, such as pre-Columbian Panama, isotope analysis offers an invaluable means of unraveling the complex sociocultural history of the region. If the present study is any indication, we should expect that future isotope studies will reveal that Panama's history was remarkably diverse, with humans subsisting and moving across the landscape for a variety of reasons that can only be explained by combining multiple lines of evidence.

CRediT authorship contribution statement

Ashley E. Sharpe: Conceptualization, Data curation, Investigation, Funding acquisition, Methodology, Visualization, Writing - original draft. **Nicole Smith-Guzmán:** Data curation, Investigation, Funding acquisition, Methodology, Writing - review & editing. **Jason Curtis:** Investigation, Resources, Writing - review & editing. **Ilean Isaza-Aizpurúa:** Resources, Writing - review & editing. **George D. Kamenov:** Investigation, Resources, Writing - review & editing. **Thomas A. Wake:** Resources, Writing - review & editing. **Richard G. Cooke:** Data curation, Funding acquisition, Resources, 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.

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Appendix A. Supplementary data

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References

Aggarwal, J., Habicht-Mauche, J., Juarez, C., 2008. Application of heavy stable isotopes in forensic isotope geochemistry: A review. Appl. Geochem. 23 (9), 2658–2666. https://doi.org/10.1016/j.apgeochem.2008.05.016.

AlQahtani, S.J., Hector, M.P., Liversidge, H.M., 2010. Brief communication: The London atlas of human tooth development and eruption. Am. J. Phys. Anthropol. 142 (3), 481–490. https://doi.org/10.1002/ajpa.21258.

Ambrose, S.H., Norr, L., 1993. Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert, J.B., Grupe, G. (Eds.), Prehistoric Human Bone: Archaeology at the Molecular Level. Springer-Verlag, Berlin, Germany, pp. 1–37. https://doi.org/10.1007/978-3-662-02894-0_1.

Ambrose, S.H., Butler, B.M., Hanson, D.B., Hunter-Anderson, R.L., Krueger, H.W., 1997. Stable isotopic analysis of human diet in the Marianas Archipelago, Western Pacific. Am. J. Phys. Anthropol. 104 (3), 343–361. https://doi.org/10.1002/(SICI)1096-8644(199711)104:3<343::AID-AJPA5>3.0.CO;2-W.

Bataille, C.P., Crowley, B.E., Wooller, M.J., Bowen, G.J., 2020. Advances in global bioavailable strontium isoscapes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 555, 109849 https://doi.org/10.1016/j.palaeo.2020.109849.

Beard, B.L., Johnson, C.M., 2000. Strontium isotope composition of skeletal material can determine the birth place and geographic mobility of humans and animals. J. Forensic Sci. 45 (5), 1049–1061. https://doi.org/10.1520/JFS14829J.

Bentley, R.A., 2006. Strontium isotopes from the earth to the archaeological skeleton: A review. J. Archaeol. Method Theory 13 (3), 135–187. https://doi.org/10.1007/s10816-006-9009-x.

Carvajal, D.R., Díaz, C.P., Sánchez Herrera, L.A., Cooke, R.G., 2006. ¿Fue Cerro Juan Díaz, una aldea precolombina en el río la villa, el pueblo de indios de Cubita? Memorias del VI Congreso Centroamericano de Historia 100–123.

Carvajal-Contreras, D.R., Cooke, R., Jiménez, M., 2008. Taphonomy at two contiguous coastal rockshelters in Panama: Preliminary observations focusing on fishing and curing fish. Quat. Int. 180 (1), 90–106. https://doi.org/10.1016/j.quaint.2007.08.027.

Chisholm, B.S., Nelson, D.E., Schwarcz, H.P., 1982. Stable-carbon isotope ratios as a measure of marine versus terrestrial protein in ancient diets. Science 216 (4), 1131–1132. https://doi.org/10.1126/science.216.4550.1131.

Clary, J., Hansell, P., Ranere, A.J., Buggey, T., 1984. The Holocene geology of the western Parita Bay coastline of central Panama. In: Lange, F.W. (Ed.), Recent Developments in Isthmian Archaeology. British Archaeological Reports (International Series), Oxford, England, pp. 55–83.

Cooke, R.G., 2001. La pesca en estuarios panameños: una visión histórica y cultural desde la Bahía de Parita. In: Heckadon-Moreno, S. (Ed.), Panamá: Puente Biológico. Smithsonian Tropical Research Institute, Panama, pp. 45–53.

