NOT BY MAIZE ALONE: ASSESSING THE EFFECTS OF TEMPORAL, GEOGRAPHIC, AND CULTURAL VARIABILITY ON A STABLE ISOTOPE MIXING MODEL OF ANCIENT MAYA DIETS

A Dissertation

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ABSTRACT

Bayesian stable isotope mixing models (SIMMs) and stable sulfur isotope analysis have seen increasing utilization in the study of ancient diets and foodways in recent years. However, the latter has only recently seen usage in understanding diets of the Ancient Maya of Central America, and the former not at all. This is despite the long history of stable isotope investigation of human remains in the region. Uptake of these techniques in the field has largely been limited on two fronts - a lack of a suitable sulfur isotope baseline (which has only recently seen publication) and the inherent difficulties of using SIMMs in circumstances where both C3 and C4 cultigens formed substantial elements of human diet. While the requisite information to use both techniques to their full potential remains a work in progress, several unknowns can currently be rectified using existing data. These include the degree to which culturally specific preparation practices affect the nutritional (and potentially isotopic) composition of key foods (particularly maize), the degree to which modern cultigens can appropriately serve as proxies for foods consumed, and the degree of regional specificity required when using sulfur isotopes for dietary reconstruction. This dissertation will explore all three of these problems by comparing diet compositions of a sample of Ancient Maya individuals derived from a Bayesian mixing model (Food Reconstruction Using Isotope Transfer Signals) incorporating nixtamalized and raw maize, regionally derived and modern/industrialized plant food proxies, and local vs. pan-Mesoamerican sulfur isotope baselines.

DEDICATION

To Betsy, Lew, and Anson, for making it worth it.

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Data not obtained solely for this dissertation by the student is cited to published sources in the References Cited section. Unpublished data was kindly made available by Dr. Erin Kennedy Thornton (Dept. Of Anthropology, Washington State University, Pullman) and was obtained through a collaborative project with Dr. Lori Wright and is cited as Thornton & Wright (n.d.). Further unpublished strontium isotope data was made available by Dr. Lori Wright and is cited as Wright (n.d.).

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CHAPTER I: INTRODUCTION

Stable isotope analysis (SIA) of archaeological skeletal material has a long history of use in the Americas and the Maya region in particular as a means to assess patterns of diet in ancient populations (Wright, 2004). The application of stable isotope techniques has become so common for skeletal remains excavated from Maya sites that at present, large-scale questions of diet can be investigated at a regional level using little more than already published data (e.g., Rand, Healy, & Awe, 2013)(Somerville et al., 2013).

I see two reasons for this wide application of SIA to the Maya region, one theoretical and one methodological. The roots of the theoretical interest in Maya diets are perhaps best understood in the context of mid-twentieth-century neo-cultural evolutionism. Maya civilization seemed to be a prehistoric global oddity, in that it is one of the few complex societies to emerge in a tropic lowland forest environment (Curtis et al., 1998). This contradicted proposed theories of the role of the environment in "limiting" cultural development (i.e., Meggers, 1954). Thus, much of the earliest investigations into ancient Maya diet and health by processual bioarchaeologists were informed by this framework. These studies, and particularly that of Haviland (1967), sought to investigate the degree of the Maya's "adaptation" to their environmental conditions as evidenced by their overall level of health and dietary quality.

As a matter of course, much of the more adaptationist perspectives faded, but this initial interest in studying ancient Maya diet is what first attracted the use of SIA. The methodological appeal of SIA – and particularly stable carbon analysis – is due to its relative effectiveness in identifying patterns of maize consumption. Maize subsistence is particularly amenable to investigation because it is one of the few domesticated staple crops (and the only one in pre-

European contact Mesoamerica) that utilizes the Hatch-Slack (C4) photosynthetic pathway for carbon fixation. In this pathway, relatively more of the heavy carbon isotope, ^{13}C, is integrated into the plant's tissues, giving it a distinct isotopic signature. When humans rely on maize as a staple food, they –through the uptake and integration of maize carbon– will be similarly enriched in the carbon isotope signature of their tissues.

This allows us to track not only how and when maize agriculture arose and spread, but also how it was distributed within society. As maize was valued not just as a food, but also as a vital ritual and religious symbol. Therefore, patterns of maize consumption can be highly informative as to the dynamics of power and prestige within Maya society. Similarly, due to the Maya's relative lack of domesticated food animals, the consumption of meat was likely considered a signifier of high prestige (Emery, 2003; Masson & Peraza Lope, 2008; Shaw, 1999). Therefore, social patterning in meat consumption as evidenced by variation in $\delta^{15}N$ values (which increase with trophic level, and therefore the degree of meat consumed) can likewise provide valuable cultural information.

Extensive sampling and isotopic analyses of skeletal material from Maya populations have yielded data on a wide variety of archaeological topics, typically through inter- and intrasite comparisons of individual diets. These include regional or residential variations in diet (Gerry & Krueger, 1997; Metcalfe et al., 2009; Rand et al., 2013; Reed, 1999); changes in diet over time (Magennis, 1999; Scherer et al., 2007; White et al., 1993, White & Schwarcz, 1989; Williams et al., 2017; Wright et al., 2010); socioeconomic and gendered patterns in diet (Mansell et al., 2006; Price et al., 2018; Scherer et al., 2007; Somerville et al., 2013; White et al., 1993; White et al., 2010; White et al., 2001; Whittington & Reed, 1997; Wright, 2006); and the relationship

between diet and large-scale environmental or societal change (Emery et al., 2000; Wright, 1997a, 1997b; Wright & White, 1996).

While a great deal of valuable information about the ancient Maya can be made available by SIA, several problems and pitfalls remain. First is the considerable overlap between the carbon isotope ratios of those consuming a maize-heavy diet and those consuming marine food resources. In many cases, this potential confusion is mitigated by the inclusion of nitrogen isotope data, which can be used to separate C4 terrestrial consumers from marine consumers. However, this is not possible in archaeological contexts where bone collagen is not preserved. Thus, studies that utilize bone apatite only for diet reconstruction (e.g., Coston et al., 1999) may risk conflating dietary carbon sources. Luckily, few studies now rely on either collagen or apatite isotopes alone. Other studies, noting the relatively constrained range of isotope signatures exhibited by the ancient Maya, have relied on whole-site averages for comparing diet variability (Harvey, 2018; Rand et al., 2013). This ignores possible intrasite variation, which can be substantial and without a ready explanation. Furthermore, this subsumes the great number of different proportions of foods consumed that may equate to the same isotope signature.

Moving forward, new stable isotope methodologies may provide fresh avenues of investigation in the long-standing field of ancient Maya diet reconstruction. First, isotopic mixing models can be used to provide data on the relative proportion of different dietary components actually consumed by individuals, allowing for more direct inter-individual and inter-site comparison (Bownes et al. 2017, Fernandes et al. 2014, Fernandes et al. 2015, Pestle and Laffoon 2018, Phillips 2012). Data generated from these models are, in many ways, preferable to raw isotope data in terms of comparability because they are estimates of actual dietary composition, while raw isotopic signatures are themselves only proxies for measuring

diet. These methods furthermore have the added benefit of being applied to data previously reported in the literature. Importantly, SIMMs have been shown by Bownes et al. (2017) to identify substantial marine resource consumption in a population of Neanderthals when none was suggested by bulk isotope signatures alone. This indicates that SIMMs may be useful in assessing the degree to which inland Maya populations relied on traded marine foods. This is significant for the Maya region because of the considerable overlap between the carbon isotope ratios of those consuming a maize-heavy diet and those consuming marine food resources.

Similarly, aquatic (freshwater) resources are broadly similar to terrestrial resources in their carbon isotope values. Furthermore, stable isotope mixing models (SIMMs) allow for quantitative comparison in the ratio of food resource contribution to diet between individuals. However, the most established uses of the techniques have taken place within Old World contexts, meaning their applicability to new world archaeological contexts has yet to be fully tested.

This dissertation, therefore, seeks to use a dataset of ancient Maya isotope signatures and Maya-specific food source isotope and nutritional composition to elucidate several unknowns concerning the use of sulfur isotope analysis and SIMMs for diet reconstruction, and specifically, the cultural, temporal, geographic factors that can affect the food reference samples necessary to accurately understand diet in the past. “Section I: Measuring Ancient Diets” introduces the theoretical underpinnings of the study of diet in anthropology, ancient Maya foodways, stable isotope analysis, and stable isotope mixing models. “Section II: Influencing Diet Estimation” presents three case studies to explore how culturally or regionally-specific questions about model parameters can affect estimates of diet using mixing models. Finally, “Section III: Future Applications of SIMM in the Maya Region” discusses the results of the case studies in the

broader methodological and theoretical context of ancient Maya diet reconstruction and explores future avenues for diet reconstruction using both SIMMs and other, cutting-edge techniques such as compound-specific isotope analysis.

SECTION I: MEASURING ANCIENT DIETS

CHAPTER II: IMPORTANCE OF DIET IN ANTHROPOLOGICAL RESEARCH

Why Study Food?

There are several reasons why food would be so central to the study of human cultures. First, food is universal – all humans need to eat and through technology and complex behaviors, we as a species can consume an incredibly wide range of foods. Second, food and eating are particular. While humans are able both through biological and technological adaptations to make use of a wide variety of food sources, with cooking alone rendering many otherwise useless foodstuffs readily available, they never do (Pelto, Goodman, & Dufour, 2000; Smith, 2006).

Third, food serves an inherently biological function. Food fulfills physiological needs, and thus what is eaten directly impacts daily function. This makes food the primary mechanism by which we most frequently directly interact with our environment. Finally, food is inherently cultural (Palmer & Van der Veen, 2002). As before stated, humans conceptualize food through learned behaviors. However, even within groups, different people eat different things at different times and with different meanings. Therefore, food does not just differentiate insiders from outsiders, but rather creates and reinforces relations between individuals.

So, food sits at the nexus of all things that concern anthropologists – essentially it is the most intrinsically holistic field of study to understand the most about a culture and the people that comprise it (Fieldhouse, 1995). As noted by Gumerman (1997, p. 106), "food is intrinsically social…social relationships are defined and maintained through food. Food systems do not entail the simple food item alone, but also represent the technologies, labor, and relationships that were necessary to produce the food. Furthermore, these relationships are equally valid in the study of human ancestors, and archaeological and modern human populations (Dufour & Piperata, 2018; Schoeninger, 1995).

Thus, examination of the food itself often reveals a great deal about the underlying social relationships present within a society. These relationships are present in all human groups, from individual hunter-gatherer bands to large complex societies. For one example, social status and diet are linked because of the intrinsic cultural nature of foods (Farb & Armelagos, 1980). To again quote Gumerman (1997, p. 126), "…within complex societies, different individuals – elites and commoners, males and females, specialists and nonspecialists, old and young – often consume different resources for a variety of reasons". Specifically, social complexity determines how food is produced, who produces it, how it is distributed, how it is consumed, and who consumes it. This is particularly true of complex societies, where there is a marked divide between producers and consumers of food; i.e. one group produces food to be primarily or completely consumed by another group (van der Veen, 2003). Perhaps unsurprisingly, food is generally seen as having even more symbolic meaning in agricultural societies (see Bennett (1943) for an ethnoarchaeological example in a modern population).

Anthropological approaches to dietary study

Since the earliest days of British socio-culturalists, anthropological research in practically any form has necessitated some discussion of a people's subsistence strategies (Messer, 1984). Subsistence has remained a constant topic of study throughout the major anthropological paradigm shifts of the past 100+ years, from the cultural particularism of Boas, the structuralism of Levi-Straus, and the materialism of Harris (Mintz & DuBois, 2002).

Admittedly, early studies tended to focus on "exotic elements of food taboos and extravagant practices related to the maintenance of power – such as ritual feasting (Gumerman, 1997). Eventually, however, subsistence strategies came to be reframed to center the underlying

insights into cultural practices and norms like social stratification, gender norms, etc. (Messer, 1984). An early example of this shift is Richards's (1995) *Land, Labour, and Diet in Northern Rhodesia,* in which the author correlated undernutrition among the Bemba of that country with recent socio-economic changes. This study exemplifies the focus of early social anthropology and its focus on the manners in which social relationships affect food production and their downstream effects (Mintz & DuBois, 2002). In the case of the Bemba, increased British mining activity in the region and the subsequent demand for local labor disrupted traditional gendered division of labor in subsistence strategy (Messer, 1984).

Studies of foodways have also proven fruitful in archaeology in particular, as food production and preparation leave behind material culture (Graff, 2017). However, foodways research in archaeology has recently transformed a simple extension of subsistence into a holistic view of cultural practices. As Graff (2017) describes, new expansions in foodways in archaeology have resulted in an increasing concern for "cooking and food preparation and how these data can elucidate social practices, social identities, socially produced relations of power, and social change". In this way, food provides a wealth of information on a people's conception of sensation, identity, and transmission of information, to name a few examples (Graff, 2020).

While the study of food and eating remained a key part of most theoretical frameworks of the early to mid-twentieth century, subsistence is arguably most frequently examined from a cultural materialist perspective. In this way, specific food choices are viewed as adaptive reactions to ecological or environmental factors, with the symbolic or otherwise immaterial element coming thereafter. Put simply, behaviors and practices that maximize the energic contribution or nutritional completeness will be favored by Darwinian selection, and the cumulative total of a culture's dietary adaptations can be viewed as its cuisine, as exemplified by

the complimentary nutrition of the “Three Sisters" or the American agricultural triad of maize, beans, and squash. Taken together, each of these cultigens largely mitigates the nutritional deficiencies of the others, and thus cultivation and consumption of the three together provide greater nutritional benefit than each alone, and are thus adaptive (Armelagos, 2009; Pelto et al., 2000). Conversely, food avoidances are similarly treated as adaptive decisions (Harris, 2009), such as the taboo on potentially toxic fish species among pregnant and lactating Fijian women (Henrich & Henrich, 2010).

Furthermore, because culture influences and determines the types of foods a people eat, and those food choices, in turn, affect the people on a physiological level –in their bone chemistry, prediction toward certain metabolic conditions, etc. – their bodies in and of themselves become material culture: physical things arising as a product of human behavior (Armelagos, 2003). As such, this work – along with most bioarcheological studies involving food – operates from a distinctly biocultural approach (Zuckerman & Armelagos, 2011). As defined by Armelagos (2009, p. 579), this approach is marked by the understanding that “a food procurement system must meet the essential nutritional requirements necessary to maintain and reproduce the population”. Thus, a society or culture’s food choices can be understood in adaptive terms considering their surrounding environment. However, it should also be noted that this approach does not (or at least should not) disregard or minimize the non-material influencers of food choice – such as economic or social differentiations – that can complicate our understanding of diet in purely adaptive terms (Armelagos, 2009).

Rather, the biocultural perspective of food and nutrition on how social and physical environments, technology, culture/idea systems, and social organization act in concert and against each other to meet individual biological and psychobiological needs (Pelto et al., 2000).

In other words, the biocultural perspective seeks to understand how humans meet their fundamental needs given the totality of the human experience, with both sociocultural and biological determinates. Both culture and physical environment determine what foods are available or are utilized, which in turn affects what nutrients are available to a given population. This then affects their nutritional status and has downstream functional results (Pelto et al., 2000). In this way, human biology is a product of both the physical environment and one's cultural adaptations to and constraints within that environment. This interplay can therefore be inferred from human remains, which exist as material evidence of this interplay between the physical environment and cultural particularity.

This perspective on food choice and subsistence has found fertile ground in the study of New World foodways, owing to the complimentary nutrition of the "Three Sisters" and their adaptive benefit (Armelagos, 2009). Similar veins of thought have been applied to the study of maize preparation techniques, discussed in greater detail in Chapter VII.

CHAPTER III: ARCHAEOLOGICAL BACKGROUND: DIET AMONG THE ANCIENT MAYA

Overview of Maya Culture History

The region in which the ancient Maya culture developed and eventually expanded includes much of present-day Central America – encompassing the entirety of the modern Mexican states of Yucatán, Campeche, and Quintana Roo, the nations of Guatemala and Belize, and large swaths of the states of Chiapas and Tabasco, and countries of Honduras and El Salvador. The first antecedents of Maya culture are seen as early as about 2000 BC, in the form of ceramic vessels in the southwestern periphery of this area.

This formative period of Maya culture, dubbed the Preclassic and further subdivided into the Early (~1,800 to 1,000 B.C.E.) and Middle (1,000 B.C.E.-300 B.C.E.) and Late (300 B.C.E.-300 C.E.) Preclassic, marks the gradual development of many hallmarks of Maya civilization (McKillop, 2004). These include the slow emergence of monumental, non-domestic architecture signifying increasing social stratification, the appearance of the first ballcourts, long-distance interaction in the form of trade of prestige or ritually significant items, hieroglyphic writing systems, and the rise of major city-states, including Altar de Sacrificios, Lamanai, Cerros, El Mirador, Cuello, and Colha (Trachman, 2007).

The ancient Maya arguably reached their zenith between 250 and 800 C.E. (McKillop, 2004). This era, known as the Classic Period, is marked by a flurry of monumental construction, urban expansion, and increased internal and external trade through the Maya world (McKillop 2004). It is during this time that some of the most characteristic Maya art, science, and architecture developed (Culbert, 1988). But more than anything, the Classic Period, particularly the Early Classic (250-600 C.E.), saw the emergence of major long-distance political interactions centered on the central Mexican city-state of Teotihuacan and the iconic lowland Maya site of Tikal. This

era saw the exchange of valuable goods from the Maya Region, such as feathers, cacao, obsidian, hardwoods, and the like, to central Mexico, and the influx of Teotihuacano cultural knowledge, most notably Talud-Tablero architecture, to the polities of the Maya Region.

The latter century of the Early Classic is marked by the "Maya hiatus", in which the former powers of Teotihuacan and Tikal wane in influence. This, however, introduces a power vacuum in which many Maya polities formerly subservient to Tikal seek to expand their influence. It is during this period, known as the Late Classic (600-800 C.E.) that many Maya city-states come into their own. This era saw massive population growth in conjunction with the proliferation of regional architectural styles, signifying a more fragmented political landscape and competition between locally entrenched, hereditary elites.

Beginning around the turn of the ninth century C.E., the trajectory of Maya culture took a surprising turn. Large-scale architecture virtually ceases, with the last known monument dedication dating to 889 B.C.E. (Willey & Shimkin, 1973). Overall population, which beforehand had been experiencing exponential growth, suddenly drops dramatically. By 900 C.E., nearly all urban centers in the central lowlands are abandoned and remained so even until the arrival of the Spanish 600 years later (McKillop 2004). This transitional period, known as the Terminal Classic, is indicative of major political and social upheaval, such that by the beginning of the Postclassic (), nearly all Maya population centers had been completely abandoned, with only occasional visitations until the period of European contact.

This sudden reversal of growth and development has been known for centuries as the Maya Collapse. While it is worth noting that this "collapse" took place over about 150 years and many urban centers along the coasts of the Yucatan and Belize continued into the contact period, it is difficult to argue with the magnitude of such a cultural shift.

Pasión Region

While the overall field of Maya bioarchaeology spans nearly three millennia and nearly all of Mesoamerica, this dissertation primarily focuses on human and faunal samples dating to the Late and Terminal Classic periods from the Pasión Region. Located in the Department of Petén, Guatemala, the Pasión Region of the Southern Maya Lowlands contains the major Maya sites of Altar de Sacrificios, Aguateca, Dos Pilas, Seibal, and Itzan in addition to several small sites including Cancuen, Tamarindito, and Arroyo de Piedra, among others (Demarest, 1997). Based on ceramic evidence, the earliest occupation for several of the main sites occurred during the Middle Preclassic (900 B.C.E.-300 B.C.E.), though the Petexbatún sites of Dos Pilas and Aguateca were not likely populated until the Late Preclassic. As with most of the Maya Lowlands, the Pasión Region consists primarily of subtropical forest and wetlands over karstic limestone bedrock.

The geographic focus of this dissertation is the site of Dos Pilas, which was one of the twin capitals of the Petexbatún dynasty, along with the nearby site of Aguateca (Demarest, 1997; Demarest et al., 2008; Foias & Bishop, 1996; Houston, 1993; Inomata, 1997; Palka, 1997; Wright, 1997a). While there is some evidence of Preclassic and Early Classic occupation in the vicinity of the site, significant expansion of the site did not occur until the Nacimiento phase of the Late Classic Period, with most major architecture constructed within a narrow timeframe (Foias, 1996; Wright, 1994). The history of Dos Pilas appears to have been short and highly militaristic, as described in the well-preserved epigraphic record of the site (Demarest, 1997; Demarest et al., 2008; Houston, 1993). As with many lowland sites, all monumental construction at Dos Pilas ceased by the Terminal Classic, likely at the time of the ruling dynasty's retreat to the twin capital of Aguateca following a siege (Foias, 1996; Houston, 1993).

Over the years, a wealth of archaeological investigation has been conducted around Dos Pilas and in the Pasión region overall (Cavallaro, 2013; Emery et al., 2000; Wright, 1994, 1997a, 1997b, 2006). Much of this was performed by the Vanderbilt Petexbatún Regional Archaeological Project, which focused primarily on the events surrounding the "Maya Collapse" within the region and how these might inform the causalities of the collapse writ large (Demarest, 1997). Specifically, these efforts sought to test the Ecological Model of the Collapse, which holds that increasing population and population densities among the Maya during the Classic Period necessitated increased agricultural exploitation of the land to feed swelling urban centers populated by a growing elite class and non-producing laborers (Culbert 1988). Eventually, this growing need exceeded carrying capacities throughout the Maya world and led to increasingly diminishing returns in land investment due to environmental degradation (Santley et al., 1986). In other words, the Maya simply grew too quickly too fast and rapidly overextended its capacity to feed itself, creating an internal and ecological collapse.

This framing of the collapse is supported by some bioarcheological evidence. Haviland (1967), in a study of burials at Tikal, argued that residents of the central lowlands show a pattern of decreasing stature throughout the Classic Period not related to genetic factors. This phenomenon was interpreted as evidence of increasing nutritional stress. Furthermore, Haviland argued that this trend also had a social dimension, as the reduction in stature was more prominent among commoners than elites. Similarly, Saul (1972), studying patterns of pathology, concluded that the Classic Period was marked by an increasing rate of infectious and metabolic diseases, likely due to increased dependency on maize and pathogen load. It is argued further that, because the Maya possessed few domestic food animals, deforestation would have the additional effect of decreasing

meat availability by eliminating the natural habitats of food animals, and thus led to an increase in conditions such as anemia (Santley et al. 1986, Saul 1972).

The Vanderbilt Petexbatún Regional Archaeological Project has been prolific in refuting many aspects of the ecological model of the collapse. Demarest et al. (1997), through extended investigations of the collapse period in the Petexbatún region, found that increased conflict and warfare coincided with the expansion of monumental architecture and preceded evidence of the environmental degradation described by the Ecological Model. Instead, Demarest and colleagues (1997) argue that ideologically driven competition between governing elites, both in the form of military expansion and the construction of ever-grander monumental architecture, precipitated the Classic Maya collapse through increasing conflicts between urban centers.

This model of ritualistic competition between elites is potentially corroborated by evidence from the site of Aguateca, which Inomata (1997) argues was abandoned rapidly after a period of intense conflict. Palka (1997) further argues that at Dos Pilas elites were most affected by the site's collapse, supporting the idea that elites were the cause of the site's collapse. From a bioarcheological perspective, dietary investigation from the Pasión Region has been instrumental in undermining the ecological model of the collapse. Wright (1997a, 1997b, 2006), in numerous studies of Classic Maya skeletons, argues that isotopic paleodietary evidence does not support the claim that maize consumption universally increased during the Classic Period, and that meat consumption did not particularly decrease (Wright and White 1996). Wright (2006) further argues that conclusions of health deterioration based on Saul's work disregard the author's explicit reservation in generalizing his findings to all of the Classic Maya, due to his small sample sizes (Wright & Chew, 1998).

Regardless of specific conclusions, the wealth of available data from the Pasión Region, and from the locality of Dos Pilas and surrounding sites, in particular, make this area ideal for the comparison of techniques for estimating diet.

Agricultural Staples

Among the ancient Maya, maize (*Zea mays*)served a dual role as both a stable food source and a ubiquitous cultural symbol. It has been estimated that the first widespread cultivation of maize began as early as 5000 B.C.E, and is vital to the subsistence of many New World cultures, but nowhere is this more evident than for the Maya (Staller et al., 2010), who were likely practicing intensive maize agriculture as early as 3400 B.C.E (Colunga-GarciaMarin & Zizumbo-Villareal, 2004; Pohl et al., 1996), with palynological evidence suggesting that widespread clear of forestland for maize cultivation was well underway by approximately 1000 B.C.E (Islebe, 1996; Magennis, 1999). This is apparent from the writings of Bishop Diego de Landa, the fifteenth-century friar tasked with converting the Maya to Catholicism, who observed that the people of the Yucatan's "principal subsistence is maize…it serves them both as food and drink" (Tozzer, 1941:89). While there was certainly temporal and regional variation in the importance of maize to ancient Maya diets, its ubiquity is difficult to overstate (Gerry & Krueger, 1997).

The social importance of maize for the ancient Maya is further apparent in its symbolic use in many aspects of Maya culture (Staller, 2010). The ancient Maya believed they were sculpted from the maize by the Maize god, whom rulers would often seek to imitate in their dress during ritual ceremonies (White et al., 2010; Joyce, 1992; Looper, 2002). Because of the ritual and economic function of maize, the dispersal and consumption of the foodstuff was a primary

concern of the ruling elite, and it is apparent from archaeological and chemical data (examples of which will be discussed below) that at many sites the degree of maize consumption seems to be correlated to status (White et al., 2010). Maize subsistence also provides a uniquely opportune chance to conduct rigorous chemical analyses of skeletal due to its isotopic signature, and many studies have focused on just that (see Ambrose et al., 2003 for a North American example).

Apart from maize, vital cultivars among the Maya, similar to many agricultural groups of North and Central America, included beans (*Phaseolus vulgaris*) and squash (*Cucurbita* sp.). Beans, which likely contributed a plurality of protein to most Maya diets, have been cultivated in the region for over four millennia (Brown, 2010; Kaplan & Lynch, 1999). Squash, on the other hand, was domesticated substantially later and would have been valued both for its fruit and seeds (Lentz et al., 1996). Other potential domesticated plant foods include manioc (*Manihot esculenta*) (Cagnato & Ponce, 2017), chiles (*Capsicum* sp.), cacao (*Theobroma cacao*, though most often reserved as a prestige good), camote (*Ipomoea batatas*), gourds (Cucurbitaceae), tomatoes (*Lycopersicon esculentum*), and avocado (*Persea americana*) (Cavallaro, 2013; Colunga-GarciaMarin & Zizumbo-Villareal, 2004; Lentz, 1991, 1999; Lentz et al., 1996; Pohl et al., 1996).

