



An isotopic examination of Maya Preclassic and Classic animal and human diets at Ceibal, Guatemala

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ABSTRACT

This study examines the carbon ($\delta^{13}\text{C}$), oxygen ($\delta^{18}\text{O}$), and strontium ($^{87}\text{Sr}/^{86}\text{Sr}$) isotopes from the dental enamel of 63 animals and compares these data to the carbon signatures from 21 humans from the Maya site of Ceibal, Guatemala. Comparing both domestic dogs and non-domestic species over a history spanning two millennia, we find that subsistence strategies and interregional relationships between Ceibal and other areas changed over time, likely because of broader sociopolitical trends that affected the entire Maya region. During the first half of Ceibal's history (1100 BCE – 250 CE), dogs consumed more maize than humans. Dogs were likely intentionally fed maize as they were a major meat source at the time, and “foreign”-born dogs were transported to the site from the volcanic highlands, two hundred kilometers to the south. The reliance on dogs as food appears to have changed during the Early Classic period (250 – 600 CE), as much of the site was abandoned and the remaining inhabitants began to focus their subsistence predominantly on maize agriculture and hunting local deer. Mammals were no longer moved from long distances to Ceibal, as the principal faunal imports were marine shells from an exchange network with the Caribbean coast. The isotope data complement other artifactual data at the site and demonstrate how Maya subsistence strategies varied over time.

1. Introduction

There has long been interest in the question of how the ancient Maya sustained their vast communities, and every year new discoveries reveal more information to illustrate the complex and diverse strategies the Maya implemented across time and space (Beach et al., 2009; Dunning et al., 1998; Emery and Brown, 2012; Emery and Thornton, 2008; Krause et al., 2019; Pohl et al., 1996; Pope et al., 2001; Fedick, 1996). There was no single technique that all Maya settlements used to sustain their populations. Although many Maya communities depended on a principal suite of domesticated plant species (maize, beans, and squash, among others), they did not use the same cultivation strategies in all

areas, nor did they all consume these principal plant species to the same extent (Fedick and Santiago, 2022; Scherer et al., 2007; Sloten et al., 2020; White, 2005; White et al., 2010; Wright et al., 2010). The Maya relationship with animals was also variable, and zooarchaeological analyses show that hunting, fishing, animal rearing, and trade of animals and their products (e.g., bone, teeth, shells) differed across communities and through time (Boileau et al., 2020; Emery, 2003, 2004a; Götz, 2014; Masson and Lope, 2008; Sharpe, 2019; Sharpe et al., 2020; Jiménez-Cano, 2019). Archaeologists now recognize that there was no single, standard “Maya diet” (Emery 2004b).

The present study aims to better understand the changing subsistence relationship between animals and humans at the Maya site of

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Ceibal, Guatemala (Fig. 1), using stable isotope analysis from dental enamel. Ceibal was occupied almost constantly for over two thousand years, from the very late preceramic period (c. 1100 BCE) to the early Postclassic period (1200 CE; Table 1; Fig. 2). This unusually long occupation makes it an ideal site for examining changing subsistence strategies at a single location. Faunal analyses at the site have shown that the types and diversity of species that inhabitants depended upon changed significantly over the centuries, with a diet of dogs and freshwater shellfish dominant in the first half of the site's history that ultimately gave way to increasing dependency on turtles, deer, and turkeys into the later periods (Sharpe, 2016; Sharpe et al., 2020). An examination of the imported marine fauna at Ceibal also revealed changing trade relationships over the centuries, with Ceibal receiving certain species for specific ritual activities that fell in and out of favor across the Maya lowlands at various times (Sharpe, 2019).

This study builds on isotope analyses of animals recovered at Ceibal, which had previously concentrated on the ceremonial core (Sharpe et al., 2018). In our prior study, we identified early evidence of dogs transported from the volcanic highlands hundreds of kilometers to the south, as well as possible captive management of local carnivores. The present study expands the initial dataset with a greater number of animals across both the site core and outlying residential and minor ceremonial groups, thereby gaining a better representation across the different parts of the site. Furthermore, we include more species from time periods that were lacking in the first set, notably the Early Classic period (250 – 600 CE), a time when Ceibal and other sites in the Maya area were experiencing significant changes following the Preclassic collapse and rearrangement of politically dominant centers. Furthermore, we include isotope data from human dental enamel to compare with the animals over time, particularly domestic dogs, in order to better understand the relationship between human and animal diets.

Based on our preliminary isotope analysis of the animals from Ceibal (Sharpe et al., 2018), we predicted we would identify more non-local animals at the site, especially during the Preclassic period as the site grew into a regional monumental center. We predicted that we might also see more non-local animals during the Terminal Classic period (810 – 950 CE), when Ceibal briefly became a regional capital, and when marine shell imports from the Caribbean were common (Sharpe, 2019). We also predicted we would find more evidence for maize-fed animals, especially deer, which may have been used to feed the growing population during this period. Finally, we predicted that we would see

Table 1

Chronology of major periods of Ceibal. Note that Late and Terminal Preclassic date ranges differ slightly compared to Sharpe et al. (2020) due to recent revisions from new radiocarbon dates.

Period	Years
Early Middle Preclassic	1000—700 BCE
Late Middle Preclassic	700—350 BCE
Late Preclassic	350 – 50 BCE
Terminal Preclassic	50 BCE – 250 CE
Early Classic	250 – 600 CE
Late Classic	600 – 810 CE
Terminal Classic	810 – 950 CE
Postclassic	1000 – 1200 CE

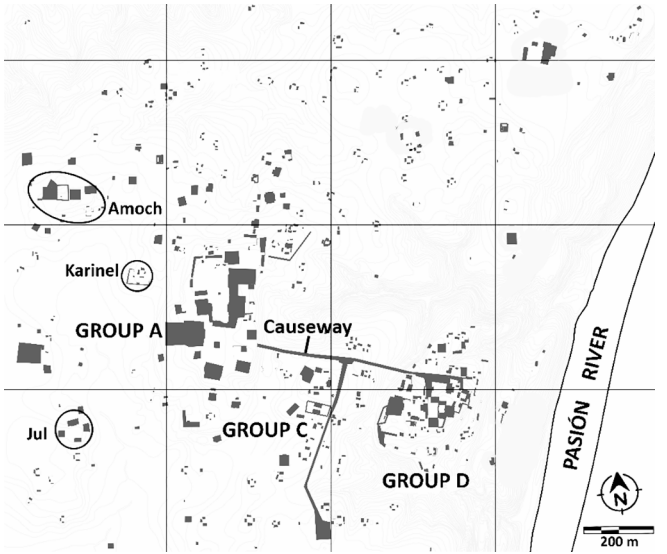


Fig. 2. Map of Ceibal, Guatemala. Map from the Ceibal-Petexbatun Archaeological Project.

comparable diets in both humans and dogs through time, assuming dogs were raised and fed by humans and were also potentially consumed as a source of meat (Cunningham-Smith et al., 2020). These predictions are tested in the present study.

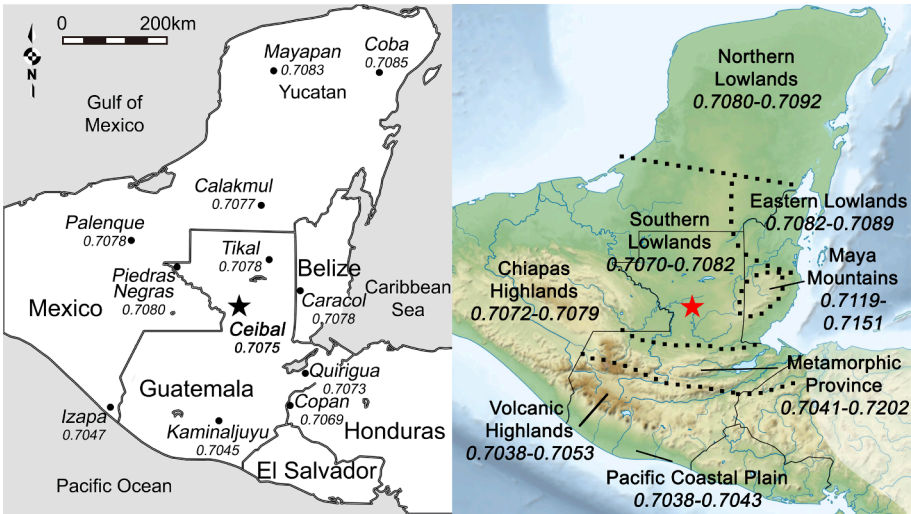


Fig. 1. Strontium isotopic values in the Maya region, including previously reported values for major centers. Strontium isotope ranges based on Freiwald et al. (2020), Hodell et al. (2004), Price et al., (2008, 2019), and Wright et al. (2010). Note that the Metamorphic Province is a geologically complex region; Hodell et al. (2004) predict the Motagua Valley that runs through this region has a $^{87}\text{Sr}/^{86}\text{Sr}$ value of 0.70598 ± 0.0018 . Maps modified from Sharpe et al. (2022), under the Creative Commons Attribution 4.0 International License.