Cooke, R.G., Ranere, A.J., 1999. Precolumbian fishing on the Pacific coast of Panama. In: Blake, M. (Ed.), Pacific Latin America in Prehistory: The Evolution of Archaic and Formative Cultures. Washington State University Press, Pullman, WA, pp. 103–122.

Cooke, R.G., Sánchez Herrera, L.A., 1998. Coetaneidad de la metalurgía, artesanias de concha y cerámica pintada en Cerro Juan Díaz, Gran Coclé Panamá. Boletín del Museo del Oro (Colombia) 42, 54–85.

Cooke, R., Jiménez, M., 2004. Teasing out the species in diverse archaeofaunas: Is it worth the effort? An example from the tropical Eastern Pacific. Archaeofauna 13, 19–35.

Cooke, R.G., Sánchez Herrera, L.A., Isaza-Aizpurúa, I.I., Pérez-Yancky, A., 1998. Rasgos mortuorios y artefactos inusitados de Cerro Juan Díaz, una aldea precolombina del 'Gran Coclé' (Panamá central). La Antigua (Panamá) 53, 127–196.

Cooke, R.G., Wake, T.A., Martínez-Polanco, M.F., Jiménez-Acosta, M., Bustamante, F., Holst, I., Lara-Kraudy, A., Martín, J.G., Redwood, S., 2016. Exploitation of dolphins (Cetacea: Delphinidae) at a 6000yr old Preceramic site in the Pearl Island archipelago, Panama. J. Archaeol. Sci. Rep. 6, 733–756. https://doi.org/10.1016/j.jasrep.2015.12.001.

Díaz, C., 1999. Estudio Bio-Antropológico de Rasgos Mortuorios de la Operación 4 del Sitio Arqueológico Cerro Juan Díaz, Panamá Central. (Unpublished graduate thesis). Universidad de los Andes, Santa Fé de Bogotá.

Dickau, R., 2010. Microbotanical and macrobotanical evidence of plant use and the transition to agriculture in Panama. In: VanDerwarker, A.M., Peres, T.M. (Eds.), Integrating Zooarchaeology and Paleoethnobotany: A Consideration of Issues, Methods, and Cases. Springer-Verlag, New York, NY, pp. 99–134. https://doi.org/10.1007/978-1-4419-0935-0_6.

Eck, C.J., DiGangi, E.A., Bethard, J.D., 2019. Assessing the efficacy of isotopic provenancing of human remains in Colombia. Forensic Sci. Int. 302, 109919 https://doi.org/10.1016/j.forsciint.2019.109919.

Ellegård, L., Alstad, T., Rütting, T., Johansson, P.H., Lindqvist, H.M., Winkvist, A., 2019. Distinguishing vegan-, vegetarian-, and omnivorous diets by hair isotopic analysis. Clin. Nutr. 38 (6), 2949–2951. https://doi.org/10.1016/j.clnu.2018.12.016.

de Espinosa, G., 1994. Relación de lo hecho por el licenciado Gaspar de Espinosa… que hiciese y cumpliese en el viaje a las provincias de Paris y Natá y Cherú y a las otras comarcanas. In: Jopling, C.F. (Ed.), Indios y negros en Panamá en los siglos XVI y XVII: Selecciones de los documentos del archivo general de indias. Centro de Investigaciones Regionales de Mesoamérica, Antigua, Guatemala, pp. 61–74.

Fernandes, R., Nadeau, M.-J., Grootes, P.M., 2012. Macronutrient-based model for dietary carbon routing in bone collagen and bioapatite. Archaeol. Anthropol. Sci. 4, 291–301. https://doi.org/10.1007/s12520-012-0102-7.

France, C.A.M., Owsley, D.W., 2012. Stable carbon and oxygen isotope spacing between bone and tooth collagen and hydroxyapatite in human archaeological remains. Int. J. Osteoarchaeol. 25 (3), 299–312. https://doi.org/10.1002/oa.2300.

Froehle, A.W., Kellner, C.M., Schoeninger, M.J., 2012. Multivariate carbon and nitrogen stable isotope model for the reconstruction of prehistoric human diet. Am. J. Phys. Anthropol. 147 (3), 352–369. https://doi.org/10.1002/ajpa.21651.