Wild Plant Resources

The ancient Maya also utilized a wide range of wild plant resources from their surrounding environments, which both widened the variety of foodstuff available in complement to agricultural staples (Lentz, 1991), and provided a buffer when such staples failed (Dine et al., 2019; Ebert et al., 2019). Some of these included chaya (*Cnidoscolus chayamansa*), coyol palm (*Acrocomia aculeata*), cohune or corozo palm (*Orbignya cohune*), nance (*Byrsonima*

crassifolia), ramón (*Brosimum alicastrum*), bactris (*Bactris* sp.), guava (*Psidium guajava*), papaya (*Carica papaya*), and sapote (*Pouteria* sp.), among many others (Cavallaro, 2013; Lentz, 1999; Lentz et al., 1996; Schwarcz et al., 2021). This continues to the modern era, with the Maya of the Northern Petén region recognizing and regularly utilizing over 400 individual species (Atran & Ucan Ek, 1999).

However, it is also debatable the degree to which the Maya may have engaged in the management of these "wild" foodstuffs, as modern patterning of dietarily important plants, such as bactris and cohune palm, suggest a higher concentration of these species than would be assumed under fully natural processes, suggesting selective management of certain high-value plants by the ancient Maya (Colunga-GarciaMarin & Zizumbo-Villareal, 2004; Lentz, 1991; McKillop, 2008; Ross, 2011). While access to non-maize plant food resources is generally thought to have been less restrictive according to status among the ancient Maya (except for cacao), Lentz (1991) did find that elite spaces tended to evidence a great variety of plant species than did common spaces at the site of Copán, suggesting that access to the widest breadth of resources may have been allocated to elites.

Terrestrial Animals

As stated above, animal goods are frequently regarded as luxuries (Curet & Pestle, 2010; Emery, 2003; Masson, 1999; van der Veen, 2003). This is particularly true for the ancient Maya, as they possessed little to no domesticated animals (with sole the exception of dogs (*Canis familiaris*)) until the Postclassic (Hamblin, 1984), when turkeys (*Meleagris* sp.) were first thought to be domesticated (Thornton et al., 2016). It thus follows that access to and consumption of such resources – both dietary and otherwise – serve as a marker of prestige and

social status (Emery, 2003). Zooarchaeological studies of elite/ritual contexts versus household groups support this line of reasoning both in the sheer number of animal remains observed and the diversity of animals seen in elite areas (Emery, 2003; Masson, 1999). This is explicable in biocultural terms as well, as nutrient-dense animal foods are often limited to individuals in a society with the wealth or power to access them (Lieberman, 2009). However, it should also be noted that the presence of a taxon in a site's assemblages does not necessarily indicate that the species was commonly used as a food source. As identified by Burke and colleagues (2020), certain species, elements, and faunal artifacts likely represent ritual importance rather than subsistence.

Of the vertebrate faunal remains commonly seen in Maya contexts, deer (*Odocoileus virginianus, Mazama americana*) and domestic dogs are among the most abundant (Hamblin, 1984). Dogs filled many roles in Maya religion, often symbolizing death, in addition to their obvious value in hunting smaller food animals (Hamblin, 1984). There is also evidence that dogs were used as a food source as well (Emery, 2003; Tykot et al., 1996). In an isotopic study of the Preclassic site of Cuello in modern-day Belize, Tykot and colleagues (1996) found that dogs likely occupied a large portion of the diet of the ruling elite. They also note that these dogs likely were fed a primarily maize-based diet before their consumption, which they interpret as ritual fattening (Tykot et al., 1996). This echoed the findings of Clutton-Brock and Hammond (1994), who found evidence for the raising of dogs for food during the Preclassic. However, this cannot be seen as universal, as in a large-scale study of animal usage by the Maya of the island of Cozumel, Hamblin (1984) observed that none of the canid remains in the region bore any signs of having been butchered. While it is certainly possible that this is due to preservation bias, it is just as likely that the residents of the island relied more on marine protein sources.

White-tailed and brocket deer typically constitute the majority of faunal remains recovered from Maya sites (Boileau, 2013; Emery, 2003; Hamblin, 1984). Patterns of deer consumption and abundance have been used to test land-use models of the collapse of the Maya, as it is believed that deer could have also subsisted on maize, thus helping to determine patterns of its cultivation and landscape usage (Emery & Thornton, 2008a, 2008b; Emery et al., 2000; Freiwald, 2010; Rivera-Araya et al., 2019). While it is possible that some deer populations were actively managed outside urban centers, most would have been hunted, and to such an extent that wild populations diminished in later periods due to overhunting (Emery, 2007; Emery & Brown, 2012).

While epigraphic, ethnoarchaeological, and zooarchaeological studies firmly cement deer as a ritually and dietary important animal for all Maya (Hamblin, 1984), it has also been noted that deer remains are far more common in elite contexts than in commoner contexts (Emery, 2003; Montero-Lopez, 2009). This fact further reinforces the nature of meat resources as luxuries in the Maya world, particularly for such difficult-to-obtain sources as deer (Blankenship-Sefczek, 2011), though there is evidence to suggest that, diets between social groups were broadly similar (Negrete et al., 2020). Other wild terrestrial animals that were likely consumed by the ancient Maya (based on the presence of their remains in assemblages) include turkeys (before their domestication), rabbits (Leporidae), armadillos (*Dasypus novemcinctus*), opossums (Didelphidae), various Mustelids, peccaries (Tayassuidae), pacas (*Cuniculus* sp.), agoutis (*Dasyprocta* sp.), iguanas (*Iguana iguana*), and tapirs (*Tapirus bairdii*) (Carr & Fradkin, 2008; Masson & Peraza Lope, 2008; Olsen, 1972; Powis et al., 1999; Thornton et al., 2016). It is worth mentioning, however, that some archaeological faunal specimens (such as deer, dogs, and armadillos) exhibit $\delta^{13}C$ and $\delta^{15}N$ values that suggest substantial maize consumption, leading to

debate over whether these animals were actively managed by the Maya, or if they simply consumed maize due to their proximity to agricultural activity (van der Merwe et al., 2002; Tykot et al., 1996; White et al., 2001).

Aquatic Animals

Among aquatic vertebrate species, turtles (Testudines) were by far the most frequently consumed by the ancient Maya (Freiwald, 2010; Olsen, 1972; Powis et al., 1999). There is also evidence to suggest that various frogs (Anura) were consumed as well as crocodiles (Crocodylidae), though less frequently (Carr & Fradkin, 2008; Olsen, 1972). Aquatic invertebrate remains are also commonplace in Maya assemblages (Healy et al., 1990). These include jute (*Pachychilus glaphyrus*) and apple snails (*Pomacea flagellata*) in particular (Dedrick, 2013; Halperin et al., 2017), in addition to other gastropods such as freshwater oysters (*Nephronaias* sp.) (Powis et al., 1999). These would have been valuable both for their meat and the usefulness of their shells in various craftworks and ritual significance (Emery & Aoyama, 2007; Halperin et al., 2017; Healy et al., 1990). Aquatic fish that have been found in Maya assemblages include gar (Lepisosteidae), guapote (*Parachromis* sp.), and freshwater catfish (Siluriformes) (Olsen, 1972; Rand et al., 2021; Sharpe & Emery, 2015; Williams et al., 2009; Wright, 2006).

Marine Animals

Marine fauna were also consumed in large quantities at coastal sites. Species of note include snapper (Lutjanidae), jack (*Caranx* sp.), grouper (Epinephelinae), marine catfish (Ariidae), rays (Myliobatoidei), parrotfish (*Scarus* sp.), barracuda (*Sphyraena* sp.), sea turtles (Cheloniidae), and manatee (*Trichechus manatus manatus*) (Götz, 2008; Götz et al., 2014;

McKillop, 1984, 1985; Newman, 2016; Powis et al., 1999; Rand et al., 2020; Sharpe & Emery, 2015; Williams et al., 2009). While most studies of Maya subsistence tend to focus on locally procured resources, the degree of coast-to-inland trade of marine foods has long been debated. Lange (1971, 1973) argued that inland Maya marine resource utilization was likely greater than previously thought. There remains some logic behind this position, as fish bones typically exhibit poor preservation bias, and thus their absence in assemblages does not necessarily mean that such foods were not widely consumed (Emery, 2004). However, this view was not widely accepted, with others suggesting that the utilization of marine species for food was likely isolated to coastal communities, where marine fauna constituted the bulk of the non-plant diet (Ball & Eaton, 1972; Götz, 2008; Maxwell, 2000; McKillop, 1984; Stemp, 2004).

In recent years, the consensus has been that traded goods consisted mostly of high-prestige or ritually significant marine goods, particularly stingray barbs, shark teeth, and bivalve shells (Ardren & Lowry, 2011; Haines et al., 2008; Masson & Peraza Lope, 2008; Moholy-Nagy, 2012; Tourtellot & Sabloff, 1972; Trubitt, 2003). Any marine species traded specifically as food would likely constitute extremely prestigious goods due to both the difficulty in procuring at inland sites and the nutritional benefits of consuming marine food resources (Larsen et al., 2011). However, there are increasing efforts to ascertain the degree to which marine food items were traded, with increasing evidence for long-distance, likely river-based trade of goods between coastal and inland communities (Graham, 1989; Graham & Pendergast, 2013; McKillop, 1996, 2002, 2009, 2010, 2019; McKillop & Aoyama, 2018; Sharpe et al., 2022; Simmons & Graham, 2016), with some market analyses suggesting that long-distance trade of both marine and terrestrial animal products was more important to non-elite Maya than originally thought (Chase et al., 2015; Cunningham, 2011; Masson & Freidel, 2012; Metcalfe et al., 2009; Rathje &

Sabloff, 1973; Sharpe & Emery, 2015; Sharpe et al., 2018; Thornton, 2011). For example, in an analysis of faunal remains from the Postclassic site of Mayapán, Masson and Peraza Lope (2008) found evidence of marine species such as barracuda, various cichlids, drum, jack, snapper, and snook. Marine fish remains have been found as far inland as Tikal and Kaminaljuyu, Guatemala (Sharpe et al., 2021), and isotopic analysis of human remains from Altun Ha, Belize has suggested surprisingly high marine resource consumption (White et al., 2001). It has been suggested that this trade may have been facilitated by salting marine fish meat for long overland travels, as evidenced by investigations of Maya saltworks in coastal areas (McKillop, 1995, 2002, 2005, 2019; McKillop & Aoyama, 2018; Robinson & McKillop, 2013; Watson & McKillop, 2019).

CHAPTER IV: THEORETICAL BACKGROUND: STABLE ISOTOPES AND DIET

Basics of Stable Isotopes

Isotopes of an element have an equal number of protons, but a different number of neutrons (Fry, 2006). Isotopes with more neutrons are referred to as "heavy", while those with fewer are dubbed "light". For example, ^{13}C is a heavy isotope of carbon and ^{12}C is a light isotope. Apart from hydrogen and helium, all elements possess a number of neutrons either equal to or greater than their protons (Fry, 2006). Some isotopes, such as ^{14}C, possess a number of neutrons that render their nuclei unstable and therefore decay into stable elements over time. Other isotopes do not experience such decay and are therefore "stable". The proportion of light to heavy stable isotopes in a substance will therefore remain stable unless subjected to chemical change.

While isotopes of the same element possess the same properties, their different atomic masses cause them to have different rates of reactivity, with light isotopes being more reactive than heavy. Because heavier isotopes react more slowly than lighter ones, in an incomplete reaction (which is to say all chemical reactions in nature), more of the lighter isotope will be present in the product relative to the remaining reactants, which are thus "depleted" in the heavy isotope. Conversely, the remaining substrate possesses a higher proportion of the heavier isotope and is therefore considered to be "enriched" in the heavy isotope (Schoeller, 1999; Schoeninger, 1995). This change in isotopic composition from the substrate to the product is called fractionation. Isotopes of different elements vary in the degree of fractionation they undergo based on a few key factors, such as their overall atomic mass and the number of oxidation states they can occupy (Anderson & Arthur, 1983; Bigeleisen, 1965; Urey, 1947). In general, fractionation rates tend to be greater between isotopes with higher relative mass differences. For

example, stable hydrogen isotopes (δD) display high rates of fractionation because the heavy isotope, deuterium (^{2}H or D), is twice that of the light isotope, protium (^{1}H). Therefore, isotopes of relatively light elements, such as hydrogen, carbon, nitrogen, and oxygen tend to be the most sensitive to isotopic change during fractionation, and thus these elements – along with some slightly heavier elements like calcium and sulfur – tend to be the most informative in their isotope ratios.

While fractionation divides an element into light and heavy isotopes, mixing is the process by which substances of different isotopic compositions are combined into a single product with an isotopic ratio that is effectively a weighted average of that of its inputs (Fry, 2006). Like fractionation, examination of isotopic mixing can be used to understand how substances move through complex systems. By modeling how elements both mix and fractionate in a set of reactions, it is possible to effectively reverse engineer the source of elements in a single product. Isotopic mixing and how it is modeled will be covered more extensively in the subsequent chapter.

Isotope Mass Spectrometry

The basic techniques for measuring the stable isotope composition in a sample are broadly similar to, and an outgrowth from, techniques for radiocarbon dating developed in the 1960s, as both measure the proportion of two isotopes of the same element within a given sample (Ambrose & Krigbaum, 2003). This typically involves either combustion of a sample followed by separation of the resulting compounds via an Elemental Analyzer or by gas or liquid chromatography, which are then passed into an isotope ratio mass spectrometer (IRMS) for analysis (Muccio & Jackson, 2009). Within the IRMS, the effluent of interest (usually along with

helium as a carrier) is given a strong positive charge and accelerated down a flight tube at high velocity.

Within the flight tube, the effluent passes through a carefully calibrated electromagnetic field created by a magnetic analyzer. This magnetic field causes the beam of particles to bend according to the strength of the magnetic field. However, molecules containing heavier isotopes of a particular element – such as $^{15}N^{14}N$ vs. $^{14}N^{14}N$ – resist bending more than their lighter isotope counterparts, and thus the particle beam separates by atomic weight as it bends. By adjusting the strength of the magnetic field, these separated beams can effectively be "aimed" at a series of Faraday detector cups, which generate a signal in proportion to the strength of the particle beam it collects. Thus, the relative abundance of different isotopes of an element can be inferred by the level of signal from each detector.

As there is no practical way to quantify the exact number of heavy vs. light isotopes within a sample, isotope signatures are expressed as a ratio of heavy-to-light isotopes within a sample vs the ratio of the same within an accepted reference standard. This "ratio of ratios" is represented by the following formula:

$$\delta^{H}X\ (‰) = [(R_{sample}/R_{standard}) - 1)*1000 \text{ (Fry, 2006)}$$

Where R_{sample} represents the heavy-to-light isotope ratio of the sample and $R_{standard}$ represents the heavy-to-light isotope ratio of the sample. The delta notation (δ) is used to signify that the given isotope value is the sample's difference from the standard, thus a negative $\delta^{13}C$ indicates that the sample contains less ^{13}C relative to ^{23}C than the standard, while a positive value indicates the opposite.

Because concentrations of heavy isotopes in naturally occurring substances are typically very low, these ratios are given in permil (‰) – parts per thousand – rather than percent. Accepted standards against which samples are compared vary according to the element being measured. The original standard for carbon isotopes for many years, for example, was PeeDee Belemnite, however, exhaustion of this resource has led to a shift toward Vienna-PDB (VPDB) in recent decades.

Stable Isotopes in Human Remains

The atoms that constitute an organism's tissues originate in the food it consumes, the water it drinks, and the air it breathes. Because stable isotopes of different elements do not change overtime, the isotopic signature of an organism's tissues will tend to represent an average of the signatures of its food and water sources (Ambrose & Krigbaum, 2003; Schoeninger, 2010; Schwarcz & Schoeninger, 1991; Schwarcz et al., 2010; Tykot, 2004). Because isotopes of a given element are not evenly distributed within nature and differ slightly in their level of reactivity (discussed below), the isotope signatures of a given organism's tissues can be used to infer what types of resources it utilizes or utilized. Therefore, given knowledge of the general isotopic composition of different possible food sources, patterns of fractionation due to biochemical processes, and potential sources of additional variation (locality, age, nutritional status, etc.), diets of individual humans can be inferred from isotopic analysis of their physical remains (Schwarcz, 1991; Schwarcz & Schoeninger, 1991).

In the context of human diet reconstruction in bioarchaeology, the most commonly investigated isotope ratios include δD, $\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$, $\delta^{34}S$, and $^{87}Sr/^{86}Sr$. Isotopic analysis of hydrogen, oxygen, and strontium is beyond the scope of this work, but fortunately carbon,

nitrogen, and sulfur are relatively easy to obtain from vertebrate skeletal tissue. Carbon can be obtained from skeletal material from both collagen – the protein component of bone – and hydroxyapatite, its mineral component. Isotopic signatures from these two materials represent different components of the diet, as discussed below. Nitrogen, on the other hand, occurs in bone collagen only, being found in the amine groups of the protein's constituent amino acids (Eastoe, 1955; Honch et al., 2012; Post, 2002). Sulfur is also found in collagen. However, unlike carbon and nitrogen, which are found in all the protein's constituent amino acids, sulfur occurs only in certain amino acids: cysteine and methionine (Nehlich & Richards, 2009). Methionine sulfur is preferentially isolated for use in isotopic analysis for two reasons. First, as an essential amino acid, it more closely represents dietary sulfur. Second, cysteine does not occur in measurable quantities in bone collagen (Eastoe, 1955; Nehlich, 2015).

Beyond the level of the primary consumer, several biochemical processes can affect isotope ratios in organisms, and therefore introduce fractionation (Schoeller, 1999). Within the context of diet reconstruction, fractionation is most observed as an offset between the isotopic contribution of the food itself and the tissues of an organism that consumes it. Various factors can influence both the manner and degree of this offset dependent on the element in question and in what tissue it is observed. Thus, the main causes of fractionation in carbon, nitrogen, and sulfur isotopes in humans are discussed in their respective sections.

Carbon-13

Of the two stable isotopes of carbon observed in nature, ^{12}C is the most common – making up approximately 98.9% of radio-stable carbon on earth. The heavier isotope, ^{13}C, is much less common at only approximately 1.1%, and the radioactive isotope ^{14}C is far less abundant at

approximately $1x10^{-12}$ % (Fry, 2006; Schoeninger, 1995). Ultimately, all carbon in the biosphere originates from atmospheric carbon dioxide via photosynthesis. Terrestrial plant carbon isotopic signatures differ from that of the atmosphere largely due to the type of photosynthetic pathway utilized (O'Leary, 1981, 1988; Tieszen, 1991; Tieszen & Fagre, 1993; van der Merwe, 1982).

Most terrestrial plants utilize the Calvin-Benson photosynthetic pathway. These, called C_3 plants due to the three-carbon molecule phosphoglycerate synthesized during photosynthesis, are relatively inefficient at carbon fixation, and therefore exhibit a high degree of ^{13}C depletion compared to atmospheric CO_2 (Hoefs, 2018; O'Leary, 1988). Therefore, C_3 plants display $\delta^{13}C$ values averaging approximately -26.5‰ (Calvin & Benson, 1948; Schoeninger, 1995; Tykot, 2004). Examples of C_3 plants include temperate trees and grasses, as well as nearly all edible fruits and vegetables.

Conversely, some tropical grasses utilize the Hatch-Slack photosynthetic pathway, which is more efficient at fixing carbon than the Calvin-Benson pathway (Hoefs, 2018). This results in less ^{13}C depletion relative to atmospheric CO_2, thus C_4 plants are more enriched in the heavy isotope of carbon than C_3, with an average $\delta^{13}C$ value of -12.5‰ (DeNiro & Epstein, 1977; M. D. Hatch & Slack, 1966; Schoeninger, 1995). C_4 plants, as these are called, are more water-efficient but less light efficient than C_3 plants, making them better suited to sunnier, dryer environments. Examples of edible C_4 plants include maize, amaranth, millet, and sorghum (Schoeninger, 1995; Tieszen & Fagre, 1993). Because of this, some of the earliest uses of carbon isotope analysis in bioarchaeology were to detect C3/C4 contribution to diet to track the adoption of maize (Price et al., 2002; Schwarcz et al., 1985; van der Merwe & Vogel, 1978).

Though much less common, some desert succulents utilize a third photosynthetic pathway, Crassulacean Acid Metabolism, or CAM (Bender et al. 1973). CAM plants yield $\delta^{13}C$

signatures intermediate to C_3 and C_4 plants and include agricultural staples such as pineapple and agave (Schoeninger, 1995; Tieszen, 1991; Tykot, 2004).

Because carbon isotopes in most organisms are ultimately dependent on the dominant primary consumer in its environment. In terrestrial ecosystems, these usually consist of either C3 or C4 plants. However, carbon in such systems originates in the atmosphere. In marine ecosystems, most of the carbon originates from phytoplankton, which fix carbon directly from the surrounding water, which is enriched in ^{13}C relative to the atmosphere by approximately 7‰. This difference is preserved through the food chain, and thus, organisms from marine ecosystems tend – or terrestrial organisms subsisting on marine species – to differ significantly from fully terrestrial organisms (Chisholm et al., 1982, 1983; Keegan & DeNiro, 1988). This also permits the estimation of marine food consumption in ancient human populations by assessment of their carbon isotope signatures (Chisholm et al., 1982, 1983; Webb et al., 2017).

Furthermore, different tissues within a consumer will disproportionately represent different macronutrient components of the diet (Jim et al., 2007; Post et al., 2007). For example, most proteins or proteinaceous tissues disproportionally represent the protein component of the diet because consumed amino acids are preferentially (and in the case of essential amino acids, almost exclusively) incorporated into bodily proteins as opposed to catabolized for energy (Ambrose & Norr, 1993; Krueger & Sullivan, 1984; Lee-Thorp et al., 1989). Therefore, when sampling a proteinaceous tissue of a mixed feeder, such as human collagen, if higher protein food items possess a different isotope signature than less protein-rich foods – such as animal meat vs. plants – the collagen will more closely resemble that of the high-protein food source (Ambrose & Norr, 1993). Conversely, some tissues are produced via a “scrambling” effect, wherein their constituent carbon is derived from protein, carbohydrates, and fat without

preference (Krueger & Sullivan, 1984). These tissues/materials, which include bone apatite, can be considered representative of the full diet (Ambrose & Norr, 1993)

Unlike nitrogen (discussed below), $\delta^{13}C$ values typically exhibit little diet-to-tissue fractionation, generally on the order of 1‰ or less (McCutchan, et al. 2003; Post, 2002). However, several factors due introduce complications or complexities in ^{13}C analysis. Other factors include the "canopy effect", in which the $\delta^{13}C$ values of plants exhibit a gradation of depletion to enrichment from forest floor to canopy (van der Merwe & Medina, 1991). It is also possible that dietary quality can affect trophic level discrimination of ^{13}C, though a definitive conclusion has yet to be reached (Warinner & Tuross, 2010; Webb et al., 2017). Furthermore, in studies of ancient samples, diagenetic alteration of isotope ratios must be considered – typically by assessment of whether the observed carbon to nitrogen ratio of the collagen is approximately what it would be from an unaltered, living specimen (Ambrose, 1990; Van Klinken, 1999). Similar tests for diagenesis have recently been explored based on bone apatite yield (Chesson et al., 2021).

Nitrogen-15

The light isotope of nitrogen, ^{14}N, is most abundant at 99.6%, with the heavy isotope, ^{15}N, at 0.4% (Fry, 2006; Schoeninger, 1995). From the outset, researchers determined that the $\delta^{15}N$ ratios of consumers tended to be enriched relative to the foods they consumed (DeNiro & Epstein, 1981; DeNiro & Schoeninger, 1983; Schoeninger & DeNiro, 1984; Schoeninger et al., 1983; Steele & Daniel, 1978). Thus, legumes and other organisms which fix nitrogen directly from the atmosphere tend to exhibit $\delta^{15}N$ signatures close to 0‰, as AIR serves as the standard for nitrogen isotope analysis. Other producers that do not fix nitrogen directly are slightly more

enriched in their $\delta^{15}N$ values, as they derived their nitrogen from the soil, which can consist of somewhat varying $\delta^{15}N$ values, though in most historical circumstances it is likely that this variation was minimal (Szpak, 2014). Primary consumers are enriched relative to the plants they eat, and so on. Therefore, $\delta^{15}N$ values tend to be used as a measure of an organism's trophic position in its given ecosystem (DeNiro & Epstein, 1981).

While the causes of carbon isotope variation within organisms can be difficult to pin down due to carbon's ubiquity, nitrogen isotope variation is highly specific. Because 98% of bodily nitrogen is found in proteins, nitrogen isotope fractionation is controlled largely by amino acid metabolism. Nitrogen fractionation among amino acids whenever the α nitrogen bond is cleaved during transamination and deamination reactions. This occurs because, like in all stable isotope fractionation, the lighter isotope, ^{14}N, forms weaker atomic bonds than the heavier isotope, ^{15}N, and therefore reacts more readily, due to its faster reaction time (Macko et al. 1986). Therefore, when any group of amino acids is transaminated, if the reaction is incomplete (which is always) there will be a greater proportion of the heavy isotope in the substrate relative to the product, thus creating the distinctive step-wise enrichment of ^{15}N of approximately 2‰ to 5‰ per trophic level observed in most ecosystems (McCutchan et al., 2003; Minagawa & Wada, 1984; Post, 2002).

This simple relationship is, however, complicated by the fact that most transamination reactions are reversible. Therefore, it is equally likely that a newly aminated amino acid will have preferentially received a light isotope from the now enriched substrate. As a result, on an organismal level, most nitrogen fractionation occurs during oxidative deamination of amino acids in the liver and kidneys, wherein the amino group is removed from its keto acid and is not rebuilt. When proteins are in excess, the amino group is removed to produce acetyl-CoA, which

can then be used for lipogenesis. When in a fasted state, amino acids from proteins are catabolized to meet energetic requirements. In either case, the resulting toxic ammonia is then excreted via the urea cycle. As a result, some nitrogen fractionation occurs at all times regardless of metabolic state. Due to the greater reactivity of ^{14}N, it is preferentially excreted, resulting in a relative buildup of ^{15}N in the body's remaining nitrogen pool. These enriched amino acids are then incorporated into tissues, resulting in an overall enrichment in ^{15}N relative to the diet.

In omnivorous species, such as humans, $\delta^{15}N$ can give insights into an individual's degree of carnivory, as animal foods are enriched in ^{15}N relative to plants and pass those higher $\delta^{15}N$ values on to their predators. Therefore, higher $\delta^{15}N$ values are generally taken to mean greater consumption of animal foods, with some correction for body size and animal age (Hedges & Reynard, 2007; Minagawa & Wada, 1984; O'Connell et al., 2012; Post, 2002). Nitrogen isotope ratios can also be used to determine marine vs terrestrial food consumption, given that animals consuming exclusively marine resources are typically 9‰ in their $\delta^{15}N$ values compared to members of the same species consuming exclusively terrestrial resources (Schoeninger & DeNiro, 1984; Schoeninger et al., 1983). This is likely due to the greater complexity of marine food chains, which typically involve more trophic levels than terrestrial ecosystems.