2. Overview of Ceibal and the research area

Ceibal persisted as an important political and ceremonial center in the south-central Maya lowlands for about two thousand years. A large earthen platform mound extending 600 by 340 m and between 6 and 15 m in height was constructed at the site between 1000 and 700 BCE (Inomata et al., 2019); thereafter, residential groups and minor ceremonial centers grew out around its vicinity (Burham, 2022; MacLellan, 2019; Triadan et al., 2017). The site expanded with increasingly large, monumental stone construction projects, including causeways and pyramids, through the Late and Terminal Preclassic period (c. 350 BCE – 250 CE). In the early part of the Early Classic (c. 350 CE) Ceibal was largely abandoned, although outlying residential groups and a central platform (Str. A-2) bear evidence of sporadic occupation. The monumental core of the site began to grow again after 600 CE, and an elite ceremonial and residential complex, Group D, was constructed by the Pasión river (Bazy and Inomata, 2017). Ceibal briefly became a capital toward the end of the 8th century, following the political defeat and abandonment of other Maya capitals in the area. By 950 CE, the site was entirely abandoned. A remnant population, perhaps a different population of settlers from another site or returning descendants of the Classic inhabitants of Ceibal, came to occupy at least one outlying structure around 1000 – 1200 CE. Today, the site lies in the El Ceibal Archaeological Park (Parque Arqueológico El Ceibal).

Two series of excavations have been conducted at Ceibal in the last century. Harvard University performed the first excavations in the 1960s, when the site was known as Seibal (Willey et al., 1975); fauna from these excavations were analyzed by Pohl (1976, 1990). An international collaborative team directed by archaeologists from Guatemala, the University of Arizona, and Ibaraki University has carried out the second series of excavations, which have been ongoing since 2005 (Inomata et al., 2013, 2017). The first isotopic assessment of animals examined fauna recovered prior to 2013, which mostly originated from Ceibal's ceremonial core, since that was where the majority of excavations were focused (Sharpe et al., 2018). The present study includes animals recovered from the 2005–2017 excavations, and covers a broader range of locations at the site, including residential groups and minor outlying ceremonial centers.

3. Isotope analyses in this study

This study measured three isotopes from dental enamel to examine diet and mobility: carbon ($\delta^{13}\text{C}$), oxygen ($\delta^{18}\text{O}$), and strontium ($^{87}\text{Sr}/^{86}\text{Sr}$). Enamel generally forms early in the life of an animal, including humans, and once an isotope is situated within the hydroxyapatite matrix it is not modified unless the enamel itself degrades, as can occur during post-depositional diagenesis. Rodents and other mammals with continuously growing dentition are the exceptions to this pattern. This study focused on clean, well-preserved enamel lacking evidence of discoloration or post-depositional wear. Enamel may contain isotopic values from the diet of the mother if the particular tooth was under development while *in utero* or during breastfeeding. The permanent teeth used in this study were fully-formed, although there is a possibility the mother's diet appears in the enamel of some teeth. The human teeth used for comparison were third molars, which begin development around the age of 9 and fully erupt by around 21 years (AlQahtani et al., 2010).

Carbon isotope values from enamel hydroxyapatite are frequently used in Mesoamerican archaeology to determine the proportion of C_4 photosynthetic plants in the diet, mainly maize (Sharpe et al., 2022; Somerville et al., 2016; Sugiyama et al., 2015; Wright et al., 2010). Maize was, and still remains, the dominant grain in the Maya diet; next to wheat and rice, it is one of the three dominant staple grains in the world (Nuss and Tanumihardjo, 2010). Yet it was not always consumed in Mesoamerica to the extent it is today, and a number of recent studies have shown that its introduction and spread across the Americas was

complex, starting in the Early Holocene (c. 9000 BP) in central Mexico (Matsuoka et al., 2002; Piperno et al., 2009) and spreading down to South America before arriving in the Maya region a second time (Kennett et al., 2020, 2022; Kistler et al., 2020; Rosenswig et al., 2015). Although maize was certainly present in the Maya region when people began to settle at Ceibal around 1100 BCE (Inomata et al., 2022; Palomo, 2020), this study uses enamel $\delta^{13}\text{C}$ from animals and humans to determine who was consuming maize, and whether there is an increase in maize dependency over time. In general, based on previous enamel studies, we would expect that ^{13}C -enriched terrestrial fauna exhibiting $\delta^{13}\text{C}$ values above -10‰ were consuming primarily C_4 plants (including maize), whereas those with lower $\delta^{13}\text{C}$ values were consuming mainly C_3 species (Sharpe et al., 2022; van der Merwe et al., 2000).

Oxygen isotope values from dental enamel primarily reflect the drinking location and behavior of an animal, and, to a lesser extent, its physiology (Pederzani and Britton, 2019). Oxygen isotopes from rivers and standing water vary across the landscape; in the Maya area, they are generally higher (0‰ or greater) near the Caribbean coast, and lower inland and along the Pacific coast (below -4‰ ; Lachniet and Patterson, 2009). Tests of $\delta^{18}\text{O}$ values from rivers and standing bodies of water across the lowland Maya region have shown that there is a degree of seasonal variability in these sources (Scherer et al., 2015). Different animal species also obtain water from different sources, including non-obligate drinkers like deer that can obtain much of their water from vegetation (Repussard et al., 2014; Sharpe et al., 2022). Thus, while oxygen isotopes can be used for rough geographic estimation of where an animal was drinking water as its tooth enamel formed, these values must be used in conjunction with other isotopic variables to support interpretations.

Strontium isotope ratios in dental enamel are a more robust means of identifying an animal's place of origin. These ratios vary according to the rock type and age in a region; in general, volcanically active areas tend to have the lowest $^{87}\text{Sr}/^{86}\text{Sr}$ values, whereas geologically old rock formations have the highest $^{87}\text{Sr}/^{86}\text{Sr}$ values (Bentley, 2006; Hodell et al., 2004). As rocks weather differently in different areas, the $^{87}\text{Sr}/^{86}\text{Sr}$ in the soil and available drinking water may resemble a mix of strontium values in an area. Most animals, including humans, incorporate strontium into their tissues through the food they consume, and to a lesser extent from the water they drink.

It is not always clear how one distinguishes a “local” from “non-local” oxygen or strontium isotope signature. Some studies in Mesoamerica have used the standard deviation around a dataset mean, either of all the archaeological data or local baseline data (Price et al., 2019; Rand et al., 2020; Sharpe et al., 2018); others calculate the interquartile range of the archaeological dataset to locate outliers (Freiwald et al., 2020; Pacheco-Forés et al., 2020) or look for a normal distribution using a Shapiro Wilk statistic (Wright, 2012). Each of these methods has benefits and drawbacks. For example, if there is a possibility that the archaeological dataset contains multiple non-local individuals, any standard deviation or interquartile range calculated from this data distribution will obfuscate the distinction between what is “local” and not. Concerning oxygen, an extensive global survey of human $\delta^{18}\text{O}$ values showed that the inter-quartile range or median absolute deviation were most accurate at distinguishing “local” individuals, but were highly dependent on the circumstances of the study population (Lightfoot and O'Connell, 2016). Variable geographic zones with similar $\delta^{18}\text{O}$ or $^{87}\text{Sr}/^{86}\text{Sr}$ ranges can also make distinguishing outliers difficult (see Casar et al., 2022 for an example in northern Mesoamerica). Thus, prior knowledge of the local $\delta^{18}\text{O}$ and $^{87}\text{Sr}/^{86}\text{Sr}$ distributions across a region is important to take into consideration, and a combination of both isotopes, rather than only one, is a more reliable means of detecting true non-local outliers.