Graustein, W.C., 1989. ^{87}Sr/^{86}Sr ratios measure the sources and flow of strontium in terrestrial ecosystems. In: Rundel, P.W., Ehlerginger, J.R., Nagy, K.A. (Eds.), Stable Isotopes in Ecological Research. Springer-Verlag, New York, NY, pp. 491–512. https://doi.org/10.1007/978-1-4612-3498-2_28.

Harmon, R.S., Wörner, G., Goldsmith, S.T., Harmon, B.A., Gardner, C.B.W., Lyons, B., Ogden, F.L., Pribil, M.J., Long, D.T., Kern, Z., Fórizs, I., 2016. Linking silicate weathering to riverine geochemistry—A case study from a mountainous tropical setting in west-central Panama. GSA Bull. 128 (11–12), 1780–1812. https://doi.org/10.1130/B31388.1.

Harrison, R.G., Katzenberg, M.A., 2003. Paleodiet studies using stable carbon isotopes from bone apatite and collagen: Examples from Southern Ontario and San Nicolas Island, California. J. Anthropol. Archaeol. 22 (3), 227–244. https://doi.org/10.1016/S0278-4165(03)00037-0.

Hedges, R.E.M., 2003. On bone collagen—apatite-carbonate isotopic relationships. Int. J. Osteoarchaeol. 13 (1–2), 66–79. https://doi.org/10.1002/oa.660.

Hillson, S., 2005. Teeth, 2nd ed. Cambridge University Press, Cambridge, UK.

Isaza-Aizpurúa, I., 2013. Diachronic developments of two pre-Columbian settlements in the southern domains of Parita's chiefdom, Gran Coclé, Panamá. In: Palumbo, S.D., Boada Rivas, A.M., Locascio, W.A., Menzies, A.C.J. (Eds.), Multiscalar Approaches to Studying Social Organization and Change in the Isthmo-Columbian Area. University of Pittsburgh, Pittsburgh, PA, pp. 15–38.

Isaza, I., 2019. Una perspectiva multidisciplinaria: el sello indeleble de la metodología arqueológica de Richard Cooke y su influencia en las investigaciones de la autora en el valle bajo del río La Villa y las islas del Parque Nacional Coiba, Panamá. Cuadernos de Antropología 29 (2), 1–20. https://doi.org/10.15517/cat.v29i2.36761.

Isaza, I., Jiménez-Acosta, M., Smith-Guzmán, N., Sharpe, A., Cooke, R. G., In Review. Precolumbian lifeways at three estuarine and two platform island sites in Pacific Panama. In Elkin, D., Delaere, C. (Eds.), Underwater and Coastal Archaeology of Latin America. Gainesville, FL: University Press of Florida.

Jørkov, M.L.S., Heinemeier, J., Lynnerup, N., 2007. Evaluating bone collagen extraction methods for stable isotope analysis in dietary studies. J. Archaeol. Sci. 34 (11), 1824–1829. https://doi.org/10.1016/j.jas.2006.12.020.

Kamenov, G.D., Lofaro, E.M., Goad, G., Krigbaum, J., 2018. Trace elements in modern and archaeological human teeth: Implications for human metal exposure and enamel diagenetic changes. J. Archaeol. Sci. 99, 27–34. https://doi.org/10.1016/j.jas.2018.09.002.

Krigbaum, J., Fitzpatrick, S.M., Bankaitis, J., 2013. Human paleodiet at Grand Bay, Carriacou, Lesser Antilles. J. Island Coastal Archaeol. 8 (2), 210–227. https://doi.org/10.1080/15564894.2012.756082.

Lachniet, M.S., Patterson, W.P., 2009. Oxygen isotope values of precipitation and surface waters in northern Central America (Belize and Guatemala) are dominated by temperature and amount effects. Earth Planet. Sci. Lett. 284, 435–446. https://doi.org/10.1016/j.epsl.2009.05.010.

Lachniet, M.S., Patterson, W.P., Burns, S., Asmerom, Y., Polyak, V., 2007. Caribbean and Pacific moisture sources on the Isthmus of Panama revealed from stalagmite and surface water δ^{18}O gradients. Geophys. Res. Lett. 34, 1–6. https://doi.org/10.1029/2006GL028469.

Laffoon, J.E., Rojas, R.V., Hofman, C.L., 2013. Oxygen and carbon isotope analysis of human dental enamel from the Caribbean: Implications for investigating individual origins. Archaeometry 55 (4), 742–765. https://doi.org/10.1111/j.1475-4754.2012.00698.x.