Despite this usefulness, several factors can introduce variation into an organism's $\delta^{15}N$ values (McMahon & McCarthy, 2016). For example, the trophic discrimination factor of ^{15}N can vary according to the abundance and quality (that is, amino acid composition) of protein in the diet, with the factor being reduced when the abundance of available protein decreases, and vice versa (Robbins et al., 2005; Vanderklift & Ponsard, 2003). Furthermore, prolonged states of fasting or nutritional stress can cause an increase in the catabolization of endogenous proteins for

energy, thus effectively creating a trophic effect within a single individual. However, it is unlikely that such states would increase $\delta^{15}N$ substantially over the entire life of the individual, likely only affecting tissues laid down over a narrow window of time and not remodeled (Canterbury et al., 2020).

Sulfur-34

Of sulfur's two most common stable isotopes, ^{32}S is most abundant at approximately 95% of stable sulfur, compared to 4% for ^{34}S. A third, stable sulfur isotope – ^{33}S – is known, occurring at a rate of less than 1% (Fry, 2006). Originally, the accepted standard against which $\delta^{34}S$ values were scaled was Canyon Diablo Troilite (CDT), obtained from the Canyon Diablo meteorite in Arizona. However, this standard was found to be unreliable in its $\delta^{34}S$ values in the 1990s (Beaudoin et al., 1994), leading to the establishment of the Vienna-Canyon Diablo Troilite (V-CDT) as a standard reference (Hoefs, 2018).

The majority of Earth's sulfur is found in the form of oceanic sulfates, which tend to be fairly uniform at approximately 20.3‰ $\delta^{34}S$ (Nehlich, 2015; Richards et al., 2001; Richards et al., 2003). However, in terrestrial and aquatic environments $\delta^{34}S$ can range widely due to the varying sulfur inputs at play. As all freshwater originates from the oceans, oceanic evaporation tends to match that of oceanic water (Nehlich, 2015). However, as clouds of oceanic vapor move inland, the heavier isotope of sulfur is preferentially released as rain earlier than the lighter isotope, meaning that $\delta^{34}S$ values of rainfall decrease with distance from the coast (Nehlich, 2015). As this increasingly depleted water collects in rivers and streams, it also leaches sulfur of varying isotopic compositions from the soil and underlying rocks and minerals, meaning that inland aquatic $\delta^{34}S$ are highly regionally dependent.

Sulfur within terrestrial plants originates in both the atmosphere (primarily) and soil. Thus, plant $\delta^{34}S$ values are highly regionally dependent, with plants typically being about 1.5‰ lower in their values than their surrounding environment, though there can be significant variability even when considering plants of the same species (Nehlich, 2015). As the sulfur within animal tissues ultimately originates from the plants in its environment, animal $\delta^{34}S$ tends to closely track those of the local plant life, with some minor variation due to trophic discrimination or metabolic disturbance (Richards et al., 2003).

As most studies of ^{34}S in humans examine collagen methionine, little trophic fraction is observed with $\delta^{34}S$. This is because methionine is an essential amino acid in humans and is therefore routed to proteins directly from the diet. However, some trophic shift has been observed in muscle or bulk tissue analyses of other species, with some variation due to dietary quality, meaning that like collagen $\delta^{13}C$, $\delta^{34}S$ may disproportionately reflect higher protein components of the diet (McCutchan et al., 2003; Nehlich, 2015; Richards et al., 2003). This suggests that while human $\delta^{34}S$ values do represent the values of their diet with great fidelity, there can still be noticeable variation within the ecosystem itself.

Because of the high degree of local variability in $\delta^{34}S$, and the fact that such isotopic values tend to be conserved from diet to consumer, sulfur isotope analysis has great utility as a maker for mobility (Linderholm, et al., 2014; Nehlich et al., 2012; Richards et al., 2001). This is done by comparing the $\delta^{34}S$ of individual humans with the local sulfur baseline. If the two are substantially dissimilar, it can be assumed that the individual was likely non-local. Furthermore, implementing $\delta^{34}S$ values in dietary analyses alongside $\delta^{13}C$ and $\delta^{15}N$ can offer greater separation between sources with otherwise overlapping values. In particular, $\delta^{34}S$ can be used to tease apart consumption of marine resources – which are fairly consistent in their $\delta^{34}S$ values –

from aquatic resources, which are much more variable and tend to be lower than marine signatures (Nehlich et al., 2011; Nehlich et al., 2012; Privat et al., 2007).

One complicating factor in $\delta^{34}S$ analysis is the "sea spray effect", wherein coastal-dwelling humans and animals exhibit more ^{34}S enrichment than otherwise expected (with $\delta^{13}C$ and $\delta^{18}O$ of carbonates similarly affected) due to the incorporation of marine sulfur via aerosols into their tissues (Norman et al., 2006), though corrections for this effect have been proposed (Göhring et al., 2020). Furthermore, the relative scarcity of sulfur in human bone tissue means that only well-preserved specimens are likely to yield reliable $\delta^{34}S$ values (Nehlich & Richards, 2009).

Finally, and perhaps most significantly, increased anthropogenic release of sulfur has rendered many modern applications of sulfur isotope analysis unreliable, as the burning of fossil fuels, use of industrial fertilizers, or mining operations increase the turnover of buried minerals into local water systems (Krouse et al., 1996; Krouse & Mayer, 2000; Nehlich, 2015; Richards et al., 2001; Strauch et al., 2001). Thus, caution should always be taken when attempting to use modern flora and fauna as a proxy for those species in past environments.

Multi-Isotopic Analyses

Early on, researchers recognized the utility of using more than one isotope in estimating human diets, as certain food sources may have overlapping values for, say, $\delta^{13}C$, but have vastly different $\delta^{15}N$ values (DeNiro & Schoeninger, 1983; Leach et al., 2003). For example, aquatic and terrestrial animals frequently exhibit indistinguishable $\delta^{13}C$ values, but aquatic organisms (especially vertebrates) tend to have higher average $\delta^{15}N$ due to the more complex foodwebs of aquatic environments. This multi-isotopic "fingerprinting" can therefore be used to track the

movement of nutrients through foodwebs much better than single isotopes alone (Peterson et al., 1985).

In addition, multiple sampling of single individuals can give insights into changes in diet over the lifetime of the induvial, particularly when elements exhibiting regular linear growth and little or no remodeling are employed, such as hair and teeth (Balasse et al., 2011). Sampling different tissues can also provide information on the origin of different macronutrients in the diet via an understanding of isotopic routing (Froehle et al., 2012; Kellner & Schoeninger, 2007). The use of stable isotopes of multiple elements also allows for greater precision in estimating diet by creating multi-dimensional isoscapes. This can be quite useful in cases where different major food sources have overlapping isotope signatures for some elements, such as the difficulty in differentiating terrestrial versus aquatic resources using carbon and nitrogen alone (Bocherens et al., 2016). This will serve as the basis of the analysis presented in Chapter VII. Also, the use of sulfur oxygen ($\delta^{18}O$), or strontium ($^{87}Sr/^{86}Sr$) isotopes alongside carbon and nitrogen allow for mobility to be considered in addition to diet (Linderholm et al., 2014; Negrete et al., 2020; Price et al., 2018; Rand et al., 2020; Wright et al., 2013).

CHAPTER V: THEORETICAL BACKGROUND: MIXING MODELS

Principles of Stable Isotope Mixing Models

It is important to understand that most diet reconstructions using stable isotopes tend to be purely descriptive. For example, stable carbon ratios may be able to distinguish maize-consuming populations from non-maize consuming (Schwarcz et al., 1985), or nitrogen isotopes may indicate if a population is utilizing significant amounts of marine protein (Schoeninger & DeNiro, 1984). However, they are less useful when attempting to determine differences by degree (Cheung and Szpak 2021). How much more maize is one group consuming than another? What percent of an individual's diet consisted of animal protein? Bulk isotope signatures alone cannot answer these questions definitively because they are effective mixtures of all the isotopic ratios of the various components of a single diet. Furthermore, there can be a degree of equifinality in interpreting diets from isotopes, as different sources may have overlapping isotope ranges.

Stable isotope mixing models (SIMMs) offer a solution to these issues by using known information concerning food source isotope composition, macronutrient composition, and the effects of fractionation due to normal metabolism to effectively "reverse engineer" the diet composition from an individual's isotope profile. Put more simply, these programs estimate the combination of known food sources could produce a given isotope signature (Phillips, 2012). This can effectively add greater refinement to our understanding of the importance of various sources and how individuals – in addition to groups – varied in their reliance on different resources, particularly in cases with isotopically complex subsistence patterns (e.g. Mora et al., 2021; Newsome et al.,2004; Pestle & Laffoon, 2018; Pinder et al., 2019; Somerville et al., 2013; Zavodny et al., 2017).

Various types of linear mixing have been developed in diet reconstruction. Early understandings of maize consumption assumed a linear relationship between $\delta^{13}C$ and the among of maize consumed (Vogel & van der Merwe, 1977), though it was recognized that this was an oversimplification (Schwarcz, 1991). Kellner and Schoeninger (2007) developed a regression model that utilized $\delta^{13}C$ values from both collagen and apatite to assess an organism's major energy source (that is, the major carbohydrate and fat components of their diet) between C3 plants, C4 plants, and marine protein. Later, this model was updated to include $\delta^{15}N$ by Froehle et al. (2012), which allowed for discrimination between protein sources by holistically integrating $\delta^{13}C$ values from apatite with $\delta^{13}C$ and $\delta^{15}N$ from bone collagen to examine different components of the diet at higher resolutions. These models have also previously been used to study Maya populations with considerable success (Somerville et al., 2013).

In recent years there has been a shift within diet reconstruction toward the use of Bayesian, rather than linear, SIMMs, as they allow for the greater assumption of uncertainty as well as integrating factors such as diet to tissue offset, digestibility, various metabolic factors, etc. (Buck & Meson, 2015; Cheung & Szpak, 2021; Newsome et al., 2004; Parnell et al., 2013; Phillips, 2012). In isotopic studies of diet, Bayesian mixing models are particularly useful in parsing sources of carbon isotopes by factoring in routing and concentration dependence of food sources (Fernandes, 2016; Fernandes et al., 2012). This provides a significant advantage over linear mixing models, as it is well established that in most cases different food sources have different concentrations of macronutrients, and therefore contribute to tissue isotope values not always in proportion to their percentage of the diet (Phillips & Koch, 2002).

This approach is not, however, without complications. For example, lipids are isotopically lighter than proteins or carbohydrates in ^{13}C (DeNiro & Epstein, 1977; Post et al.,

2007). Thus, corrective measures should be applied to account for this, which can cause substantial differences in diet estimations depending on the technique employed (Arostegui et al., 2019). Moreover, Bond and Diamond (2011) found that variations in trophic discrimination factors could significantly impact estimates of diet composition. This is a substantial finding, given that widely accepted and cited discrimination factors can vary widely between sources, suggesting that context-specific factors be determined before using SIMMs. Also, a typical practice is to limit the number of food sources to the number of proxies (that is, isotope values used) plus one, otherwise, models are likely to fail (Phillips & Gregg, 2003). This may not always be possible when examining human groups with many possible food sources. Like any model, SIMMs are also only as reliable as the data input into them, thus care must be taken to ensure that only high-quality and reliable data are used to construct necessary baselines (Phillips et al., 2014).

Finally, the adoption of Bayesian techniques in fields like archaeology –concerning diet estimation or otherwise– requires an understanding of the mechanics and methods employed in the underlying model, otherwise results produced from Bayesian modeling cannot be properly evaluated or retested for validity (Buck & Meson, 2015; Phillips, 2001; Phillips et al., 2014). Similarly, the level of technical expertise of the researchers, research design, and overall goals can and should determine the specific model and features utilized (Cheung & Szpak, 2021).

Food Reconstruction Using Stable Isotope Transfer Signals (FRUITS)

While several Bayesian isotope mixing models for dietary reconstruction have been developed (e.g. SIMMS, MixSIAR, Isosource), Food Reconstruction Using Isotopic Transferred Signals (FRUITS) is unique in that it was developed expressly for use in reconstructing past

human diets, concordant with the methods and practices of human paleonutrition (Fernandes et al., 2014). Importantly, FRUITS is designed to work on data sets with multiple isotope signals per a single individual, representing ratios of different skeletal tissues (e.g., Kaupová et al., 2018).

In paleodiet reconstruction, this would frequently include $\delta^{13}C_{apatite}$, $\delta^{13}C_{collagen,}$ and $\delta^{15}N_{collagen}$. This allows the user to account for isotopic routing in their target data by incorporating "offsets'' for various target "signals" or isotope ratios (Ambrose & Norr 1993; Fernandes et al. 2012; Froehle et al., 2010; Kellner & Schoeninger 2007). For example, the carbon of collagen is derived primarily, but not entirely, from dietary protein. Therefore. It is assumed that the $\delta^{13}C$ value of collagen will overrepresent that of protein over carbohydrates and lipids by approximately 3 to 1 (Fernandes et al. 2012). Conversely, $\delta^{15}N$ from collagen can be expected to 100% represent that of dietary protein, and $\delta^{13}C$ of apatite all dietary fractions equally. Furthermore, additional prior information can be inputted based on assumptions about the individuals to be modeled. For example, it is reasonable to assume a priori that in a healthy individual, protein will comprise between 5% and 45% of the diet (Fernandes et al., 2015).

The user begins by assembling a "source" database of potential food consumed with relevant nutritional information. This includes percent macronutrient composition and individual isotopic ratios for each source. These sources are then categorized based on the dietary composition of interest. These could be, for example, C3 plants, C4 plants, marine animal protein, and terrestrial animal protein. Consumer, or "target", isotope ratios are then entered. Finally, any prior assumptions of diet as described above can be included.

With all source, target, and prior data entered, FRUITS then models possible combinations of source contributions capable of producing the given target isotope signatures

within the given prior parameters. The result is output for each consumer with the estimated average percent contribution (per each iteration of the model) of each source to the diet. This is beneficial for paleodiet reconstruction because unlike bulk isotopic ratios alone, these modeled diets are directly comparable between individuals, provided that the same parameters are followed.

SECTION II: FACTORS INFLUENCING DIET ESTIMATION

CHAPTER VI: FRUITS MODEL GENERAL PARAMETERS

The following experiments utilize a common set of FRUITS model parameters, except when otherwise noted. In general, model parameters follow methods outlined by Fernandes et al. (2015) and Pestle and Laffoon (2018) and can be seen in Izzo et al. (2022).

Proxies & Targets

All models utilize target $\delta^{13}C$ and $\delta^{15}N$ signatures as proxies for diet. To better separate the protein component of the diet from bulk ratios, carbon isotopes from both hydroxyapatite and collagen are utilized due to macronutrient routing, apart from sulfur isotope ratios (described below). Chapter IX differs from the previous models only in that it incorporates a fourth proxy – stable isotope ratios of sulfur derived from collagen methionine. All human isotope data analyzed here originate from the Pasión Region and date primarily to the Late and Terminal Classic, except for a single sample from a Preclassic burial from the site of Tamarindito. All samples used for models for which $\delta^{13}C$ and $\delta^{15}N$ are the only proxies can be found in Table 6.1. All human burials were excavated as part of the Vanderbilt Petexbatún Regional Archaeological Project between 1989 and 1994 (Demarest, 1997).

A subset of the burials presented in Table 6.1 either have $\delta^{34}S$ available or were analyzed for $\delta^{34}S$ as part of this study. The $\delta^{34}S$ data for half of these samples were obtained from Thornton and Wright (n.d.), which sought to investigate ^{34}S ratios within the Pasión Region among both human and faunal remains. Those human samples can be found in Table 6.2.

This sample contains several notable individuals. TA6 from Tamarindito possibly represents the ruler "Chanal Balam" as identified by Valdés (1997). DP30 likely represents Dos Pilas's "Ruler 2", likely the son of the first documented ruler of the site, and DP20,

epigraphically known as the "Woman of Cancuen", the wife of Ruler 2's son, "Ruler 3" (Wright, 1994, 2006). Furthermore, several samples -DPA, DPB, DPE, DPG, DPH, DPI, DP9, DP10A, DP10B, and DP12- represent decapitated crania dating to the Terminal Classic (Wright, 2006). Additionally, LP1 and AP4 likely represent royal and elite individuals, respectively, based on associated grave goods (Wright, 2006). Citations, age and sex estimates, and additional provenience information for all samples can be found in Appendix A.

Source Data

The models used herein utilize isotope data from modern floral and both modern and archaeological faunal samples. Selected taxa are generally representative of those archaeological or epigraphically known to be Maya food items. In addition to data derived from the literature, I also performed $\delta^{13}C$ and $\delta^{15}N$ analysis on a further 16 modern botanical samples. Bulk organic analysis of these samples was performed using a Thermo EA Isolink and Delta V Advantage IRMS at the Stable Isotope Geosciences Facility at Texas A&M University. All isotope signatures represent the edible portion of the source (where available) or are derived from accepted offsets between edible portions (generally skeletal muscle) and bone tissues, as described below. Carbon isotope values of modern taxa (both flora and fauna) were corrected by +1.5‰ due to the Suess effect (Marino & DeNiro, 1987). Procedures follow the methods described by Fernandes et al. (2015).

Individual taxa are further separated into source groups. For floral specimens, grouping is based on photosynthetic pathway. Therefore, floral sources are C3 and C4 for all models. Plants utilizing CAM photosynthesis are excluded from the analysis. This group does include some cultivars that were known to the ancient Maya – including pinuela (*Bromelia karatas*) and nopal

Table 6.1: Human Target Data for $\delta^{13}C$ and $\delta^{15}N$ Analysis (N=45)

FRUITS ID	Burial ID	Site	Period	$\delta^{13}C_{apatite}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)
1	TR3-1	Tamarindito	Preclassic	-7.9	-12.6	8.8
2	DP52	Dos Pilas	Late Classic	-3.8	-8.6	10.5
3	TA4	Tamarindito	Late Classic	-7.2	-9.1	9.8
4	TA6	Tamarindito	Late Classic	-4.1	-8.9	10.2
5	CC1	Cerro de Cheyo	Late Classic	-5.2	-9.1	10.2
6	LP1	La Pacencia	Late Classic	-4.6	-10.3	9.6
7	DP55	Dos Pilas	Late Classic	-2.8	-8.6	10.1
8	AP4	Arroyo de Piedra	Late Classic	-3.2	-9.7	2.3
9	AG1	Aguateca	Late Classic	-5.8	-9.9	9.1
10	QCH5	Aguateca	Late Classic	-4.1	-9.9	7.9
11	QCH6	Aguateca	Late Classic	-8.3	-11.0	10.1
12	DP2	Dos Pilas	Terminal Classic	-5.0	-8.9	8.7
13	DPA	Dos Pilas	Terminal Classic	-5.3	-8.4	11.6
14	DPB	Dos Pilas	Terminal Classic	-6.3	-11.3	9.6
15	DPE	Dos Pilas	Terminal Classic	-6.3	-12.0	12.7
16	DPG	Dos Pilas	Terminal Classic	-6.9	-11.2	9.7
17	DPH	Dos Pilas	Terminal Classic	-4.9	-8.6	9.1
18	DPI	Dos Pilas	Terminal Classic	-5.3	-8.8	10.4
19	DP4	Dos Pilas	Late Classic	-5.1	-9.1	9.7
20	DP9	Dos Pilas	Terminal Classic	-5.2	-9.6	9.5
21	DP10B	Dos Pilas	Terminal Classic	-4.6	-9.0	11.6
22	DP10A	Dos Pilas	Terminal Classic	-4.1	-8.6	9.1
23	DP12	Dos Pilas	Terminal Classic	-3.9	-7.8	12.4
24	DP16	Dos Pilas	Terminal Classic	-7.2	-9.7	7.5
25	DP17	Dos Pilas	Terminal Classic	-7.2	-9.7	10.3
26	DP20	Dos Pilas	Late Classic	-6.2	-9.6	11.0
27	TA1A	Tamarindito	Late Classic	-4.7	-9.3	8.1
28	TA2	Tamarindito	Late Classic	-6.4	-13.0	8.2
29	DP22	Dos Pilas	Late Classic	-4.6	-7.7	10.6
30	DP29	Dos Pilas	Late Classic	-4.3	-9.7	10.1
31	DP43	Dos Pilas	Late Classic	-6.7	-8.6	10.1
32	DP45	Dos Pilas	Late Classic	-4.1	-8.2	10.3
33	DP47	Dos Pilas	Late Classic	-6.4	-8.3	11.1

Table 6.1 Continued

FRUITS ID	Burial ID	Site	Period	$\delta^{13}C_{apatite}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)
34	DP50	Dos Pilas	Late Classic	-5.6	-9.1	9.7
35	TR3/2	Tamarindito	Late Classic	-6.6	-9.7	10.9
36	DP1	Dos Pilas	Late Classic	-7.1	-7.0	9.3
37	DP49	Dos Pilas	Late Classic	-6.4	-10.1	9.9
38	DP33	Dos Pilas	Late Classic	-5.9	-9.5	8.3
39	DP5	Dos Pilas	Late Classic	-6.4	-8.6	7.7
40	DP3	Dos Pilas	Terminal Classic	-6.6	-8.2	8.2
41	DP13	Dos Pilas	Terminal Classic	-8.0	-9.8	9.1
42	DP30	Dos Pilas	Late Classic	-7.6	-8.5	8.9
43	AG5B	Aguateca	Late Classic	-7.3	-9.3	9.1
44	AG5A	Aguateca	Late Classic	-5.5	-8.8	8.0
45	DP44	Dos Pilas	Late Classic	-8.3	-11.3	10.2

(*Opuntia* sp.). However, it is unlikely that plants from this group constituted a large enough portion of any diet to greatly influence the model.

Faunal specimens are likewise terrestrial, marine, and aquatic species. This affects individual isotope signatures in that it largely determines the basal isoscape of the specimens' food web, which varies between environments. While certain specimens may spend time in (and, more importantly, consume resources from) different environments, for the sake of simplicity they are grouped here according to the environment in which they spend at least 50% of their time. For example, all species of turtle are considered aquatic animals for modeling. Hereafter, faunal sources are referred to as TP (terrestrial protein), AP (aquatic protein), and MP (marine protein).

A full list of source taxa, their provenience, isotope values, and appropriate citations can be found in Appendix B.

Table 6.2: Human Target Data for $\delta^{34}S$ Analysis (N=18)

FRUITS ID	Burial ID	Site	Period	$\delta^{13}C_{apatite}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)
1S	AG5A	Aguateca	Late Classic	-5.5	-8.8	8.0
2S	AG1	Aguateca	Late Classic	-5.8	-9.9	9.1
3S	AG5B	Aguateca	Late Classic	-7.3	-9.3	9.1
4S	DP30	Dos Pilas	Late Classic	-7.6	-8.5	8.9
5S	DP17	Dos Pilas	Terminal Classic	-7.2	-9.7	10.3
6S	DP1	Dos Pilas	Terminal Classic	-7.1	-7.0	9.3
7S	DP4	Dos Pilas	Terminal Classic	-5.1	-9.1	9.7
8S	DP13	Dos Pilas	Terminal Classic	-8.0	-9.8	9.1
9S	DP5	Dos Pilas	Terminal Classic	-6.4	-8.6	7.7
10S	CC1	Cerro de Cheyo	Late Classic	-5.2	-9.1	10.2
11S	DP55	Dos Pilas	Late Classic	-2.8	-8.6	10.1
12S	DP2	Dos Pilas	Late Classic	-5.0	-8.9	8.7
13S	DPG	Dos Pilas	Terminal Classic	-6.9	-11.2	9.7
14S	DP9	Dos Pilas	Terminal Classic	-5.2	-9.6	9.5
15S	DP10B	Dos Pilas	Terminal Classic	-4.6	-9.0	11.6
16S	DP49	Dos Pilas	Late Classic	-6.4	-10.1	9.9
17S	DP10A	Dos Pilas	Terminal Classic	-4.1	-8.6	9.1
18S	DP12	Dos Pilas	Terminal Classic	-3.9	-7.8	12.4

Source Proxy Values

The mean and standard error of each proxy value ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$) were calculated from each source group. These values can be found in Tables 6.3 and 6.4.

Table 6.3: Plant Source Proxy Values (‰)

Group	$\delta^{13}C_{bulk}$	$\delta^{15}N_{bulk}$
C3	-27.5±0.25	4.81±0.42
C4	-8.84±2	5.05±2

Table 6.4: Animal Source Proxy Values (‰)

Group	$\delta^{13}C_{apatite}$	$\delta^{13}C_{collagen}$	$\delta^{15}N_{collagen}$	$\delta^{34}S_{methionine}$
Terrestrial	-9.72±0.4	-19.29±0.61	5.48±0.15	12.47±0.26
Aquatic	-2.82±6.51	-19.97±0.68	7.84±7.84	7.6±0.75
Marine	-3.35±0.61	-3.35±1.35	9.41±0.53	9.94±2.52

Fractions

Three or four source fractions are considered, depending on the model being used. Fractions are standard across all models and follow those originally described by Fernandes et al. (2015). These include BULK – the isotopic composition of the full diet regardless of nutrient breakdown, PROTEIN – the isotope value of the protein component of the diet alone – and ENERGY – the isotope value of the carbohydrate and fat components of the diet. In models where sulfur isotopes are employed, a fourth fraction is also used, METHIONINE, representing the sulfur isotope value of the amino acid methionine. Where isotope values are derived from animal (terrestrial, marine, or aquatic) collagen, offsets are further employed to determine the isotope composition of the animal's edible portions using fractionation factors derived by Fernandes (2016) from consensus values from previous feeding studies. These offset values and their accompanying uncertainties can be found in Table 6.4**.** The application of these discrimination factors yields the expected contribution of each fraction from the sources to the respective proxies, which can be found in Table 6.5. Conservative uncertainties of ±1‰ were used for all fractions except $\delta^{34}S_{methionine}$, for which an even more conservative of ±2‰ was used due to low sample sizes and model complexity.

Concentrations

Source concentrations present a particular challenge, particularly in the case of domesticated taxa. Humans select for various qualities in a food source, and therefore there can be temporal as

well as geographic variation in the macronutrient concentrations of a single food source. Most SIMM studies, for example, utilize standards of food nutritional composition derived from the United States Department of Agriculture (USDA) FoodData Central database.