In some regions, geological foundations and thus strontium isotope ratios do not vary considerably for many kilometers around a site, while in other regions, rock types and drinking sources may be variable, and

there may be a wide range of possible isotope values within a single kilometer. At Ceibal, four baseline samples of limestone bedrock, terrestrial snails (*Orthalicus princeps*), and a possibly post-occupation opossum (*Philander opossum*) have shown that the local value is 0.70749 ($2\sigma = 2.84 \times 10^{-5}$; Sharpe et al., 2018). Terrestrial snails (*Neocyclotus dysoni*) at the site of Caobal, three kilometers to the west of Ceibal's Group A, had a value of 0.70750. The site of Aguatega about 18 km southwest of Ceibal has reported local values of 0.7075 (Price et al., 2008) and 0.7077 (Thornton, 2011; note the latter was pooled from samples taken from a neighboring site). Cancuen, located about 50 km south of Ceibal on the Pasión River, has an average value of 0.7074 (Thornton, 2011). Considering that the karstic geology in the Petexbatun region of Guatemala is relatively similar in age, the strontium isotope ratio throughout much of the region is likely ~ 0.70750 with little variation. In this study, we consider any values between 0.70746 and 0.70752 as *immediately* local to Ceibal (within 2σ of the local norm), and ~ 0.70740 – 0.70760 as potentially “local” in origin to the general area, within several kilometers. Individuals with values outside this range are potentially “non-local”.

There are many reasons animals were moved long distances in the past. An animal could have been brought to the site by humans as a pet, tribute, or exchange item, as has been identified at the ceremonial centers of large sites like Teotihuacan in central Mexico (Sugiyama et al., 2022) and Kaminaljuyu in Guatemala (Sharpe et al., 2022). They may have been transported post-mortem as a material resource, such as an animal skin for clothing, costume, or ornament, representatives of which have been identified in the surviving tribute records like the Codex Mendoza from Mexico (Berdan and Anawalt, 1997). They may have been hunted or fished at a distant location, evidence for the latter having been found throughout the northern Yucatan Peninsula (Jiménez-Cano, 2019; Jiménez-Cano and Masson, 2016). If the animal belonged to a species known to have a broad territorial or home range, such as tapirs (Reyna-Hurtado et al., 2016) or peccaries (Keuroghlian et al., 2004), they may have naturally moved many kilometers during their lifetime. We explore each of these possibilities in this study.

4. Materials and methods

This study examines the enamel of 63 different individual non-human mammals. Of these, 31 are newly tested, and 32 were previously reported in the first isotopic analysis (Sharpe et al., 2018). The 21 additional human molars were previously reported in Inomata et al. (2022).

Animal remains were identified by Sharpe using comparative osteological collections at the Florida Museum of Natural History (USA) and the Smithsonian Tropical Research Institute (Panama). Teeth were photographed and measured prior to sampling. Only teeth that could be securely matched to *different* individuals were used, to avoid accidentally resampling the same individual. We attempted to sample a broad array of species, time periods, and locations at the site, in order to gain a broad understanding of trends across space and time. However, the number of species that were available for analysis differed by time period, likely for reasons inherent in the Maya subsistence and cultural practices over time. For example, there were more dog teeth available in the Preclassic assemblages, as the number of dog remains overall drops by more than half in assemblages dating to the Late and Terminal Classic periods (Sharpe et al., 2020). There were more deer teeth available to test from the Classic period deposits because dense middens containing deer bones were more common near residences at that time.

With the exception of dogs and small rodents, there is a general lack of mammal crania and mandibles across Ceibal during all time periods. This might be due to the ceremonial deposition of crania/mandibles by hunters, often in sacred locations in the forest, as is still done in some areas of the Maya region today (Brown and Emery, 2008; Santos-Fita et al., 2015). The animal crania might also have been used for ornaments or clothing, but if that was the case, these parts were not disposed

of near the excavated portions of the site. We acknowledge that the lack of crania/mandibles, and therefore lack of associated teeth, may lead to sample bias since we do not have as many “wild” animals to test as we do dogs.

Isotopic preparation methods for the animal samples followed those described in Sharpe et al. (2018). Briefly, visible surface contaminants on teeth were cleaned manually with a dental pick and sonication in distilled-deionized water (DI-H₂O). Enamel samples were drilled with a diamond-tipped Brasseler NSK Z500 drill, removing surface residues and dentin. About 30–50 mg of enamel was selected from each tooth, and then divided for either the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analysis or the $^{87}\text{Sr}/^{86}\text{Sr}$ analysis. The sample destined for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analysis was ground using an agate mortar and pestle, switching to a clean set between samples to avoid contamination. Enamel powder was placed in a microcentrifuge tube for 16 h with ~ 1 – 1.5 ml of 2.5 % NaOCl, agitating occasionally, and then rinsed to neutral pH with DI-H₂O. The tubes containing enamel were then filled with ~ 1 – 1.5 ml of 0.2 M acetic acid (CH₃-COOH) for another 16 h, with occasional agitation, and again rinsed to neutral pH afterward. Excess water was removed by a pipette and then samples were frozen before being placed in a freeze dryer for 2–3 days. Samples were then weighed, placed in glass vials and loaded in a Kiel carbonate prep device connected to a Finnegan MAT 252 isotope ratio mass spectrometer at the Light Stable Isotope Mass Spectrometry Laboratory in the Department of Geological Sciences at the University of Florida. One sample from the original isotope study (Specimen 15; Sharpe et al., 2018) was retested for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ at the Washington State University Stable Isotope Core Laboratory, since it had only strontium data previously. The precision for the NBS-19 standard ($n = 20$) was 0.023 ‰ for $\delta^{13}\text{C}$ and 0.041 ‰ for $\delta^{18}\text{O}$ (see Sharpe et al., 2018 for prior NBS-19 precision data).

The enamel samples destined for strontium analysis were sent to the class 100 clean lab at the Department of Geological Sciences at the University of Florida. Samples were weighed and placed in clean Teflon vials and 2 ml of 8 N nitric acid (HNO₃, Optima) solution was added. To obtain Sr concentrations, a small fraction of each solution was removed, following the procedure outlined in Kamenov et al. (2018). Trace elements were analyzed on an Element2 HR-ICP-MS. The remaining portion was placed on a hot plate at 100 °C and evaporated to dryness. The strontium fraction was separated using ion chromatography and a strontium-selective crown ether resin (Sr-spec; Eichrom Technologies) with multiple washes of 3.5 M HNO₃, following Pin and Bassin (1992). Samples were measured with a Nu-Plasma multiple-collector inductively coupled plasma mass spectrometer (MC-ICP-MS). The $^{87}\text{Sr}/^{86}\text{Sr}$ of the NBS 987 standard was 0.710246 ($2\sigma = 0.000030$) for the original pre-2013 sample set (Sharpe et al., 2018). The NBS 987 standard for the new set was 0.710244 ($2\sigma = 0.000028$). A few samples were re-drilled and processed on two separate occasions in order to assess the accuracy of results (see Supplementary Information tables).

5. Results

5.1. Strontium and oxygen analyses

Tooth enamel from a total of 56 different individual animals were tested for their strontium isotopic composition (Fig. 3, Table 2). Additionally, teeth from 63 individual animals were tested for oxygen isotopes, including all individuals that were tested for $^{87}\text{Sr}/^{86}\text{Sr}$. These results represent nine different taxa from the Middle Preclassic through Terminal Classic periods. Table 3 shows the statistical summary of the two most abundant species in the dataset, dogs (45 individuals) and deer (7 individuals). We did not perform a more detailed statistical test of the sample set due to the low number of individuals represented in each taxon category.

A total of 28.6 % ($N = 16$) of the animals analyzed for strontium fall into a $^{87}\text{Sr}/^{86}\text{Sr}$ range of 0.70746–0.70752, considered to be “local” to the immediate vicinity of Ceibal. Using a more general range of

