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The Zooarchaeological Dimension of Preceramic Human-Environment Dynamics in the Highlands of Southwestern Honduras

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THE ZOOARCHAEOLOGICAL DIMENSION OF PRECERAMIC HUMAN-ENVIRONMENT DYNAMICS IN THE HIGHLANDS OF SOUTHWESTERN HONDURAS

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THE ZOOARCHAEOLOGICAL DIMENSION OF PRECERAMIC HUMAN-ENVIRONMENT DYNAMICS IN THE HIGHLANDS OF SOUTHWESTERN HONDURAS

A Dissertation Presented to the Graduate Faculty of the

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in

Partial Fulfillment of the Requirements

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Doctor of Philosophy

with a

Major in Anthropology

by

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It took me ten years to understand that writing a dissertation is more about the journey than the destination. I have been fortunate to have excellent companions throughout every step of this journey, and though this manuscript is of my own making, it was shaped by those who walked beside me and encouraged me along the way, whom I wish to acknowledge here. I am fortunate to have received funding to carry out and write my research, which made walking this path a little easier. My research was funded by a Wenner-Gren Dissertation Fieldwork Grant and its writing was made possible thanks to writing fellowships from the Ford Foundation and the Quest Archaeological Research Program at SMU. I could not have asked for a better dissertation committee and am still astonished, and thankful, that they all said “yes”. My chair, Dr. Chris Roos, has been a mentor and guide since before I attended the program at SMU, and has thoughtfully prodded, guided, and encouraged me through every step of this process, including offering feedback and support on eight different versions of a dissertation grant proposal (yes, I kept track), various job application materials, and countless letters of recommendation. Through Dr. David Meltzer I fell in love with the Late Pleistocene and Early Holocene and learned the importance and value of telling a good story from the bits and pieces of the distant past we gather and study. Dr. Karen Lupo was my guide through all things zooarchaeological, and I will be forever thankful for her time and patience in introducing me to this realm. Dr. Ken Hirth was the most gracious host at Penn State, and his willingness to grant me access to the El Gigante materials, his wealth of archaeological knowledge, and his friendship made this research possible

and State College feel like home. I also owe a debt of gratitude to Tim Scheffler, whom I consider an honorary committee member because of his constant encouragement and because his careful and precise work at El Gigante is allowing many of us to continue to study this incredible site.

This dissertation was researched and written at three different institutions across three different states, leading to many friendships and collaborations along the way. At SMU, Drs. Kacy Hollenback and Sunday Eiselt offered their keen advice and support on what became successful grant and dissertation writing proposals. Rachel Burger walked me through zooarchaeological methods, protocols, codes, forms, and references, and I simply could not have done any of my analyses without her help. At Penn State, Sarah McClure graciously opened the doors to her zooarchaeology lab for me, which she had equipped with comparative specimens from the tropics specifically for work at El Gigante. She invited me to the zooarchaeology working group meetings at PSU and made sure I felt a part of the department, for which I am incredibly thankful. Martin Welker was always willing to help me identify a bit of bone or share a funny story about raptors, making time at the lab enjoyable. Doug Kennett, Gina Buckley, and Laurie Eccles offered their expertise and advice for analyzeing the composition of some of the El Gigante faunal materials, which I stubbornly refuse to accept are unable to be dated. At the University of Missouri, Lee Lyman unquestioningly granted me access to his incredible zooarchaeology collection, and though our conversations have been few, they have always been enlightening and I know they are the first of many more to come. Libby Cowgill granted me access to her photo room in the anthropology department, which helped me immensely with preparing the figures for the dissertation. Brooke Morgan and Meredith Mahoney at the Illinois State Museum helped me secure a loan for a peccary skeleton, which came in very handy for a number of bones that refused to be identified otherwise. Ashley Sharpe at STRI was always willing to help me make some tentative identifications from digital photographs, including and especially the crab specimens.

Though this dissertation is based solely on laboratory and collections research, I am fortunate to have visited El Gigante on many occasions and even more so to have met some of the wonderful people who care for and protect this and countless other archaeological sites in southwestern Honduras. These are the Lenca indigenous and ladino communities of La Estanzuela, Marcala, and the broader Mancomunidad de Municipios Lencas de la Sierra de La Paz (MAMLESIP), with whom I have had the pleasure and honor of working in the past. They expect me to return and share with them what I have done, just as they shared their knowledge and expertise with me every time I visited. I hope I have done them and their ancestors justice.

In the end, I was able to navigate and complete this journey thanks to the love and companionship of those who I feel have always been with me. Ma y pa, you taught me what I needed to know before I embarked on any adventure and showed me how to walk with love and patience. Whitney, Mati, Joey, and Gifi, you are the loves of my life and my companions of all days. Though we never know where we'll end up, I know by your side things will always be wonderful. Los amo.

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The Zooarchaeological Dimension of Preceramic Human-Environment Dynamics In The Highlands Of Southwestern Honduras

Advisor: Professor Christopher I. Roos

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In this dissertation I evaluate different hypotheses regarding human-environment dynamics in the Mesoamerican neotropics during the Preceramic period (ca. 11000-7400 cal B.P.) by examining the largest extant faunal assemblage dated to this time. The Preceramic was characterized by major climatic and ecological changes following the end of the Pleistocene, including the extinction of megafauna and the expansion of tropical forests. This period ended with a series of behavioral adaptations suited to this transformed landscape such as increased territoriality, sedentism, agriculture, and domestication. Three hypotheses have been proposed to explain these dynamics: the Broad-Spectrum Revolution hypothesis suggests post-Pleistocene resource uncertainty and unpredictability pushed foragers to reduce their mobility and expand their diet, particularly in marginal areas people had been driven to occupy as population sizes increased in the region. The Plant Food Production hypothesis posits that a decline in high-ranked resources (i.e., megafauna) following the end of the Pleistocene pulled foraging populations towards food-producing behaviors centered on plants. The Niche Construction hypothesis predicts that human-environment dynamics at this time changed in contexts of environmental abundance and not depletion, as foraging groups settled particularly productive environments and expanded their diet and modified their surroundings to maximize the productivity of these landscapes.

In this this dissertation I present the results of analyses of a large faunal assemblage and sediment samples obtained from the El Gigante rockshelter, a multi-component site located in the highlands of southwestern Honduras occupied episodically between 11,000-980 cal B.P. My results show that the shelter's initial occupations (ca. 11,010-9550 cal B.P.) were characterized by a narrow diet focused on the consumption of a limited number of animal resources, namely deer, and some plants. This 1400-year period of little behavioral change was likely the product of relative climatic stability aided by the unique physiography of the highlands of southwestern Honduras. Over time, deer became scarce on the landscape and El Gigante's inhabitants began overhunting this resource and heavily processed what prey they captured for obtaining marrow and fat. Consequently, the shelter was largely abandoned for 1400 years, with the exception of a few episodes of intense activity centered on the consumption of plant resources. This shift suggests plants, rather than animals, might have been what attracted populations to occupy the shelter during this time. These behavioral patterns continued to intensify during the subsequent phase of occupation, the Middle Marcala (7610-7430 cal B.P.). The rockshelter was occupied either longer or more intensively, bones were more heavily broken and processed, and the plant component of the diet continued to expand as the faunal component contracted slightly.

By focusing on the role that animals played during this key period of transition in Mesoamerica, my dissertation expands our understanding of the processes behind Preceramic adaptive changes, which predated experimentation with plant cultivation and extended far back into earliest Holocene. It also advances our knowledge of Preceramic lifeways and how these shaped major economic and social changes over time in Mesoamerica and beyond.

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Dedicated to the Lenca peoples of the Sierra de La Paz, who have shared their homes, their food, their coffee, and their heritage and to whom I am eternally grateful. Gracias.

In loving memory of Francisco Manuel Rodríguez Mota.

CHAPTER 1:

INTRODUCTION

In this dissertation I evaluate different hypotheses developed to explain the human-environment dynamics of foraging groups in the neotropics during the Preceramic period (ca. 11,000-7400 cal B.P.) by examining the largest known faunal assemblage in Middle America dated to this period, recovered from the El Gigante rockshelter in southwestern Honduras. Archaeology has contributed greatly to our understanding of human societies following the end of the last ice age. However, relatively little is known about human adaptations to changes taking place in the world's tropical forests at this time (i.e., Bush and Flenley 2006; Cochrane 2009; Mercader 2003; Roberts et al. 2017). This is especially true of the Preceramic in the neotropics of Middle America. The name alone suggests this period has been defined by the absence of social and behavioral traits that appear later in time, specifically agriculture, sedentism, and pottery. This period is important because it yields insights into human adaptations to and modifications of the region, and because it set the stage for later socio-cultural developments. However, the mechanisms that contextualized and drove changes in patterns of subsistence and mobility remain largely unexplored and have largely been addressed solely through the study of human-plant interactions. By focusing on the role that animals played during this key period of transition in Mesoamerica, my dissertation research expands our current understandings of the processes behind Preceramic adaptive changes, which may predate experimentation with plant cultivation and could extend far back into the earliest Holocene. El Gigante's exceptional faunal assemblage offers a unique opportunity to explore these issues and advance our knowledge of Preceramic lifeways and how these shaped broader economic and social changes over time in Middle America and beyond.

The Pleistocene-Holocene transition (PHT) was a time of major climatic and ecological changes that led to, among other transformations, the expansion of tropical forests, the extinction of megafauna, and a general decline in the amount of fauna on the landscape (Aceituno et al. 2013; Piperno 2006, 2011; Piperno and Pearsall 1998; Piperno et al. 2017). This transition ended with a widespread series of behavioral changes among human foragers including more diverse diets, increased territoriality and reduced residential mobility, and the first indications of horticulture, arboriculture, and domestication (Flannery 1969, 1986; Piperno and Pearsall 1998; Piperno et al. 2017). Three alternative hypotheses were developed to explain these natural and behavioral changes. The first hypothesis, known as the Broad-Spectrum Revolution (BSR; Flannery 1969, 1986) suggests that post-Pleistocene resource uncertainty and unpredictability pushed foragers to reduce their mobility and expand their diet in order to mitigate these changes. The effects were most significant in marginal areas where people were pushed as population sizes increased in the region. The second hypothesis, which I term the Plant Food Production (PFP) model, posits that a decline in high-ranked resources following the end of the Pleistocene (i.e., megafauna) led foraging populations to adopt food-producing behaviors centered on the acquisition and consumption of plants in order to maintain adequate levels of dietary returns (Piperno and Pearsall 1998; Piperno et al. 2017). The third hypothesis, based on the tenets of Niche Construction Theory (NCT), postulates that landscapes with rich and predictable resources attracted foraging populations to occupy them early in the history of the region. The abundance of predictable and high value resources is predicted to favor reduced mobility, a diverse diet, and eventually the adoption of landscape modification or “niche construction” practices (Smith 2015, 2016; Zeder 2012, 2016).