Table 6.5: Animal Macronutrient to Collagen Offset (derived from Fernandes, 2016)

	$\Delta^{13}C_{protein\text{-}collagen}$	$\Delta^{13}C_{lipids\text{-}collagen}$	$\Delta^{15}N_{protein\text{-}collagen}$
Terrestrial Animals	-2‰ ± 1‰	-8‰ ± 1‰	+2‰ ± 1‰
Fish	-1‰ ± 1‰	-7‰ ± 1‰	+2‰ ± 1‰

Table 6.6: Source Fraction Values

		$\delta^{13}C_{apatite}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)
C3	Bulk	-27.5			
	Protein		-29.5	4.81	
	Energy		-27		
	Methionine				6.82
C4	Bulk	-8.84			
	Protein		-10.84	5.05	
	Energy		-8.34		
	Methionine				4.36
Terrestrial	Bulk	-21.87			
	Protein		-21.29	7.48	
	Energy		-27.29		
	Methionine				12.47
Aquatic	Bulk	-21.59			
	Protein		-20.97	9.84	
	Energy		-26.97		
	Methionine				7.6
Marine	Bulk	-5.16			
	Protein		-4.35	11.41	
	Energy		-10.35		
	Methionine				9.94

However, the foods included in this database reflect a generally industrialized, Western dietary menu. This can create problems when attempting to understand the nutritional profiles of

foods generally unseen in Western cuisine, and especially in past populations. While the significance of this variation is tested in subsequent chapters, a summary of the macronutrient concentrations of the sources and their associated uncertainties derived from USDA data can be found in Table 6.6. To test the appropriateness of regional or temporal variation in macronutrient concentrations, Table 6.7 contains nutritional data derived from the Institute of Nutrition of Central America and Panama (INCAP) of Guatemala City and the National Institutes of Health of Bethesda, Maryland (Leung & Flores, 1961). This database contains compositional data of foodstuffs common to and collected from Central America. All uncertainties are derived from the standard error of the mean of the given dataset. In cases where only one data point is available, a conservative uncertainty of 2% is employed. Complete tables of macronutrient concentrations by source group and taxon can be found in Appendix C.

Table 6.7: Macronutrient Concentrations – USDA Data (US Department of Agriculture & Agricultural Research Service, 2019)

Food Group	Bulk %	S.E.	% Protein	S.E.	% Energy	S.E.	Methionine %	S.E.
C3	100	0	13.34	4.68	86.66	4.68	100	0
C4	100	0	10.98	2	89.02	2	100	0
Terrestrial	100	0	89.24	1.61	10.76	1.61	100	0
Aquatic	100	0	87.42	2.29	12.58	2.29	100	0
Marine	100	0	80.56	14.44	19.44	14.44	100	0

Table 6.8: Macronutrient Concentrations – INCAP Data (Leung & Flores, 1961)

Food Group	Bulk %	S.E.	% Protein	S.E.	% Energy	S.E.	Methionine %	S.E.
C3	100	0	11.97	1.89	88.03	1.89	100	0
C4	100	0	7.94	2	92.06	2	100	0
Terrestrial	100	0	90.91	3.64	9.09	3.64	100	0
Aquatic	100	0	92	3.08	8	3.08	100	0
Marine	100	0	92.28	1.33	7.72	1.33	100	0

Offsets and Weights

FRUITS software controls for human diet-to-tissue routing and fractionation through the use of offsets and weights. Offsets represent the fractionation factor between each isotope and its integration into human tissues. Weights represent routing by accounting for the relative contribution of different macronutrients to different tissues. For instance, because $\delta^{13}C_{apatite}$ represents a "scrambled egg" model of dietary carbon, it faithfully represents the Bulk signature of the diet. Collagen, however, tends to overrepresent the protein component of the diet due to the preferential routing of amino acids to bodily proteins. Thus, $\delta^{13}C_{collagen}$ represents Protein to Energy by a factor of approximately 3 to 1 (Fernandes et al., 2012). As methionine is an essential amino acid, it represents the methionine of the total diet and thus weights 100% methionine.

Offsets used in these analyses follow accepted standards of carbon to apatite fractionation, and carbon and nitrogen to collagen fractionation (Fernandes, 2016; Fernandes et al., 2012). Again, because methionine is an essential amino acid in humans, it is assumed to exhibit no fractionation from diet to tissue, as the reactivity of sulfur plays no role in the likelihood of methionine being catabolized. Data for Offsets and weights used in all models can be found in Table 6.8.

Table 6.9: Offsets and Weights (‰)

	Offset	S.E.	Bulk	S.E.	Protein	S.E.	Energy	S.E.	Methionine	S.E.
$\delta^{13}C_{apatite}$	10.1	0.5	100	0	0	0	0	0	0	0
$\delta^{13}C_{collagen}$	4.8	0.5	0	0	74	4	26	0	0	0
$\delta^{15}N_{collagen}$	5.5	0.5	0	0	100	0	0	0	0	0
$\delta^{34}S_{methionine}$	0	0.5	0	0	0	0	0	0	100	0

Priors

Following the methods of Fernandes et al. (2015), the model employed here assumes that all measured individuals consumed a nutritionally satisfactory diet, or at least over the length of time represented by bone deposition, their diet tended toward adequate. This is a broad assumption, given the variation in periods, sites, and social circumstances of the individuals. This also has implications for both the degree of diet-to-tissue offset, as recent studies have shown that states of nitrogen imbalance during periods of nutritional stress (Carroll et al., 2018; Hatch et al., 2006; Petzke et al., 2010), disease (Katzenberg & Lovell, 1999; Olsen et al., 2014) or pregnancy (Fuller et al., 2010) can introduce variations in both nitrogen and carbon isotope fractionation. However, limited experimental studies have shown the effect to be minimal compared to other sources of variation (Canterbury et al., 2020). In this study, I, therefore, assume that all diets consist of between 5% and 45% protein (Fernandes et al., 2014b).

CHAPTER VII: REGIONAL SPECIFICITY IN SOURCE MACRONUTRIENT COMPOSITION

Overview

As before stated, there has been a proliferation in recent years in the use of SIMMs to reconstruct diets in archaeology. While many of these incorporate macronutrient concentration as a parameter, almost none derive the nutritional composition of key foods for the given population as a course of the analysis. Rather, most utilize available data from the United States Department of Agriculture's FoodData Central. This database provides nutritional profiles of experimental and branded commercial foods, among others, but of particular interest to diet, reconstruction is the Standard Reference (SR) Legacy dataset. The SR served as the major food composition data type of the USDA, and "provides the foundation for most food composition databases in the public and private sectors" (US Department of Agriculture & Agricultural Research Service Nutrient Data Laboratory, 2018, p. 4). In 2012, it was recognized that the SR was no longer practical given the rapid pace of change in the U.S. and global food supply, and so USDA ceased updating SR in 2015 in favor of other databases such as the Global Branded Food Products Database and was released for the final time in 2018 as SR Legacy (Fukagawa et al., 2022).

The appeal of SR Legacy data in diet reconstruction is fairly obvious, it is standardized, publicly accessible data, containing over 7,000 individual food items and as many as 150 food components accrued over nearly a century (US Department of Agriculture & Agricultural Research Service Nutrient Data Laboratory, 2018). However, it should be noted that before 2015 the SR was a living document constantly updated, and thus subject to temporal variation.

However, more of a concern than the variability in the isotope composition of foods is the nutritional variability. As humans tend to select for particular, desirable traits over time, there can be substantial temporal variation in macronutrient composition, which, as discussed in the

previous chapter, can also introduce isotopic variability due to different portions of isotopically dissimilar macromolecules. Examination of the FoodData Central's data reveals a median 6% drop in total protein among 43 common crops during the latter half of the twentieth century alone (Davis et al., 2004). This says nothing of the corresponding dilution in key micronutrients in many cultivars over approximately the same period (White & Broadley, 2005), though likely not enough to affect the overall dietary intake of populations on the whole.

Even within the USDA's database, there can be significant variability in the macronutrient composition of different varieties. For example, in a study of the drought hardiness of Maya cultivars, Fedick and Santiago (2022) use USDA's nutritional data for raw modern yellow sweet corn (NDB Ref: 11167), which has a protein content of approximately 14% of its dry mass. In contrast, the default maize variety in this volume where USDA data is used is dried Navajo corn (NDB Ref: 35134), which is only 11% protein by dry mass but is likely much more similar in composition to the agricultural staple cultivated by the ancient Maya. This distinction is not made by Fedick and Santiago (2022). This can be problematic as, even after over a century of industrialization of agriculture, modern maize in the Yucatan displays a vast degree of diversity, and it should be expected that this would have only been greater in the past (Tuxill et al., 2010). Finally, there can be further issues when considering data not just from the USDA, but from various regional and international databases as well. Multiple food compositional databases are used simultaneously, as there can be considerable variation in both the types of foods included and the compositions of those foods (Merchant & Dehghan, 2006).

This, in turn, could have implications for diet reconstructions when its data are used as proxies for foods in the distant past if macronutrient compositions have changed from ancient

foods as a result of artificial selection. For example, Huelsemann et al., (2013) found that modern pigs and poultry were significantly depleted in ^{15}N relative to their historical counterparts. This is possibly due to changes in feeding regimens but could also be caused by recent intensive selection for rapid growth among modern livestock. This is because rapid growth of tissue has been associated with a depletion in an organism's ^{15}N pool as more of the light isotope remains bound in bodily proteins instead of catabolized for energy (Fuller et al., 2004; K. A. Hatch et al., 2006; Waters-Rist & Katzenburg, 2010). Luckily, the isotopic composition of animal foods can be inferred from analysis of archaeofaunal remains, and while isotopic data of floral remains are few and far between, their isotope composition can also be estimated from fauna when relevant trophic discrimination factors are well established.

Given our knowledge of how the nutritional composition of foods can change over time, particularly for domestic plants and animals since the Second World War, and across space, such as between industrialized and non-industrialized nations, very little attention is paid in diet reconstruction to regional and temporal variation in food composition. Indeed, USDA data has been used as proxies for ancient food items in such disparate circumstances as Neolithic Germany (Fernandes et al., 2015), medieval Bohemia (Kaupová et al., 2018), pre-Columbian Chile (Mora et al., 2021), and the prehistoric U.S. Virgin Islands (Pestle & Laffoon, 2018).

Given this variability, it stands to reason that food source data should apply to the archaeological context in terms of their nutritional composition in addition to their isotope composition. Unfortunately, reliable data on the nutritional composition of ancient foodstuffs is largely lost except in very specific circumstances. However, it is likely that the foodstuffs of largely subsistence-based agricultural populations descended from and currently occupying the ancestral lands of past populations will likely resemble those cultivated in the past closely than

do the databases of modern industrialized nations. In the case of Mesoamerica, one such dataset currently exists. The Food Composition Table for Use in Latin America – a 1961 joint effort of the Institute of Nutrition of Central America and Panama (INCAP) of Guatemala City and the National Institutes of Health of Bethesda, Maryland (Leung and Flores, 1961). "INCAP", as it is commonly known, contains compositional data of foodstuffs common to and collected from Central and South America, and includes many local foods known to the Maya but absent from the USDA database including chaya, armadillo, and iguana. Furthermore, some food items exhibit marked differences in reported composition between the two datasets. Some examples of these discrepancies can be found in Table 7.1. This could be due either to regional variation in nutrient composition or measurement accuracy between agencies given the technology available at the time (K. Kubena, pers. comm., 2022).

Table 7.1: Nutritional Composition of Some Maya Foods in INCAP vs. USDA FoodData Central

	INCAP		**USDA**	
Species	**Protein (wt/100g)**	**Energy (wt/100g)**	**Protein (wt/100g)**	**Energy (wt/100g)**
Annona muricata (soursop)	1	15.3	1	20.1
Brosimum alicastrum (ramón/breadfruit)	11.4	77.7	5.97	47.2
Capsicum sp. (chile)	1.9	8.6	0.91	11.08
Phaseolus vulgaris (bean)	9.8	28.1	22.3	62.3
Persea americana (avocado)	1.7	20.2	1.96	24.04
Zea mays (maize, dry kernel)	3.9	45.2	9.88	80.12
Meleagris sp. (turkey)	20.2	0	22.6	1.9
Odocoileus virginianus (whitetail deer)	29.5	2.2	21.5	2.66

This section will therefore seek to compare the results of FRUITS models using nutritional data derived from INCAP and the USDA FoodData Central, respectively, to ascertain the degree of difference that regional or cultural specificity of the reference data can have on diet composition estimates.

Methods

Source datasets were compared by running five (C3, C4, TP, AP, and MP), four (C3, C4, TP, and AP), and three-source (C3, C4, and TP) models for both datasets. As such, all macronutrient concentration data for the INCAP and USDA models were derived from their respective datasets alone. The human isotope presented in Table 6.1 (n=45, $\delta^{13}C_{collagen}$, $\delta^{13}C_{apatite}$, and $\delta^{15}N_{collagen}$) was used for this comparison.

Both databases possess a wealth of maize/corn varietals from which to choose. The effects of maize processing techniques on SIMM results are explored in the next chapter, and therefore both models use C4 composition data derived from raw, dry maize. Some discretion was utilized in selecting the maize proxy for the USDA model that would best represent that cultivated by the Pre-Contact Maya. As before stated, Navajo dry maize was selected to fill this role. Protein and energy concentrations for all source groups from each dataset can be found in Table 7.2.

Table 7.2: Macronutrient Concentration Parameters by Model Iteration (INCAP vs. USDA)

	INCAP		USDA	
Source	**% Protein**	**% Energy**	**% Protein**	**% Energy**
C3	11.97	88.03	10.94	89.06
C4	10.67	89.33	10.98	89.02
Terrestrial Protein	90.91	9.09	89.24	10.76
Aquatic Protein	92	8.0	87.42	12.58
Marine Protein	92.28	7.72	84.99	15.01

All other model parameters were identical to those presented in the previous chapter. For the sake of simplicity, paired two-sample t-tests (α=0.05) were used to assess statistical significance for each source and individual between model iterations. To test for model integrity,

in each three-source model, the estimation of TP consumption was plotted against $\delta^{15}N$ for each individual. It is expected that in a simply three-source model these should be highly correlated.

Results

Four (C3, C4, TP, AP) and five-source (C3, C4, TP, AP, MP) models failed to produce results for both iterations due to model complexity (number of sources > number of proxies). However, three-source models (C3, C4, TP) were ultimately successful, and the estimated proportion of each source for each individual can be found in Table 7.3.

As expected, both iterations produced results suggesting diets high in maize for all individuals, with C3 plants generally clustered between 20% and 30% of diet. Terrestrial protein is much less prevalent in the diets of most individuals, which averages approximately 5-6% in both model iterations. However, there is also a considerable interindividual variation with this source, with some estimates over 10% and, in one case, 20% of overall diet. This fits within expectations of generally unequal access to high-value animal resources, and this is born out in both models.

The results of the two model iterations did produce significantly different (TP: $t=-4.44$, $N=45$, $p<0.01$) estimates for all three sources. The INCAP model, on average, estimated significantly more C3 plant consumption than did the USDA model, which correspondingly estimated significantly more maize and terrestrial protein consumption. Despite their statistical significance, the actual difference between model iterations was small, on the order of 1-2%.

Finally, TP values in both three-source model iterations appear to be highly correlated with individual $\delta^{15}N$, with correlation coefficients of 0.732 and 0.737 for the INCAP and USDA models, respectively. These values can be seen plotted in Figure 7.1

Conclusion

From the given data, it can be said with confidence that the choice of source dataset can have some impact on estimated diet compositions, but that the magnitude of these differences is likely to be small enough to make no practical difference in interpretation. More importantly, the high amount of maize consumption estimated and the degree of correlation between %TP and $\delta^{15}N$ observed in both model iterations suggests that each can produce realistic estimations of human diets.

Interestingly, both FRUITS models estimated less meat consumption than the $\delta^{15}N$ variability would suggest. Only three individuals were estimated to consume meat as 10% or more of their total diet. All three, DPE (15), DP12 (23), and DP10B (21) are decapitated remains dating to the Terminal Classic (Wright, 1994). This possibly indicates status-based access to meat, as such decapitated assemblages are often interpreted as either an overthrow of the ruling elite, the sacrifice of high-status prisoners, or a high-status invading army (Wright, 1994, 1997b, 2006). This relationship is, however, belied by the fact that AP4 (8) can be interpreted as having consumed little to no animal protein from both the FRUITS models and their $\delta^{15}N$ signature. This burial has been postulated to represent an elite individual based on associated grave goods (Wright, 1994).

The USDA's FoodCentral Database has the advantage of being easily accessible and, as demonstrated here and in other studies, able to produce consistent results in concentration-dependent SIMMs and is invaluable in any study where context-specific data is unavailable. However, within the context of ancient Maya diet reconstruction, the INCAP dataset is likely the preferable choice. It contains nutritional data on many foodstuffs known to have been used by the Maya that are absent from a broader western context. However, its utility will likely be greatly improved by supplementation with data from other databases, like FoodCentral,

Table 7.3: Results of INCAP vs. USDA Macronutrient Parameters

Target	Burial ID	Source	INCAP Mean %	INCAP s.d.	USDA Mean %	USDA s.d.
1	TR3-1	C3	42.61%	6.75%	41.32%	6.12%
		C4	52.46%	4.11%	53.96%	3.95%
		TP	4.93%	7.44%	4.72%	6.74%
2	DP52	C3	17.91%	6.66%	17.30%	6.43%
		C4	74.60%	4.11%	75.31%	3.91%
		TP	7.48%	6.52%	7.39%	6.47%
3	TA4	C3	30.47%	5.15%	28.89%	5.13%
		C4	65.66%	3.91%	67.11%	3.89%
		TP	3.86%	4.41%	4.00%	4.55%
4	TA6	C3	19.88%	6.67%	19.17%	6.42%
		C4	73.02%	3.96%	73.86%	4.00%
		TP	7.10%	6.75%	6.98%	6.51%
5	CC1	C3	23.79%	6.37%	22.60%	6.44%
		C4	69.91%	3.93%	70.79%	3.90%
		TP	6.31%	6.41%	6.61%	6.51%
6	LP1	C3	25.47%	7.29%	24.28%	7.44%
		C4	67.24%	4.07%	68.34%	4.13%
		TP	7.29%	7.92%	7.38%	8.19%
7	DP55	C3	16.03%	6.26%	15.37%	6.17%
		C4	76.97%	3.91%	77.48%	4.00%
		TP	7.00%	6.04%	7.16%	6.23%
8	AP4	C3	21.90%	3.96%	21.77%	4.21%
		C4	77.79%	3.95%	77.91%	4.19%
		TP	0.31%	0.32%	0.33%	0.34%
9	AG1	C3	29.74%	5.65%	28.64%	5.23%
		C4	66.26%	3.81%	67.30%	3.79%
		TP	4.00%	5.39%	4.07%	5.01%
10	QCH5	C3	26.57%	5.34%	25.83%	4.98%
		C4	70.51%	3.79%	71.53%	3.81%
		TP	2.92%	4.88%	2.65%	3.90%
11	QCH6	C3	37.26%	6.25%	35.70%	7.08%
		C4	56.54%	4.13%	57.18%	4.39%
		TP	6.19%	7.03%	7.12%	8.21%
12	DP2	C3	25.50%	4.96%	24.07%	4.85%
		C4	71.51%	3.76%	72.82%	3.71%
		TP	2.99%	3.94%	3.11%	3.96%
13	DPA	C3	19.47%	6.94%	17.86%	6.76%
		C4	71.40%	4.20%	72.52%	4.17%
		TP	9.13%	7.34%	9.62%	7.52%
14	DPB	C3	32.90%	7.39%	31.47%	7.31%
		C4	60.04%	4.21%	61.19%	4.17%
		TP	7.06%	8.28%	7.35%	8.42%
15	DPE	C3	21.35%	9.10%	19.84%	8.68%
		C4	54.27%	4.59%	54.81%	4.68%
		TP	24.38%	10.85%	25.35%	10.63%
16	DPG	C3	33.94%	7.20%	32.72%	7.20%
		C4	59.16%	4.13%	60.19%	4.25%
		TP	6.90%	8.10%	7.10%	8.30%

Table 7.3 Continued

Target	Burial ID	Source	INCAP Mean %	INCAP s.d.	USDA Mean %	USDA s.d.
17	DPH	C3	24.03%	5.06%	22.91%	5.11%
		C4	72.63%	3.85%	73.64%	3.79%
		TP	3.34%	3.93%	3.45%	4.19%
18	DPI	C3	23.18%	6.24%	21.92%	6.32%
		C4	70.75%	3.86%	71.43%	4.00%
		TP	6.07%	5.94%	6.65%	6.49%
19	DP4	C3	24.53%	5.88%	23.33%	6.02%
		C4	70.36%	3.88%	71.32%	3.89%
		TP	5.12%	5.71%	5.35%	5.89%
20	DP9	C3	26.57%	5.83%	25.32%	6.04%
		C4	68.50%	3.86%	69.49%	3.91%
		TP	4.93%	5.64%	5.19%	5.95%
21	DP10B	C3	17.86%	7.34%	16.88%	7.02%
		C4	70.76%	4.30%	71.57%	4.22%
		TP	11.38%	8.02%	11.55%	7.99%
22	DP10A	C3	21.55%	5.58%	20.44%	5.29%
		C4	74.53%	3.92%	75.54%	3.84%
		TP	3.92%	4.54%	4.03%	4.61%
23	DP12	C3	12.56%	6.36%	11.32%	6.16%
		C4	76.20%	4.13%	76.92%	4.27%
		TP	11.24%	6.82%	11.75%	7.01%
24	DP16	C3	34.12%	4.15%	32.88%	4.25%
		C4	64.43%	3.81%	65.62%	3.87%
		TP	1.45%	2.20%	1.51%	2.27%
25	DP17	C3	31.06%	6.12%	29.38%	6.07%
		C4	63.25%	4.01%	64.59%	3.98%
		TP	5.69%	6.38%	6.03%	6.38%
26	DP20	C3	25.48%	7.36%	24.09%	7.54%
		C4	65.35%	4.23%	66.20%	4.35%
		TP	9.17%	8.09%	9.72%	8.75%
27	TA1A	C3	26.59%	4.50%	25.37%	4.43%
		C4	71.11%	3.69%	72.28%	3.65%
		TP	2.30%	3.27%	2.35%	3.03%
28	TA2	C3	39.74%	7.83%	39.14%	6.97%
		C4	55.22%	3.83%	56.12%	4.05%
		TP	5.04%	8.57%	4.74%	7.82%
29	DP22	C3	18.21%	5.86%	17.22%	5.65%
		C4	76.07%	3.88%	76.85%	3.85%
		TP	5.72%	5.12%	5.93%	5.36%
30	DP29	C3	22.01%	7.26%	21.56%	6.84%
		C4	69.98%	3.98%	70.74%	3.97%
		TP	8.00%	7.65%	7.69%	7.17%
31	DP43	C3	27.39%	5.38%	25.82%	5.32%
		C4	68.41%	4.07%	69.69%	3.92%
		TP	4.20%	4.60%	4.49%	4.92%
32	DP45	C3	18.67%	6.22%	17.73%	5.73%
		C4	75.25%	3.97%	76.28%	3.85%
		TP	6.07%	5.67%	5.99%	5.57%

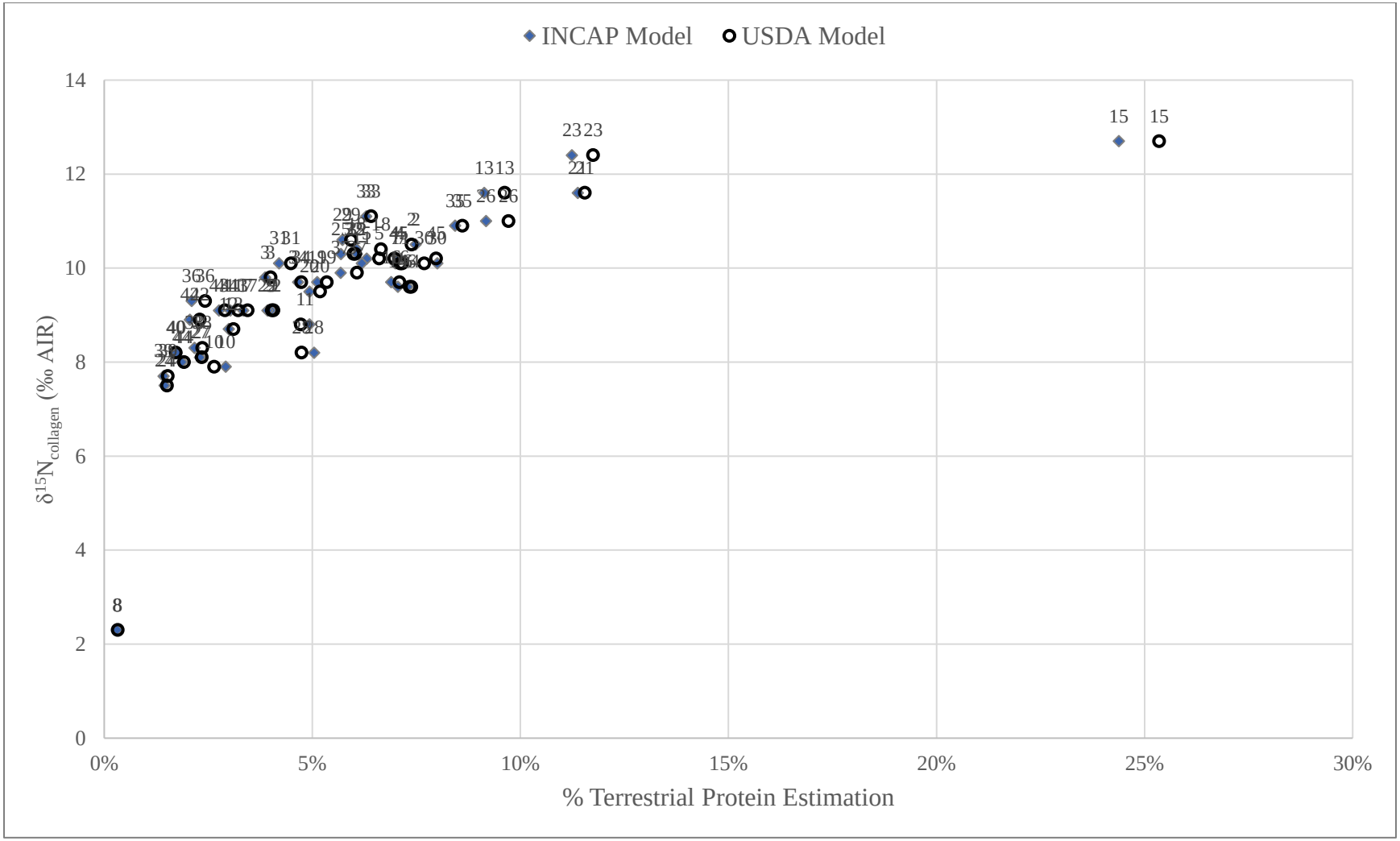
Table 7.3 Continued

Target	Burial ID	Source	INCAP Mean %	INCAP s.d.	USDA Mean %	USDA s.d.
33	DP47	C3	23.79%	6.01%	22.63%	6.03%
		C4	69.92%	4.06%	70.96%	3.99%
		TP	6.30%	5.99%	6.41%	6.09%
34	DP50	C3	26.12%	5.68%	25.02%	5.68%
		C4	69.22%	3.85%	70.24%	3.80%
		TP	4.66%	5.19%	4.73%	5.44%
35	TR3/2	C3	27.40%	7.32%	26.14%	7.09%
		C4	64.17%	4.18%	65.25%	4.19%
		TP	8.43%	8.03%	8.61%	8.25%
36	DP1	C3	24.42%	4.32%	22.84%	4.57%
		C4	73.48%	3.82%	74.74%	3.93%
		TP	2.10%	2.27%	2.43%	2.79%
37	DP49	C3	30.38%	6.32%	29.00%	6.41%
		C4	63.94%	3.99%	64.93%	4.05%
		TP	5.68%	6.43%	6.08%	6.86%
38	DP33	C3	29.97%	4.43%	28.69%	4.35%
		C4	67.86%	3.84%	68.95%	3.75%
		TP	2.17%	2.83%	2.36%	3.03%
39	DP5	C3	28.54%	3.90%	27.50%	3.95%
		C4	70.03%	3.61%	70.97%	3.67%
		TP	1.43%	1.67%	1.53%	1.94%
40	DP3	C3	27.92%	4.38%	26.39%	4.06%
		C4	70.34%	3.96%	71.89%	3.71%
		TP	1.74%	2.23%	1.72%	2.22%
41	DP13	C3	35.29%	4.71%	33.93%	4.53%
		C4	61.68%	3.76%	63.16%	3.82%
		TP	3.03%	3.94%	2.91%	3.55%
42	DP30	C3	30.82%	4.26%	29.33%	4.24%
		C4	67.12%	3.73%	68.37%	3.79%
		TP	2.06%	2.46%	2.30%	2.84%
43	AG5B	C3	32.25%	4.64%	30.51%	4.91%
		C4	64.99%	3.82%	66.27%	3.97%
		TP	2.76%	3.47%	3.22%	4.16%
44	AG5A	C3	26.92%	4.27%	25.85%	4.08%
		C4	71.21%	3.77%	72.23%	3.66%
		TP	1.87%	2.23%	1.92%	2.30%
45	DP44	C3	37.77%	6.62%	35.93%	7.29%
		C4	55.15%	4.27%	56.09%	4.49%
		TP	7.08%	7.83%	7.98%	8.78%

or through new data collection. Notably absent from INCAP's data are nutritional compositions of freshwater mollusks, and particularly *Pachychilus*, the shells of which are ubiquitous at Maya sites of all sizes (Dedrick, 2013; Healy et al., 1990).