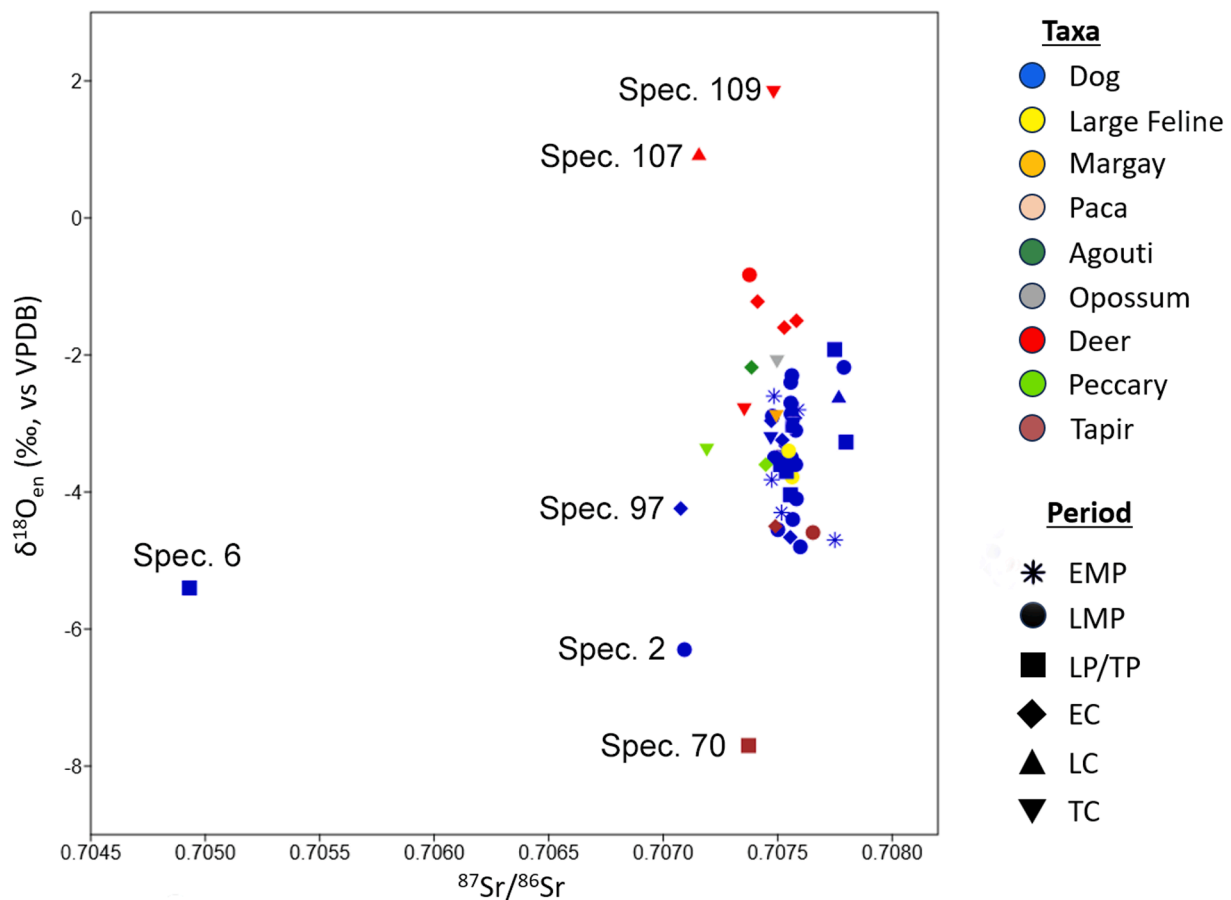


Fig. 3. Strontium and oxygen isotopes from animal tooth enamel at Ceibal, Guatemala. Period designations include: Early Middle Preclassic (EMP), Late Middle Preclassic (LMP), Late Preclassic/Terminal Preclassic (LP/TP), Early Classic (EC), Late Classic (LC), and Terminal Classic (TC).

0.70740–0.70760 representing a broader local region, this proportion becomes 80.4 % (N = 45). Contrary to expectations, the dogs exhibit the most significant variation in $^{87}\text{Sr}/^{86}\text{Sr}$ compared to the local value. A dog that was previously identified as an extreme outlier and non-local individual (Specimen 6, $^{87}\text{Sr}/^{86}\text{Sr} = 0.70493$), sharing a $^{87}\text{Sr}/^{86}\text{Sr}$ value with Guatemala's volcanic highlands (Hodell et al., 2004; Wright et al., 2010), is still the most significant outlier. Interestingly, the second most significant outlier (Specimen 2, $^{87}\text{Sr}/^{86}\text{Sr} = 0.70703$) shares a similar strontium value with a new dog tested from elsewhere at the site (Specimen 97, $^{87}\text{Sr}/^{86}\text{Sr} = 0.70708$). These two dogs, Specimens 2 and 97, match $^{87}\text{Sr}/^{86}\text{Sr}$ values from the southern part of the Peten and Alta Verapaz regions, located in central Guatemala where elevation increases toward the highlands. The low $\delta^{18}\text{O}$ values of these dogs, as well as the possible highland dog (Specimen 6), add further evidence to suggest they are from a more southerly part of Guatemala, and from an area with higher elevation. Five dogs (Specimens 28, 32, 85, 92, and 95), all from different time periods, have slightly elevated $^{87}\text{Sr}/^{86}\text{Sr}$ (0.7077–0.7078). These may have been from sites further to the north of Ceibal, where these higher strontium ratios are most common.

There is some evidence in support of the idea that animals may have been hunted from a region kilometers away from the site. Two deer exhibit elevated $\delta^{18}\text{O}$ values that are statistical outliers compared to other deer in the study (Specimens 107 and 109; $\delta^{18}\text{O} = 0.9\text{‰}$ and 1.8‰ , respectively). One of these (Specimen 107) had a $^{87}\text{Sr}/^{86}\text{Sr}$ value below the local range (0.70716). As was mentioned, mammal skulls besides those of dogs and rodents were exceedingly rare at Ceibal, and thus only a few deer teeth could be tested. The deer from the Early Classic period appear to be local to the Ceibal area. The two Late/Terminal Classic period deer with anomalously high $\delta^{18}\text{O}$ values come from different areas of the site (the Karinel Group and Group D's West Plaza).

The elevated $\delta^{18}\text{O}$ values may be a sign of water stress or drought (Repussard et al., 2014), but may also be an indication that these deer were drinking from an ^{18}O -enriched water source with elevated $\delta^{18}\text{O}$, such as lakes, as their teeth developed. There is already evidence that some water sources in the inland Maya region exhibit elevated $\delta^{18}\text{O}$ values, particularly one of the largest lakes in the Maya lowlands, Peten Itza in northeast Guatemala ($1.5\text{--}2.6\text{‰}$; Scherer et al., 2015; Table 1). These two deer have lower $^{87}\text{Sr}/^{86}\text{Sr}$ than the Peten Itza area (Freiwald et al., 2020; Hodell et al., 2004), so were likely not from such a far distance away. Further testing of the $\delta^{18}\text{O}$ ranges across the inland Maya area is needed to determine the extent of variability in the area.

Many of the other non-domestic animals at Ceibal have slightly lower $^{87}\text{Sr}/^{86}\text{Sr}$ than the expected 0.7074–0.7076 range. These include a peccary (Tayassuidae), an agouti (*Dasyprocta punctata*, a housecat-sized rodent), and a tapir (*Tapirella bairdii*). In the case of the tapir (Specimen 70), one of three tested, this individual also had the lowest $\delta^{18}\text{O}$ value of any animal in the sample set (-7.7‰). This tapir was previously reported in an earlier study (Sharpe et al., 2018), and it was posited that it may have come from an area slightly to the south or west of Ceibal. The unusually low $\delta^{18}\text{O}$ value may be a product of tapirs' natural propensity for spending most of their time in the water (DeSantis, 2011). Two new tapir enamel values show that, while tapirs may have lower $\delta^{18}\text{O}$ compared to the other mammals (-4.6‰ and -4.5‰), they are not outliers compared to the rest of the animal sample set. The tapir with exceedingly low $\delta^{18}\text{O}$ is likely a non-local individual.

5.2. Carbon and oxygen isotope assessment of diet

Carbon and oxygen isotopes were obtained from the same sample set of 63 individuals (Fig. 4, Table 2). There appear to be two distinct groups

Table 2

Carbon, oxygen, and strontium isotope results from archaeological animal tooth enamel at Ceibal, Guatemala. See Supplementary Information section for more information for each specimen. Specimen numbers follow order from Sharpe et al. (2018).