The above hypotheses are predicated on the interplay between four key processes: climatic and ecological change, resource depression and/or the loss of foraging efficiency, changes in diet and mobility, and the human modification of the landscape. However, the presence and timing of these processes have been only partially evaluated using botanical, archaeological, and paleoecological data from a small number of sites (see Lohse et al. 2021 and Piperno et al. 2017 for reviews of this literature). Little is known about the timing of these ecological and behavioral changes and the full range of resources exploited by these populations, especially how the presence and distribution of animal prey affected the behaviors of foraging groups at this time. Consequently, the Preceramic period represents one of the most significant lacunae in our understanding of the peoples of Middle America, yet it has great potential for informing us about social and economic behaviors that developed during this time and persisted throughout the prehistory of the region. My research begins to address this gap by analyzing the well-preserved faunal assemblage and a sample of the sedimentary assemblage recovered from the El Gigante rockshelter, a multi-component site occupied episodically between 11,000-980 cal B.P. located in the mountainous highlands of southwestern Honduras (Iceland and Hirth 2021; Kennett et al. 2017; Scheffler 2008; Scheffler et al. 2012).

The Preceramic faunal materials from El Gigante that I analyzed for this dissertation suggest that the southwestern highlands remained a dry and open (i.e. not heavily forested) refugium for certain species such as jackrabbits (*Lepus* sp.) well into the Holocene and through at least 7670 cal B.P. This is in agreement with paleoecological studies of the *highlands* of Middle America that indicate a dry early Holocene through ca. 7000 cal B.P. (see Caballero et al.

2019 and Lozano Garcia et al. 2015 for overviews of existing datasets). This is in contrast to the *lowlands* of the region, where records show an increase in moisture levels starting at ca. 10,000 cal B.P. (e.g., Correa-Metrio et al. 2012; Hodell et al. 2008; Lachniet et al. 2013). In addition, my results suggest the inhabitants of the highlands of southwestern Honduras, whether intentionally or not, modified their surroundings in ways that helped attract disturbance-loving species including white-tailed deer (*Odocoileus virginianus,* hereafter WTD), nine-banded armadillos (*Dasypus novemcinctus*), and certain rodent species (i.e., neotominae, sigmodontinae). This might indicate this was an increasingly disturbed landscape during the Preceramic, and perhaps remained (or was made) patchy through burning or clearing (e.g., Aceituno and Loaiza 2014, 2018; Aceituno et al. 2013). However, the highly fragmented nature of the El Gigante assemblage does not allow me to make stronger inferences regarding the productivity or openness of this landscape.

My analyses of a sample of El Gigante's zooarchaeological materials, when combined with existing analyses of the macrobotanical and lithic assemblages from this site (Figueroa and Scheffler 2021; Iceland and Hirth 2021; Scheffler 2008) support earlier proposals that foraging populations utilized the shelter and its environs sporadically throughout the Preceramic period, likely as part of a broader seasonal round (e.g., Scheffler 2008; Scheffler et al. 2012). In addition, it appears foraging populations began utilizing the shelter and its landscape more intensively in response to a reduction in foraging efficiency and resource depression in this area. I argue that this might have been a product of the El Gigante landscape remaining relatively stable and productive and thus attractive to foragers during most of the Preceramic, as indicated by evidence of repeated visits to the site despite decreases in the availability of high-ranked prey, namely WTD. It was only after a prolonged period of little ecological and behavioral change that faunal resource depression occurred at El Gigante during the Early Marcala occupation (ca. 8990-7670 cal B.P.) The shelter was occupied very sporadically over this 1,300-year span, suggesting its inhabitants lived and utilized other, more productive landscapes. Occupations of the shelter during this phase were short but intensive, as indicated by the presence of living floors dated to this time as well as an increase in the use, processing, and discard of plants (Figueroa and Scheffler 2021; Scheffler 2008). In response to a marked decrease in available WTD, the shelter's inhabitants consumed a wider variety of animals and plants than before, though their diet remained highly focused on the acquisition of deer and tree fruits. These behavioral patterns intensified during the final Preceramic phase of occupation, the Middle Marcala (ca. 7610-7430 cal B.P.). This phase is the shortest but has the highest abundance of bone and plant remains of the Preceramic. While the faunal component of the diet contracted slightly from the previous phase, the amount and diversity of plants consumed continued to increase, indicating a sustained shift in the subsistence system towards the acquisition of floral resources. Additionally, an increase in the abundance of species that are attracted to anthropogenically disturbed environments as well as an increase in the abundance of plant species that require human propagation in the diet suggests the El Gigante landscape was increasingly managed, though these behaviors likely began much earlier in the occupational sequence of the shelter. Lastly, while the number and age structure of WTD hunted rebounded during this time, populations continued to diversify their diet and reduce their foraging radius, which might indicate populations grew at this time.

I argue that the strongly seasonal nature of the botanical assemblage recovered from this site and the diverse and heavily processed faunal assemblage found in the earliest phases of occupation suggest El Gigante's inhabitants were drawn to this landscape by plant resources, most likely fruit-bearing trees with highly predictable productivity cycles. In this scenario, human-flora relations were perhaps more important to the inhabitants of El Gigante and likely conditioned subsistence decisions to a larger degree than the acquisition of animal prey. Over time, populations at El Gigante artificially selected and propagated certain fruit-bearing tree species (i.e., avocado, *Persea americana*, see Figueroa and Scheffler 2021; Scheffler 2008), which created landscapes with abundant and predictable resources that were "inherited" by future populations, making re-occupation and re-visitation more advantageous, all while having cumulative effects on faunal resources (*sensu* O'Brien and Laland 2012; Odling-Smee et al. 2003).

Critically, these results support arguments made elsewhere (e.g., Lupo et al. 2020; Piperno and Pearsall 1998; Stiner 2001) that generalizations regarding how foraging groups rank their resources (i.e., larger animals are higher ranked) are problematic, and should instead be based on a more complete understanding of subsistence systems and the landscapes that sustain them. This study also highlights the mutualistic nature of human-environment relations and the importance of developing explanatory models that utilize theoretical perspectives and approaches that examine and integrate the ecological, historical, and cultural contexts of foraging decisions over long spans of time. Lastly, it presents a baseline for examining other archaeological assemblages from the Pleistocene-Holocene transition (PHT) elsewhere in Middle America and beyond.

1.1 Theoretical approaches to the Pleistocene-Holocene Transition (PHT) in Archaeology

The PHT was characterized by global-scale climatic, environmental, and human behavioral changes, the latter of which culminated with the critical transition from a foraging to a farming way of life. Since the 1980s, research into these adaptive changes has employed models developed from the field of Human Behavioral Ecology (HBE) and especially Optimal Foraging Theory (OFT) to evaluate the effects of PHT environmental changes on human behavior, including and especially the loss of foraging efficiency concomitant with resource depression. The latter is often defined in archaeology as a decline in the abundance of high-ranked resources (Broughton 1994a, b). Recently, HBE studies of the PHT have come under criticism by proponents of Niche Construction Theory (NCT), who argue that this transition did not necessarily involve environmental degradation and resource depression. Rather, it is posited that these behavioral changes took place in contexts of abundance rather than scarcity, and that this abundance was in many cases the result of deliberate human niche construction (Jones and Hurley 2017; Smith 2011a, 2011b, 2014, 2015, 2016; Zeder 2012, 2015a, b, 2016). Proponents of these two approaches have created models that make predictions about human behavior in relation to the cultural, biological, and environmental contexts of decision-making, and specify the variables that condition forager subsistence and mobility, among other behaviors.

Research has continued to show HBE and NCT are not mutually exclusive and can complement one another when combined within an evolutionary approach to economic and environmental changes (Ready and Price 2021; Stiner and Kuhn 2016). Although a combination of natural and cultural processes such as climate and environmental change and demographic growth and expansion likely affected the behavioral changes taking place during the Preceramic, some of these potentially had a greater influence than others at particular times in the past, leading to feedbacks and sequences that must be parsed.

1.2 The PHT in Mesoamerica

The onset of the Holocene in Mesoamerica was marked by increases in temperature and humidity, both of which led to the expansion of tropical forests at the expense of other habitats, namely forest-savannah and forest-grassland mosaics (see Piperno and Pearsall 1998, Piperno et al. 2017 for a review of this literature). Research of human-environment dynamics during this time is focused on the reconstruction of human-plant interactions such as understanding the origins of the region's plant domesticates (e.g., Piperno 2011; Piperno et al. 2007, 2017). What little we know about human-animal dynamics during the PHT is limited to a handful of securely-dated megafauna kill sites (see Acosta 2008 and Gonzalez et al. 2003, 2006 for a review of these) and three faunal assemblages that indicate these groups had a diverse faunal component of the diet (Acosta 2008; Flannery 1986; Orsini 2016). Extensive zooarchaeological research of later periods highlights continuity in the importance of wild animals in subsistence, commercial exchange, and ritual (e.g., Boileau et al. 2020; Emery 2004; Sharpe et al. 2020).

Existing research (Piperno and Pearsall 1998; Piperno et al. 2017) has applied models derived from OFT – and some argue NCT (see Piperno et al. 2017) – to suggest that Preceramic adaptive changes initially took place in the tropical lowlands, which expanded and became more densely vegetated at the end of the Pleistocene (e.g., Correa-Metrio et al. 2013). These dense forests did not support large-bodied fauna (80% from animals smaller than an average-sized dog; see Piperno and Pearsall 1998: 67), routinely inferred to be the highest-ranked resources in forager diets (Piperno and Pearsall 1998), which would presumably have been pursued by Late Pleistocene hunters until their extinction or drop in abundance over time. Current scholarship based on NCT and OFT suggests that widespread resource depression during the PHT forced populations to expand their diet to include increasing numbers of plant and animal species and to modify parts of the landscape to improve the abundance and predictability of desired resources. Greater investment in lower-ranked resources made longer stays in modified landscapes advantageous, further compounding these density-dependent relationships (Bliege-Bird et al. 2020; Gremillion and Piperno 2009; Kennett et al. 2006; Piperno and Pearsall 1998). This model has been supported by evidence from across the region, which shows that some Preceramic groups modified the availability and distribution of key resources through patch clearing and burning to maintain early successional stages of tropical forests (Aceituno et al. 2018; Acosta et al. 2018; Gnecco and Aceituno 2006; Piperno 2011; Piperno et al. 1990, 2017; Vecino et al. 2014). Studies elsewhere in the world (e.g., Bird et al. 2016; Stiner et al. 2012) suggest that PHT behavioral adaptations and the modification of landscapes by foraging populations were the result of changing human-animal relations, though this has yet to be evaluated in the neotropics.