Additionally, in this study, I decided to use modern pigs as a nutritional proxy for peccary (Tayassuidae) in the absence of a better alternative. This is even though the two constitute different families within the suborder Suina (Tayassuidae vs. Suidae) and modern pigs have been subject to intense artificial selection over approximately the past 10,000 years (Ottoni et al., 2013). For example, modern pigs are likely to have higher fat content than their New World-native counterparts. However, in the absence of any more appropriate nutritional proxies, this was determined to be the best approximation of the nutritional composition of peccary meat consumed in the past. Unfortunately, nutritional information on many foods of interest, such as paca, agouti, opossum, and dog, remains elusive in any database.

Figure 7.1: Scatterplot of $\delta^{15}N$ vs. % Terrestrial Protein for Both Model Iterations



Note: Data labels are Target ID numbers, see Appendix A for full details.

CHAPTER VIII: EFFECT OF CHEMICAL PROCESSING TECHNIQUES ON ESTIMATES OF DIET COMPOSITION

Overview

As Solomon Katz (1990) identified, food processing techniques are as integral to a biocultural understanding of diet as the foods themselves. Perhaps no other processing technique has received more attention in this regard than nixtamalization. Nixtamalization is the process by which raw maize kernels are processed with an alkaline solution prior to final preparation and consumption. The resulting maize is known as nixtamal, a Hispanicized form of the Nahuatl *nextamalli* (Cheetham, 2010). While the origins of nixtamalization remain murky, one possible explanation is that the process developed from the stone-boiling of maize kernels using limestone (Ellwood et al., 2013).

The overall process has changed little since ancient times: raw maize kernels are immersed in an alkaline solution. Historically this solution would consist of water mixed with ground and slaked limestone, burned invertebrate shells, or hardwood ash (Cheetham, 2010), but in modern times slaked lime ($Ca(OH)_2$) or lye (NaOH) are also used (Wacher, 2003). The kernels may be boiled in the solution for a period of time, or simply added to a hot solution and left to soak. The now softened kernels are frequently washed and (often) ground into a type of corn dough, known as masa among Spanish-speaking populations.

Nixtamal or masa has several practical benefits over raw corn. It allows for the hard, indigestible pericarp surrounding the germ and endosperm to be easily removed during the washing phase (Wacher, 2003). Furthermore, once ground the maize can be easily worked and

shaped into any number of forms during further cooking, such as flattened into quick-cooking tortillas.

Regardless of the specific process utilized, nixtamalization has been found to initiate several chemical changes to maize in addition to the physical changes described above. There is between approximately 5% and 15% loss of overall dry mass during both soaking and the grinding process (Bressani et al., 1958; Wacher, 2003). There is also a loss of crude fiber, riboflavin, niacin, thiamin, and overall protein, with some variation based on the variety of maize (Bressani et al., 1958; Saldana & Brown, 1984). Other changes include a small increase in Ca and Mg (likely from the lime used in processing) and small losses in Na and K (Bressani et al., 1990; Pappa et al., 2010). However, the degree of chemical/nutritional change can vary depending on the variety of maize (Bressani et al., 1990).

Despite the general reduction in overall protein and dry mass, experimental studies (Warinner & Tuross, 2009) have nevertheless shown that animals exhibit a greater growth rate when subsisting on a diet of nixtamalized corn compared to raw (Katz et al., 1974). This is because during nixtamalization there is a somewhat paradoxical increase in the bioavailability of certain key nutrients in the maize despite the net loss. Maize is naturally deficient in lysine, tryptophan, and niacin (of which tryptophan is a precursor) (Bressani et al., 1958; Katz et al., 1974). It is therefore believed that the nixtamalization process causes protein to be released more readily compared to raw corn (though this may be due more to the cooking itself than the alkaline nature of the cooking liquid) (Bressani, 2009; Bressani et al., 1958; Martínez-Velasco et al., 2018). Nixtamalization also exhibits increased bioavailability of niacin and a more optimal leucine-to-isoleucine ratio compared to raw maize (Bressani, 2009). The process also means the nutrient-rich germ is maintained in the final dough – improving both its nutritional quality and

workability (Martínez-Bustos et al., 2001; Sefa-Dedeh et al., 2004), and has the added benefit of eliminating any toxic fungal growth on the kernels (Bressani, 2009). Furthermore, the pericarp, which is removed during nixtamalization, contains phytates, which can hinder intestinal absorption of iron.

Nearly all New World cultures that utilized maize as a staple crop also practiced some form of alkaline cooking, though it is likely the conscious goal of the process was likely to simply remove the pericarp, rather than its nutritional benefits (Cheetham, 2010). Conversely, those that cultivated, but did not necessarily depend on maize as a staple were less likely to have such practices, as, without nixtamalization, societies subsisting on maize would require substantial supplementation from other sources to avoid significant malnutrition (Katz et al., 1974).

Given that nixtamalization introduces such a radical chemical change in raw maize, and that the practice is and was so widespread, its effects on both the macronutrient and isotope composition of maize must be understood to accurately reconstruct ancient diets. To date, the effect of food processing techniques on stable isotope ratios has largely focused on the propensity for boiling or heating water to affect $\delta^{18}O$ values (Tuross et al., 2017), particularly in fermented beverages (e.g. Brettell et al., 2012; Gagnon et al., 2015).

However, recent works have also begun to address issues of culturally moderated behaviors, such as baking and intentional putrefaction on $\delta^{13}C$ and $\delta^{15}N$ values as well (Bostic et al., 2015; Foecke, 2022; Speth, 2017). For example, in an experimental study, Doering found that cooking salmon by direct fire treatment significantly lowered $\delta^{13}C$ values, albeit at a level that “may be too slight to warrant incorporation into dietary mixing models” (2017, p. 497).

In terms of maize processing specifically, contact with the alkaline wastewater produced during nixtamalization (*nejayote*) may alter the isotope ratios of faunal bone in midden assemblages, thus confounding human diet estimations based on the isotope composition of those faunal materials. In addition, Lovis et al., (2011) found that isotopic signatures of maize can be masked in residue analyses of ceramic vessels due to the nixtamalization process. However, these effects, if they did occur, are likely negligible for diet reconstruction (Colaninno et al., 2019). Moreover, most research indicates that the isotopic ratios of most plant cultivars are conserved through most typically cooking processes, nixtamalization of maize included (Marino & DeNiro, 1987; Wright, 1994).

Much more impactful can be the changes in the macronutrient composition of foods introduced by certain preparation techniques, and how these can have downstream effects on isotope composition. For example, most cooking practices involve a greater reduction in lipid content than protein, as fat renders out of a food during cooking. As fat is typically depleted in ^{13}C relative to protein, this macronutrient loss can affect the isotope composition of the food as a whole (Fernandes et al., 2014a).

Most SIMM studies include maize or C4 plants generally either use raw maize (Fernandes et al., 2014a; Pestle & Laffoon, 2018) or do not specify the type or variety of maize used (Kaupová et al., 2018; Mora et al., 2021; Pinder et al., 2019). This section, therefore, seeks to elucidate how SIMM estimates of diet composition can be affected by variations in the macronutrient composition of maize attributable to nixtamalization.

Methods

The human isotope presented in Table 6.1 (n=45, $\delta^{13}C_{collagen}$, $\delta^{13}C_{apatite}$, and $\delta^{15}N_{collagen}$) was used to compare different maize preparations. Ideally, data for tamales would be used in this analysis, given that they would have been the major preparation of maize well into the Postclassic. However, in the absence of nutrient composition data for tamales, I used tortillas as a proxy for foodstuffs consumed in the past based on similarity in overall production techniques. In addition, only macronutrient data derived from INCAP was used in this analysis.

The INCAP nutritional composition tables include several corn-based products, but the most relevant for Mesoamerican diets are found in Table 8.1. INCAP 13 was used as a proxy for dry, unprocessed maize kernels. To best approximate the composition of a fully prepared food item, ash (INCAP 23) and lime treated (INCAP 25) tortillas (traditionally made directly from masa dough) were used, respectively, as proxies for prepared nixtamal.

All other model parameters were identical to those presented in Chapter VI. For the sake of simplicity, paired two-sample t-tests (α=0.05) were used to assess statistical significance for each source and individual between model iterations.

Table 8.1: Macronutrient Concentrations of Maize Preparation Techniques (Leung & Flores, 1961)

INCAP #(s)*	Preparation	Variety	Protein (% Dry Weight)	Energy (% Dry Weight)
20, 21	Corn dough, Lime treated	White and Yellow	9.41%	90.59%
13, 14	Corn, whole kernel, dry	White, Black, Yellow	10.67%	89.33%
23, 24	Tortilla, ash treated	Yellow, White	7.94%	92.06%
25, 26	Tortilla, lime treated	Yellow, White	8.90%	91.10%

* Multiple numbers indicate different varieties (yellow, white, etc.) of identical composition.

Results

Four- (C3, C4, TP, AP) and five-source (C3, C4, TP, AP, MP) models failed to produce results for all iterations due to model complexity (number of sources > number of proxies). The model using lime-treated tortilla data also failed to produce results in the three-source model (C3, C4, TP). Results for model variations using dry maize kernels and ash-treated tortillas can be found in Table 8.2).

The type of maize product used does significantly alter the estimated contribution of all three sources to individual diets (C4: $t=-4.56, N=45, p<0.01$), with the dry maize model estimating a greater proportion of TP on average, and the ash-treated maize model estimating greater contribution of C3 plants and maize. However, the absolute difference for each is relatively minuscule for all sources. The ash-treated maize model estimated, on average, 0.16% more C3 plants, 0.17% more maize, and 0.33% less terrestrial animal protein.

Conclusion

The significance of the difference between model outputs reifies our understanding that macronutrient composition can significantly impact concentration-dependent SIMMs. However, much like the results of the regional database comparison, the small degree of difference between both the original composition values and the computed diet compositions suggests that nixtamalization has very little impact on SIMM output when all factors are considered. The failure of the three-source, lime-treated model is perplexing, but possibly due to the overlap of its protein content with that of C3 plants when their relative uncertainties are factored in. However, given that the lime-treated variety is intermediate in its protein-to-energy content between raw maize and ash-treated (much more common practice in the North American Southwest than in

Table 8.2: Results of Dry vs. Alkaline Processed Maize

Target	Burial ID	Source	Dry Maize Kernels Mean	Dry Maize Kernels SD	Tortilla, ash treated Mean	Tortilla, ash treated SD
1	TR3-1	C3	42.40%	6.64%	42.46%	6.36%
		C4	52.67%	4.07%	53.00%	4.07%
		TP	4.93%	7.36%	4.54%	7.03%
2	DP52	C3	17.68%	6.64%	18.47%	6.27%
		C4	74.72%	3.97%	74.80%	3.87%
		TP	7.60%	6.54%	6.73%	6.10%
3	TA4	C3	30.37%	5.06%	30.38%	5.26%
		C4	65.81%	3.76%	65.87%	3.87%
		TP	3.83%	4.31%	3.75%	4.82%
4	TA6	C3	19.88%	6.58%	20.49%	6.37%
		C4	73.03%	3.96%	73.12%	3.92%
		TP	7.09%	6.58%	6.39%	6.38%
5	CC1	C3	23.82%	6.24%	23.91%	6.35%
		C4	70.11%	3.85%	70.29%	3.95%
		TP	6.07%	6.19%	5.80%	6.26%
6	LP1	C3	25.44%	7.30%	25.79%	7.26%
		C4	67.32%	4.01%	67.62%	3.98%
		TP	7.24%	7.83%	6.59%	7.71%
7	DP55	C3	15.88%	6.43%	16.06%	6.43%
		C4	76.92%	3.88%	76.98%	3.91%
		TP	7.20%	6.17%	6.96%	6.27%
8	AP4	C3	21.27%	4.19%	22.44%	4.20%
		C4	78.41%	4.18%	77.32%	4.20%
		TP	0.32%	0.33%	0.24%	0.26%
9	AG1	C3	29.81%	5.60%	30.02%	5.19%
		C4	66.28%	3.77%	66.63%	3.77%
		TP	3.91%	5.29%	3.36%	4.58%
10	QCH5	C3	26.74%	5.36%	26.86%	5.22%
		C4	70.59%	3.82%	70.68%	3.74%
		TP	2.67%	4.47%	2.46%	4.58%
11	QCH6	C3	37.95%	6.04%	37.43%	6.81%
		C4	56.22%	4.02%	56.42%	4.09%
		TP	5.83%	6.60%	6.15%	7.64%
12	DP2	C3	25.39%	5.00%	25.79%	4.67%
		C4	71.58%	3.82%	71.67%	3.76%
		TP	3.04%	3.91%	2.54%	3.48%
13	DPA	C3	19.25%	7.02%	19.82%	6.69%
		C4	71.39%	4.21%	71.61%	4.08%
		TP	9.37%	7.34%	8.57%	6.81%
14	DPB	C3	32.96%	7.24%	33.14%	7.09%
		C4	60.20%	4.11%	60.47%	3.99%
		TP	6.84%	8.05%	6.39%	7.90%
15	DPE	C3	20.78%	9.04%	20.28%	9.19%
		C4	54.05%	4.73%	54.59%	4.84%
		TP	25.18%	10.76%	25.13%	11.16%
16	DPG	C3	34.07%	7.09%	34.05%	7.34%
		C4	59.23%	4.06%	59.29%	4.18%
		TP	6.70%	7.94%	6.66%	8.37%

Table 8.2 Continued

Target	Burial ID	Source	Dry Maize Kernels Mean	Dry Maize Kernels SD	Tortilla, ash treated Mean	Tortilla, ash treated SD
17	DPH	C3	23.79%	5.06%	23.96%	4.91%
		C4	72.91%	3.81%	72.94%	3.80%
		TP	3.29%	3.84%	3.09%	3.77%
18	DPI	C3	23.22%	6.07%	23.51%	6.15%
		C4	70.77%	3.79%	70.70%	3.94%
		TP	6.00%	5.92%	5.79%	5.89%
19	DP4	C3	24.05%	6.17%	24.56%	6.00%
		C4	70.57%	3.93%	70.42%	3.81%
		TP	5.37%	5.97%	5.02%	5.83%
20	DP9	C3	26.40%	6.04%	26.21%	6.22%
		C4	68.58%	3.78%	68.77%	3.79%
		TP	5.01%	5.94%	5.02%	6.36%
21	DP10B	C3	17.82%	7.23%	18.19%	7.21%
		C4	70.86%	4.20%	71.13%	4.17%
		TP	11.32%	7.97%	10.68%	7.82%
22	DP10A	C3	21.47%	5.62%	22.02%	5.27%
		C4	74.52%	3.77%	74.50%	3.92%
		TP	4.02%	4.80%	3.48%	4.28%
23	DP12	C3	12.76%	6.33%	12.50%	6.24%
		C4	76.18%	4.20%	76.61%	4.13%
		TP	11.05%	6.75%	10.89%	6.48%
24	DP16	C3	34.22%	4.05%	34.31%	4.06%
		C4	64.45%	3.76%	64.47%	3.72%
		TP	1.33%	1.81%	1.22%	1.97%
25	DP17	C3	30.67%	6.23%	31.28%	5.95%
		C4	63.32%	4.05%	63.49%	3.91%
		TP	6.02%	6.44%	5.23%	5.93%
26	DP20	C3	25.73%	7.13%	26.17%	7.18%
		C4	65.56%	4.12%	65.66%	4.14%
		TP	8.71%	7.72%	8.17%	7.91%
27	TA1A	C3	26.26%	4.91%	26.53%	4.84%
		C4	71.15%	3.84%	71.32%	3.87%
		TP	2.59%	3.72%	2.15%	3.65%
28	TA2	C3	39.71%	7.52%	39.93%	7.60%
		C4	55.32%	4.14%	55.46%	3.96%
		TP	4.97%	8.36%	4.61%	8.51%
29	DP22	C3	18.33%	6.05%	18.55%	5.77%
		C4	75.87%	4.03%	76.15%	3.95%
		TP	5.80%	5.32%	5.30%	5.06%
30	DP29	C3	22.29%	7.20%	22.14%	7.29%
		C4	69.91%	3.98%	70.11%	4.00%
		TP	7.80%	7.69%	7.75%	7.61%
31	DP43	C3	27.34%	5.34%	27.51%	5.05%
		C4	68.44%	3.86%	68.76%	3.83%
		TP	4.22%	4.60%	3.73%	4.19%
32	DP45	C3	18.32%	5.86%	18.47%	5.92%
		C4	75.56%	3.82%	75.85%	3.92%
		TP	6.12%	5.52%	5.68%	5.36%

Table 8.2 Continued

Target	Burial ID	Source	Dry Maize Kernels Mean	Dry Maize Kernels SD	Tortilla, ash treated Mean	Tortilla, ash treated SD
33	DP47	C3	24.17%	5.98%	23.82%	6.02%
		C4	69.83%	4.09%	70.14%	3.99%
		TP	6.00%	5.70%	6.04%	5.64%
34	DP50	C3	26.07%	5.66%	26.29%	5.73%
		C4	69.30%	3.87%	69.35%	3.93%
		TP	4.63%	5.22%	4.36%	5.53%
35	TR3/2	C3	27.15%	7.08%	27.82%	6.74%
		C4	64.36%	4.20%	64.62%	4.21%
		TP	8.49%	7.83%	7.56%	7.52%
36	DP1	C3	24.36%	4.42%	24.49%	4.21%
		C4	73.49%	3.89%	73.58%	3.71%
		TP	2.15%	2.33%	1.93%	2.13%
37	DP49	C3	29.97%	6.61%	30.25%	6.16%
		C4	63.86%	4.12%	64.35%	3.94%
		TP	6.17%	6.87%	5.40%	6.42%
38	DP33	C3	29.73%	4.76%	30.31%	4.07%
		C4	67.86%	3.78%	67.88%	3.66%
		TP	2.42%	3.67%	1.81%	2.32%
39	DP5	C3	28.76%	4.02%	28.61%	3.91%
		C4	69.76%	3.70%	70.15%	3.74%
		TP	1.48%	1.99%	1.24%	1.63%
40	DP3	C3	27.96%	4.19%	27.88%	4.31%
		C4	70.32%	3.81%	70.53%	3.87%
		TP	1.72%	2.13%	1.59%	2.84%
41	DP13	C3	35.52%	4.47%	35.35%	4.64%
		C4	61.66%	3.76%	61.88%	3.67%
		TP	2.81%	3.51%	2.76%	3.94%
42	DP30	C3	30.80%	4.22%	30.38%	4.65%
		C4	67.10%	3.76%	67.36%	4.15%
		TP	2.11%	2.38%	2.26%	2.98%
43	AG5B	C3	32.51%	4.76%	32.32%	4.68%
		C4	64.77%	3.93%	65.08%	3.79%
		TP	2.73%	3.35%	2.59%	3.61%
44	AG5A	C3	27.24%	4.25%	27.20%	4.32%
		C4	70.98%	3.65%	71.15%	3.81%
		TP	1.78%	2.27%	1.65%	2.45%
45	DP44	C3	37.68%	7.22%	37.25%	7.25%
		C4	54.78%	4.43%	55.45%	4.38%
		TP	7.54%	8.36%	7.30%	8.51%

Mesoamerica, where treatment with slaked lime would have been more common), it is highly unlikely that the specific treatment method would create a substantial difference.

CHAPTER IX: EFFECT OF LOCALITY IN DIET ESTIMATIONS USING ^{34}S

Overview

Sulfur isotopic analysis has proven an increasingly useful tool for investigating both mobility and diet in ancient populations for several years. To date, most sulfur isotope applications have taken place in the Old World (Bocherens et al., 2016; Linderholm et al., 2014; Nehlich, 2015; Nehlich et al., 2010; Nehlich et al., 2011; Nehlich et al., 2012; Richards et al., 2003). However, large-scale, systematic studies of the sulfur isotope distributions of Mesoamerica have recently been published (Ebert et al., 2021; Rand et al., 2021; Rand & Grimes, 2017). The primary focus of these studies this far has been to assess migration patterns, adding to the rich body of migration data derived from strontium isotope analysis. However, sulfur isotopes also offer great potential in researching a long-neglected aspect of ancient Mesoamerican diet reconstruction: the use of marine and riverine food resources. These have been difficult to assess using previously available means given preservation bias against fish remains and the degree of overlap between such resources and maize (as C4 resources were not a component of Old-World diets until recently, this problem is not present in many other applications of sulfur analysis).

However, as discussed previously, sulfur isotope ratios are highly dependent upon regionality in inland environments, being largely dependent on precipitation and local geology Linderholm et al., 2014; Linderholm et al., 2008). Therefore, an in-depth understanding of local baselines is necessary to determine whether variations in human $\delta^{34}S$ values reflect differences in diet or regional origin.

Sulfur isotope analysis is relatively new to ancient Maya archaeology. However, its use for both diet and mobility in the region has proliferated recently, going from preliminary modeling (Rand & Grimes, 2017) to an extensive $\delta^{34}S$ baseline derived from faunal signatures (Rand et al.,

2021) in just four years. Despite this progress, the actual use of $\delta^{34}S$ analysis to answer questions about diet and mobility among the ancient Maya remains in its infancy. At the time of writing, publications are limited to Ebert et al.'s (2021) regional survey in the Eastern lowlands and Rand et al.'s (2020) site-based study at Nakum, Guatemala.

A reasonable step towards securing the utility of ^{34}S in reconstructing Maya diets would be to understand the degree to which geographic variation in sulfur isotope impacts dietary inference. In other words, within the context of Mesoamerica, does geographic location or diet exert a greater influence on the sulfur isotope signatures observed in human remains? This section will address this problem using diet estimates from a sample of humans from the ancient Maya site of Dos Pilas, Guatemala, and its surrounding environs. FRUITS models will be run on human isotope samples from the site using a sulfur isotope baseline derived from the local area only and a larger Pan-Mesoamerican baseline (Rand et al., 2021).

Methods

The human isotope presented in Table 6.2 (n=45, $\delta^{13}C_{collagen}$, $\delta^{13}C_{apatite}$, and $\delta^{15}N_{collagen}$) was used to compare sulfur baselines. In addition, only macronutrient data derived from INCAP was used in this analysis. Given the results of the previous chapter, the nutrient composition of ash-treated tortillas (INCAP 23) was used as a proxy for maize in these models.

Nine previously prepared samples of human bone collagen for which $\delta^{13}C_{collagen}$, $\delta^{13}C_{apatite}$, and $\delta^{15}N_{collagen}$ values were reported by Wright (1994) were selected for additional ^{34}S analysis. Also, $\delta^{34}S$ for a further nine individuals from Dos Pilas was provided by Thornton & Wright (n.d.) for use in this analysis. These collagen samples were previously reported by Wright (1994; 2006) and remained desiccated before their ^{34}S analysis. To further investigate the possibility of using $\delta^{34}S$ from botanicals, twelve samples of maize originating from various rural

areas of Guatemala (Wright, 1994) and three samples of C3 botanicals (*Brosimum alicastrum* and 2 samples of *Sechium edulis*) were subjected to ^{34}S to compare with expected values given the current $\delta^{34}S$ baseline. Botanical and human collagen samples retained from Wright (1994; 2006) were analyzed at the Stable Isotope Geosciences Facility (SIGF) at Texas A&M University via a Thermo Fisher Flash Elemental Analyzer and Scientific Delta V Advantage Isotope Ratio Mass Spectrometer. For the FRUITS models, a conservative standard error of ±2‰ was used for all botanical $\delta^{34}S$ data owing to the small sample sizes.

The local baseline for Dos Pilas-only iteration was derived from faunal $\delta^{34}S$ data from Thornton & Wright (n.d.) and presented here. Conversely, the Pan-Maya Region iteration baseline is derived from all available $\delta^{34}S$ for the Maya region (Rand et al., 2021). These $\delta^{34}S$ source values can be found in Table 9.1.

Table 9.1: $\delta^{34}S$ Baselines

	Dos Pilas Baseline		**Pan-Maya Region Baseline**	
Source	$\delta^{34}S_{methionine}$ (‰ VCDT)	S.E.	$\delta^{34}S_{methionine}$ (‰ VCDT)	S.E.
C3	6.82*	2*	6.82*	2*
C4	4.36*	2*	4.36*	2*
TP	4.0	1.13	12.47	0.26
AP	0.11	1.75	7.6	0.75
MP**	9.94	2.52	9.94	2.52

** Values are derived from Dos Pilas botanicals only, see below.*
*** As no marine life can be considered local to the Pasión region, the Pan-Mesoamerican value was used for both model iterations.*

All other model parameters were identical to those presented in Chapter VI. For the sake of simplicity, paired two-sample t-tests (α=0.05) were used to assess statistical significance for each source and individual between model iterations.