Specimen No.	Scientific Name	Common Name	Location at Site	Period	$\delta^{13}\text{C}$ (‰, vs VPDB)	$\delta^{18}\text{O}$ (‰, vs VPDB)	$^{87}\text{Sr}/^{86}\text{Sr}$
2a	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Middle Preclassic	n/a	n/a	0.707026
2b	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Middle Preclassic	-2.5	-6.3	0.707093
4	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Middle Preclassic	-3.9	-4.8	0.707599
6a	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Preclassic	-2.7	-5.4	0.704931
6b	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Preclassic	n/a	n/a	0.705007
7	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Early Middle Preclassic	-9.0	-2.6	0.707484
9	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Early Middle Preclassic	-9.0	-3.4	0.707529
11	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Middle Preclassic	-9.2	-4.4	0.707566
13	<i>Canis lupus familiaris</i>	Domestic Dog	Jul Group	Late Middle Preclassic	-6.4	-2.7	0.707557
15	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Preclassic	-2.9	-2.7	0.707575
17	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Middle Preclassic	-4.2	-3.5	0.707560
18	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Middle Preclassic	-2.3	-3.5	0.707535
19	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Middle Preclassic	-8.5	-3.5	0.707486
20	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Middle Preclassic	-8.9	-2.3	0.707562
21	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Middle Preclassic	-4.8	-3.1	0.707579
22	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Preclassic	-2.4	-3.6	0.707513
23	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Middle Preclassic	-3.5	-4.1	0.707582
24	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Middle Preclassic	-6.0	-2.4	0.707557
25	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Early Middle Preclassic	-8.9	-3.5	0.707516
26	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Early Middle Preclassic	-7.7	-4.3	0.707517
28	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Classic	-3.2	-2.6	0.707767
29	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Terminal Preclassic	-4.2	-3.7	0.707538
30	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Late Middle Preclassic	-2.0	-3.6	0.707579
31	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Early Middle Preclassic	-5.0	-2.8	0.707590
32	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Early Middle Preclassic	-5.9	-4.7	0.707750
35	<i>Felidae (Panthera onca?)</i>	Large Feline (Jaguar?)	Group A	Late Middle Preclassic	-8.4	-3.4	0.707548
37	<i>Leopardis wiedii</i>	Margay	Group A	Terminal Classic	-15.1	-2.9	0.707494
53	<i>Odocoileus virginianus</i>	White-tailed Deer	Group A	Early Classic	-13.7	-1.6	0.707529
54	<i>Odocoileus virginianus</i>	White-tailed Deer	Group A	Early Classic	-12.8	-1.5	0.707582
55	<i>Odocoileus virginianus</i>	White-tailed Deer	Group D	Terminal Classic	-13.9	-2.8	0.707354
68	<i>Tayassuidae</i>	Peccary	Group A	Early Classic	-6.7	-3.6	0.707448
70	<i>Tapirella bairdii</i>	Baird's Tapir	Group A	Late Preclassic	-16.4	-7.7	0.707373
71	<i>Tapirella bairdii</i>	Baird's Tapir	Karinel Group	Early Classic	-14.0	-4.5	0.707490
73	<i>Philander opossum</i>	Gray four-eyed opossum	Group A	Terminal Classic or later	-13.5	-2.1	0.707497
81	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Middle Preclassic	-4.97	-3.80	n/a
82	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Late Middle Preclassic	-11.27	-2.89	0.707477
83	<i>Canis lupus familiaris</i>	Domestic Dog	Group A	Early Middle Preclassic	-4.13	-3.82	0.707474
84	<i>Canis lupus familiaris</i>	Domestic Dog	Group D	Terminal Classic	-0.31	-2.43	n/a
85	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Late Middle Preclassic	-9.55	-2.18	0.707789
86	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Late Middle Preclassic	-4.28	-2.86	0.707558
87	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Early Classic	-3.78	-2.96	0.707472
88	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Early Classic	-2.65	-4.66	0.707555
89	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Late Middle Preclassic	-8.34	-2.38	n/a
90	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Early Classic	-2.88	-3.24	0.707520
91	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Late Middle Preclassic	-5.14	-4.55	0.707501
92	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Late Preclassic?	-9.07	-1.92	0.707749
93	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Late Middle Preclassic	-6.48	-4.83	n/a
94	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Late Classic	-2.32	-3.20	n/a
95	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Terminal Preclassic	-5.80	-3.27	0.707799
96	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Early Classic	-3.77	-2.65	n/a
97	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Early Classic	-1.76	-4.24	0.707077
98	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Early Classic	-4.41	-3.06	n/a
99	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Late Preclassic?	-6.84	-4.04	0.707556
100	<i>Canis lupus familiaris</i>	Domestic Dog	Karinel Group	Early Classic	-5.10	-2.92	0.707576
101	<i>Canis lupus familiaris</i>	Domestic Dog	Amoch Group	Early Classic	-1.93	-3.56	0.707535
102	<i>Canis lupus familiaris</i>	Domestic Dog	Group D	Terminal Classic?	-4.80	-3.22	0.707470
103	cf. <i>Panthera onca</i>	Jaguar	Karinel Group	Late Middle Preclassic	-14.49	-3.78	0.707563
104	<i>Cuniculus paca</i>	Lowland Paca	Karinel Group	Early Classic	-16.26	-3.47	0.707500
105	<i>Dasyprocta punctata</i>	Central American Agouti	Karinel Group	Early Classic	-8.73	-2.18	0.707386
106	<i>Odocoileus virginianus</i>	White-tailed Deer	Karinel Group	Late Middle Preclassic	-14.9	-0.83	0.707377
107a	<i>Odocoileus virginianus</i>	White-tailed Deer	Karinel Group	Late Classic	-14.34	0.94	0.707156
107b	<i>Odocoileus virginianus</i>	White-tailed Deer	Karinel Group	Late Classic	-14.21	0.11	n/a
108	<i>Odocoileus virginianus</i>	White-tailed Deer	Karinel Group	Early Classic	-15.92	-1.22	0.707412
109	<i>Odocoileus virginianus</i>	White-tailed Deer	Group D	Late/Terminal Classic	-14.30	1.83	0.707482
110	<i>Tapirella bairdii</i>	Baird's Tapir	Karinel Group	Late Middle Preclassic	-14.63	-4.59	0.707654
111	<i>Tayassuidae</i> cf. <i>Dicotyles tajacu</i>	Collared (?) Peccary	Karinel Group	Terminal Classic	-6.77	-3.39	0.707190

Table 3
Descriptive statistics of the dog and deer tooth enamel isotopes by chronological period. Period designations include: Early Middle Preclassic (EMP), Late Middle Preclassic (LMP), Late Preclassic/Terminal Preclassic (LP/TP), Early Classic (EC), and Late Classic/Terminal Classic (LC/TC).

		$\delta^{13}\text{C}_{\text{en}}$ (‰, vs VPDB)			$\delta^{18}\text{O}_{\text{en}}$ (‰, vs VPDB)			$^{87}\text{Sr}/^{86}\text{Sr}$		
		Mean	sd	Range	Mean	sd	Range	Mean	sd	Range
EMP	Dogs (7)	-7.1	2.1	-9.0 to -4.1	-3.6	0.8	-4.7 to -2.6	0.70755	9.5x10-5	0.70747 to 0.70775
LMP	Dogs (19)	-5.9	2.7	-11.3 to -2.0	-3.6	1.1	-6.3 to -2.2	0.70751 (of 17)	1.8x10-4	0.70703 to 0.70779
	Deer (1)	-14.9	n/a	n/a	-0.8	n/a	n/a	0.70738	n/a	n/a
LP/TP	Dogs (7)	-4.9	2.3	-9.1 to -2.4	-3.5	1.0	-5.4 to -1.9	0.70724	1.0x10-3	0.70493 to 0.70780
EC	Dogs (8)	-3.3	1.2	-5.1 to -1.8	-3.4	0.7	-4.7 to -2.7	0.70746	1.9x10-4	0.70708 to 0.70758
	Deer (3)	-14.1	1.6	-15.9 to -12.8	-1.4	0.2	-1.6 to -1.2	0.70751	8.9x10-5	0.70741 to 0.70758
LC/TC	Dogs (4)	-2.7	1.9	-4.8 to -0.3	-2.9	0.4	-3.2 to -2.4	0.70762 (of 2)	2.1x10-4	0.70747 to 0.70778
	Deer (3)	-14.2	0.2	-14.3 to -13.9	0	2.5	-2.8 to 1.8	0.70733	1.6x10-4	0.70716 to 0.70748