Existing research suggests human-plant interactions and human modifications of the landscape have very deep roots in Mesoamerica. However, little is known about how these early populations interacted with animals. In addition, contexts where we can examine the interplay between landscape modification, climate change, and diet and mobility remain limited in Middle America. As a result, there is no holistic understanding of Preceramic diets because faunal records are rare, degraded, or too fragmentary to provide information. For my dissertation I developed a model that integrates the theoretical programs of OFT and NCT for examining the faunal assemblage from the El Gigante rockshelter to evaluate behavioral responses to resource depression and disentangle the sequence in which human-environment dynamics associated with the PHT might have unfolded. Evaluating the presence of niche construction in a particular landscape requires detailed knowledge of its cultural and natural composition. El Gigante’s large faunal collection, while being a single case study, offers a unique opportunity to evaluate how its

Preceramic inhabitants navigated changes taking place as a result of climate and environmental change or human actions, and offer a baseline to be evaluated and built upon by future research in the area.

1.3 The El Gigante Rockshelter

Prior research on the Preceramic period in Honduras is limited to the southwestern highlands, which are part of the Central American Continental Divide (Figure 1.1). The El Gigante rockshelter is the only site in the area that has been intensively excavated, largely due to its unique and well-preserved deposits that were first identified and excavated in the late 1990s (Scheffler 2008: 49). The interior of the shelter remained a closed system for millennia, and no water, sediments, or other materials percolated in from the outside, creating a dry sediment sink for at least the past 11,000 years (Scheffler 2008). Moreover, the breakdown of the shelter's tuff walls and the accumulation of anthropogenic ash significantly increased the pH of the shelter's matrix. This in addition to the dry nature of the shelter inhibited bacterial growth and created suitable conditions for the preservation of archaeological materials such as bone, macrobotanical remains, textiles, and leather (Scheffler 2008; Scheffler et al. 2012). Ongoing analyses of El Gigante's lithic materials and preliminary analyses of the macrobotanical and faunal remains show a higher accumulation of these materials over time, indicating longer and more frequent occupation of the shelter throughout the Preceramic (Iceland and Hirth 2021; Kennett et al. 2017; Scheffler 2008; Scheffler et al. 2012). In addition, ongoing analyses of the site's botanical materials have identified an increasingly diverse diet as the inhabitants of the shelter added Mesoamerican staples such as maize and squash as complements to an already rich diet (Figueroa and Scheffler 2021). As tantalizing as these results are, they address just one part of the dietary changes associated with the PHT – an increase in the consumption of plants – and only hint at how humans interacted with their surroundings. In addition, the chronology of these changes has not been compared across the different datasets, which is fundamental to interpreting the role of human decision-making and agency in response to demographic and ecological change.

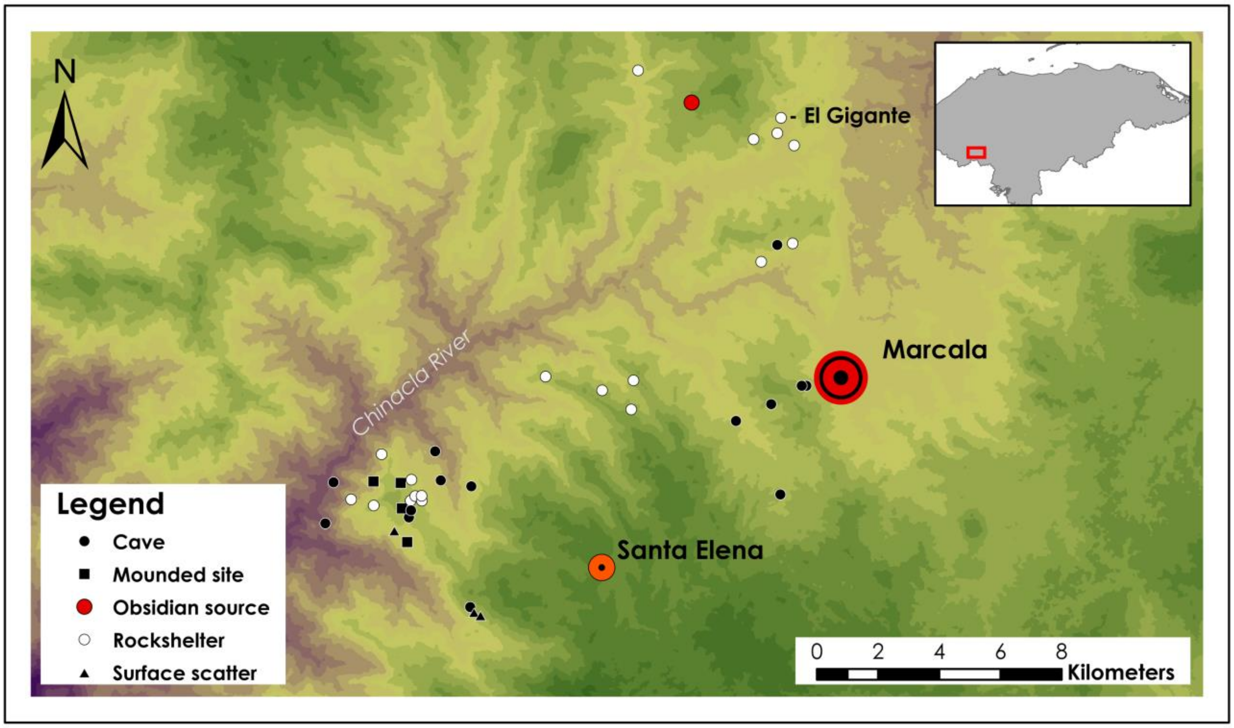

Figure 1.1 Location of the El Gigante rockshelter within southwestern Honduras.

1.4 Research Questions and Hypotheses

Over the course of this dissertation I explore the ways in which Preceramic foraging populations inhabiting El Gigante interacted with their surroundings by answering the following questions: Did the landscape surrounding the rockshelter change following the end of the

Pleistocene or in the wake of land-use intensification? How much agency did these populations have in responding to or even counteracting some of these environmental changes? Did environmental change "push" people to adapt? Or did this landscape "pull" people to change their subsistence and mobility before environmental change took place? To what degree did El Gigante's inhabitants occupy, utilize, and possibly modify their surroundings over time?

Existing and ongoing research at El Gigante has only identified some of the behavioral changes associated with the PHT: an expansion of the diet and an increase in the frequency and duration of occupations of the shelter over time (Figueroa and Scheffler 2021; Scheffler 2008; Scheffler et al. 2012). Analyses of the few existing Preceramic faunal assemblages recovered in the region have also identified broad changes in forager subsistence and mobility but have not yet determined whether and when resource depression took place nor how these populations responded to it in the near and long term (Acosta et al. 2018; Flannery 1986; Orsini 2016; Solis-Torres et al. 2020). In addition, while this research has identified the general trajectory of some of these behavioral changes, the timing, rate, and temporal relationships between these processes are key to interpreting the role of human decision-making and human agency in response to changing social and natural environments. The large and well-dated faunal assemblage recovered from El Gigante presents a unique opportunity to evaluate Preceramic adaptive change over time.

In this dissertation I evaluate the following hypotheses created to explain the ecological and behavioral changes of the PHT: The BSR hypothesis predicts that a decrease in mobility caused by demographic packing of the landscape coupled with post-Pleistocene climatic and environmental change caused resource depression and forced foraging populations to use the local landscape more intensively or return to it less frequently (Flannery 1969, 1986). The PFP hypothesis predicts that post-Pleistocene ecological change, namely the expansion of tropical forests, led to the depression of high-ranked prey – including megafauna – and caused groups to adopt a broader diet focused on the consumption of plant resources, which are energetically higher-ranked than animals in neotropical forests (Piperno 2006, 2011; Piperno and Pearsall 1998; Piperno et al. 2017). The NCT hypothesis predicts that an expansion of the diet breadth and a reduction in residential mobility occurred prior to the onset of resource depression and ecological change and were instead the result of populations adapting to resource-rich environments (Smith 2015, 2016; Zeder 2012, 2016).

The chronological order in which cultural and natural changes might have unfolded was a critical variable in this exercise, and my key archaeological goals were to evaluate each response independently and disentangle the sequence of events that led to these adaptive changes in order to obtain a better understanding of the consequences and potential feedbacks among these processes. I collected four independent lines of evidence to evaluate these hypotheses: (1) the relative abundances of artiodactyls to other prey, as measured by the Artiodactyl Index as a proxy for foraging efficiency and resource depression (AI; Bayham 1979; Broughton 1994a, 1994b); (2) mortality profiles for deer and measures of carcass processing as indicative of resource depression independent of diet breadth (Broughton 2002; Church and Lyman 2003; Lupo and Schmitt 1997; Lyman 1994; Outram 2001, 2002, 2004; Wolverton 2008; Wolverton et al. 2008), and; (3) the richness and diversity of the faunal assemblage as a proxy for diet breadth. These datasets are complemented by the existing large radiocarbon chronology established for the site (Kennett et al. 2017), a limited analysis of 11 sediment samples recovered during excavation and carried out by me, a detailed analysis of the site's Preceramic lithic assemblage (Hirth et al. 2018; Iceland and Hirth 2021), and existing and ongoing analyses of the shelter's large macrobotanical assemblage (Figueroa and Scheffler 2021; Scheffler 2008; Scheffler et al. 2012).

1.5 Organization of the dissertation

There are six chapters that follow. In Chapter 2, I present the theoretical and research framework for this dissertation, which approaches the study of mobility and subsistence from the perspective of evolutionary ecology. First, I review the major tenets of Optimal Foraging Theory and Niche Construction theory, both of which have been used by researchers to approach the study of adaptive change in the region. I conclude the chapter with a model I developed to determine the context in which adaptive changes unfolded in the Middle American neotropics. This model combines principles and expectations derived from both OFT and NCT that I used to inform the hypotheses I evaluated as part of this study.

Chapter 3 provides the paleoclimatic, paleoecological, and archaeological context for this study. I first review what we know about the paleoenvironment and paleoclimate of Middle America during the Preceramic period. I then present ecological, climatic, and archaeological datasets that help situate the natural and behavioral changes associated with the PHT that have some bearing on understanding the archaeological record of the highlands of southwestern Honduras. I then synthesize existing research of the Preceramic in Middle America to understand the behavioral patterns associated with this major transition and identify gaps in our knowledge of this topic and conclude the chapter with an overview of prior and ongoing research on the vast material assemblage recovered from the El Gigante rockshelter pertinent to this dissertation.