Results

Among the analyses run specifically for this section, two human, one C3, and one maize sample failed quality control during ^{34}S measurement, and therefore are not considered further. The two remaining C3 plant samples yielded one value within the expected value and one outside and are therefore equivocal in their usefulness.

Results of the maize ^{34}S can be found in Table 9.2 below. As can be seen, while there is some patterning by location, $\delta^{34}S$ are highly variable both within and between groups. There is also no clear patterning by treatment. Although the sample size is limited, these results support, along with the C3 results, the assertion that modern botanicals – regardless of their provenance – do not possess $\delta^{34}S$ signatures that are of use when investigating past diets or migration due to sulfur pollution resulting from fossil fuel emissions (Nehlich, 2015).

Table 9.2: Results of $\delta^{34}S$ Analysis of Maize Kernels

Region/Site	Treatment	% S	$\delta^{34}S$ (‰ VCDT)
Chimaltenango	Untreated	0.12%	4.65
Chimaltenango	Lime soaked & boiled	0.11%	6.89
Chimaltenango	Lime soaked	0.12%	3.88
Pacific Coast	Untreated	0.12%	7.03
Pacific Coast	Lime soaked & boiled	0.08%	7.54
Pacific Coast	Lime soaked & boiled	0.06%	6.70
Pacific Coast	Lime soaked & boiled	0.09%	6.80
Pacific Coast	Lime soaked	0.08%	0.77
San Juan Comalapa	Lime soaked & boiled	0.09%	0.23
San Juan Comalapa	Lime soaked	0.11%	3.86

In the FRUITS analysis, four- (C3, C4, TP, AP) and five-source (C3, C4, TP, AP, MP) models failed to produce results for both iterations due to model complexity. In this case, the cause cannot be attributed to model complexity, but rather overlap between $\delta^{34}S$ values due to repetition (see below). In the three-source model (C3, C4, TP), the Pan-Maya $\delta^{34}S$ baseline, on average, estimated significantly more C3 plant consumption and less TP consumption than did the Dos Pilas-only baseline (C3: $t=3.68, N=16, p<0.01$). There was no statistically significant

Table 9.3: Results of Human $\delta^{34}S$ Analysis

FRUITS ID	Site	Period	$\delta^{13}C_{apatite}$ (‰ VPDB)*	$\delta^{13}C_{collagen}$ (‰ VPDB)*	$\delta^{15}N_{collagen}$ (‰ AIR)*	$\delta^{34}S_{methionine}$ (‰ VCDT)
1S	Aguateca	Late Classic	-5.531	-8.78	7.98	11.99**
2S	Aguateca	Late Classic	-5.790	-9.87	9.06	10**
3S	Aguateca	Late Classic	-7.341	-9.34	9.13	10.56**
4S	Dos Pilas	Late Classic	-7.564	-8.53	8.9	10.21**
5S	Dos Pilas	Terminal Classic	-7.172	-9.65	10.3	10.81**
6S	Dos Pilas	Terminal Classic	-7.109	-7.04	9.31	8.04**
7S	Dos Pilas	Terminal Classic	-5.055	-9.07	9.67	8.89**
8S	Dos Pilas	Terminal Classic	-7.967	-9.84	9.13	9.03**
9S	Dos Pilas	Terminal Classic	-6.394	-8.58	7.66	5.49**
10S	Cerro de Cheyo	Late Classic	-5.171	-9.11	10.19	3.79
11S	Dos Pilas	Late Classic	-2.819	-8.64	10.08	-1.46
12S	Dos Pilas	Late Classic	-5.023	-8.94	8.69	9.75
13S	Dos Pilas	Terminal Classic	-6.895	-11.16	9.70	11.07
14S	Dos Pilas	Terminal Classic	-5.223	-9.59	9.46	5.29
15S	Dos Pilas	Terminal Classic	-4.626	-8.95	11.63	6.9
16S	Dos Pilas	Late Classic	-6.430	-10.10	9.90	9.56

** Previously reported data, see Wright (1994).*
*** $\delta^{34}S$ data provided by Thornton & Wright (n.d.)*

difference in maize estimates. While the absolute degree of difference remained quite small (less than approximately 3% difference), discrepancies between model iterations were more pronounced than in previous model comparisons. However, it is likely that in this model there are several other confounding variables.

Conclusion

Most importantly, $\delta^{34}S$ signatures of terrestrial fauna at Dos Pilas average 4‰. This fits perfectly within Rand and Grimes's (2017) modeled range of 0 to +8‰ for the southern lowland interior, suggesting that further exploration of $\delta^{34}S$ in the region could prove fruitful. In addition, the fact

Table 9.4: Local vs. Regional $\delta^{34}S$ Baseline Comparison

Target	Burial ID	Source	Dos Pilas Baseline Mean	Dos Pilas Baseline SD	Pan-Mesoamerican Baseline Mean	Pan-Mesoamerican Baseline SD
1S	AG5A	C3	28.94%	4.94%	26.67%	5.93%
		C4	69.96%	4.74%	70.82%	4.29%
		TP	1.10%	1.26%	2.51%	5.05%
2S	AG1	C3	31.25%	5.54%	27.61%	8.60%
		C4	66.23%	4.62%	65.27%	4.60%
		TP	2.51%	3.36%	7.11%	10.14%
3S	AG5B	C3	36.90%	4.70%	32.81%	6.09%
		C4	61.49%	4.37%	63.57%	4.22%
		TP	1.62%	1.80%	3.61%	5.77%
4S	DP30	C3	35.86%	4.78%	31.67%	5.14%
		C4	62.82%	4.47%	66.01%	3.96%
		TP	1.31%	1.49%	2.32%	4.13%
5S	DP17	C3	35.27%	5.49%	27.70%	9.49%
		C4	61.67%	4.57%	61.77%	4.96%
		TP	3.07%	3.28%	10.53%	11.51%
6S	DP1	C3	30.15%	4.81%	26.01%	4.49%
		C4	68.41%	4.51%	72.08%	4.02%
		TP	1.44%	1.52%	1.91%	2.36%
7S	DP4	C3	26.38%	5.92%	24.10%	7.02%
		C4	70.09%	4.42%	69.96%	4.21%
		TP	3.53%	4.13%	5.94%	7.24%
8S	DP13	C3	40.03%	4.97%	35.74%	6.63%
		C4	58.11%	4.40%	59.99%	4.29%
		TP	1.86%	2.35%	4.27%	7.26%
9S	DP5	C3	32.81%	4.41%	30.00%	4.10%
		C4	66.19%	4.21%	68.88%	3.92%
		TP	1.00%	1.34%	1.13%	1.43%
10S	CC1	C3	24.55%	7.05%	25.59%	5.38%
		C4	69.31%	4.47%	70.19%	3.79%
		TP	6.14%	6.59%	4.22%	4.21%
11S	DP55	C3	13.88%	6.16%	17.31%	4.99%
		C4	79.39%	4.12%	79.46%	3.79%
		TP	6.73%	6.03%	3.23%	3.18%
12S	DP2	C3	27.08%	5.21%	26.01%	5.75%
		C4	70.90%	4.48%	70.56%	3.94%
		TP	2.02%	2.76%	3.43%	5.40%
13S	DPG	C3	37.69%	5.46%	26.62%	12.31%
		C4	59.30%	4.58%	56.45%	5.39%
		TP	3.02%	3.53%	16.93%	15.24%
14S	DP9	C3	27.18%	6.60%	27.78%	5.83%
		C4	68.08%	4.42%	68.22%	3.93%
		TP	4.74%	5.97%	4.00%	4.91%
15S	DP10B	C3	19.87%	7.50%	17.66%	7.47%
		C4	70.37%	4.55%	70.64%	4.39%
		TP	9.77%	7.25%	11.70%	8.18%
16S	DP49	C3	33.54%	5.80%	27.41%	9.40%
		C4	62.97%	4.46%	62.37%	4.70%

that human $\delta^{34}S$ from the site is substantially higher than the local baseline suggests some contribution of either non-local or (more likely) aquatic resource consumption, though currently available comparative data generated via SIMMs fail to bear this out.

The failure of the original four and five-source models are concerning at first, given that the addition of another dietary proxy in $\delta^{34}S_{methionine}$ should enable a greater number of sources to be considered. However, on closer inspection, there are several likely explanations. While $\delta^{34}S$ values separate aquatic animals from other sources, the degree of overlap between the remaining groups is likely sufficient to cause the model to fail. In particular, marine $\delta^{34}S$ values are expected to fall around the oceanic baseline of approximately 20‰, but the current Mesoamerican baseline is much lower at about 10‰. As Rand et al. (2021) point out, marine fish found within inland sites were likely caught close to shore in reef (or marine) environments. Waters in these areas can be generally depleted in ^{34}S relative to the oceanic average due to a mixture of freshwater with proportionately lower $\delta^{34}S$ and sulfate reduction by microbes in certain environments, which has a depleting effect on ^{34}S.

The greater divergence based between estimates in these models compared to those based on macronutrient concentrations reinforces that isotope values are the key determinate of model output. In other words, models are overall quite robust against small variations in concentration, trophic discrimination, etc., but $\delta^{34}S$ variation based on locality can have a much more significant impact. Furthermore, this analysis demonstrates why $\delta^{34}S$ analysis of plant foods themselves should usually be avoided when developing isotope baselines for different sources. In this case, the $\delta^{34}S$ analyses were conducted on bulk botanical samples. However, only sulfur within methionine is bioavailable to consumers.

Future Considerations

One consistent theme with all models is the low estimated proportion of terrestrial protein in the diet. On the one hand, this is not completely unexpected. Maya foodways reconstruction has largely supported low quantities of meat consumed. However, another possibility is that the lower quality of protein available primarily from maize is to some extent masking what consumption did take place. As Bond and Diamond (2011) note, relatively small changes in diet-to-tissue offsets for $\delta^{13}C$ and $\delta^{15}N$ can lead to highly variable estimates of diet components. In this case, the somewhat high trophic discrimination factor for ^{15}N ($\Delta^{15}N$) of +5.5% could potentially cause the model to underestimate the relative trophic level of foods being consumed and therefore result in extremely small estimates of animal protein. Furthermore, $\Delta^{15}N$ can vary based on the organism's diet overall. When an individual's diet is relatively protein-deficient, $\Delta^{15}N$ can decrease as more dietary protein is routed directly to building tissue, similar to the ^{15}N depletion observed when animals enter anabolic states (Chikaraishi et al., 2015; Fuller et al., 2004; K. A. Hatch et al., 2006; Hughes et al., 2018; Y. I. Naito et al., 2015). However, it should be noted that this effect is not universal (Robbins et al., 2005). A lower $\Delta^{15}N$ of approximately +3‰ would likely result in estimates of higher animal meat as a proportion of the diet while remaining well within acceptable ranges for diet-to-tissue fractionation.

Similarly, Warinner and Tuross (2009) have found that pigs fed alkaline-treated maize exhibited approximately 1‰ greater diet-to-tissue spacing in their $\delta^{13}C_{collagen}$ values than pigs fed raw maize; a small but statistically significant difference. This would suggest that nixtamalization likely could have more of an impact on FRUITS estimates of maize consumption than the results presented here would suggest. This study used a standard $\Delta^{13}C_{bulk\text{-}protein}$ of -2‰ for both C3 and C4 plants. If it could be assumed that most of the C4 plants in question consisted

of alkaline-treated maize, as would have been the case with the ancient Maya, Warinner and Tuross's (2009) results suggest that the offset should be slightly greater than that for C3. In addition to a reduction in the protein concentration of maize of about 2-3%, future models could also incorporate $\Delta^{13}C_{bulk\text{-}protein}$ of approximately -3‰, for C4 plants, vs. -2‰ for C3.

In light of these considerations, a FRUITS model incorporating a $\Delta^{15}N_{collagen\text{-}diet}$ offset of +3‰ (instead of 5.5‰), a $\Delta^{13}C_{bulk\text{-}protein}$ of -3‰, for C4 plants, and a terrestrial $\delta^{34}S$ baseline of 4.0±1.13‰ was executed. This new set of parameters did yield a viable four-source model, the results of which can be found in Table 9.5.

Estimations generated with this model fall largely in line with those generated in previous chapters, but with animal protein (both terrestrial and aquatic) forming a larger share of diets overall. Maize remains between 60-70% of the diet for most individuals, indicating that the inclusion of aquatic protein as a source generally has the greatest effect on the estimation of C3 plant consumption. Interestingly, a single Late Classic individual of indeterminate age and sex, DP55 (11) was estimated to have a C3 consumption of less than 10% of their diet, with correspondingly high maize and aquatic resource consumption. This individual exhibited a surprisingly low $\delta^{34}S$ of -1.46‰, lower even than the site's AP baseline of 0.11‰. This cannot be considered an artifact of this model iteration, as other models generated as part of this dissertation also indicated low C3 consumption for this individual in models not utilizing $\delta^{34}S$ as a proxy. DP55's $\delta^{34}S$ may represent a non-local signal, however available $\delta^{18}O$ and $^{87}Sr/^{86}Sr$ data do not immediately suggest that this individual was a migrant to the area (Wright, n.d.). This would therefore indicate that this individual possibly consumed substantial quantities of marine foods –a fact belied by the relatively ordinary nature of their interment (Wright, 2006).

Table 9.5: Results of Pasión 4-Source Model

Burial ID	Time	Age	Sex	C3	C4	TP	AP
AG1	Late Classic	Young Adult	M	23.05%	67.19%	6.91%	2.85%
AG5A	Late Classic	Teen	F	22.59%	72.48%	3.46%	1.48%
AG5B	Late Classic	Mature Adult	F	28.32%	65.33%	3.94%	2.41%
CC1	Late Classic	Teen	?	14.38%	68.49%	9.53%	7.60%
DP1	Late Classic	Mature Adult	M	20.95%	73.20%	3.37%	2.48%
DP30	Late Classic	Old Adult	M	26.78%	67.60%	3.56%	2.07%
DP4	Late Classic	Young Adult	F	17.42%	70.80%	7.84%	3.94%
DP49	Late Classic	Young Adult	M	24.26%	64.17%	7.45%	4.12%
DP5	Late Classic	Mature Adult	F	25.60%	68.74%	4.00%	1.65%
DP55	Late Classic	Ind.	Ind.	8.00%	76.68%	7.21%	8.11%
DP10B	Terminal Classic	Teen	M	10.74%	70.25%	8.67%	10.34%
DP13	Terminal Classic	Mature Adult	F	31.37%	61.06%	4.89%	2.68%
DP17	Terminal Classic	Young Adult	M	26.08%	64.39%	5.53%	4.00%
DP2	Terminal Classic	Young Adult	M	20.18%	72.28%	5.17%	2.37%
DP9	Terminal Classic	Mature Adult	M	18.45%	67.02%	9.60%	4.93%
DPG	Terminal Classic	Mature Adult	M	29.65%	60.46%	6.52%	3.37%

SECTION III: FUTURE APPLICATIONS OF SIMM IN THE MAYA REGION

CHAPTER X: DISCUSSION AND CONCLUSIONS

Overall, the results of this work demonstrate the robustness of FRUITS models to small variations in macronutrient concentration. Moreover, the study of $\delta^{34}S$ requires a well-established local baseline is necessary to produce reliable results, but some variability in the $\delta^{34}S$ baseline is not likely to greatly affect conclusions. The failure of the original four and five-source models could potentially be due to low levels of actual consumption of aquatic and marine foods. FRUITS will always seek to quantify the proportion of a source group in the diet, regardless of whether the target individual consumed the resource at all. Therefore, the models may have failed because AP and MP were low enough to be negligible for most individuals, either due to literal availability or social allocation of certain high-value resources. However, it is equally likely that the overlap in source isotope signatures produces equifinality in target estimations, especially given that the one successful four-source model did estimate considerable AP consumption for some individuals.

In the future, compound-specific isotope analysis (CSIA) of amino acids may aid in resolving issues of overlapping course isotope signatures such as we see in more complex diet models (Fogel & Tuross, 2003). Newly analyzed modern maize samples from the region did not largely correlate with what would have been expected given the either the Dos Pilas or Pan-Mesoamerican faunal baselines. This could be due to exogenous sulfur originating in the nixtamalization liquid. This sulfur would be detected in the bulk analysis of the grain, but would not be incorporated into bone collagen, as it is not within methionine or cystine, the only true sources of sulfur in bone collagen. CSIA of the constituent amino acids of collagen may help to circumvent this issue completely by analyzing only methionine and cysteine. While the relatively low concentration of both amino acids has made them difficult to isolate, recent advances in

liquid chromatography suggest that this may not be the case for much longer (Phillips et al., 2021).

CSIA would also add greater clarity to the issue of aquatic resource consumption among the ancient Maya. As this work demonstrates, the detection of aquatic foods is inherently difficult in a complex isotopic ecosystem. However, several techniques have been developed using CSIA to differentiate aquatic, marine, and terrestrial resource consumption, including the comparison of $\delta^{13}C$ signatures of essential vs. non-essential amino acids (Webb et al., 2018), using glutamic acid and phenylalanine $\delta^{15}N$ signatures to simultaneously assess terrestrial vs. aquatic vs. marine consumption and trophic level (Yuichi I. Naito et al., 2016), and glycine-phenylalanine spacing to detect high degrees of marine protein consumption (Corr et al., 2005).

While limited, these results support the assertion that meat consumption did not substantially decrease from the Late to Terminal Classic, as TP did not noticeably decrease between periods, and maize consumption likewise did not substantially increase. This follows previous works which undermine the ecological model of the collapse within the region (Emery, 2008; Emery et al., 2000; Wright, 1994, 2006), but allows for direct comparisons of meat consumption between sites given the totality of isotopic evidence available.

More than anything, this analysis demonstrates the importance of considering the entirety of the biocultural model of diet when constructing parameters for a SIMM of human diets. Most models concern themselves primarily with the physical and cultural environments in which they are situated. In other words, they consider only what foods were likely to have been consumed by individuals within the particular cultural setting.

This belies several facts about human food and cuisine. From the advent of domestication, humans (and by extension, civilizations) have directed the biology and nutritional value of their foods. Thus, it is not always appropriate to assume that the nutritional profiles of modern foods are identical to those of previous generations. Moreover, very little attention is given to the technological systems that can affect not only the foods consumed but how those foods are biologically utilized from a nutritional standpoint. As demonstrated here, the technological adaptation of nixtamalization can significantly impact interpretations of diet from individual isotope signatures. In this way, cultural practices have a direct and measurable impact on human biology (Armelagos, 2003; Pelto et al., 2000).

As this dissertation has shown, when conducting human diet reconstruction using stable isotope mixing models (SIMMs), careful consideration must be given to selecting appropriate source data, accounting for culturally moderated physical or chemical changes to sources, and designing projects in a manner that is informed of the given context and realistic in scope. That said, it has been demonstrated that such models are relatively robust to minor variations, and therefore their use is only likely to increase. While there are problems that can arise from unsystematic applications of such techniques, the ability to present diet reconstructions in terms of actual percent compositions promises to make diet information more accessible and serviceable in archaeology writ large. Therefore, every aspect of the biocultural model of human food systems and cuisine should be considered to mitigate potential complications. This includes how particular technologies, physical environments, social environments, idea systems, and social organizations can interact to produce culture-specific isoscapes that should be considered on a case-by-case basis.

The potential of stable isotope mixing models (SIMMs), and Food Reconstruction Using Isotope Transfer Signals (FRUITS) in particular, to further our understanding of ancient foodways has only just begun, especially in the case of ancient Maya archaeology. Even more promising is the fact that several new and not-so-new methods and techniques, such as ^{34}S analysis, are not only breaking into the field but offering synergistic benefits as well. SIMMs can allow for the quantification of diet components at the individual level while controlling for fraction offsets, trophic discrimination, and variations in macronutrient concentration. Where these techniques fall short, methods such as CSIA of amino acids can resolve problems like detecting aquatic resource consumption that have vexed the field for decades. And all of this is occurring as more human, floral, and faunal isotope data than ever is available in the literature. Much like the Three Sisters of the ancient Maya (and others), these disparate methods are poised to offer a more complete view of ancient foodways than ever before.

Appendix A: Human Isotope Data

Appendix A.1: Human Target Data for $\delta^{13}C$ and $\delta^{15}N$ Analysis (N=45)

FRUITS ID	Burial ID	Site	Period	Sex	Age	$\delta^{13}C_{apatite}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	Source
1	TR3-1	Tamarindito	Preclassic	M?	Middle Adult (35-49)	-7.9	-12.6	8.8	Wright, 1994
2	DP52	Dos Pilas	Late Classic	F	Adult	-3.8	-8.6	10.5	Wright, 1994
3	TA4	Tamarindito	Late Classic	M	Young Adult (20-34)	-7.2	-9.1	9.8	Wright, 1994
4	TA6	Tamarindito	Late Classic	M	Young Adult (20-34)	-4.1	-8.9	10.2	Wright, 1994
5	CC1	Cerro de Cheyo	Late Classic	Ind.	Adolescent (12-19)	-5.2	-9.1	10.2	Wright, 1994
6	LP1	La Paciencia	Late Classic	M?	Middle Adult (35-49)	-4.6	-10.3	9.6	Wright, 1994
7	DP55	Dos Pilas	Late Classic	Ind.	Adult	-2.8	-8.6	10.1	Wright, 1994
8	AP4	Arroyo de Piedra	Late Classic	M?	Young Adult (20-34)	-3.2	-9.7	2.3	Wright, 1994
9	AG1	Aguateca	Late Classic	F	Old Adult (50+)	-5.8	-9.9	9.1	Wright, 1994
10	QCH5	Aguateca	Late Classic	M	Middle Adult (35-49)	-4.1	-9.9	7.9	Wright, 1994
11	QCH6	Aguateca	Late Classic	M	Middle Adult (35-49)	-8.3	-11.0	10.1	Wright, 1994
12	DP2	Dos Pilas	Terminal Classic	M	Young Adult (20-34)	-5.0	-8.9	8.7	Wright, 1994
13	DPA	Dos Pilas	Terminal Classic	M	Middle Adult (35-49)	-5.3	-8.4	11.6	Wright, 1994
14	DPB	Dos Pilas	Terminal Classic	M	Middle Adult (35-49)	-6.3	-11.3	9.6	Wright, 1994
15	DPE	Dos Pilas	Terminal Classic	F	Young Adult (20-34)	-6.3	-12.0	12.7	Wright, 1994
16	DPG	Dos Pilas	Terminal Classic	M	Middle Adult (35-49)	-6.9	-11.2	9.7	Wright, 1994
17	DPH	Dos Pilas	Terminal Classic	F	Young Adult (20-34)	-4.9	-8.6	9.1	Wright, 1994
18	DPI	Dos Pilas	Terminal Classic	M	Young Adult (20-34)	-5.3	-8.8	10.4	Wright, 1994
19	DP4	Dos Pilas	Late Classic	F	Young Adult (20-34)	-5.1	-9.1	9.7	Wright, 1994
20	DP9	Dos Pilas	Terminal Classic	M	Middle Adult (35-49)	-5.2	-9.6	9.5	Wright, 1994

Appendix A.1 Continued

FRUITS ID	Burial ID	Site	Period	Sex	Age	$\delta^{13}C_{apatite}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	Source
21	DP10B	Dos Pilas	Terminal Classic	M	Adolescent (12-19)	-4.6	-9.0	11.6	Wright, 1994
22	DP10A	Dos Pilas	Terminal Classic	M	Young Adult (20-34)	-4.1	-8.6	9.1	Wright, 1994
23	DP12	Dos Pilas	Terminal Classic	M	Young Adult (20-34)	-3.9	-7.8	12.4	Wright, 1994
24	DP16	Dos Pilas	Terminal Classic	F	Young Adult (20-34)	-7.2	-9.7	7.5	Wright, 1994
25	DP17	Dos Pilas	Terminal Classic	M	Middle Adult (35-49)	-7.2	-9.7	10.3	Wright, 1994
26	DP20	Dos Pilas	Late Classic	F	Old Adult (50+)	-6.2	-9.6	11.0	Wright, 1994
27	TA1A	Tamarindito	Late Classic	M	Middle Adult (35-49)	-4.7	-9.3	8.1	Wright, 1994
28	TA2	Tamarindito	Late Classic	F	Young Adult (20-34)	-6.4	-13.0	8.2	Wright, 1994
29	DP22	Dos Pilas	Late Classic	M	Young Adult (20-34)	-4.6	-7.7	10.6	Wright, 1994
30	DP29	Dos Pilas	Late Classic	F	Middle Adult (35-49)	-4.3	-9.7	10.1	Wright, 1994
31	DP43	Dos Pilas	Late Classic	F	Middle Adult (35-49)	-6.7	-8.6	10.1	Wright, 1994
32	DP45	Dos Pilas	Late Classic	M	Adult	-4.1	-8.2	10.3	Wright, 1994
33	DP47	Dos Pilas	Late Classic	M	Young Adult (20-34)	-6.4	-8.3	11.1	Wright, 1994
34	DP50	Dos Pilas	Late Classic	M	Young Adult (20-34)	-5.6	-9.1	9.7	Wright, 1994
35	TR3/2	Tamarindito	Late Classic	Ind.	Adult	-6.6	-9.7	10.9	Wright, 1994
36	DP1	Dos Pilas	Late Classic	M	Middle Adult (35-49)	-7.1	-7.0	9.3	Wright, 1994
37	DP49	Dos Pilas	Late Classic	M	Young Adult (20-34)	-6.4	-10.1	9.9	Wright, 1994
38	DP33	Dos Pilas	Late Classic	F	Adolescent (12-19)	-5.9	-9.5	8.3	Wright, 1994
39	DP5	Dos Pilas	Late Classic	F	Middle Adult (35-49)	-6.4	-8.6	7.7	Wright, 1994
40	DP3	Dos Pilas	Terminal Classic	M	Young Adult (20-34)	-6.6	-8.2	8.2	Wright, 1994
41	DP13	Dos Pilas	Terminal Classic	F	Young Adult (20-34)	-8.0	-9.8	9.1	Wright, 1994
42	DP30	Dos Pilas	Late Classic	M	Old Adult (50+)	-7.6	-8.5	8.9	Wright, 1994
43	AG5B	Aguateca	Late Classic	F	Middle Adult (35-49)	-7.3	-9.3	9.1	Wright, 1994
44	AG5A	Aguateca	Late Classic	F	Adolescent (12-19)	-5.5	-8.8	8.0	Wright, 1994
45	DP44	Dos Pilas	Late Classic	F	Adult	-8.3	-11.3	10.2	Wright, 1994

Appendix A.2: Human Target Data for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ Analysis (N=16)