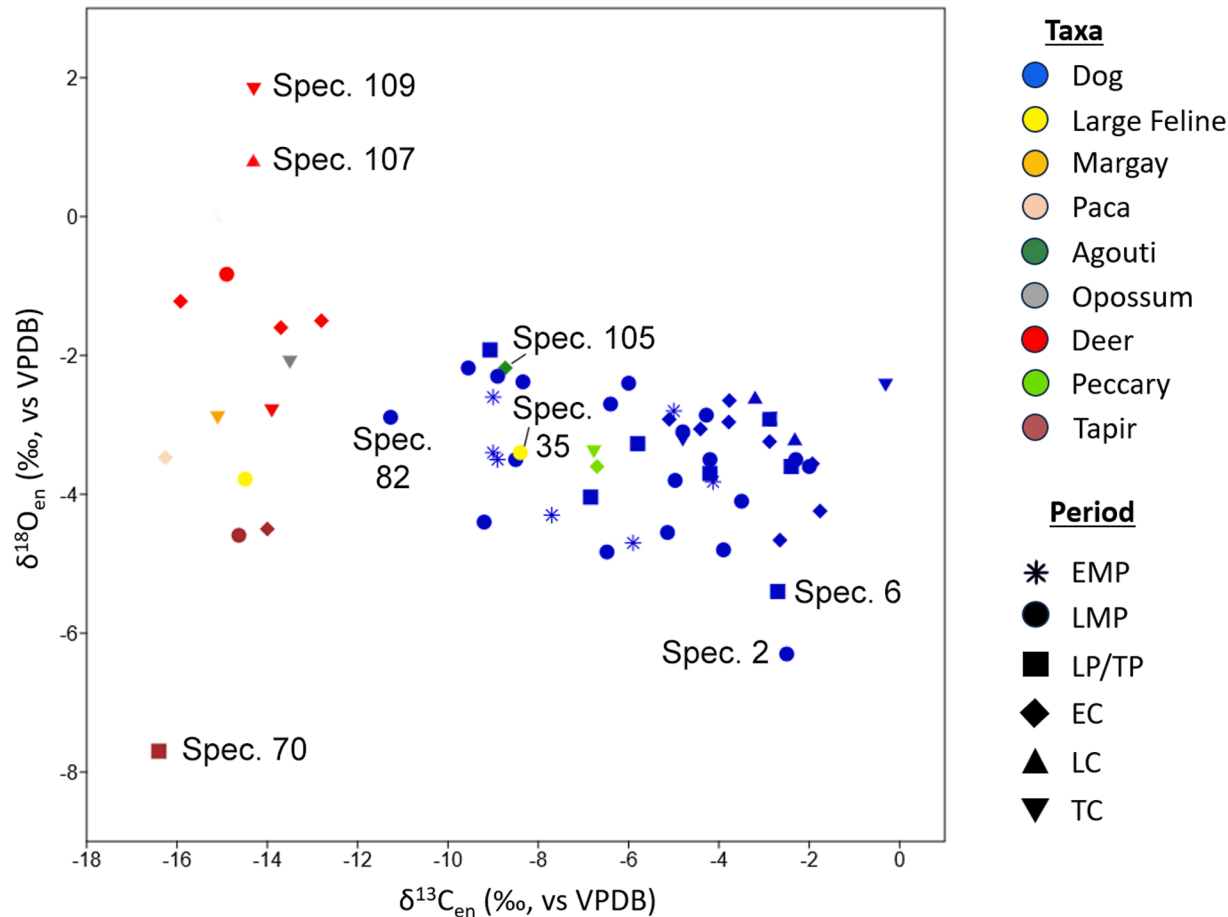


Fig. 4. Carbon and oxygen isotopes from animal enamel at Ceibal, Guatemala. Period designations include: Early Middle Preclassic (EMP), Late Middle Preclassic (LMP), Late Preclassic/Terminal Preclassic (LP/TP), Early Classic (EC), Late Classic (LC), and Terminal Classic (TC).

in the $\delta^{13}\text{C}$ data, above and below -10‰ . The group exceeding -10‰ , which includes all dogs, both peccaries, the agouti, and one large feline, were likely consuming a regular or semi-regular diet of C_4 plant species. All other animals appear to have been consuming a predominantly C_3 diet. One dog (Specimen 82) has a $\delta^{13}\text{C}$ value of -11.3‰ , falling between both groups; it may have been consuming less maize than the other dogs.

The $\delta^{18}\text{O}$ values of most animals appear to be determined by their species' drinking behavior and location of origin. There is no evidence that the deer were directly fed maize by humans, as their $\delta^{13}\text{C}$ values are below -10‰ and do not overlap with the dogs. We can therefore conclude that the deer with elevated $\delta^{18}\text{O}$ values are a product of natural drinking behavior, and likely not a direct influence by humans. The dogs, conversely, all have elevated $\delta^{13}\text{C}$ values, suggesting they

consumed maize to varying extents. They likely relied on the humans at Ceibal for subsistence, and their $\delta^{18}\text{O}$ values reflect what they were drinking at the site. The only exceptions would be those dogs with non-local $^{87}\text{Sr}/^{86}\text{Sr}$ values; the dogs with the lowest $^{87}\text{Sr}/^{86}\text{Sr}$ (Specimens 2 and 6) had lower $\delta^{18}\text{O}$ than the other dogs ($<-5\text{‰}$), indicating that the water sources they had used during enamel growth were non-local. The omnivores (peccaries, opossums, agoutis) have $\delta^{18}\text{O}$ values comparable with the dogs. In the case of the two large felines, one with low $\delta^{13}\text{C}$ (-14.5‰) and one with elevated $\delta^{13}\text{C}$ (-8.4‰), both had comparable $\delta^{18}\text{O}$ values (-3.8‰ and -3.4‰ , respectively). A margay (*Leopardus wiedii*) with low $\delta^{13}\text{C}$ (-15.1‰) also had comparable $\delta^{18}\text{O}$ (-2.9‰). This suggests that many carnivores and omnivores may have similar $\delta^{18}\text{O}$ values in the area, regardless of whether they lived in captivity or not, although herbivores (tapirs, deer) appear to have more variable $\delta^{18}\text{O}$

dependent on their species.

5.3. Comparison of Ceibal human and dog diets

When we compare the 45 dogs with enamel $\delta^{13}\text{C}$ data at Ceibal with the third molar data of 21 humans, a distinct temporal trend emerges (Fig. 5; Supplementary Information Table 2). As has been noted from ongoing isotope analyses of the humans at Ceibal (Inomata et al., 2022; Palomo, 2020), the proportion of maize in the diet appears to increase over time. Combined with the dog data, however, we see that not only do dog and human diets shift increasingly toward a diet dominated by maize, but that the shift is most noticeable during the Preclassic/Classic transition (c. 250 CE). Furthermore, our data show that the increase in maize consumption is temporally offset between the dogs and humans, which is surprising if the dogs were presumably eating the residues of human food.

During the early Middle Preclassic (1000 – 700 BCE), human and dog diets mostly overlap, with dogs consuming lower quantities of maize on average than humans. A shift occurs in the late Middle Preclassic period (700 – 350 BCE), as dogs begin to consume more maize, and humans, surprisingly, do not. The difference between dog and human diets is still not statistically different ($p = 0.13$ using Student's t -test), but the range of variation is much more distinct between the two than in other periods. The trend indicates that the shift toward maize consumption appears chronologically earlier in dogs than in humans during the later part of the Middle Preclassic period.

The Late/Terminal Preclassic period (350 BCE – 250 CE) had the greatest variability in both human and dog diets, compared to other periods in Ceibal's history. Dogs continue to increase in their

dependency on maize in their diet, but although humans generally follow suit, there is more variability in the human dietary proportion of maize. This suggests the shift toward a maize-focused diet was not consistent among everyone during this period (although a larger sample set would no doubt reveal more nuances to this trend). By the Early Classic period (250 – 600 CE), all dogs have a $\delta^{13}\text{C}$ value exceeding -6‰ . All of these dogs were found at either the Karinel or Amoch Groups of the periphery, rather than the center of the site, which was mostly abandoned at this time. No human third molar data are available yet to compare from this period. Late and Terminal Classic (600 – 950 CE) humans and dogs both have elevated $\delta^{13}\text{C}$ values and continue to overlap, but humans possess a more restricted $\delta^{13}\text{C}$ range in their diets (-3.5‰ to -1.2‰ as opposed to -4.8‰ to -0.3‰ for dogs).

6. Discussion

The isotopic results of the animals from Ceibal reflect broad socio-political and economic changes in the Maya world over a period of two thousand years. In order to interpret patterns evident in the data, it is necessary to understand what was happening within the Ceibal community during the periods when these animals were hunted, reared, or transported to the site. The following sections compare the mobility and dietary data from a temporal perspective.

6.1. Animal mobility and interregional exchange at Ceibal

At the start of the study, we predicted that we would see more non-local animals brought to Ceibal during the two periods of the site's greatest population growth, being the later part of the Preclassic period