Chapter 4 is a review of the various methods I employed to generate the datasets I used to evaluate these hypotheses, including a suite of faunal and geoarchaeological analyses. In Chapter

4 I also include a description of information pertinent to each of the major taxa I identified in the El Gigante assemblage in order to assist my interpretations. Chapter 5 provides the results of the various faunal analyses I carried out to evaluate the decisions made by El Gigante's Preceramic inhabitants regarding subsistence, mobility, and landscape modification. I also present the results of geoarchaeological analyses I conducted on a small sample of sediments obtained from the site during previous excavations.

In Chapter 6, I synthesize and interpret the results of my analyses of the faunal and sedimentary records recovered from the Preceramic levels of El Gigante and integrate them with existing and independent ongoing analyses of the site's macrobotanical and lithic assemblages. My results suggest that foraging groups in Middle America maintained relatively high levels of mobility well into the Holocene. These groups modified their subsistence and mobility behaviors as a result of decreased returns and/or because their movements became more restricted as the region became more populated. The faunal assemblage from El Gigante shows that animal prey was scarce even in areas that were re-visited by foragers over millennia, and that the diet of groups inhabiting this region – particularly seasonally dry forests – was instead likely focused on procuring, processing, and consuming plant resources.

In Chapter 7, I situate my research within the current state of the study and knowledge of human-environment dynamics taking place during the Pleistocene-Holocene Transition in the neotropics and beyond. I first discuss how the research program at El Gigante complements previous research in the region (i.e., Piperno and Pearsall 1998; Piperno et al. 2017) and elsewhere in the tropics (e.g., Hunt et al. 2012; Levis et al. 2018; Lombardo et al. 2020; Roberts et al. 2017; Summerhayes et al.2017) aimed at reconstructing and explaining the long history of human occupation, use, and modification of these environments. I also note the importance of combining multiple and independent lines of evidence for parsing out the interplay between ecological and behavioral change over long spans of time, particularly the need to examine human diet holistically rather than through a single material class. Lastly, I echo others (e.g. Ready and Price 2020; Stiner and Kuhn 2016) in highlighting the need to develop a robust theoretical framework that integrates the models and expectations of OFT and NCT to examine the mutualistic and long-term dynamics of how humans adapted to and modified their surroundings.

CHAPTER 2:

THE EVOLUTIONARY ECOLOGY OF HUMAN MOBILITY AND SUBSISTENCE

In this chapter, I present the research framework for my dissertation and review its theoretical underpinnings. I apply models derived from evolutionary ecology (EE) and evolutionary developmental biology (Evo-Devo) in order to evaluate the context of and develop major expectations regarding the adaptive changes taking place during the Preceramic period in the highlands of southwestern Honduras. Preceramic foraging populations across Middle America experienced ecological and environmental change, loss of habitat productivity, and demographic growth and expansion, all of which influenced subsistence and mobility decisions (see Acosta 2008; Piperno and Pearsall 1998; Piperno et al. 2017 for reviews of this research).

Existing research has focused on describing these changes rather than explaining the processes and circumstances prior to, during, and following these natural and cultural transformations. This is because Late Pleistocene and Early Holocene archaeological assemblages are extremely rare and highly fragmented. For example, paleoecological data show dense tropical forests expanded across the region following the onset of the Holocene approximately 11,000 years ago, which resulted in a reduction of habitats favorable to large-bodied species including and especially megafauna (Piperno and Pearsall 1998; Piperno et al. 2017). However, these changes did not occur simultaneously across the region, and their timing and impact were dependent on local factors such as altitude, topography, and proximity to coasts (e.g. Correa-Metrio et al. 2013). Moreover, archaeological research across Middle America has identified dietary diversification associated with increased levels of territoriality and reduced residential mobility over time during the Preceramic (Aceituno and Loaiza 2018; Aceituno et al. 2013; Acosta et al. 2018; Dickau et al. 2015; Flannery 1986; Lohse et al. 2006; Prufer et al. 2019). Evidence for human hunting of megafauna is extremely rare in the region, and indicates the earliest known populations already had a broad subsistence base (see Acosta and Perez 2012; Barnosky and Lindsey 2010). In addition, existing studies have not definitively demonstrated if and/or when resource depression, either anthropogenically or environmentally driven, occurred in the neotropics.

The rich and well-dated material record recovered from the El Gigante rockshelter presents a rare opportunity to address this knowledge gap because it provides evidence of both changes in the landscape as well as human behavior during this critical period. Based on previous research at El Gigante, I create a model that shows for the first time that resource depression occurred at this site. I then use other lines of evidence to explore the circumstances that preceded and followed the onset of resource depression in the highlands of southwestern Honduras. My model integrates the approaches and expectations of Optimal Foraging Theory (OFT) and Niche Construction Theory (NCT) to study the long-term contexts and consequences, both positive and negative, of human-environment dynamics, and can test various hypotheses related to the ecological and behavioral changes taking place during the PHT.

2.1 Background to theoretical approaches to the Pleistocene-Holocene Transition (PHT) in Archaeology

The adaptive changes that occurred during the PHT across the globe have long been hypothesized as a direct result of the climatic and ecological changes taking place at this time. This adaptive change was first referred to as the ‘Neolithic Revolution’ by Gordon Childe

(1936), who examined this transition in the Near East. Childe hypothesized that following the end of the Pleistocene humans and animals retreated to ‘oases’ that had been spared the effects of climatic and environmental change (Childe 1935). Close interaction between humans, plants, and animals in these areas as well as competition for limited resources led to the subsequent modification of these environments, from which Childe argued domestication and agriculture arose. Childe’s hypothesis was first tested by Braidwood and others (Braidwood 1951; Braidwood and Willey 1962), who argued that it was environmentally deterministic and not supported by the data, which showed the Near East became wetter instead of drier following the end of the Pleistocene. Instead, Braidwood (1963) argued that the domestication of plants and animals and the development of agriculture were the result of accumulated ecological knowledge on plant and animal resources that spread out from “nuclear zones”, as well as human’s proclivity to experiment.

Binford (1968) built upon the work of Childe and Braidwood and suggested that a warmer and wetter climate and demographic expansion during the PHT created a disequilibrium in human-environment dynamics, resulting in a broadening of the subsistence base, a scenario he called the ‘Broad-spectrum revolution’ (BSR) hypothesis. He argued that changes in the sea-level forced population packing in favorable zones and circumscription stressed the local carrying capacity of environments, resulting in a loss of foraging efficiency and leading populations to expand into previously “marginal” and unoccupied environments (Binford 1968: 328). Importantly, he predicted that this likely occurred in environmentally marginal areas with strong seasonality that were adjacent to more resource-rich landscapes that encouraged a more sedentary lifestyle, namely aquatic environments such as coasts and river valleys. These marginal areas would receive “excess” populations, stressing the local environmental carrying capacity and pushing these populations to develop more efficient ways to obtain food.

Flannery (1969, 1986) evaluated and expanded Binford’s BSR hypothesis using archaeological data, first from the Middle East and later from Mesoamerica. In 1969, he argued population growth in resource-rich ecosystems such as coasts and valleys pushed populations toward more marginal areas. These marginal areas included seasonally dry woodlands where biodiversity was low compared to the neighboring lowlands but where fruit-bearing trees and edible grasses and legumes could grow in relatively dense and predictable stands. Continued demographic growth in these areas depressed environmental carrying capacity and led these populations to consume a wider variety of formerly less desirable but seasonally predictable resources. Demographic packing also led to circumscription and reduced mobility, furthering the cycle of diet expansion and experimentation with other resources, including plants, eventually leading to domestication and agriculture. Flannery revised his model in 1986 following several years of archaeological research on this transition by himself and others (e.g., Hassan 1981). These studies had consistently shown population growth had never been large enough to truly stress environmental carrying capacities, particularly in Mesoamerica. These findings led many to call for revisions to the BSR model. Flannery proposed that environmental changes following the end of the Pleistocene created uncertainty and unpredictability in obtaining resources and that the broadening of the diet and a reduction in residential mobility was a strategy for mitigating this uncertainty while taking into account population circumscription. Under this revised scenario, resource depression and/or high population densities are not necessary precursors for the emergence of the BSR.

The expectations of the BSR hypothesis in Middle America as developed by Flannery (1969, 1986) are as follows: (1) increased climatic seasonality and environmental changes following the end of the Pleistocene led to the establishment of a more heterogeneous landscape composed of plant and animal resources whose distributions varied according to precipitation patterns in the wet and dry seasons; (2) Paleoindian populations continued expanding in size and began exploiting a wider variety of ecosystems as they became familiar with them and their resources, leading to demographic packing of the landscape and eventual circumscription, and; (3) human populations living in more marginal landscapes (i.e. with less abundant and less predictable resources) adopted a variety of behaviors to decrease environmental uncertainty and increase social resiliency, including and especially expanding their diet.

Archaeologists around the world have tested the revised BSR model as proposed by Flannery and the body of evidence accumulated so far largely supports this hypothesis (see Stiner 2001 for a list of sources). By the 1970s, as archaeological datasets grew and following the development of processual archaeology, the expectations of this hypothesis were ripe for testing using models developed in the field of EE (e.g., Keegan 1986). Piperno and Pearsall (1998) applied OFT models to test the BSR hypothesis and develop what I call the plant food production (PFP) hypothesis, which derives from it. This hypothesis predicts that post-Pleistocene environmental changes, namely the expansion of tropical forests, created a landscape with fewer animal resources that pushed human populations to significantly expand their diet and shift the focus of their subsistence systems to the collection and consumption of plants. They argue that this is because plant cultivation is more energetically efficient than hunting and gathering in tropical forests (Piperno 2006, 2011; Piperno and Pearsall 1998; Piperno et al. 2017).

The latest effort to explain post-Pleistocene environmental and behavioral change is based on the tenets of Niche Construction Theory (NCT), developed in the field of evolutionary developmental biology (Evo-Devo; Odling-Smee et al. 2003). The NCT hypothesis makes the following predictions (see Smith 2015, 2016; Zeder 2012, 2016): (1) landscapes with abundant and predictable resources led populations to reduce their residential mobility before the onset of environmental degradation and/or resource depression; (2) long-term use of these landscapes led to the adoption of subsistence strategies that favored the expansion of the diet and the modification of the landscape; this "niche construction" maintained or improved environmental productivity without the need to alter subsistence or mobility strategies. Under this scenario, expansion of the diet and reduction of mobility are the course of action that entails the lowest risk especially in situations in which an investment was already made on the landscape, for example by burning, clearing, or the propagation of certain species. Niche Construction Theory has provided theoretical and methodological tools with which to formally address the interplay of genes, memes (units of cultural transmission), and environments (Odling-Smee et al. 2003). Perhaps most importantly, models developed using NCT allow archaeologists to evaluate human decisions within a broader ecological context that includes their actions and long-term consequences (Piperno et al. 2017; Ready and Price 2021). While the idea that humans modified and constructed the landscapes they utilized and inhabited throughout their evolutionary history is not new (see Piperno and Pearsall 1998), NCT explicitly addresses a theoretical and methodological gap by expanding existing models and theories to include the effects of the transmission of knowledge and the products of human behavior on selection (Laland and O'Brien 2010).