FRUITS ID	Burial ID	Site	Period	Sex	Age	$\delta^{13}C_{apatite}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
1S	AG5A	Aguateca	Late Classic	F	Adolescent (12-19)	-5.531	-8.78	7.98	11.99	Wright, 1994; Thornton & Wright, n.d.
2S	AG1	Aguateca	Late Classic	F	Old Adult (50+)	-5.790	-9.87	9.06	10	Wright, 1994; Thornton & Wright, n.d.
3S	AG5B	Aguateca	Late Classic	F	Adolescent (12-19)	-7.341	-9.34	9.13	10.56	Wright, 1994; Thornton & Wright, n.d.
4S	DP30	Dos Pilas	Late Classic	M	Old Adult (50+)	-7.564	-8.53	8.9	10.21	Wright, 1994; Thornton & Wright, n.d.
5S	DP17	Dos Pilas	Terminal Classic	M	Middle Adult (35-49)	-7.172	-9.65	10.3	10.81	Wright, 1994; Thornton & Wright, n.d.
6S	DP1	Dos Pilas	Terminal Classic	M	Middle Adult (35-49)	-7.109	-7.04	9.31	8.04	Wright, 1994; Thornton & Wright, n.d.
7S	DP4	Dos Pilas	Terminal Classic	F	Adult	-5.055	-9.07	9.67	8.89	Wright, 1994; Thornton & Wright, n.d.
8S	DP13	Dos Pilas	Terminal Classic	F	Young Adult (20-34)	-7.967	-9.84	9.13	9.03	Wright, 1994; Thornton & Wright, n.d.
9S	DP5	Dos Pilas	Terminal Classic	F	Middle Adult (35-49)	-6.394	-8.58	7.66	5.49	Wright, 1994; Thornton & Wright, n.d.
10S	CC1	Cerro de Cheyo	Late Classic	Ind.	Adolescent (12-19)	-5.171	-9.11	10.19	3.79	Wright, 1994
11S	D55	Dos Pilas	Late Classic	Ind.	Adult	-2.819	-8.64	10.08	-1.46	Wright, 1994
12S	DP2	Dos Pilas	Late Classic	M	Young Adult (20-34)	-5.023	-8.94	8.69	9.75	Wright, 1994
13S	DPG	Dos Pilas	Terminal Classic	M	Middle Adult (35-49)	-6.895	-11.16	9.70	11.07	Wright, 1994
14S	DP9	Dos Pilas	Terminal Classic	M	Middle Adult (35-49)	-5.223	-9.59	9.46	5.29	Wright, 1994
15S	DP10B	Dos Pilas	Terminal Classic	M	Adolescent (12-19)	-4.626	-8.95	11.63	6.9	Wright, 1994
16S	DP49	Dos Pilas	Late Classic	M	Young Adult (20-34)	-6.430	-10.10	9.90	9.56	Wright, 1994

Appendix B: Source Isotope and Nutrition Values

Appendix B.1: Isotope Composition of C3 Plants Used in Constructing FRUITS Models

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Agastache mexicana	Toronjil	Modern	-27.5	5.5		Warinner et al., 2013
Annona muricata	Soursop	Modern	-26.22	5.21		Wright, 2006
Annona sp.	Anona fruit	Modern	-28.48			Wright, 2006
Anonna scleroderma	Bandesopa, poshte	Modern	-24.4	7.6		Warinner et al., 2013
Arctosaphylos pungens	Pinguica	Modern	-24.2			Warinner et al., 2013
Asclepias curassavica	Cancerillo	Modern	-33.2	6.3		Warinner et al., 2013
Astrocaryum mexicanum	Chapay nut	Modern	-29.94			Wright, 2006
Astrocaryum mexicanum	Chapay nut	Modern	-30.12			Wright, 2006
Astrocaryum mexicanum	Chapay nut	Modern	-29.2	2.35		*This analysis*
Astrocaryum mexicanum	Chapay nut	Modern	-27.99	1.98		*This analysis*
***Bactris* sp.**	Chiquijul	Modern	-25.8	1.0		Warinner et al., 2013
Bixa orellana	Achiote	Modern	-28.21			Wright, 2006
Bixa orellana	Achiote	Modern	-26.08	1.4		*This analysis*
Brosimum alicastrum	Ramón	Modern	-26.2			Wright, 2006
Brosimum alicastrum	Ramón	Modern	-25.53			Wright, 2006
Brosimum alicastrum	Ramón	Modern	-23.28	3.86		*This analysis*
Brosimum alicastrum	Ramón	Modern			5.31	*This analysis*
Byrsonima crassifolia	Nance	Modern	-25.6			Wright, 2006
Byrsonima crassifolia	Nance	Modern	-27.3	5.10		Warinner et al., 2013
Byrsonima crassifolia	Nance	Modern	-23.87	2.74		*This analysis*
Capsicum annum	Chile	Modern	-24.8	3.5		Warinner et al., 2013
Capsicum annum	Chile anachito	Modern	-31.7	7.0		Warinner et al., 2013
Capsicum annum	Chile dulce	Modern	-23.3	6.2		Warinner et al., 2013

Appendix B.1 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Capsicum annum	Chile picante	Modern	-25.7	2.4		Warinner et al., 2013
Capsicum chinense	Chile habañero	Modern	-27.9	9.9		Warinner et al., 2013
Capsicum sp.	Chile	Modern	-28.51			Wright, 2006
Capsicum sp.	Chile	Modern	-26.25			Wright, 2006
Carica papaya	Papaya	Modern	-23.6	10.1		Warinner et al., 2013
Carica sp.	Wild papaya	Modern	-24.87	5.49		Wright, 2006
Chenopodium ambrosioides	Epazote	Modern	-27.7	13.4		Warinner et al., 2013
Cnidoscolus chayamansa	Chaya	Modern	-27.1	4.6		Warinner et al., 2013
***Crotelaria* sp.**	Chipil	Modern	-26	0.7		Warinner et al., 2013
Cucurbita mixta	Pipian squash	Modern	-26	5.6		Warinner et al., 2013
***Cucurbita* sp.**	Squash	Modern	-26	7.3		Warinner et al., 2013
***Cucurbita* sp.**	Squash	Modern	-23.6	7.9		Warinner et al., 2013
***Cucurbita* sp.**	Squash	Modern	-28.3	7.7		Warinner et al., 2013
Dialium guianese	Wild tamarind	Modern	-24.61			Wright, 2006
Dialium guianese	Wild tamarind	Modern	-22.32	-0.01		*This analysis*
Dioscorea alata	Macal/Yam	Modern	-23.56			Wright, 2006
Helianthus annuus	Sunflower	Modern	-27.3	9.9		Warinner et al., 2013
Ipomaea batatas	Camote/Potato	Modern	-26.1	6.2		Warinner et al., 2013
Ipomoea batatas	Camote/Potato	Modern	-24.94			Wright, 2006
Junco Palm Leaf		Modern	-25.16	4.01		Wright, 2006
Licania platypus	Sunzapote	Modern	-27.78			Wright, 2006
Lingua de vaca		Modern	-25.31			Wright, 2006
Lingua de vaca		Modern	-23.37	0.17		*This analysis*
Lycopersicon esculentum	Jitomate rojo	Modern	-27.2	4.6		Warinner et al., 2013
Lycopersicon esculentum	Jitomate verde	Modern	-23.1	4.8		Warinner et al., 2013

Appendix B.1 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Manihot esculenta	Yuca	Modern	-26	2.2		Warinner et al., 2013
Manilkara zapotilla	Chicozapote	Modern	-25.8	6.7		Warinner et al., 2013
Orbignya cohune	Corozo nut	Modern	-28.15			Wright, 2006
Orbignya cohune	Corozo nut	Modern	-26.8			Wright, 2006
Orbignya cohune	Corozo nut	Modern	-24.73	5.6		*This analysis*
Pachyrhizus erosus	Jicama	Modern	-25.2	7.2		Warinner et al., 2013
Parmentiera edulis	Guajilote	Modern	-25.3	5.4		Warinner et al., 2013
Passiflora edulis	Maracuya	Modern	-26.8	2.6		Warinner et al., 2013
Persea americana	Avocado	Modern	-26	10.4		Warinner et al., 2013
Phaseolus vulgaris	Bean	Modern	-26.25	3.94		Wright, 2006
Phaseolus vulgaris	Bean (bayo)	Modern	-26.6	3.1		Warinner et al., 2013
Phaseolus vulgaris	Bean (blanco)	Modern	-25.1	2.8		Warinner et al., 2013
Phaseolus vulgaris	Bean (flor de mayo)	Modern	-25.8	4.1		Warinner et al., 2013
Phaseolus vulgaris	Bean (negro)	Modern	-23.9	8.1		Warinner et al., 2013
Phaseolus vulgaris	Beans	Modern	-23.59	0.71		*This analysis*
Pouteria mamosa	Zapote (fruit)	Modern	-25.6			Wright, 2006
Pouteria mamosa	Zapote (fruit)	Modern	-26.63			Wright, 2006
Pouteria mamosa	Zapote (seed)	Modern	-26.32	0.56		Wright, 2006
Pouteria mamosa	Zapote (seed)	Modern	-28.54			Wright, 2006
Pouteria mamosa	Zapote	Modern	-26.52	0.7		*This analysis*
Pouteria sapota	Mamey	Modern	-25.9	0.9		Warinner et al., 2013
Psidium guajava	Guava	Modern	-25.77			Wright, 2006
Psidium guajava	Guava	Modern	-27.9	10.6		Warinner et al., 2013
Psidium guajava	Guava	Modern	-26.3	1.1		Warinner et al., 2013
Psidium guajava	Guava	Modern			8.32	*This analysis*

Appendix B.1 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Sechium edulis	Chayote, fruit	Modern	-25.4	8.1		Warinner et al., 2013
Sicana odorifera	Melocoton	Modern	-24.3	5.5		Warinner et al., 2013
Theobroma cacao	Cacao	Modern	-32.64	3.69		Wright, 2006
Theobroma cacao	Cacao	Modern	-30.56	2.1		*This analysis*
Water lilly		Modern	-23.05			Wright, 2006
Xanthosoma sagittifolium	Macal/Cocoyam	Modern	-25.6	3.7		Warinner et al., 2013

Appendix B.2: Isotope Composition of Maize (C4 Plants) Used in Constructing FRUITS Models

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Zea mays	Maize	Modern	-9.7	6.07		Wright, 2006
Zea mays	Maize	Modern	-8.9	6.2		Warinner et al., 2013
Zea mays	Maize	Modern	-8.9	2.6		Warinner et al., 2013
Zea mays	Maize	Modern	-7.85	5.32		*This analysis*
Zea mays	Maize	Modern (Pacific Coast, Untreated)			7.03	*This analysis*
Zea mays	Maize	Modern (Chimaltenango, Untreated)			4.65	*This analysis*
Zea mays	Maize	Modern (Pacific Coast, lime soaked and boiled)			7.54	*This analysis*
Zea mays	Maize	Modern (Chimaltenango, Lime soaked and boiled)			6.89	*This analysis*
Zea mays	Maize	Modern (San Juan Comalapa, lime soaked and boiled)			0.23	*This analysis*
Zea mays	Maize	Modern (Pacific Coast, lime soaked)			0.77	*This analysis*
Zea mays	Maize	Modern (Chimaltenango, lime soaked)			3.88	*This analysis*
Zea mays	Maize	Modern (San Juan Comalapa, lime soaked)			3.86	*This analysis*

Appendix B.3: Isotope Composition of Terrestrial Animals Used in Constructing FRUITS Models

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Canis familiaris	Dog	Flores		-10.7	7.2		Gerry, 1993
Canis familiaris	Dog	Flores		-9.4	7.3		Gerry, 1993
Canis familiaris	Dog	Flores		-10.2	6.9		Gerry, 1993
Canis familiaris	Dog	Altar		-7.8	8.2		Gerry, 1993
Canis familiaris	Dog	Copan		-9.7	4.5		Gerry, 1993
Canis familiaris	Dog	Copan		-8.4	6.8		Gerry, 1993
Canis familiaris	Dog	Copan		-8.7	5.6		Gerry, 1993
Canis familiaris	Dog	Copan		-9	6.7		Gerry, 1993
Canis familiaris	Dog	Copan	-4.6	-8.4	4.3		Gerry, 1993
Canis familiaris	Dog	Copan	-4.6	-7.5	5.1		Gerry, 1993
Canis familiaris	Dog	Copan	-6.8	-9.8	6.1		Gerry, 1993
Canis familiaris	Dog	Copan	-4.2	-8.1	5.2		Gerry, 1993
Canis familiaris	Dog	Copan	-5	-9.5	6.3		Gerry, 1993
Canis familiaris	Dog	Caye Coco			9.59	8.5	Rand et al., 2021
Canis familiaris	Dog	Caye Coco			7.61	10.7	Rand et al., 2021
Canis familiaris	Dog	Ceibal	-10.35	-14.9	10.6		Sharpe et al., 2019
Canis familiaris	Dog	Ceibal	-8.32	-13.5	9.8		Sharpe et al., 2019
Canis familiaris	Dog	Ceibal	-8.31	-14.51	8.8		Sharpe et al., 2019
Canis familiaris	Dog	Ceibal	-7.95	-11.24	8.3		Sharpe et al., 2019
Canis familiaris	Dog	Ceibal	-7.6	-12.65	9.7		Sharpe et al., 2019
Canis familiaris	Dog	Ceibal	-7.56	-11.49	7.0		Sharpe et al., 2019
Canis familiaris	Dog	Ceibal	-7.24	-8.47	7.2		Sharpe et al., 2019
Canis familiaris	Dog	Ceibal	-6.98	-10.17	11.5		Sharpe et al., 2019
Canis familiaris	Dog	Ceibal	-6.67	-9.55	9.3		Sharpe et al., 2019
Canis familiaris	Dog	Ceibal		-8.36	9.5		Sharpe et al., 2019
Canis familiaris	Dog	Laguna de On Island			6.62	12.6	Rand et al., 2021

Appendix B.3 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Canis familiaris	Dog	Chanlacan			8.16	3.0	Rand et al., 2021
Canis familiaris	Dog	Chanlacan			9.60	12.2	Rand et al., 2021
Canis sp.	Dog	Arroyo de Piedra		-19.19	6.57		Wright, 2006
Canis sp.	Dog	Dos Pilas		-8.96	4.37		Wright, 2006
Canis sp.	Dog	Dos Pilas		-9.57	7.91		Wright, 2006
Cervid	Deer	Dos Pilas		-21.64	2.23		Wright, 2006
Cervidae	Deer	Pacbitun			4.16	16.9	Rand et al., 2021
Cervidae	Deer	Nakum			1.53	12.8	Rand et al., 2021
Cervidae	Deer	Nakum			6.35	12.5	Rand et al., 2021
Cervidae	Deer	Nakum			4.58	13.8	Rand et al., 2021
Cervidae	Deer	Nakum			5.93	13.5	Rand et al., 2021
cf. *Odocoileus virginianus*	cf Whitetail deer	Nakum			3.82	14.4	Rand et al., 2021
cf. *Odocoileus virginianus*	cf Whitetail deer	Nakum			7.02		Rand et al., 2021
cf. *Odocoileus virginianus*	cf Whitetail deer	Nakum			4.41	14.5	Rand et al., 2021
cf. *Odocoileus virginianus*	cf Whitetail deer	Nakum			6.00	14.4	Rand et al., 2021
cf. Odocoileus virginianus	cf Whitetail deer	Nakum			6.78	13.5	Rand et al., 2021
cf. *Odocoileus virginianus*	cf Whitetail deer	Nakum			4.68	13.9	Rand et al., 2021
Cuniculus paca	Lowland paca	Modern		-21.47	5.78		Wright, 2006
Cuniculus paca	Lowland paca	Modern		-21.14	5.28		Wright, 2006
Cuniculus paca	Lowland paca	Copan	-5.9	-8.9	6.2		Gerry, 1993
Cuniculus paca	Lowland paca	Ceibal	-11.12	-20.96	4.6		Sharpe et al., 2019
Cuniculus paca	Lowland paca	Pacbitun			8.55	13.6	Rand et al., 2021
Cuniculus paca	Lowland paca	Pacbitun			5.14	15.5	Rand et al., 2021
Cuniculus paca	Lowland paca	Pacbitun			2.32	18.8	Rand et al., 2021

Appendix B.3 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Cuniculus paca	Lowland paca	Caye Coco			6.58	13.0	Rand et al., 2021
Cuniculus paca	Lowland paca	Oxtankah			5.82	16.6	Rand et al., 2021
Dasyprocta punctata	Central American agouti	Oxtankah			5.57	18.0	Rand et al., 2021
Dasyprocta punctata	Central American agouti	Oxtankah			6.68	15.8	Rand et al., 2021
Dasyprocta punctata	Central American agouti	MSJ		-21.44	2.78	12.9	Thornton & Wright, n.d.
Dasyprocta punctata	Central American agouti	Aguateca		-14.5	8.11	7.7	Thornton & Wright, n.d.
***Dasyprocta* sp.**	Agouti	Pacbitun			2.08	17.2	Rand et al., 2021
***Dasyprocta* sp.**	Agouti	Caye Coco			4.70	14.8	Rand et al., 2021
***Dasyprocta* sp.**	Agouti	Chanlacan			2.65	13.7	Rand et al., 2021
***Dasyprocta* sp.**	Agouti	Yaxha		-19.67	7.26	11.7	Thornton & Wright, n.d.
***Dasyprocta* sp.**	Agouti	Lamanai		-20.1	8.97	12.1	Thornton & Wright, n.d.
***Dasyprocta* sp.**	Agouti	Aguateca		-18.13	5.60	10.3	Thornton & Wright, n.d.
***Dasyprocta* sp.**	Agouti	Dos Pilas		-21.64	2.23	5.4	Thornton & Wright, n.d.
***Dasyprocta* sp.**	Agouti	Punta de Chiminos		-21.5	3.05	10.8	Thornton & Wright, n.d.
Dasypus novemcinctus	Nine-banded armadillo	Modern		-20.12	8.66		Wright, 2006
Dasypus novemcinctus	Nine-banded armadillo	Laguna de On Island			6.61	14.6	Rand et al., 2021
Dasypus novemcinctus	Nine-banded armadillo	Laguna de On Island			7.63	13.5	Rand et al., 2021
Dasypus novemcinctus	Nine-banded armadillo	Laguna de On Island			7.39	11.7	Rand et al., 2021
Dasypus novemcinctus	Nine-banded armadillo	Laguna de On Island			7.91	12.8	Rand et al., 2021
Dasypus novemcinctus	Nine-banded armadillo	Laguna de On Island			8.53	13.9	Rand et al., 2021

Appendix B.3 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Dasypus novemcinctus	Nine-banded armadillo	Caye Coco			8.06	12.2	Rand et al., 2021
Dasypus novemcinctus	Nine-banded armadillo	Caye Coco			8.54	13.2	Rand et al., 2021
Dasypus novemcinctus	Nine-banded armadillo	Caye Coco			6.81	12.4	Rand et al., 2021
Dasypus novemcinctus	Nine-banded armadillo	Caye Coco			8.84	9.5	Rand et al., 2021
Dasypus novemcinctus	Nine-banded armadillo	Chanlacan			8.22	13.8	Rand et al., 2021
Dasypus novemcinctus	Nine-banded armadillo	Chanlacan			6.60	13.2	Rand et al., 2021
Dasypus novemcinctus	Nine-banded armadillo	Chanlacan			6.41	14.0	Rand et al., 2021
Dasypus novemcinctus	Nine-banded armadillo	Laguna de On Shore			4.04	15.8	Rand et al., 2021
Dasypus novemcinctus	Nine-banded armadillo	Ichpaatun			6.20	16.5	Rand et al., 2021
Didelphidae	Opossum	Laguna de On Island			6.49	13.5	Rand et al., 2021
Didelphidae	Opossum	Laguna de On Island			8.25	13.8	Rand et al., 2021
Didelphis marsupialis	Common opossum	Caye Coco			9.27	13.3	Rand et al., 2021
Didelphis virginiana	Virginia opossum	Oxtankah			6.41		Rand et al., 2021
Felidae	Feline	Pacbitun			8.70	14.5	Rand et al., 2021
Hystricognathi	Agouti or paca	Caye Coco			5.21	12.8	Rand et al., 2021
Iguana iguana	Iguana	Marco Gonzales	-9.1	-19.1	5.8		Williams et al., 2009
Leporidae	Rabbit	Chanlacan			5.10	14.2	Rand et al., 2021
Mazama americana	Red Brocket Deer	Copan	-9.9	-18.3	5.2		Gerry, 1993
Mazama americana	Red Brocket Deer	Copan		-22.7	6.6		Gerry, 1993
Mazama americana	Red Brocket Deer	Punto de Chimino		-21.5	3.1		Wright, 2006

Appendix B.3 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Mazama americana	Red Brocket Deer	Aguateca		-14.04	5.08		Wright, 2006
Mazama americana	Red Brocket Deer	Modern		-22.76	5.92		Wright, 2006
Mazama americana	Brocket Deer	Marco Gonzales	-11.95	-22.1	5.9		Williams et al., 2009
Mazama americana	Red Brocket Deer	Laguna de On Island			6.80	13.9	Rand et al., 2021
Mazama americana	Red Brocket Deer	Laguna de On Island			5.73	13.3	Rand et al., 2021
Mazama americana	Red brocket deer	Vista Alegre			6.67	14.9	Rand et al., 2021
***Mazama* sp.**	Brocket deer	Pacbitun			4.82	15.0	Rand et al., 2021
***Mazama* sp.**	Brocket deer	Pacbitun			3.78	15.5	Rand et al., 2021
***Mazama* sp.**	Brocket Deer	Laguna de On Island			4.02	14.5	Rand et al., 2021
***Mazama* sp.**	Brocket deer	Caye Coco			4.69	13.9	Rand et al., 2021
***Mazama* sp.**	Brocket deer	Caye Coco			5.00	14.0	Rand et al., 2021
***Mazama* sp.**	Brocket deer	Caye Coco			5.33	15.9	Rand et al., 2021
***Mazama* sp.**	Brocket deer	Caye Coco			6.52	13.0	Rand et al., 2021
***Mazama* sp.**	Brocket deer	Chanlacan			4.60	13.2	Rand et al., 2021
***Mazama* sp.**	Brocket deer	Chanlacan			6.03	14.3	Rand et al., 2021
***Mazama* sp.**	Brocket deer	Nakum			6.34	12.9	Rand et al., 2021
***Mazama* sp.**	Brocket deer	Vista Alegre			6.21	14.2	Rand et al., 2021
***Mazama* sp.**	Brocket deer	Oxtankah			7.43	16.0	Rand et al., 2021
***Mazama* sp.**	Brocket deer	San Miguelito			7.26	13.7	Rand et al., 2021
***Mazama* sp.**	Brocket Deer	Tayasal			4.42		Rand et al., 2021
***Mazama* sp.**	Brocket deer	Trinidad		-14.44	4.76	13.4	Thornton & Wright, n.d.
***Mazama* sp.**	Brocket deer	Cancuen		-24.02	4.97	8.4	Thornton & Wright, n.d.
***Mazama* sp.**	Brocket deer	Lamanai		-22.58	5.52	12.1	Thornton & Wright, n.d.
Meleagris gallopavo	Northern turkey	Modern		-8.43	8.29		Wright, 2006
Meleagris gallopavo	Northern turkey	Ceibal	-5.2	-9.68	6.3		Sharpe et al., 2019

Appendix B.3 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Meleagris gallopavo	Northern turkey	Ceibal	-5.11	-8.06	8.9		Sharpe et al., 2019
Meleagris gallopavo	Northern turkey	Laguna de On Island			11.44	13.6	Rand et al., 2021
Meleagris gallopavo	Northern turkey	Laguna de On Island			7.69	14.9	Rand et al., 2021
Meleagris ocellata	Ocellated turkey	Ceibal	-9.07	-17.76	8.6		Sharpe et al., 2019
Meleagris ocellata	Ocellated turkey	Vista Alegre			7.42	15.7	Rand et al., 2021
Meleagris ocellata	Ocellated turkey	Vista Alegre			7.89	15.0	Rand et al., 2021
Meleagris ocellata	Ocellated turkey	Vista Alegre			7.66	13.1	Rand et al., 2021
Meleagris ocellata	Ocellated turkey	Vista Alegre			6.37	16.5	Rand et al., 2021
***Meleagris* sp.**	Turkey	Ceibal	-11.45	-22.72	5.4		Sharpe et al., 2019
***Meleagris* sp.**	Turkey	Ceibal	-6.39	-14.1	5.2		Sharpe et al., 2019
***Meleagris* sp.**	Turkey	Pacbitun			4.64	15.8	Rand et al., 2021
***Meleagris* sp.**	Turkey	Caye Coco			7.04	14.7	Rand et al., 2021
***Meleagris* sp.**	Turkey	Caye Coco			7.33	13.7	Rand et al., 2021
***Meleagris* sp.**	Turkey	Caye Coco			7.59	10.7	Rand et al., 2021
***Meleagris* sp.**	Turkey	Caye Coco			9.03		Rand et al., 2021
***Meleagris* sp.**	Turkey	Chanlacan			6.42	14.0	Rand et al., 2021
***Meleagris* sp.**	Turkey	Chanlacan			7.00	13.2	Rand et al., 2021
***Meleagris* sp.**	Turkey	Caye Muerto			3.05		Rand et al., 2021
***Meleagris* sp.**	Turkey	Nakum			6.05	14.0	Rand et al., 2021
***Meleagris* sp.**	Turkey	Xunantunich			7.96		Rand et al., 2021
Mustelidae	Weasel	Laguna de On Island			5.67	12.4	Rand et al., 2021
Odocoileus virginiana	Whitetail deer	Copan	-11.2	-19.7	4		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan	-11.2	-20.6	3.4		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan	-9.2	-20.7	2.8		Gerry, 1993

Appendix B.3 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Odocoileus virginiana	Whitetail deer	Copan	-11.7	-21.1	4.5		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan	-11.8	-21	2.8		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan	-11	-19.3	3.2		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan	-10.1	-20.6	3.8		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan	-9.9	-20	3.5		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan	-10.3	-20.8	2.7		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan	-9.3	-22.2	4.2		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan	-9.9	-20.4	8		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan	-10.8	-21.3	5.6		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-22.2	2.7		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-20.1	3.5		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-21.6	3.6		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Flores		-20.7	4.4		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Flores		-22	4.7		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Flores		-21.5	5.2		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Flores		-19	4.7		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Flores		-20.1	4.4		Gerry, 1993

Appendix B.3 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Odocoileus virginiana	Whitetail deer	Altar		-22.2	5.1		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Altar		-19.4	5.4		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Altar		-21.5	4.3		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Altar		-22.3	5.2		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Altar		-21.5	3.8		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Altar		-22.5	3.6		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-21.9	3.5		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-22.3	3.7		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-20.7	4.7		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-20.8	4.9		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-21.2	4.9		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-21.9	7.4		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-22.3	7.8		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-21.4	4.3		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-22.1	3.9		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Holmul		-21.4	6.8		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-20.6	3.5		Gerry, 1993