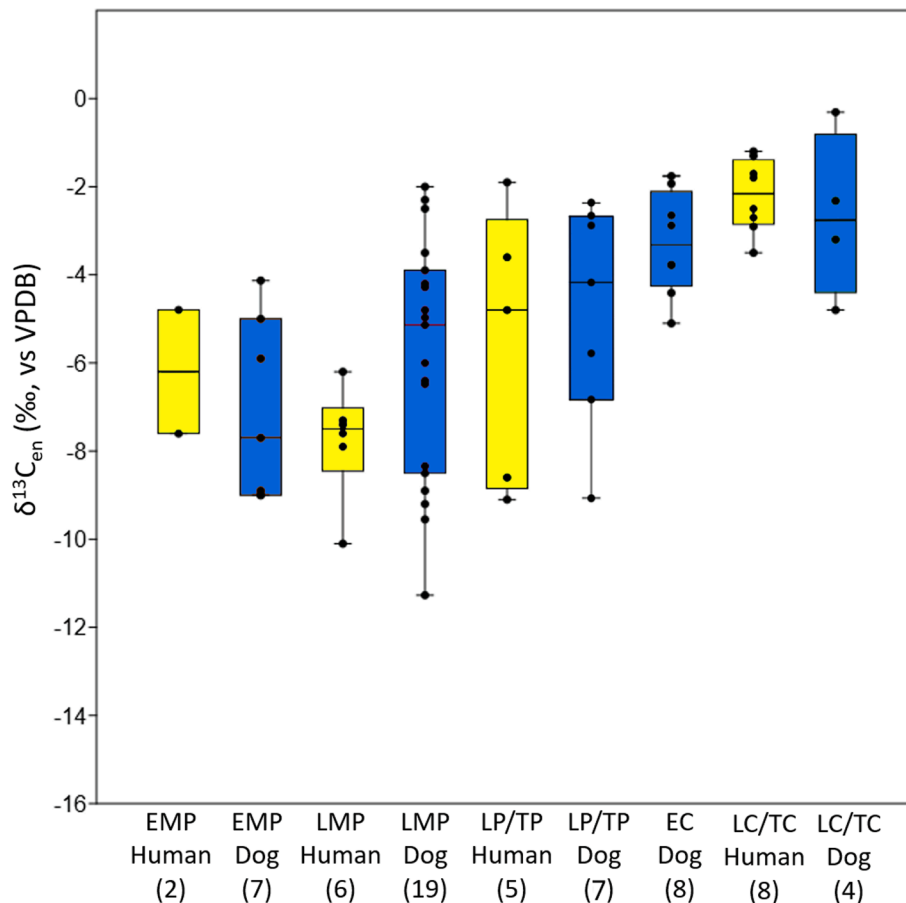


Fig. 5. Comparison of human and dog $\delta^{13}\text{C}$ enamel values over time. Box plots include the 25–75% quartile range, with the interior horizontal line indicating the median. Parentheses indicate the number of sampled specimens. Period designations include: Early Middle Preclassic (EMP), Late Middle Preclassic (LMP), Late Preclassic/Terminal Preclassic (LP/TP), Early Classic (EC), and Late Classic/Terminal Classic (LC/TC).

and the end of the Late Classic and Terminal Classic periods. Instead, the strontium and oxygen isotope data at Ceibal show that non-local animals were moved to the site by humans at various times throughout the site's history, and from different directions.

A growing number of animal isotope projects in the Maya region have begun to show two remarkable patterns: first, non-local mammals (or their products) appear at both Preclassic and Classic sites (Rand et al., 2020, 2021; Sharpe et al., 2018, 2022; Sugiyama et al., 2018; Thornton, 2011), and second, non-local animals often appear in ritually significant and ceremonial deposits (e.g., caches, dedicatory offerings, human burials). The first point reflects the mobility of human populations in the Maya area over time (Ebert et al., 2021; Locker et al., 2023; Price et al., 2010, 2015, 2019; Wright, 2005, 2012; Wright et al., 2010), where in all periods humans had the tendency to move and resettle many kilometers' distant from the place where they were born. Animal remains with non-local signatures are indicative of the movement of people (for example, of dog-owners) and also their close interactions across long distances through trade (for example, of non-domestic animals or their products such as teeth or skins). This also follows patterns observed in the number and variety of marine shells apparent at sites throughout the Maya region; at Ceibal, for example, marine shells from the Caribbean are most common in the later Middle Preclassic and Terminal Classic, but they can be found across the site at every period (Sharpe, 2019).

When the Maya began to transition to sedentary settlements following the advent of ceramic technology during the Early Preclassic/Middle Preclassic transition, they continued to maintain contact with other communities near and far. At least one of Ceibal's non-local dogs dates to the Middle Preclassic period (Specimen 2), and the dog that may have come from the highlands dates to the Late Preclassic period (Specimen 6). Dogs may have come with their human owners, unless they were transported specifically for an economic or ceremonial purpose. The movement of dogs may have been related to the obsidian exchange network from its source in the volcanic highlands (Aoyama, 2017), although at present this link is unclear.

During the Classic period, a few of the wild animals may have been hunted from other locations and brought back to the site, and some of the dogs do not appear to have come from the immediate area around Ceibal; however, no mammals in the Classic period appear to have come from regions a hundred or more kilometers away, as they had done in the Preclassic. This is contrary to what we anticipated at the start of the study, for the Classic period was the height of Maya urbanization in the Guatemala lowlands, and human and animal movements have been identified at other Classic sites (Rand et al., 2020, 2021; Somerville et al., 2016; Thornton, 2011; Wright, 2012). Ceibal, located in the far interior of Guatemala and politically subservient to larger centers throughout much of the Classic period (Bazy and Inomata, 2017), may not have been as actively involved in animal resource exchange during that time. It is possible that the lack of non-local, Classic period mammals is due to sample bias since no mammals directly associated with a ceremonial context were tested from the Classic period, but since mammals from elite contexts were tested (Group D and the Group A royal palace) where ceremonies likely took place, we believe this is evidence that mammals were not as frequently moved to the site during this time.

Many, but not all, of the non-local animals at Ceibal come from unique deposits. Two previously-identified non-local Preclassic dogs (Specimens 2 and 6) were found in two of the largest and oldest pyramids at the ceremonial center of the site (Strs. A-10 and A-18). However, newly identified non-local dogs and other species come from all parts of the site, including the Karinel residential group, and not from special deposits. All mammals recovered in the immediate vicinity of the Terminal Classic palace, including the palace middens, were apparently local. Interestingly, marine shells, and even sea urchins and a shark tooth, have been recovered in the palace deposits (Sharpe, 2019; Sharpe et al., 2020). The ruling elite had access to non-local taxa, but these

apparently did not include mammals during the Classic period.

Another interesting trend that emerged from the mammal dataset is that, unlike the marine shells that mainly came from the Caribbean (Sharpe, 2019), most non-local mammals came from the south and west. None of the mammals thus far tested isotopically at Ceibal match the elevated $^{87}\text{Sr}/^{86}\text{Sr}$ values diagnostic of the northern Maya lowlands or Belize (>0.7080). The dogs with $^{87}\text{Sr}/^{86}\text{Sr}$ values above 0.7077 may have come from the northern or eastern parts of Guatemala; significantly, these dogs span all periods of Ceibal's history, and may have come to the site for different reasons. Animal mobility at Ceibal therefore appears to have been focused on interactions with communities to the south and west of the site, as opposed to the densely-populated northeast.

The possibility that animals came from the southwest during the Preclassic period coincides with extensive evidence for obsidian access and blade production at Ceibal at that time (Aoyama, 2017). During the later Middle Preclassic, evidence for obsidian blade production and the ceremonial interment of exhausted obsidian cores indicate strong socioeconomic ties existed between the inhabitants of Ceibal and those in control of the obsidian sources in the Guatemalan highlands (Aoyama et al., 2017). The exchange of animals and their products may have been part of this same trade network.

6.2. Maize consumption among animals at Ceibal

Ceibal lies in the humid forested lowlands of north-central Guatemala, besides the Pasión River and expansive wetlands to the east; there are no immediate savannas in the vicinity, although much of the region outside the natural park is deforested for cattle ranching today. Extensive surveys over the last 50 years as well as very recent and intensive LiDAR mapping efforts reveal a lack of residential and monumental construction beyond the site limits (Inomata et al., 2018). Therefore, we can assume that much of the region around Ceibal was forested or agricultural land in the past. Areas used in *milpa* farming (mixed-crop farming on minimally cleared lands) would have included extensive maize planting, likely a primary source of C_4 plants in the local animal diet. Wild animals may have foraged along the borders of the *milpa* fields and in household gardens. The wetlands across the river immediately east of the site would have limited much of this agricultural activity to the southwest, including the area between Ceibal, Caobal, and other smaller satellite sites in the region.

Animals with elevated $\delta^{13}\text{C}$ enamel values at Ceibal include an agouti, two peccaries, and a jaguar. The agouti (Specimen 105) and one of the peccaries (Specimen 111, possibly a collared peccary due to the shape and size of the canine tooth) have $^{87}\text{Sr}/^{86}\text{Sr}$ values that fall below the "local" range of the Ceibal area (0.70739 and 0.70719, respectively). Collared and white-lipped peccaries can have home ranges that vary in size according to local ecology, seasonal variability, and group dynamics; generally, they range within several square kilometers per year, with herds of white-lipped peccaries roaming greater distances (Charre-Medellín et al., 2018; Hofman et al., 2016; Hurtado et al., 2020; Keuroghlian et al., 2004). Agoutis have small home ranges, often within a square kilometer (Aliaga-Rossel et al., 2008). Thus, these two individuals were likely hunted or managed elsewhere before being moved to Ceibal, although it is possible the peccary had roamed naturally during its life.