Laffoon, J.E., Sonnemann, T.F., Shafie, T., Hofman, C.L., Brandes, U., Davies, G.R., 2017. Investigating human geographic origins using dual-isotope (^{87}Sr/^{86}Sr, δ^{18}O) assignment approaches. PLoS One 12 (2), e0172562. https://doi.org/10.1371/journal.pone.0172562.

Linares de Sapir, O., 1971. Cerro Brujo: A tiny Guaymí hamlet of the past. Expedition Mag. 13 (2), 27–35.

Linares, O.F., Ranere, A.J. 1980. Adaptive Radiations in Prehistoric Panama. Peabody Museum Monographs No. 5. Cambridge, MA: Peabody Museum of Archaeology and Ethnology.

Longin, R., 1971. New method of collagen extraction for radiocarbon dating. Nature 230 (5291), 241–242. https://doi.org/10.1038/230241a0.

Martín, J.G., Sánchez Herrera, L.A., 2007. El Istmo Mediterráneo: Intercambio, simbolismo y filiación social en la bahía de Panamá durante el periodo 500–1000 DC. Arqueología del Área Intermedia 7, 113–122.

Martín, J.G., Cooke, R.G., Bustamante, F., Holst, I., Lara, A., Redwood, S., 2016. Ocupaciones prehispánicas en Isla Pedro González, archipiélago de Las Perlas, Panamá: Aproximación a una cronología con comentarios sobre las conexiones externas. Latin Am. Antiq. 27 (3), 378–396. https://doi.org/10.7183/1045-6635.27.3.378.

Martyr D'Anghera, P., 1912. De orbe novo: The Eight Decades of Peter Martyr D'Anghera. Translated by F. A. MacNutt. New York, NY: G.P. Putnam's Sons.

Mayo Torné, J.C., Cooke, R.G., 2005. La industria prehispánica de conchas marinas de Gran Coclé, Panamá: Análisis tecnológico de los artefactos de concha del basurero-taller del Sitio Cerro Juan Díaz, Los Santos, Panamá. Archaeofauna 24, 285–298.

McGimsey, C.R., 1956. Cerro Mangote: A Preceramic site in Panama. Am. Antiq. 22 (2), 151–161. https://doi.org/10.2307/276817.

Norr, L., 1991. Nutritional Consequences of Prehistoric Subsistence Strategies in Lower Central America (Unpublished doctoral dissertation). University of Illinois, Urbana.

Norr, L., 1995. Interpreting dietary maize from bone stable isotopes in the American tropics: The state of the art. In: Stahl, P.W. (Ed.), Archaeology in the Lowland American Tropics: Current Analytical Methods and Recent Applications. Cambridge University Press, Cambridge, UK, pp. 198–223. https://doi.org/10.1017/CBO9780511521188.010.

Norr, L., 2002. Bone isotopic analysis and prehistoric diet at the Tutu site. In: Righter, E. (Ed.), The Tutu Archaeological Village Site: A Multidisciplinary Case Study in Human Adaptation. Routledge, New York, NY, pp. 263–273.

O'Connell, T.C., Hedges, R.E.M., 1999. Investigations into the effect of diet on modern human hair isotopic values. Am. J. Phys. Anthropol. 108 (4), 409–425. https://doi.org/10.1002/(SICI)1096-8644(199904)108:4<409::AID-AJPA3>3.0.CO;2-E.

Pearson, G.A., Martín, J.G., Castro, S., Jiménez-Acosta M., Cooke, R. G. 2020. Mid-Holocene occupation of the Pearl Islands, A case of unusual insular adaptations in Panama Bay. Quat. Int. https://doi.org/10.1016/j.quaint.2020.07.036.

Pederzani, S., Britton, K., 2019. Oxygen isotopes in bioarchaeology: Principles and applications, challenges and opportunities. Earth Sci. Rev. 188, 77–107. https://doi.org/10.1016/j.earscirev.2018.11.005.

Pestle, W.J., Laffoon, J., 2018. Quantitative paleodietary reconstruction with complex foodwebs: An isotopic case study from the Caribbean. J. Archaeol. Sci. Rep. 17, 393–403. https://doi.org/10.1016/j.jasrep.2017.11.032.

Pin, C., Bassin, C., 1992. Evaluation of a strontium-specific extraction chromatographic method for isotopic analysis in geological materials. Anal. Chim. Acta 269 (2), 249–255. https://doi.org/10.1016/0003-2670(92)85409-Y.