2.2 Human Behavioral Ecology and Foraging Behavior

Human behavioral ecology (HBE) studies the fitness of human behaviors under particular ecological contexts (Bird and O'Connell 2006; Broughton and O'Connell 1999). The most common models employed by HBE proponents – notably diet breadth and patch choice – are derived from Optimal Foraging Theory (OFT), which was first developed by MacArthur and Pianka (1966) to evaluate the choices foragers make in order to enhance their fitness by maximizing the rate of resource or nutrient acquisition. In archaeology, these models are used to examine human behavior in relation to the cultural and environmental contexts of decision-making, and specify the variables that condition forager subsistence and mobility (Hawkes and O'Connell 1992; Hawkes et al. 1991). Several models have been developed under the umbrella of OFT but I will focus on the four models that have the most direct bearing on human mobility and subsistence as related to the testing of the BSR hypothesis: 1) the prey choice or diet breadth model (PreyCM), 2) the patch choice model (PatchCM), 3) central place foraging models (CPF), and 4) the ideal free distribution model (IFD). These models are explicitly reductionist, meaning they are simplified, provide testable hypotheses, and are meant to be heuristic tools, not reflections of particularistic cases or processes. These characteristics make them attractive to archaeologists, who seek to derive clear material expectations from these hypotheses and their implications (Cannon and Broughton 2010; Smith and Winterhalder 1992). These models are based on the assumption that natural selection has favored behavioral traits that maximize an individual's reproductive fitness. In addition, because these models aim to identify correlations between behaviors and ecological contexts, they assume that it is difficult and unnecessary to understand how behaviors were inherited or transmitted – an assumption called the "phenotypic gambit" (Bird and O'Connell 2006; Cannon and Broughton 2010; Stephens and Krebs 1986).

2.2.1 OFT Models in Archaeology

OFT models share a series of key components: (1) all evaluate behaviors in terms of a fitness-related goal, (2) behavioral decisions are evaluated within the context of that goal, (3) trade-offs associated with each decision are all measured, (4) some currency is used to evaluate trade-offs, and, (5) all models specify the constraints that define or limit behaviors under particular circumstances (Bird and O'Connell 2006: 146; Stephens and Krebs 1986: 19). The prey choice model (hereafter PreyCM), also known as the diet breadth model, makes predictions about how foragers select their diet from a range of options. This model assumes that resources are encountered at random on a landscape and that resources can be ranked according to their post-encounter energetic return rate. The latter is determined by the time or energy required to pursue something after it is encountered, processed (butcher, roast, shell, etc.), and consumed (MacArthur and Pianka 1966). High-ranked resources are those that provide a high energetic return rate, often measured in calories per item or calories earned per unit of energy expenditure. Low-ranked resources, conversely, are those that provide a low energetic return rate as a result of increased acquisition and processing costs.

The PreyCM has three central predictions: 1) resources enter and leave the diet in rank order, 2) high-ranked resources are always pursued whenever encountered, regardless of abundance, and; 3) low-ranked resources are not included in the diet as a function of their own abundance but only as a function of the availability of high-ranked resources (MacArthur and Pianka 1966; Stephens and Krebs 1986; Winterhalder and Smith 2000). This means foragers will add resources into their diet in rank order until the average return rate for the diet as a whole begins to decline (MacArthur and Pianka 1966; Stephens and Krebs 1986). For example, if the abundance of high-ranked resources declines, foragers will respond by adding lower-ranked resources into the diet. This will decrease foraging efficiency as lower ranked resources, which are costlier to process, will increasingly be incorporated into the diet (Charnov et al. 1976). Because lower-ranked resources may be more abundant on the landscape but often involve increased acquisition and/or processing costs, foragers will spend more time handling these resources.

The PatchCM is used to predict which resource patches are exploited by foragers in an environment where resources are heterogeneously encountered on the landscape. It can be applied at many different scales including the habitat and landscape. This model posits that foragers select which patches to exploit as a function of the energetic yields of each particular patch measured against the cost (measured in terms of time and distance to the next patch) of moving to a more productive one (MacArthur and Pianka 1966). Similar to the PreyCM, the PatchCM assumes foragers will add patches to their subsistence and mobility strategies in rank order until the average return rate per patch begins to decline.

The Marginal Value Theorem (MVT; Charnov 1976), is often used in association with the PatchCM and is applied to circumstances in which foragers face diminishing returns over time in a particular patch. The MVT predicts when rate-maximizing foragers will leave that patch when the marginal return rate within a patch equals the overall average return rate for a suite of patches within a habitat, including travel costs. The PatchCM when used with the MVT has the following basic predictions: (a) foragers should leave a patch when its energetic return declines and when foraging in another patch will yield higher returns, (b) as the productivity of a habitat increases, foragers will spend less time in one patch, (c) if the costs of travel between patches are low, foragers should spend less time in any one patch (Charnov 1976; MacArthur and Pianka 1966).

CPF models examine how foragers tradeoff transport and travel against processing costs and how this affects which resources foragers will transport for consumption or distribution at a central location (Orians and Pearson 1979; Schoener 1979). These models assume foraging occurs in a radial pattern from a central place strategically positioned to maximize the amount of energy delivered to it. As a result, one of the major variables considered by this model is travel to and from the central place, sometimes measured as the maximum transport distance (MTD), the distance a resource will be carried before energetic returns decrease or become negative (Jones and Madsen 1989; Madsen et al. 2000). Other variables that need to be considered under this model are the volume and weight of resources to be carried, travel speed, and the cost of resource acquisition. The major predictions of the central place model are that as travel costs increase, foragers will increase field processing time in order to maximize nutrient return per trip taken (e.g., Bettinger et al. 1997; Bird and Bliege Bird 1997; Reeder-Myers 2014; Winterhalder and Kennett 2006).

The IFD model examines forager choices at a broader scale than the patch and is focused on the habitat scale, defined as an area inhabited and colonized by a species and composed of multiple patches (Fretwell and Lucas 1970). Under this model, the rank of a habitat is based on the quality (i.e., rank) and abundance of resources and the degree to which the habitat is occupied and used by populations. The IFD model predicts foragers will occupy habitats in rank order and that a decline in habitat rank will cause groups to move to an adjacent habitat if it is feasible and cost-effective to do so (Fretwell and Lucas 1970). Over time, as populations increase and habitat qualities decrease, increasingly marginal and lower quality habitats are expected to be occupied. A variant of this model, called the Allee principle (Allee et al. 1949) suggests that habitat quality might initially increase rather than decrease with the arrival and growth of populations because of habitat modification or due to economies of scale (Codding and Bird 2015; Kennett et al. 2006; Winterhalder and Kennett 2006). For example, populations are known to affect the availability and distribution of certain resources, such as through the maintenance of early successional stages of forests through fire or clearing, as has been seen in the neotropics (Gnecco and Aceituno 2006; Piperno 2011; Piperno and Pearsall 1998) and Oceania (Kennett et al. 2006).

Each of the models described above make certain assumptions that may not always be applicable. For example, all four models assume foragers have complete information of patch and prey distribution and assume that all prey and patch types are unambiguous and known to the forager. However, if incomplete information or resource ambiguity is assumed, it is predicted that foragers must spend time sampling and recognizing resources or patches before deciding on whether or not they are worth pursuing, creating an additional cost which must be considered. Based on this expectation, stable patches and predictable and easily identifiable resources will lead to reduced sampling and recognition costs, and thus will be ranked higher (Stephens and Krebs 1986).

2.2.2 Archaeological Applications of OFT models

Although OFT was adopted from the field of evolutionary ecology, its application in archaeology has benefitted from the discipline’s study of long-term processes and mechanisms. OFT models require the integration of various lines of quantitative evidence and provide mechanisms and expectations that are easy to operationalize under a variety of different settings, including robust hypothesis-testing, which facilitates the comparison of results and interpretations. OFT models also allow archaeologists to vary the currencies, constraints, and goals of the forager, thus allowing archaeologists to apply them to a variety of cultural and historical contexts and circumstances. Lastly, OFT models allow for the examination of long-term change and the use of multiple scales of analysis, from individual patches to entire habitats or macroregions (Bird and O'Connell 2006; Lupo 2007; Winterhalder and Kennett 2006).

Archaeologists have operationalized OFT models by first defining the currencies with which trade-offs and decisions are evaluated, as well as the various constraints that limit behavioral responses (see for example Bird and O'Connell 2006; Bliege Bird et al. 2009; Codding and Bird 2015; Codding et al. 2010, 2016; Lupo et al. 2020). One of the most critical components of the models described above is the ranking of habitats, patches, and resources, which archaeologists have often assumed is based on the energetic returns of these various choices (Lupo 2007). Moreover, because it is difficult if not impossible to apply actual return rate data to the archaeological record, zooarchaeologists have relied on prey body-size as a reliable proxy for energetic rank when applying the PreyCM (see Broughton et al. 2011; Lupo et al. 2020 for a review of the literature). However, a number of studies continue to show resource ranks are more often based on an evaluation of the risk and energy requirements associated with that resource (see Lupo and Schmitt 2016; see also Lupo et al. 2020 for a comprehensive discussion of this issue). Risk in this case refers to the probability of failure associated with pursuing and acquiring a particular resource relative to others. For example, research shows that ease of capture or prey mobility plays a major role in how resources are ranked by foragers, and that high pursuit costs also lead to higher handling costs, decreasing the post-encounter energetic return of those resources (Lupo and Schmitt 2016; Lupo et al. 2020). As a result, technological advances that alleviate costs of search and capture and reduce the risk of acquiring resources must also be taken into account (e.g., Bird et al. 2009; Jones 2016; Lupo et al. 2020; Lupo and Schmitt 2016; Munro et al. 2016; Stiner and Munro 2011; Stiner et al. 2000).