Both peccaries and agoutis are omnivores, with mixed diets. Agoutis prefer fruits, seeds, and leaves; they frequently live near residences today and consume organic vegetable waste from cooking activities tossed outdoors (personal observation from the first author, who regularly watches agoutis scavenge from neighbors' compost). Although collared peccaries generally avoid humans, they are known to forage in gardens, occasionally entering urbanized zones. Thus, both of these individuals may have been living near human agricultural fields, but not at Ceibal. Interestingly, the Karinel Group dog with the unusually low $^{87}\text{Sr}/^{86}\text{Sr}$ value (Specimen 97) was found in the same deposit as the

agouti, dated to the same ceramic phase. It is possible that there is an association between the two. The peccary came from a nearby part of the same residential group, but from a later occupational period.

Regarding the two peccaries, it is unclear if their elevated $\delta^{13}\text{C}$ values are the result of direct human influence (i.e., feeding in captivity) or opportunistic foraging in maize crops. There are few comparable $\delta^{13}\text{C}$ values from peccary enamel in the Maya lowlands (van der Merwe et al., 2000) report a value of -13.8‰ for one tooth from Cuello, Belize). Peccary bones have been tested for $\delta^{13}\text{C}$ values previously at Ceibal (Sharpe et al., 2018), and indicate diets that vary from full C_3 -based to partial C_4 influence (collagen $\delta^{13}\text{C} = -22.3\text{‰}$ to -14.4‰). Due to the complex omnivorous habits of peccaries, it is important that more isotopic research be done on this taxon, to be able to distinguish the possibility of maize-feeding from captivity in their diets.

The large feline with the elevated $\delta^{13}\text{C}$ value was reported previously (Sharpe et al., 2018), and its significance can now be interpreted within a larger dataset. Although this value may be the result of a carnivore feeding on other animals that foraged in maize fields (Sugiyama et al., 2020), there are several reasons to believe this individual was reared in captivity. First, both the tooth and bone $\delta^{13}\text{C}$ values of the animal were elevated ($\delta^{13}\text{C}_{\text{en}} = -8.4\text{‰}$; $\delta^{13}\text{C}_{\text{col}} = -15.2\text{‰}$). This implies that the animal consumed a consistent diet throughout its life. The majority of non-domestic species at Ceibal consumed a predominantly C_3 diet, including all the deer. Second, the other wild cats tested from Ceibal have consistently low $\delta^{13}\text{C}$ values, including a jaguar from the Karinel Group dating to the same period (late Middle Preclassic). Lastly, the feline's mandible was recovered from a unique deposit of concentrated artifacts in the core of Str. A-18, which also included one of the non-local dogs (Specimen 2). This concentration of fauna may have been refuse from an event or activity at the ceremonial center of the site. It would seem more likely that the feline was captured while young, and perhaps was reared on meat from dogs, which have sufficiently high $\delta^{13}\text{C}$ values to maintain an elevated $\delta^{13}\text{C}$ in a carnivore.

6.3. Comparing dog and human diets

The development of maize agriculture and its cultural significance in the Maya region was a long and complex story (Ebert et al., 2021; Kennett et al., 2020, 2022; White, 2005; White et al., 2010). Based on $\delta^{13}\text{C}$ data from humans in the lowland Maya area and at Ceibal, we know that maize dependency increased over time, with individuals from the Late and Terminal Classic period consuming a near-100 % maize diet (Inomata et al., 2022; Palomo, 2020; White et al., 2010). We would therefore anticipate the diets of domestic dogs, presumably dependent on humans for food, to reflect the isotopic trends of humans over time. The tendency for dog diets to reflect that of humans in a community is so widespread that archaeologists have developed the “canine surrogacy approach”, which is a method used to predict human diets from the isotopic values of dogs at the same site (Guiry, 2012, 2013). While not without caveats (Hart, 2023; Perri et al., 2019), the method has been used increasingly since its introduction, especially at sites where there are many dog remains but far fewer humans.

Interestingly, Ceibal appears to be a case where the surrogacy approach works in a general sense, and better in some time periods than others. While a larger dataset is needed, the results of Fig. 5 show that human and dog diets were not entirely consistent during the Preclassic period. Maize did not yet comprise the majority of human diets in the Middle Preclassic period. Dogs, however, started to consume maize more consistently before humans during the late Middle Preclassic. By the Late Preclassic period, dogs and humans consumed similar amounts of maize, although individual diets for both were highly variable. Only during the Classic period did both dogs and humans consume maize on a regular basis.

What is the reason for this dietary difference during the Middle Preclassic? We suspect it may have to do with the role of dogs in Maya society. As was previously reported at Ceibal (Sharpe et al., 2020), dogs

were fairly numerous during the Middle Preclassic through Early Classic components of the site's history. During the Late and Terminal Classic period, there were overall fewer dogs. A general trend toward fewer dogs in the Classic period has been noted across the Maya region (Cunningham-Smith et al., 2020). Dogs were likely consumed as food at least part of the time during the Preclassic period, and were possibly used for ceremonial purposes as well. A recent analysis of Middle Preclassic middens and crafting activities at Ceibal revealed that all cut marks resembling “butchery” activity were found on dogs, although in later periods such cut marks could be found on other species as well (Sharpe and Aoyama, 2023). We propose that the dogs reared by the Preclassic Ceibal inhabitants were fed proportionally more maize than humans at that time, likely processed in the form of a bread (e.g., tortillas, tamales) or gruel, perhaps as a means to fatten them before consumption. This practice appears to have begun in the latter part of the Middle Preclassic, as Ceibal's population was growing. Although the human consumption of dogs reared on maize may have elevated $\delta^{13}\text{C}$ values, it appears that, at least during the Preclassic, humans were consuming more C_3 plant species relative to maize than they were in later periods. We also do not know how common dog consumption was on a daily basis, although the proportional lack of deer and other game animals compared to dogs in the Preclassic period suggests that dogs were a principal source of mammal meat.

7. Conclusions

A review of the enamel isotopes at Ceibal over a period of two thousand years reveals new information concerning subsistence and interregional exchange at a site located in the center of the Maya world. During the Middle Preclassic period, maize did not yet dominate human diets, and dogs were provisioned with greater quantities of maize than humans consumed. This was likely because dogs were a major meat source at that time. Dogs were such a significant part of the Maya livelihoods during the Preclassic that some were transported from considerable distances to Ceibal's site core. We do not yet know why dogs would be moving such great distances, but it may have been due to the mobility of humans at that time. During the Middle and Late Preclassic periods, Ceibal was a major ceremonial center in the southern lowlands. Important resources such as obsidian and greenstone were brought to the site in considerable quantities. Individuals transporting these items may have also brought their dogs.

By the Late and Terminal Classic periods, the inhabitants of Ceibal depended more on deer hunted from the forest and perhaps agricultural fields than dogs for their terrestrial meat source. Based on the broad spread of oxygen values of deer at this time, it would appear that deer were hunted from different locations, not in the immediate vicinity of Ceibal but perhaps in the lowlands nearby. This may have been done with hunting parties moving further and further away from the urbanized areas, or through trade or tribute with neighboring sites. Interestingly, there is a distinct absence of non-local mammals originating from great distances in the Classic period, despite the fact that Ceibal was a regional capital during the Terminal Classic.

This study has shown that Preclassic and Classic Maya populations had different subsistence practices. This revelation is not new; a number of other studies have shown that there is no consistent Maya “diet”, and that both cultivation strategies and hunting/fishing activities varied across the landscape and through time. It is likely that such variations were the product of technological adaptations to local habitat and landscape differences, as well as regional cultural trends that depended on greater or lesser degrees of interaction with other sites. With every new study, we move closer toward defining the intricacies of these variations across space and time.

CRedit authorship contribution statement

Ashley E. Sharpe: Writing – review & editing, Writing – original

draft, Visualization, Validation, Supervision, Software, Resources, Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration. **Juan Manuel Palomo:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Takeshi Inomata:** Writing – review & editing, Validation, Resources, Project administration, Investigation. **Daniela Triadan:** Writing – review & editing, Validation, Resources, Project administration, Investigation. **Flory Pinzón:** Writing – review & editing, Validation, Resources, Project administration, Investigation. **Jason Curtis:** Formal analysis, Validation, Writing – review & editing. **Kitty Emery:** Funding acquisition, Validation, Writing – review & editing. **George Kamenov:** Formal analysis, Methodology, Supervision, Validation, Writing – review & editing. **John Krigbaum:** Methodology, Resources, Supervision, Validation, Writing – review & editing. **Jessica MacLellan:** Resources, Validation, Writing – review & editing. **María Paula Weihmüller:** Formal analysis, Investigation, 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.

Data availability

All data used in the article is in the text/tables or Supplemental files.

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Appendix A. Supplementary data

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