Appendix B.3 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Odocoileus virginiana	Whitetail deer	Copan		-21.6	4.9		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-20.4	3.7		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-21.5	3.7		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-20.8	5.1		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan		-19.1	4.6		Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan	-9.7				Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan	-9.2				Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan	-10.3				Gerry, 1993
Odocoileus virginiana	Whitetail deer	Copan	-10.2				Gerry, 1993
Odocoileus virginiana	Whitetail deer	Aguateca		-18.13	5.6		Wright, 2006
Odocoileus virginiana	Whitetail deer	Dos Pilas		-21.4	4		Wright, 2006
Odocoileus virginiana	Whitetail deer	Punto de Chimino		-21.48	6.6		Wright, 2006
Odocoileus virginiana	Whitetail deer	Modern		-20.36	7.2		Wright, 2006
Odocoileus virginiana	Whitetail deer	Modern		-22.13	7.86		Wright, 2006
Odocoileus virginiana	Whitetail deer	Marco Gonzales	-11.15	-19.55	5.4		Williams et al., 2009
Odocoileus virginianus	Whitetail deer	Ceibal	-14.78	-24.08	5.4		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-14.47	-22.46	3.0		Sharpe et al., 2019

Appendix B.3 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Odocoileus virginianus	Whitetail deer	Ceibal	-12.95	-21.14	5.2		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-12.14	-21.92	5.2		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-12.02	-20.48	4.1		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-11.31	-21.34	8.4		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-11.12	-22	6.1		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-10.82	-21.55	4.5		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-10.68	-20.11	3.0		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-10.66	-20.98	7.1		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-10.63				Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-10.63	-21.59	3.7		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-10.42	-22.23	2.8		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-10.3	-20.86	6.6		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-9.99	-21.74	3.7		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-9.99	-22.45	3.7		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-9.96	-19.48	6.0		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-9.76	-20.54	6.0		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-9.46	-19.22	7.0		Sharpe et al., 2019

Appendix B.3 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Odocoileus virginianus	Whitetail deer	Ceibal	-9.1	-20.4	3.3		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-9.04	-20.17	4.0		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Ceibal	-9.04	-21.96	3.2		Sharpe et al., 2019
Odocoileus virginianus	Whitetail deer	Pacbitun		-20.05	5.30	17.7	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Pacbitun		-21.54	3.84	17.1	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Pacbitun		-21.8	3.35	6.5	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Pacbitun		-19.03	6.77	13.8	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Pacbitun		-19.76	6.66		Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Laguna de On Island		-22.67	5.24	14.0	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Laguna de On Island		-23.35	4.82	15.5	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Laguna de On Island		-22.19	4.41	8.6	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Laguna de On Island		-18.78	4.76	12.5	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Laguna de On Island		-22.52	4.83	13.5	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Laguna de On Island		-21.13	5.07	11.7	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Laguna de On Island		-21.17	5.62	13.3	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Caye Coco		-22.32	4.53		Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Caye Coco		-22.62	3.45	12.1	Rand et al., 2021

Appendix B.3 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Odocoileus virginianus	Whitetail deer	Caye Coco		-22.52	3.51	14.0	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Caye Coco		-22.08	4.66	12.2	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Caye Coco		-21.35	6.35	12.3	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Caye Coco		-22.6	5.44	~~17.1~~	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Caye Coco		-21.02	7.41	14.1	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Chanlacan		-22.33	3.76	13.0	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Chanlacan		-22.47	6.06	13.8	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Chanlacan		-22.48	3.39	12.4	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Caye Muerto		-20.2	3.94	13.3	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Nakum		-20.25	6.42	12.7	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Nakum		-21.06	3.82	13.1	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Nakum		-20.38	6.59	5.0	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Nakum		-21.86	4.21	13.0	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Vista Alegre		-20.88	5.06	15.1	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Vista Alegre		-20.76	6.32	12.6	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Vista Alegre		-7.35	8.45		Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Oxtankah		-17.16	7.45	16.0	Rand et al., 2021

Appendix B.3 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Odocoileus virginianus	Whitetail deer	San Miguelito		-19.68	7.36	12.3	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Caracol		-20.34	3.91		Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Caracol		-20.48	3.90		Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Xunantunich		-21.42	4.70	16.7	Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Tayasal		-21.49	5.14		Rand et al., 2021
Odocoileus virginianus	Whitetail deer	Trinidad		-21.09	5.60	11.7	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Trinidad		-22.37	7.38	11.1	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Trinidad		-23.92	5.50	11.0	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Trinidad		-20.77	4.70	9.5	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	MSJ		-22.3	4.97	8.5	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Yaxha		-21.64	4.63	9.3	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Yaxha		-21.34	5.14	9.4	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Cancuen		-21.07	4.16	7.2	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Cancuen		-19.64	6.48	7.9	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Cancuen		-21.16	3.20	9.7	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Cancuen		-21.42	8.09	6.9	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Cancuen		-19.51	5.98	11.0	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Cancuen		-20.23	2.96	8.0	Thornton & Wright, n.d.

Appendix B.3 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Odocoileus virginianus	Whitetail deer	Cancuen		-13.74	5.58	7.6	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Aguateca		-20.09	5.15	1.9	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Lamanai		-22	4.51	11.1	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Lamanai		-22.4	7.66	5.6	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Lamanai		-21.89	7.39	3.2	Thornton & Wright, n.d.
Odocoileus virginianus	Whitetail deer	Aguateca		-19.29	8.37	3.7	Thornton & Wright, n.d.
Pecari tajacu	Collared Peccary	Xunantunich		-20.87	6.32	14.9	Rand et al., 2021
Pecari tajacu	Collared Peccary	Tayasal		-22.6	3.99		Rand et al., 2021
Philander opossum	Grey four-eyed opossum	Oxtankah		-19.36	7.86	14.8	Rand et al., 2021
Procyon lotor	Raccoon	Caye Coco		-20.28	2.95		Rand et al., 2021
Tayassu pecari	While-lipped peccary	Punto de Chimino		-24.4	3.3		Wright, 2006
Tayassu pecari	While-lipped peccary	Modern		-22.16	4.73		Wright, 2006
Tayassu pecari	While-lipped peccary	Modern		-11.49	6.07		Wright, 2006
Tayassu pecari	While-lipped peccary	Modern		-16.1	6.32		Wright, 2006
Tayassu pecari	White-lipped peccary	Pacbitun			4.59	14.8	Rand et al., 2021
Tayassu pecari	White-lipped peccary	Laguna de On Island			3.74	14.6	Rand et al., 2021
Tayassu pecari	White-lipped peccary	Laguna de On Island			4.14	11.1	Rand et al., 2021
Tayassuidae	Peccary	Flores		-22.7	3.5		Gerry, 1993
Tayassuidae	Peccary	Flores		-21	4.1		Gerry, 1993

Appendix B.3 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Tayassuidae	Peccary	Flores		-22.1	3		Gerry, 1993
Tayassuidae	Peccary	Flores		-23.5	4.1		Gerry, 1993
Tayassuidae	Peccary	Altar		-20.8	4.4		Gerry, 1993
Tayassuidae	Peccary	Altar		-23.3	7.5		Gerry, 1993
Tayassuidae	Peccary	Altar		-22.9	3.9		Gerry, 1993
Tayassuidae	Peccary	Altar		-22.7	3.8		Gerry, 1993
Tayassuidae	Peccary	Altar		-17.5	4.7		Gerry, 1993
Tayassuidae	Peccary	Altar		-22.2	4.3		Gerry, 1993
Tayassuidae	Peccary	Copan		-18.1	4.2		Gerry, 1993
Tayassuidae	Peccary	Copan		-21.9	3.2		Gerry, 1993
Tayassuidae	Peccary	Copan		-19.6	3.6		Gerry, 1993
Tayassuidae	Peccary	Copan		-10.6	4.5		Gerry, 1993
Tayassuidae	Peccary	Copan		-21.6	4		Gerry, 1993
Tayassuidae	Peccary	Quirigua		-22.9	6.4		Gerry, 1993
Tayassuidae	Peccary	Quirigua		-22.9	6.2		Gerry, 1993
Tayassuidae	Peccary	Copan		-22.4	4.5		Gerry, 1993
Tayassuidae	Peccary	Copan		-21.2	3.8		Gerry, 1993
Tayassuidae	Peccary	Copan		-22.3	2.6		Gerry, 1993
Tayassuidae	Peccary	Copan		-17.9	3.4		Gerry, 1993
Tayassuidae	Peccary	Copan	-10.2	-22.2	3.5		Gerry, 1993
Tayassuidae	Peccary	Copan	-9.2	-19	2.1		Gerry, 1993
Tayassuidae	Peccary	Copan	-11.1	-19.2	3.4		Gerry, 1993
Tayassuidae	Peccary	Copan	-12	-21.7	3.9		Gerry, 1993
Tayassuidae	Peccary	Copan	-8.1	-15.7	2.6		Gerry, 1993
Tayassuidae	Peccary	Copan	-10.3	-20.2	3.3		Gerry, 1993
Tayassuidae	Peccary	Copan	-11.7	-20.9	3.9		Gerry, 1993
Tayassuidae	Peccary	Copan	-11.4	-19.8	4		Gerry, 1993

Appendix B.3 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Tayassuidae	Peccary	Copan	-9.9	-21	2.8		Gerry, 1993
Tayassuidae	Peccary	Copan	-11	-19	4.6		Gerry, 1993
Tayassuidae	Peccary	Copan	-12.4	-20.6	5.8		Gerry, 1993
Tayassuidae	Peccary	Ceibal	-13.22	-21.34	3.4		Sharpe et al., 2019
Tayassuidae	Peccary	Ceibal	-11.64	-22.25	5.4		Sharpe et al., 2019
Tayassuidae	Peccary	Ceibal	-10.61	-20.37	5.3		Sharpe et al., 2019
Tayassuidae	Peccary	Ceibal	-9.81	-18.67	5.4		Sharpe et al., 2019
Tayassuidae	Peccary	Ceibal	-9.13	-20.97	4.4		Sharpe et al., 2019
Tayassuidae	Peccary	Ceibal	-8.48	-14.45	3.9		Sharpe et al., 2019
Tayassuidae	Peccary	Pacbitun		-21.99	4.01	15.2	Rand et al., 2021
Tayassuidae	Peccary	Laguna de On Island		-22.51	3.16	11.8	Rand et al., 2021
Tayassuidae	Peccary	Caye Coco		-22.98	5.12		Rand et al., 2021
Tayassuidae	Peccary	Caye Coco		-22.13	3.34	12.4	Rand et al., 2021
Tayassuidae	Peccary	Caye Coco		-21.07	4.24	12.5	Rand et al., 2021
Tayassuidae	Peccary	Chanlacan		-21.61	3.96	13.0	Rand et al., 2021
Tayassuidae	Peccary	Chanlacan		-7.26	8.06	8.1	Rand et al., 2021
Tayassuidae	Peccary	Chanlacan		-19.5	6.97	13.3	Rand et al., 2021
Tayassuidae	Peccary	Cancuen		-15.71	4.66	9.3	Thornton & Wright, n.d.
Tayassuidae	Peccary	MSJ		-19.11	5.73	7.1	Thornton & Wright, n.d.
Tayassuidae	Peccary	Yaxha		-19.23	4.94	10.1	Thornton & Wright, n.d.
Tayassuidae	Peccary	Aguateca		-22.83	4.45	1.6	Thornton & Wright, n.d.
Tayassuidae	Peccary	Lamanai		-16.09	4.23	11.4	Thornton & Wright, n.d.
Tayassuidae	Peccary	Lamanai		-21.53	5.49	6.0	Thornton & Wright, n.d.

Appendix B.4: Isotope Composition of Aquatic Animals Used in Constructing FRUITS Models

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Aramus guarauna	Limpkin	Vista Alegre		-11.01	7.45	13.5	Rand et al., 2021
Aramus guarauna	Limpkin	Vista Alegre		-10.98	8.00	14.2	Rand et al., 2021
Aramus guarauna	Limpkin	Vista Alegre		-9.98	7.19	16.0	Rand et al., 2021
Aramus guarauna	Limpkin	Vista Alegre		-8.47	7.17	16.0	Rand et al., 2021
Arius	River catfish	Marco Gonzales		-6.4	11.2		Williams et al., 2009
***Chrysemys* sp.**	Pond turtle	Modern		-25.07	7.29		Williams et al., 2009
***Chrysemys* sp.**	Pond turtle	Modern		-25.07	7.29		Wright, 2006
Crocodylidae	Crocodile	Laguna de On Island		-15.8	10.33	8.6	Rand et al., 2021
Crocodylidae	Crocodile	Laguna de On Island		-19.89	9.31	13.3	Rand et al., 2021
Crocodylidae	Crocodile	Laguna de On Island		-23.12	7.29	4.6	Rand et al., 2021
Crocodylidae	Crocodile	Laguna de On Island		-21.81	8.66	6.8	Rand et al., 2021
Crocodylidae	Crocodile	Chanlacan		-4.33	6.69		Rand et al., 2021
Crocodylidae	Crocodile	Caye Muerto		-10.97	6.47		Rand et al., 2021
Crocodylidae	Crocodile	Caye Coco		-23.16	10.16		Rand et al., 2021
Crocodylidae	Crocodile	Caye Muerto		-10.97	6.47		Rand et al., 2021
Crocodylidae	Crocodile	Marco Gonzales	10.2	-18.2	8.9		Williams et al., 2009
Dermatemys mawii	Central American river turtle	Marco Gonzales	-9.8	-21	6.8		Williams et al., 2009
Dermatemys mawii	Central American river turtle	Tayasal		-19.65	9.04		Rand et al., 2021
Dermatemys mawii	Central American river turtle	Trinidad		-24.93	6.14	3.57	Thornton & Wright, n.d.
Dermatemys mawii	Central American river turtle	Trinidad		-17.92	9	5.45	Thornton & Wright, n.d.
Dermatemys mawii	Central American river turtle	MSJ		-16.90	3.82	4.33	Thornton & Wright, n.d.
Dermatemys mawii	Central American river turtle	MSJ		-18.46	7.6	4	Thornton & Wright, n.d.

Appendix B.4 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Dermatemys mawii	Central American river turtle	Yaxha		-14.59	3.84	10.11	Thornton & Wright, n.d.
Dermatemys mawii	Central American river turtle	Aguateca		-22.97	8.4	0.17	Thornton & Wright, n.d.
Dermatemys mawii	Central American river turtle	Aguateca		-22.58	6.9	2.37	Thornton & Wright, n.d.
Dermatemys mawii	Central American river turtle	Lamanai		-21.20	3.57	1.36	Thornton & Wright, n.d.
Dermatemys mawii	Central American river turtle	Lamanai		-24.70	3.95	1.36	Thornton & Wright, n.d.
Dermatemys mawii	Central American river turtle	Lamanai		-20.96	4.49	4.5	Thornton & Wright, n.d.
Dermatemys mawii	Central American river turtle	Lamanai		-22.82	4.16	3.89	Thornton & Wright, n.d.
Dermatemys mawii	Central American river turtle	Lamanai		-23.29	3.8	3.78	Thornton & Wright, n.d.
Dermatemys mawii	Central American river turtle	Yaxha		-16.48	7.62	11.12	Thornton & Wright, n.d.
Emydidae	Pond turtle	Marco Gonzales	-8.85	-16.35	4.35		Williams et al., 2009
Emydidae	Pond turtle	Chanlacan		-22.03	8.78	2.3	Rand et al., 2021
Emydidae	Pond turtle	Aguateca		-24.18	9.81	-5.07	Thornton & Wright, n.d.
Emydidae	Pond turtle	Aguateca		-15.23	9.98	5.07	Thornton & Wright, n.d.
freshwater crab		Modern		-19.72	3.21		Wright, 2006
***Ictalurus* sp.**	Catfish	Modern		-20.78	11.59		Wright, 2006
Kinosternidae	Turtle	Pacbitun		-24.09	10.37	15.6	Rand et al., 2021
Kinosternidae	Turtle	Pacbitun		-22.67	6.82	13.5	Rand et al., 2021
Kinosternon cf. acutum	Pond turtle	Cancuen		-15.74	11.31	7.16	Thornton & Wright, n.d.
Pachychilus glaphyrus	Jute	Modern		-32.09	4.87		Wright, 2006
Pachychilus glaphyrus	Jute	Modern		-28.5	5.49		Wright, 2006

Appendix B.4 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
***Parachromis* sp.**	Guapote	Modern		-29.3	9.3		Wright, 2006
***Parachromis* sp.**	Guapote	Modern		-28.36	11.51		Wright, 2006
Petenia splendida	Bay snook	Modern		-28	12.30		Wright, 2006
Petenia splendida	Bay snook	Modern		-28.1	11.90		Wright, 2006
Siluriformes	Freshwater catfish	Laguna de On Island	-14.81	9.91			Rand et al., 2021
Siluriformes	Freshwater catfish	Laguna de On Island	-16.59	9.55			Rand et al., 2021
Staurotypus triporcatus	Mexican Musk Turtle	Tayasal		-20.99	6.08		Rand et al., 2021
Testudines	Freshwater turtle	Pacbitun		-22.22	8.06	13.3	Rand et al., 2021
Testudines	Freshwater turtle	Pacbitun		-24.28	10.52	13.8	Rand et al., 2021
Testudines	Freshwater turtle	Laguna de On Island	-23.02	4.03	3.9		Rand et al., 2021
Testudines	Freshwater turtle	Laguna de On Island	-15.5	10.36	9.5		Rand et al., 2021
Testudines	Freshwater turtle	Laguna de On Island	-9.86	10.31	11.2		Rand et al., 2021
Testudines	Freshwater turtle	Laguna de On Island	-18.99	14.26			Rand et al., 2021
Testudines	Freshwater turtle	Laguna de On Island	-18.01	10.94	10.1		Rand et al., 2021
Testudines	Freshwater turtle	Laguna de On Island	-25.91	9.36	13.4		Rand et al., 2021
Testudines	Freshwater turtle	Punto de Chimino		-23.8	7.4		Wright, 2006
Testudines	Freshwater turtle	Punto de Chimino		-25	6.4		Wright, 2006
Testudines	Freshwater turtle	MSJ		-20.89	6.28	5.7	Thornton & Wright, n.d.
Testudines	Freshwater turtle	Lamanai		-24.11	3.76	5.8	Thornton & Wright, n.d.
Trachemys scripta	Pond slider	Trinidad		-19.78	6.08	4.99	Thornton & Wright, n.d.
Trachemys scripta	Pond slider	Trinidad		-17.40	10.29	6.48	Thornton & Wright, n.d.
Trachemys scripta	Pond slider	MSJ		-15.47	5.66	8.2	Thornton & Wright, n.d.

Appendix B.4 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
Trachemys scripta	Pond slider	Aguateca		-20.78	11.49	-1.99	Thornton & Wright, n.d.
Trachemys venusta	Mesoamerican slider	Laguna de On Island	-24.8	7.12	10.2		Rand et al., 2021
Trachemys venusta	Mesoamerican slider	Laguna de On Island	-22.16	12.38	13.6		Rand et al., 2021
Trachemys venusta	Mesoamerican slider	Laguna de On Island	-25.3	7.14	2.6		Rand et al., 2021
Trachemys venusta	Mesoamerican slider	Caye Coco		-23.23	7.15	8.5	Rand et al., 2021
Trachemys venusta	Mesoamerican slider	Caye Coco		-27.21	8.90	12.3	Rand et al., 2021
Trachemys venusta	Mesoamerican Slider	Nakum		-22.59	7.46	14.6	Rand et al., 2021
Trachemys venusta	Mesoamerican slider	Vista Alegre		-9.35	7.64	3.4	Rand et al., 2021
Viejas p.	“colorada”	Modern		-27.1	9.2		Wright, 2006
Viejas p.	“colorada”	Modern		-25.89	10		Wright, 2006

Appendix B.5: Isotope Composition of Marine Animals Used in Constructing FRUITS Models

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
***Acanthurus* sp.**	Surgeon Fish	Marco Gonzales	-5.3	-10.1	5.8		Williams et al., 2009
Ariidae	Sea catfish	Laguna de On Island		-16.12	8.90		Rand et al., 2021
Ariidae	Sea catfish	Laguna de On Island		-11.15	10.99		Rand et al., 2021
Ariidae	Sea catfish	Laguna de On Island		-14.82	8.64		Rand et al., 2021
Ariidae	Sea catfish	Laguna de On Island		-12.52	10.90		Rand et al., 2021
Ariidae	Sea catfish	Laguna de On Island		-13.09	12.19		Rand et al., 2021
Ariidae	Sea catfish	Laguna de On Island		-13.77	10.04		Rand et al., 2021
***Balistes* sp.**	Trigger	Marco Gonzales	-4.2	-7	7.1		Williams et al., 2009
***Caranx* sp.**	Jackfish	Marco Gonzales	-3.4	-4.7	11.2		Williams et al., 2009
Caranx hippos	Crevalle jack	Vista Alegre		-8.25	10.35		Rand et al., 2021
Caretta caretta	Loggerhead sea turtle	Vista Alegre		-13.59	11.12	13.6	Rand et al., 2021
Caretta caretta	Loggerhead sea turtle	Vista Alegre		-20.01	6.95	13.5	Rand et al., 2021
Caretta caretta	Loggerhead sea turtle	Ichpaatun		-7.6	4.79		Rand et al., 2021
Caretta caretta	Loggerhead sea turtle	Vista Alegre		-12.42	10.30	11.1	Rand et al., 2021
***Centropomus* sp.**	Snook	Marco Gonzales	-3.60	-2.2	8.90		Williams et al., 2009
Cheloniidae	Sea Turtle	Laguna de On Island		-21.06	10.62	14.2	Rand et al., 2021
Gerridae	Mojarras	Caye Coco		-19.12	12.90		Rand et al., 2021
***Haemulon* sp.**	Grunt	Marco Gonzales	-3.5	-4.8	4.6		Williams et al., 2009
Lutjanidae	Atlantic Snapper	Vista Alegre		-2.63	8.61	-1.3	Rand et al., 2021
***Lutjanus* sp.**	Snapper	Marco Gonzales	1.50	-4	7.80		Williams et al., 2009
Mammalia	Marine mammal	Oxtankah		-17.25	7.54	16.1	Rand et al., 2021

Appendix B.5 Continued

Taxon	Common Name	Site/Area	$\delta^{13}C_{bulk}$ (‰ VPDB)	$\delta^{13}C_{collagen}$ (‰ VPDB)	$\delta^{15}N_{collagen}$ (‰ AIR)	$\delta^{34}S_{methionine}$ (‰ VCDT)	Source
***Mycteroperca* sp.**	Grouper	Marco Gonzales	-1.95	-6.3	8.83		Williams et al., 2009
***Scarus* sp.**	Parrot Fish	Marco Gonzales	-4.1	-5.6	8.8		Williams et al., 2009
***Sphyraena* sp.**	Barracuda	Marco Gonzales	-4.8	-5.9	11.1		Williams et al., 2009
***Trachinotus* sp.**	Pompano	Marco Gonzales	-4.1	-6.2	16.6		Williams et al., 2009
Trichechus manatus manatus	Caribbean manatee	Moho Cay		-4.44	3.82	2.4	Rand et al., 2021

Appendix C: Macronutrient Concentrations of Food Sources Used in Constructing FRUITS Models

Appendix C.1: Macronutrient Concentrations of Food Sources Used in Constructing FRUITS Models

Taxon	Common Name	Group	INCAP #	% Protein INCAP	% Energy INCAP	USDA Ref	% Protein USDA	% Energy USDA
Annona muricata	Soursop	C3	455	6.13	93.87			
Arius	River catfish	AP	624	86.89	13.11			
***Bactris* sp.**	Chiquijul	C3	456	4.73	95.27			
Bixa orellana	Achiote	C3	705	0	100			
Brosimum alicastrum	Ramón	C3	508	12.79	87.21	170552	11.23	88.77
Byrsonima crassifolia	Nance	C3	320	5.42	94.58			
Capsicum sp.	Chile	C3	195	18.1	81.9	168576	11.7	88.3
Carica papaya	Papaya	C3	417	5.62	94.38			
Carica sp.	Wild papaya	C3				169926	4.07	95.93
Chenopodium ambrosioides	Epazote	C3	156	31.4	68.6			
Cnidoscolus chayamansa	Chaya	C3	119	34.07	65.93			
Crocodylidae	Crocodile	AP	524	91.57	8.43			
***Crotelaria* sp.**	Chipil	C3	138	41.42	58.58			
***Cucurbita* sp.**	Squash	C3	250	7.14	92.86			
Dasypus novemcinctus	Nine-banded armadillo	TP	525	84.3	15.7			
Dialium guianese	Wild Tamarind	C3	463	4.25	95.75			
Dioscorea alata	Macal/Yam	C3	278	7.55	92.45			
Helianthus annuus	Sunflower	C3	518	24.81	75.19			
***Ictalurus* sp.**	Catfish	AP				174186	85.31	14.69
Iguana iguana	Iguana	TP	558	96.44	3.56			
Ipomaea batatas	Camote/Potato	C3	257	4.3	95.7			
Leporidae	Rabbit	TP	550	80.77	19.23			
Licania platypus	Sunzapote	C3	449	4.43	95.57			

Appendix C.1 Continued

Taxon	Common Name	Group	INCAP #	% Protein INCAP	% Energy INCAP	USDA Ref	% Protein USDA	% Energy USDA
***Lutjanus* sp.**	Snapper	MP	652	90.95	9.05			
Lycopersicon esculentum	Jitomate rojo	C3	263	14.04	85.96			
Meleagris gallopavo	Turkey	TP	590	100	0	5167	92.14	7.86
Marine fish (unspecified)	Surgeon Fish	MP	625	93.61	6.39			
***Mycteropercas*sp.**	Grouper	MP				15031	95	5
Odocoileus virginianus	Whitetail deer	TP	595	93.06	6.94	167622	88.99	11.01
Pachychilus glaphyrus	Jute	AP				90560	92	8
Pachyrhizus erosus	Jicama	C3	279	10.08	89.92			
Parmentiera edulis	Guajilote	C3	321	11.57	88.43			
Passiflora edulis	Maracuya	C3	420	7.35	92.65			
Persea americana	Avocado	C3	80	7.76	92.24			
Phaseolus vulgaris	Bean	C3	88	25.86	74.14	173745	26.36	73.64
Pouteria mamosa	Zapote, fruit	C3	283	4.68	95.32			
Psidium guajava	Guava	C3	367	14.31	85.69			
Sechium edulis	Chayote, fruit	C3	120	10.23	89.77			
Sicana odorifera	Melocoton, Cassabanana	C3	325	5.03	94.97			
Tayassu sp.	Peccary	TP				17158	86.59	13.41
Theobroma cacao	Cacao	C3	707	12.9	87.1			
***Trachinotus* sp.**	Pompano	MP				15068	66.12	33.88
Testudines	Freshwater turtle	AP	659	97.54	2.46	782753	84.96	15.04
Xanthosoma sagittifolium	Macal/Cocoyam	C3	175	5.17	94.83			
Zea mays	Maize	C4	202	7.94	92.06	35134	10.98	89.02

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