Piperno, D.R., 2011. The origins of plant cultivation and domestication in the New World tropics: Patterns, process, and new developments. Curr. Anthropol. 52 (S4), S453–S470. https://doi.org/10.1086/659998.

Piperno, D.R., Holst, I., 1998. The presence of starch grains on prehistoric stone tools from the humid Neotropics: Indications of early tuber use and agriculture in Panama. J. Archaeol. Sci. 25 (8), 765–776. https://doi.org/10.1006/jasc.1997.0258.

Pors Nielsen, S., 2004. The biological role of strontium. Bone 35 (3), 583–588. https://doi.org/10.1016/j.bone.2004.04.026.

Price, T.D., Gestsdóttir, H., 2006. The first settlers of Iceland: an isotopic approach to colonisation. Antiquity 80 (307), 130–144. https://doi.org/10.1017/S0003598X00093315.

Price, T.D., Burton, J.H., Sharer, R.J., Buikstra, J.E., Wright, L.E., Traxler, L.P., Miller, K.A., 2010. Kings and commoners at Copan: Isotopic evidence for origins and movement in the Classic Maya Period. J. Anthropol. Archaeol. 29, 15–32. https://doi.org/10.1016/j.jaa.2009.10.001.

Price, T.D., Burton, J.H., Fullagar, P.D., Wright, L.E., Buikstra, J.E., Tiesler, V. 2015. Strontium isotopes and the study of human mobility among the ancient Maya. In A. Cucina (Ed.), Archaeology and Bioarchaeology of Population Movement among the Prehispanic Maya (pp. 119–132). SpringerBriefs in Archaeology, Springer International Publishing. https://doi.org/10.1007/978-3-319-10858-2_11.

Price, T.D., Tiesler, V., Freiwald, C., 2019. Place of origin of the sacrificial victims in the sacred Cenote, Chichén Itzá, Mexico. Am. J. Phys. Anthropol. 170 (1), 98–115. https://doi.org/10.1002/ajpa.23879.

Redwood, S.D., 2020. Late Pleistocene to Holocene sea level rise in the Gulf of Panama, Panama, and its influence on early human migration through the Isthmus. Caribbean J. Earth Sci. 51, 15–31.

Reitsema, L.J., 2013. Beyond diet reconstruction: Stable isotope applications to human physiology, health, and nutrition. Am. J. Hum. Biol. 25 (4), 445–456. https://doi.org/10.1002/ajhb.22398.

Renson, V., Navarro-Castillo, M., Cucina, A., Culleton, B.J., Kennett, D.J., Neff, H., 2019. Origin and diet of inhabitants of the Pacific Coast of Southern Mexico during the Classic Period - Sr, C and N isotopes. J. Archaeol. Sci. Rep. 27, 101981 https://doi.org/10.1016/j.jasrep.2019.101981.

Sánchez Herrera, L.A. 1995. Análisis Estilístico de Dos Componentes Cerámicos de Cerro Juan Díaz: Su Relación con el Surgimiento de las Sociedades Cacicales en Panamá. (Unpublished licenciatura thesis). Facultad de Ciencias Sociales, Escuela de Antropología y Sociología Universidad de Costa Rica, San José.

Schoeninger, M.J., 2009. Stable isotope evidence for the adoption of maize agriculture. Curr. Anthropol. 50 (5), 633–640. https://doi.org/10.1086/605111.

Schoeninger, M.J., 2010. Diet reconstruction and ecology using stable isotope ratios. In: Larsen, C.S. (Ed.), A Companion to Biological Anthropology. Blackwell Publishing, Hoboken, NJ, pp. 445–464. https://doi.org/10.1002/9781444320039.ch25.

Schoeninger, M.J., DeNiro, M.J., 1984. Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. Geochim. Cosmochim. Acta 48, 625–639. https://doi.org/10.1016/0016-7037(84)90091-7.

Schoeninger, M.J., Moore, K., 1992. Bone stable isotope studies in archaeology. J. World Prehistory 6 (2), 247–296. https://doi.org/10.1007/BF00975551.

Schoeninger, M.J., DeNiro, M.J., Tauber, H., 1983. Stable nitrogen isotope ratios of bone collagen reflect marine and terrestrial components of prehistoric human diet. Science 220 (4604), 1381–1383. https://doi.org/10.1126/science.6344217.