Previous applications of the PreyCM model to the study of the adaptive changes taking place during the PHT in the neotropics have used ethnographic data to rank resources according to body size (in the case of animals), with megafauna being the highest ranked and plants being the lowest ranked resources. However, plants possess other qualities not reflected in energy that make them more valuable. For example, seeds and grasses are usually lower-ranked because of high search and processing costs but the former decrease significantly in cases where these resources are super abundant, reliable, and renewable on the landscape, as in for example dense stands of teosinte, the wild antecessor to maize (Piperno and Pearsall 1998). In addition, plant resources such as seeds and nuts are also storable, unlike meat, which can confer an added value on some resources making them higher ranked than their return rates based on energy suggest (Piperno and Pearsall 1998; Piperno et al. 2017). Related to the above, a review of return rates for both horticulture and foraging practices in neotropical forests by Piperno and Pearsall (1998) indicates horticulture provides a much higher energetic return (but see Barlow 2002). These authors argue that this was linked to a decrease in the abundance of high-ranked prey (i.e., animals, including megafauna) following the PHT expansion of dense tropical forests that were less hospitable to these species.

Archaeologists have also operationalized the key components of the PatchCM. For example, there is ample evidence that patches or environments with dense distributions of high-ranked prey resulted in high levels of residential mobility by foraging groups that habitually exploited these over time (e.g., Andrews et al. 2008; Surovell 2009). Archaeologists studying the adaptive changes that took place during the PHT have also examined the expectations of the

PatchCM related to behavioral responses to resource depression (Piperno and Pearsall 1998). Most of these studies have argued that external forces such as climate change and demographic pressure led to resource depletion and demographic packing and forced foraging groups to expand their diet to include lower-ranked items, including small animals and edible plants, and become increasingly sedentary. As I discussed above, major climate changes following the end of the Pleistocene in the neotropics caused the expansion of tropical forests depauperate of animal resources, which required foragers to seek alternative sources of fat and protein (Gremillion and Piperno 2009; Piperno 2006; Piperno and Pearsall 1998). This resulted in increases in search time for high-ranked prey and consequently in broader diets, followed by a reduction in residential mobility and increased experimentation with practices of landscape modification and plant propagation (Aceituno et al. 2013; Dickau et al. 2015; Piperno 2011; Piperno and Pearsall 1998).

The expectations set forth by the CPF overlap in several ways with those of the prey and patch choice models, particularly regarding optimal central place location. It can be argued that archaeological sites located at the confluence of resource rich areas, such as in ecotones, are central places that allow for the maximization of nutrient returns, which explains why most of these sites are re-occupied extensively over time. Single activity sites such as kill sites have been interpreted as being representative of resource procurement under a central-place subsistence strategy, and the degree of carcass processing is seen as indicative of proximity to the central place or camp, or transport costs (Andrews et al. 2008). Proximity to the central place thus conditions the degree of carcass processing, and distance to a central place must be taken into account in addition to time invested in processing, energetic return, and resource abundance.

The application of models derived from OFT by archaeologists to the study of forager subsistence and mobility has clearly been and continues to be a valuable and productive endeavor. The clarity and simplicity of the models being utilized has facilitated the development and evaluation of various hypotheses and their implications against the archaeological record. However, subsequent theoretical and methodological advances in evolutionary ecology, population genetics, and archaeology have suggested that these models do not fully capture the complex dynamic between human culture, genetics, and their environment. These limitations have been addressed first by gene-culture coevolutionary theory (GCT).

2.3 Gene-Culture Coevolutionary Theory (GCT) in Archaeology

GCT, also known as ‘dual inheritance theory’ or simply ‘coevolutionary theory’, studies the effects of cultural and genetic transmission on evolutionary processes and aims to understand the various conditions under which cultural transmission occurs (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981). GCT was developed from models of population genetics and in response to perceived inadequacies of HBE and OFT, namely the lack of treatment of cultural transmission, cultural evolution, and human agency (Durham 1976a, 1976b). GCT proponents argue that by relying on the phenotypic gambit, OFT models treat culture as just another aspect of the human phenotype, whose expression is probabilistically influenced by selective pressures on genes (Durham 1991). The GCT framework sees culture as transmissible and postulates that genes and culture are two independent systems of information inheritance with the potential to influence behavior and drive evolution, social and biological (Boyd and Richerson 1985; Durham 1991). GCT further posits that because humans are biological and cultural organisms subject to selection and decision making, cultural traits can be transmitted and inherited in nonrandom ways and can affect behavior and fitness independently from genes (Boyd and Richerson 1985; Durham 1991). Lastly, GCT suggests that the transmission of cultural traits is a function of genotype, culture, and the environment; the selection of a particular behavior is a function of its inclusive fitness benefits, measured by the cost of time and energy expended to carry it out (Durham 1976a).

Expectations derived from GCT have direct implications for the OFT models reviewed earlier. If cultural transmission and cultural evolution are inserted into the PreyCM and PatchCM, then humans are given a much larger role in reacting to selective pressures through the persistent transmission and adoption of cultural traits, whether these are fitness enhancing or not. Yet despite these advantages, archaeologists have not operationalized GCT nearly as much as models of OFT, perhaps given the increased complexity of defining the various material correlates of cultural transmission and cultural evolution. However, GCT makes various predictions regarding the primacy of certain modes of transmission under particular environmental contexts and circumstances. First, just as the PatchCM predicts that stable patches are higher-ranked and thus make decreased mobility favorable, GCT predicts these behaviors lead to the development of cultural traditions – defined as persistent cultural traits that have been transmitted over time and which enhance a group's selective fitness. These traditions are the result of groups gaining detailed knowledge about a particular patch and its resources as a function of the time spent there (Boyd and Richerson 1985). However, cultural *transmission* occurs irrespective of patch quality, and it can thus be predicted that the persistence of certain behaviors such as the consistent utilization of certain resources can eventually lead to the deliberate or accidental intensification of plant-animal mutualistic relationships (Rindos 1996). Cultural transmission and the persistence of certain behaviors – such as intentional resource management – can result in certain resources becoming more predictable, thus increasing their dietary rank and their abundance in the diet, as predicted by the PreyCM. Given these expectations, external factors such as climate change or population pressure do not necessarily drive reduced mobility (though they can), particularly when this change is associated with increased investment in a particular environment.

By introducing cultural inheritance as a second inheritance system in human evolution, GCT suggests that acquired characteristics have a direct bearing on evolutionary processes. This acknowledges that humans have a cultural history and cumulative and inherited knowledge, which allows them to make more informed decisions regarding not only which patches and resources will be exploited, but how they will go about doing so. One of these behaviors is the capacity to modify their environments in an effort to increase their fitness and transmit this information and its associated behaviors over time, a point that is expanded upon by niche construction theory (NCT), which I review below.

2.4 Niche Construction Theory in the Context of other NeoDarwinian Approaches

NCT builds upon and complements OFT and GCT by recognizing organisms' ability to modify their environments and the selective pressures that influence their behavior, and by accounting for mechanisms of genetic, cultural and environmental inheritance (Odling-Smee et al. 2003). Under this theory, the environment is not just the static backdrop and enforcer of evolution through natural selection but is itself influenced by the behavior of organisms. In terms of its impacts on human evolution, the introduction of a third system of inheritance – ecological inheritance, which parallels genetic and cultural inheritance –, leads to new selective pressures, which may drive new cultural or evolutionary changes, thus perpetuating a system of feedbacks in which selection pressures are intimately connected to adaptations (O'Brien and Laland 2012; Odling-Smee et al. 2003). Ecological inheritance refers to the biological and non-biological changes made by niche-constructing organisms that affect selection pressures on populations that inherit them. While OFT models and GCT allow for the possibility of habitat modification and its role in adaptive responses to changing natural and anthropogenic circumstances (see Codding and Bird 2015; Gremillion et al. 2014; Piperno et al. 2017), NCT is more explicit in its treatment of the persistent and long-term use of particular environments by humans, and how this promotes the acquisition and transmission of knowledge and skills necessary to anticipate or dampen environmental variability and unpredictability.

Niche construction can take several forms (1) perturbation, or the active modification of less suitable environments; (2) relocation, which involves the migration of an organism to a new environment which it subsequently modifies; (3) it can be initiated by an organism in order to improve its inclusive fitness, or; (4) be the result of a response to a change in its environment. Furthermore, niche construction can be positive or negative, meaning it can result in the increase or decrease of an organism's fitness, respectively. Given the tenets of GCT, CNC is knowledge-based, active, and proactive, and results in an inheritance system which is an intermediary between genes and culture (O'Brien and Laland 2012; Odling-Smee et al. 2003). Lastly, CNC produces two types of responses: culturally adaptive responses and naturally or genetically adaptive responses. Culturally adaptive responses can be tracked by archaeology, since these include material culture as part of humans' ecological inheritance (Odling-Smee et al. 2003). Identifying long-term evolutionary change resulting from CNC in the archaeological record is much more difficult and complicated because it requires both evidence of CNC and CNC-driven genetic change, both of which remain rare in the literature (though see Laland and O'Brien 2010; Odling-Smee et al. 2003; O'Brien and Laland 2012 for examples).

Yet despite its utility in drawing attention to the dynamic nature of human-environment-genetic interactions and to the long-term consequences of short-term foraging decisions – the focus of OFT models (see Stiner and Kuhn 2016 for a discussion of the multi-scalar interactions between OFT and NCT) – NCT remains a largely descriptive and heuristic framework rather than an explanatory or predictive one (Gupta et al. 2017; Wallach 2016). For example, archaeologists have employed NCT to adequately describe scenarios in which humans modified their surroundings and created long-term feedbacks (positive or negative) on plant and animal resources (e.g., Bird et al. 2016; Broughton et al. 2010; Zeanah 2017). However, these applications of NCT make no predictions or explanations as to why CNC behaviors occurred where and when they did (Piperno et al. 2017; Wallach 2016). In addition, critics of NCT rightly point out that most of the claims made by its proponents, including the role of landscape modification on the adaptive changes taking place during the PHT, were already made under the umbrella of OFT and GCT, albeit under a different name (e.g., Piperno et al. 2017; Wallach 2016). As a result, the utility of NCT to archaeologists remains limited. This framework certainly highlights the role human agency played in long-term adaptive processes such as domestication and agriculture and helps bridge the short-term human-environment dynamics examined by OFT and GCT and their long-term effects.

2.4.1 Archaeological Applications of NCT

The tenets of NCT fit within the expectations and constraints of other models from OFT and GCT, and the cultural and natural expectations put forward by this approach can be and have been operationalized by archaeologists. First, positive niche construction necessitates previously acquired knowledge of the niche in question and is only expected to occur in localities that have been persistently used by humans for extended periods of time if it is to have a selective impact. Under these circumstances, positive niche construction can be a conscious effort by human populations to dampen environmental variability and unpredictability (Laland and O'Brien 2010). There is ample archaeological evidence for the long-term persistent use of and familiarity with particular landscapes and resources, and under conditions of no migration or diffusion the development of niche construction behaviors is usually gradual and cumulative rather than abrupt (see Smith 2007, 2011a for a review of some of this literature).

Recent archaeological research has also focused on positive niche construction as an alternative response to resource depression (see Zeder 2012 for a detailed overview). If resource depression occurs, NCT predicts that foragers will modify the habitat in order to increase patch stability and resource predictability, reduce search and handling costs, and increase prey and patch rank as defined by OFT models (Bird and O'Connell 2006; Laland and O'Brien 2010; Odling-Smee et al. 2003). This approach has been applied to examine how populations modified landscapes in order to reduce search or handling costs associated with preferred prey, which would increase patch quality and promote longer stays (Bliege Bird et al. 2013; Codding and Bird 2015). For example, some groups in the neotropics modified the availability and distribution of key resources such as palms and fruit trees through patch burning to maintain early successional stages during the Preceramic period (Acosta et al. 2018; Gnecco and Aceituno 2006; Piperno 2011; Piperno et al. 1990, 2017). Under the NCT framework, populations respond to resource depression by carrying out additional niche construction, which can sometimes result in the adoption of more intensive food production strategies, such as agriculture (Laland and

O'Brien 2010). Lastly, NCT also predicts that when populations are unfamiliar with a particular niche and its resources, niche construction behaviors imported from different contexts can have deleterious effects such as resource depletion and the translocation of foreign species that disrupt local foodwebs, which affects patch return rates and subsequently diet breadth and mobility (Broughton et al. 2010; Christensen and Weisler 2013; Dixon 2015).

The framework of NCT complements models developed under OFT and GCT by re-examining the habitats, patches, and preys they refer to as the result of past human actions and decisions. In this way, NCT provides a more detailed understanding of the ecological context in which subsistence and mobility decisions evaluated by OFT and GCT are made. However, NCT does not directly address how and why and in what circumstances or conditions humans alter their subsistence and mobility behaviors or why they construct niches, and as such must rely on the expectations of OFT and GCT to make these predictions and interpretations (Codding and Bird 2015; Gremillion et al. 2014; Mohlenhoff et al. 2015). As a result, NCT, OFT, and GCT are inseparable and must complement each other if we are to more fully understand how human-environment relations changed over time.

2.5 A Theoretical Model for Evaluating the Context of Broad-Spectrum Revolution in the Neotropics

All major behavioral transitions in human history are a result of complex dynamics between humans and their socio-ecological surroundings, none more so than the transition away from a foraging way of life, which defined most of our evolutionary history. Applications of NeoDarwinian theories and models are the most recent and robust effort by archaeologists to parse these dynamics and evaluate each of their individual components against archaeological and paleoenvironmental data. Perhaps most importantly, and contrary to recent claims (Smith

2011a, 2011b, 2015, 2016; Zeder 2012, 2015, 2016), OFT and NCT are not mutually exclusive approaches, and when combined may improve our understanding of the economic and environmental dynamics taking place during the Preceramic period in the neotropics (Freeman et al. 2015; Gremillion et al. 2014; Mohlenhoff et al. 2015; Piperno et al. 2017; Ready and Price 2020; Stiner and Kuhn 2016).

Our understanding of Preceramic environmental and human adaptive changes in the neotropics is based largely on paleoecological studies and a small number of archaeological sites and material assemblages, which I summarize in the following chapter. This dearth of archaeological evidence is due to a lack of sustained research into this time period and neotropical taphonomic processes – such as weathering due to the extremely waterlogged and acidic soils of the region – that significantly impact the preservation of materials necessary to evaluate changes in diet and mobility, namely animal bones and macrobotanical remains.

Thus far, only five archaeological sites have yielded faunal materials dated to this time period (see Table 2.1): the Guila Naquitz and Cueva Blanca caves of the Tehuacan Valley (Flannery 1986; Flannery and Hole 2019), the Santa Marta cave in the Central Depression of Chiapas (Acosta 2008, 2010; Acosta et al. 2018; Eudave 2008; Solis-Torres et al. 2020), Mayahak Cab Pek cave in Belize (Orsini 2016; Prufer 2018; Prufer et al. 2019), and the El Gigante rockshelter in southwestern Honduras (Figueroa and Scheffler 2021; Kennett et al. 2017; Scheffler 2008; Scheffler et al. 2012).

Table 2.1 Extant Preceramic Faunal Assemblages from Middle America (data obtained from Eudave 2008; Flannery 1986; Flannery and Hole 2019; Orsini 2016; Scheffler 2008).

Site	**Total (approx.)**	**Identifiable**
Maya Hak Cab Peck	1,051	337
Guilá Naquitz	500	360
Cueva Blanca	1,051	389
Tehuacan Valley (several sites)	8,000	4,713
El Gigante	60,000	7,560 (estimate)

El Gigante is unique among these due its large, well-preserved, and well-dated macrobotanical and faunal assemblages dating from ca. 11,010-980 cal B.P. El Gigante thus offers a unique opportunity to examine Preceramic human-environment dynamics in Middle America.

In order to examine these adaptive changes at El Gigante, I am evaluating existing hypotheses developed to explain the timing and sequence of climatic, ecological, and economic changes that unfolded during the Preceramic as well as the processes and contexts that precipitated them. I do so by integrating the expectations of OFT, GCT and NCT with our existing knowledge of ecological and behavioral changes taking place both at El Gigante and in Middle America in general during the Preceramic period. Niche construction, for example, can lead to changes in an ecosystem that can restructure the rank of patches and resources and affect the behaviors that are considered the most optimal according to each model. In addition, niche construction is a response to environmental variation and unpredictability as a result of climatic of anthropogenic perturbations, a factor that has not received enough attention to date and which also has significant impact on the expectations of OFT models (see Ready and Price 2021; Stiner and Kuhn 2016).

Existing hypotheses developed to explain PHT changes are predicated on the interplay of four key processes: (1) climate and environmental change; (2) a loss of foraging efficiency and concomitant resource depression; (3) changes in forager subsistence and mobility; (4)

anthropogenic landscape modification (i.e., niche construction). I will first determine whether these processes occurred at El Gigante and its surroundings by examining the site's faunal and sedimentary assemblages and combining my results with those of existing and ongoing studies of the shelter's macrobotanical and lithic assemblages (Figueroa and Scheffler 2021; Scheffler 2008; Scheffler et al. 2012). I then disentangle the sequence in which these processes unfolded during the Preceramic period at this site. The critical variable of the proposed study is thus the chronological order in which cultural and natural changes happened, and our key archaeological goals are to evaluate each change independently and when they took place in order to obtain a better understanding of the consequences and potential feedbacks among these processes. By integrating OFT, GCT, and NCT, this dissertation also adds to our knowledge of the factors and contexts that preceded the PHT adaptive changes in the region, while also building on and evaluating recent advances regarding the mutualistic and long-term nature of human-environment relationships in the neotropics and beyond. When applied to the material assemblage of El Gigante, the expectations of existing hypotheses are as follows:

Hypothesis 1 (based on the BSR model): A decline in residential mobility occurred prior to environmental change at El Gigante taking place during the Early Holocene. This was followed by a loss of foraging efficiency and resource depression, and its inhabitants adapted by utilizing the local landscape more intensively.

This hypothesis assumes foraging populations were unable (or unwilling) to relocate to other habitats either because these were already populated or because these patches were also not as productive (Broughton et al. 2010; Charnov 1976; Stiner et al. 2012). Because populations did not relocate, they began to use El Gigante's landscape more intensively, possibly leading to the overhunting of high-ranked prey, an increase in within-bone nutrient extraction behaviors, and the expansion of the diet. Testable implications for this hypothesis include:

- Evidence for the loss of residential mobility during the earliest occupations of the shelter, including evidence for an increase in the use of the shelter and the utilization of local sources of stone
- Evidence for climatic and environmental change after a decrease in residential mobility
- Continuous decline in the abundance of high-ranked prey in the faunal assemblage following evidence for environmental degradation
- Continuous increase in diet breadth, indicated by an initially low richness and diversity of the faunal assemblage that increased over time
- Higher-utility portions of hunted prey are abundant at first but over time larger proportions of each carcass are transported to the site as prey is exploited more intensively
- Overhunting of high-ranked prey, including the capture of younger individuals with no/slight changes in body size (as more forage becomes available to surviving prey) and/or more intensive and extensive exploitation of carcasses for the extraction of marrow and/or grease

Hypothesis 2 (based on the PFP model): Climatic and environmental change occurred during the Early Holocene at El Gigante, causing a loss of foraging efficiency and resource depression, and its inhabitants adapted by expanding their diet and actively modifying the landscape to improve the distribution and predictability of desired resources.

This hypothesis assumes that El Gigante's Preceramic inhabitants responded to resource depression by modifying their surroundings in order to decrease the cost of searching for high-ranked prey and increase the abundance and thus reduce the handling costs of acquiring plant resources. This hypothesis is supported by archaeological and paleoenvironmental research in Panama and Colombia (Gnecco and Aceituno 2006; Piperno 2011; Piperno et al. 1990), where it is believed that anthropogenic niche construction aimed to recreate natural openings or 'gaps' (Richards and Coley 2007) in the tropical forest in order to increase the availability of forage available to high-ranked prey that thrive in early successional environments, such as deer (Whitaker 2009: 99).

The creation and maintenance of early successional forests is also supported by prior research at El Gigante, which suggests that avocado trees (*Persea americana* var. *guatemalensis*) were directionally selected in order to increase their energetic yield (Figueroa and Scheffler 2021; Scheffler 2008, 2014). Avocado trees are "small-gap specialists" (Wolstenholme and Whiley 1999: 9) and thrive in early successional habitats such as those following tree falls, selective clearings, or burns. The long-term selection of fruit trees such as avocado would have elevated the rank of these resources by making them more predictable and abundant in particular patches, leading to decreased search times, which would have made longer stays at El Gigante possible and even advantageous. Alternatively, the clearing and/or burning of forests for the maintenance of early successional stages to improve the search costs of animal prey could have had the unintended result of favoring the growth and spread of "gap specialists" such as avocados. This hypothesis has the following testable implications:

- Evidence for climatic and environmental change beginning during the initial occupation of the shelter

- Decline in the abundance of high-ranked prey (i.e., deer) that precedes evidence for anthropogenic landscape modification, followed by a recovery in the abundance of these populations, including a consequent increase in age and increase in body size, as more forage became available to these populations
- Initial decrease in landscape patchiness (climate driven), which then increased (following resource depression) as foragers created artificial gaps through burning or clearing
- Continuous but slight increase in diet breadth over time
- Continuous and intensive occupations of the rockshelter
- Longer and more intensive occupations of the shelter later in time driven by labor investments in habitat modification (costs) as well as increased abundance in preferred resources (benefits).