Sharpe, A.E., Emery, K.F., Inomata, T., Triadan, D., Kamenov, G.D., Krigbaum, J., 2018. Earliest isotopic evidence in the Maya region for animal management and long-distance trade at the site of Ceibal, Guatemala. Proc. Natl. Acad. Sci. 115 (4), 3605–3610. https://doi.org/10.1073/pnas.1713880115.

Smith-Guzmán, N.E., Cooke, R.G., 2018. Interpersonal violence at Playa Venado, Panama (550–850 AD): A reevaluation of the evidence. Latin Am. Antiq. 29 (4), 718–735. https://doi.org/10.1017/laq.2018.48.

Smith-Guzmán, N.E., Cooke, R.G., 2019. Cold-water diving in the tropics? External auditory exostoses among the pre-Columbian inhabitants of Panama. Am. J. Phys. Anthropol. 168 (3), 448–458. https://doi.org/10.1002/ajpa.23757.

Smith-Guzmán, N.E., Sánchez Herrera, L.A., Cooke, R.G., in review. Patterns of disease and culture in ancient Panama: A bioarchaeological analysis of the early graves at Cerro Juan Díaz. Bioarchaeol. Int.

Smith-Guzmán, N.E., Toretsky, J.A., Tsai, J., Cooke, R.G., 2018. A probable primary malignant bone tumor in a pre-Columbian human humerus from Cerro Brujo, Bocas del Toro, Panamá. Int. J. Paleopathol. 21, 138–146. https://doi.org/10.1016/j.ijpp.2017.05.005.

Sugiyama, N., Martínez-Polanco, M.F., France, C.A.M., Cooke, R.G., 2020. Domesticated landscapes of the neotropics: Isotope signatures of human-animal relationships in pre-Columbian Panama. J. Anthropol. Archaeol. 59, 101195 https://doi.org/10.1016/j.jaa.2020.101195.

Tieszen, L.L., Fragre, T., 1993. Effect of diet quality and composition on the isotopic composition of respiratory CO_2, bone collagen, bioapatite, and soft tissues. In: Lambert, J.B., Grupe, G. (Eds.), Prehistoric Human Bone-Archaeology at the Molecular Level. Springer-Verlag, Berlin, Germany, pp. 121–153. https://doi.org/10.1007/978-3-662-02894-0_5.

Wake, T.A., de Leon, J., Fitzgerald Bernal, C., 2004. Prehistoric Sitio Drago, Bocas del Toro, Panama. Antiquity 78 (300).

Wake, T.A., Mojica, A.O., Davis, M.H., Campbell, C.J., Mendizábal, T., 2012. Electrical resistivity surveying and pseudo-three-dimensional tomographic imaging at Sitio Drago, Bocas del Toro, Panama. Archaeol. Prospection 19, 49–58. https://doi.org/10.1002/arp.1417.

Wake, T.A., Doughty, D.R., Kay, M., 2013. Archaeological investigations provide Late Holocene baseline ecological data for Bocas del Toro, Panama. Bull. Mar. Sci. 89 (4), 1015–1035. https://doi.org/10.5343/bms.2012.1066.

Wright, L.E., 2012. Immigration to Tikal, Guatemala: Evidence from stable strontium and oxygen isotopes. J. Anthropol. Archaeol. 31 (3), 334–352. https://doi.org/10.1016/j.jaa.2012.02.001.

Wright, L.E., Schwarcz, H.P., 1998. Stable carbon and oxygen isotopes in human tooth enamel: Identifying breastfeeding and weaning in prehistory. Am. J. Phys. Anthropol. 106 (1), 1–18. https://doi.org/10.1002/(SICI)1096-8644(199805)106:1<1::AID-AJPA1>3.0.CO;2-W.

Wright, L.E., Valdes, J.A., Burton, J.H., Price, T.D., Schwarcz, H.P., 2010. The children of Kaminaljuyu: Isotopic insight into diet and long distance interaction in Mesoamerica. J. Anthropol. Archaeol. 29 (2), 155–178. https://doi.org/10.1016/j.jaa.2010.01.002.

Zohar, I., Cooke, R.G., 1997. The impact of salting and drying on fish bones: Preliminary observations on four marine species from Parita Bay, Panama. Archaeofauna 6, 59–66.

Zohar, I, Cooke, R.G., 2019. The role of dried fish: A taphonomical model of fish butchering and long-term preservation. J. Archaeol. Sci. Rep. 26, 101864 https://doi.org/10.1016/j.jasrep.2019.05.029.