Hypothesis 3 (based on the NCT model): Behavioral change in SW Honduras (mobility, subsistence, and niche construction) occurred independent of environmental degradation and resource depression and drove changes in subsistence and mobility during the Preceramic period.

This hypothesis suggests that the behavioral changes associated with the PHT occurred not as a response to resource depression but as a result of environmental advantages offered by human modification of the landscape (*sensu* Smith 2011a, 2011b, 2015, 2016; Zeder 2012, 2015, 2016). This hypothesis predicts that the Preceramic landscape surrounding El Gigante had abundant and predictable resources, which allowed its inhabitants to develop and sustain a broad diet, making decreased mobility more advantageous during the earliest occupations of the shelter. Lengthier occupations of the shelter over time allowed foragers to accumulate traditional ecological knowledge and practice behaviors that increased the productivity, abundance, and/or predictability of particular resources through niche construction or landscape modification (Smith 2011a: 267; Zeder 2012: 259). Longer human occupation of the habitat surrounding El Gigante would have also created an anthropogenic environment that favored plant and animal resources that thrive in disturbed environments, including white-tailed deer (Odocoileus virginianus) and avocado. This hypothesis also predicts that knowledge of the environment allowed El Gigante's inhabitants to mitigate landscape degradation (either purposefully or unintentionally), through the maintenance of open and disturbed areas, although resource depression could have occurred later as a result of population packing, population growth, or climate change (Zeder 2012). This hypothesis is partially supported by previous research at El Gigante, which suggests that the site's Preceramic inhabitants already had a broad diet in the Early Holocene (Scheffler 2008). This hypothesis has the following testable implications:

- Diet breadth is initially broad and remains broad throughout the Preceramic, as populations took advantage of abundant and predictable resources near the shelter
- Continuous and intensive occupations of the rockshelter
- Evidence for anthropogenic niche construction, in the form of sustained landscape patchiness, that precedes any evidence of environmental change, loss of foraging efficiency, and resource depression and is penecontemporaneous with decreased mobility, as noted above

Although the above hypotheses and their material expectations help guide my research, they are by no means the only possible scenarios in which Preceramic human-environment dynamics unfolded in the region. By focusing my research on identifying the presence, timing, and sequence of the four key processes purportedly taking place at this time (environmental change, foraging efficiency and resource depression, changes in diet and mobility, and landscape modification), my research model is able to propose new hypotheses not accounted for by existing data. El Gigante is unique in the region because of its large, well-preserved and well-dated assemblage spanning the entirety of the Preceramic, and its study can contribute to establishing a more robust evidence-based baseline from which to evaluate the environmental and behavioral changes taking place at this time in Middle America and beyond.

CHAPTER 3:

THE PALEOCLIMATIC, PALEOECOLOGICAL, AND ARCHAEOLOGICAL CONTEXT OF THE BROAD-SPECTRUM REVOLUTION IN MIDDLE AMERICA

In this chapter, I situate my research, as well as other research conducted at El Gigante, within the broader study of the ecological and behavioral changes taking place during the Pleistocene-Holocene Transition (PHT) in Middle America, the geographic area that spans from central Mexico to Panama (Figure 3.1). Paleoenvironmental and paleoclimatic research has highlighted the diverse and multi-scalar nature of the climatic and environmental changes that occurred following the end of the Pleistocene which are believed to have played a significant role in the subsistence and mobility decisions made by human foragers at this time. Archaeological work in this region has also identified many of the behavioral changes associated with this transition including an expansion of the diet and an increase in the intensity and length of use of particular landscapes and localities (e.g., Acosta et al. 2018; Flannery 2009, 2019; Orsini 2016; Piperno et al. 2017). This research also highlights the myriad ways in which human populations occupied, modified, and were impacted by their surroundings, and how these behavioral changes were not uniform in time or space in Middle America and were instead mediated by local landscapes and resources and the mutualistic interactions between these and the human populations that inhabited them. Critically, existing explanations for the processes that drove behavioral change during the Preceramic rely almost exclusively on macrobotanical datasets, and little is known about the role faunal resources played at this time (Flannery 2009;

Piperno et al. 2017). This dissertation helps balance our understanding of the natural and anthropogenic changes taking place during the PHT by integrating the analysis of a large faunal assemblage and a limited number of sediment saples with the lithic and macrobotanical data thus far collected at the El Gigante rockshelter.

Figure 3.1 Colored and shaded relief topographic satellite image of Middle America (NASA/JPL/NIMA 2002).

A review and synthesis of the ecological and behavioral changes that have been documented in the region before and during the Preceramic period (13,000-7000 cal B.P.) contextualizes the various hypotheses I evaluate in this dissertation, as well as the interpretations of the results. A synthesis and review of this body of knowledge assists me in addressing the major goals of this dissertation by helping me make inferences about the environment and climate of southwestern Honduras during the Preceramic period and delimit the types of habitats and resources available to El Gigante's Preceramic inhabitants. This review also helps identify the range of subsistence and mobility behaviors practiced by foraging populations elsewhere in the region during this time and helps constrain the expectations for each of my hypotheses.

My review of existing paleoecological and paleoclimatic studies indicates that, similar to other seasonally dry highland forests in Middle America, the topographic and altitudinal heterogeneity of the highlands of southwestern Honduras (from 650-2,100 m asl within <50km) helped buffer an increase in moisture and temperature that took place beginning in the Terminal Pleistocene (see Correa-Metrio et al. 2013; Harvey et al. 2019). High topographic diversity supported significant environmental heterogeneity and biodiversity for a longer span of time and favored a wide variety of plant and animal species, some now extinct, that used this landscape as a refugium from areas more strongly impacted by these climatic and environmental changes. Elsewhere in the region, environmental heterogeneity in the midst of less favorable environments made human occupation and re-occupation of such landscapes advantageous (Piperno and Pearsall 1998; Piperno et al. 2017).

A review of the archaeological studies focused on the behavioral changes taking place during the PHT in Middle America (Acosta 2008; Flannery 2009, 2019; Orsini 2016) demonstrates that the core expectations of resource depression and reduced habitat productivity following the end of the Pleistocene (see Piperno and Pearsall 1998; Piperno et al. 2017) have never been evaluated because the archaeofaunal records necessary to test this have not yet been recovered or analyzed with this goal in mind. The recovery of a rich and well-dated faunal assemblage from El Gigante addresses this gap in our knowledge, although its analysis needs to be part of a broader examination of the entire material assemblage at the site, including lithic and macrobotanical materials. Existing analyses of these data point towards major adaptive changes taking place between the Early Esperanza and Middle Marcala phases (11,010-7430 cal B.P.) at the site and correlate well with patterns identified elsewhere in Middle America: namely, a diversification of the diet and a reduction in residential mobility over time. However, evaluating the critical expectations of whether or not resource depression and a reduction of habitat productivity occurred and how these processes impacted human behavior are the central goals of this dissertation.

3.1 The Late Pleistocene and Early Holocene Paleoenvironment and Paleoclimate of Middle America

The first neotropical forests that human populations encountered during their southward migration were located in central Mexico and, as stated by Piperno (2011: 193), "moving through southern Central America and entering South America without encountering and living in a forest some of the time may not have been possible." As a result of earlier interactions with these environments, populations moving south, including those that came to inhabit El Gigante, would presumably already have a large body of accumulated ecological knowledge (see Meltzer 2009).

Paleoecological research indicates that millennial-scale changes in temperature and humidity including higher temperatures and increased precipitation in Middle America were driven in large part by changes in insolation, increasing atmospheric CO_2 and other greenhouse gases, and pronounced seasonality at the end of the Pleistocene and onset of the Holocene (Figure 3.2). These global climate drivers were mitigated at the century-scale by proximity to glaciers – such as those located in the Basin of Mexico – and oceans and topographic and altitudinal heterogeneity (Caballero et al. 2019; Correa-Metrio et al. 2013; Lachniet et al. 2013; Lozano-Garcia et al. 2015; Metcalfe et al. 2015). Broadly, this work indicates that the Pleistocene-Holocene transition was characterized by a time-transgressive shift that began at the Last Glacial Maximum (ca. 23,000 cal B.P.) with dry and cold conditions and ended with wet and warm conditions comparable to those of the present appearing by the Middle Holocene (ca. 5000 cal B.P.; Correa-Metrio et al. 2012, 2013; Hodell et al. 2000, 2008; Markgraf 1989; Schmidt et al. 2004). Some of the mountainous highlands of the region experienced lower rates of climatic and ecological change and led to the creation of microrefugia in places with particularly high levels of biodiversity and endemism that remained stable despite high temperature fluctuations, highlighting the capacity of heterogeneous habitats to survive abrupt climate change (Caballero-Rodriguez et al. 2018; Correa-Metrio et al. 2013; Gomez-Perez and Carbot-Chanona 2012; Perez-Crespo et al. 2015; Piperno and Jones 2003).

Throughout Middle America local variability in elevation and topography affected the kind, degree, and rapidity of climatic and environmental change. In Central Mexico, a region characterized by the mountainous Trans-Mexican Volcanic Belt (TMVB), paleoenvironmental and paleoclimatic data obtained from lacustrine and terrestrial records indicate cold and dry conditions during the glacial and Terminal Pleistocene periods, including the LGM. This was followed by a wet deglacial period (19,500-11,500 cal B.P.) during which various lakes and other wetlands were created in this region (Almeida-Lenero et al. 2005; Caballero et al. 1999, 2010, 2019; Correa-Metrio et al. 2013; Ortega et al. 2010; Solleiro-Rebolledo et al. 2006, 2011).

Recently available paleontological evidence from the TMVB suggests that the development of these wetland and lacustrine environments was particularly attractive to large Pleistocene mammals, which in some cases became mired and were easily hunted and scavenged by early human populations inhabiting this area (Metcalfe et al. 2007: 321). These data also show a transition from a highly seasonal environment in which smaller lakes would freeze in the winter and thaw in the summer, to less seasonality during the Holocene (ca. 10,000 cal B.P.). Sites on the western and eastern fringes of the TMVB show some variability in these patterns (Bradbury 2000; Metcalfe et al. 2007). Researchers believe that these differences are due to proximity to oceans, changes in sea surface temperatures, and corresponding ocean and wind currents, which resulted in variable amounts of moisture received throughout the region at this time (Caballero et al. 2019; Lachniet et al. 2013; Lozano-Garcia et al. 2015; Metcalfe et al. 2015).

Research south of the TMVB along the southern margin of the Sierra Madre del Sur indicates a complex interplay between moisture sources in the Caribbean and the Pacific that were affected by sea surface temperatures and the ITCZ (Bernal et al. 2011). For example, at Juxtlahuaca Cave, oxygen isotope analysis of a speleothem suggests an active North American Monsoon during the LGM indicative of wet conditions at this time in the south, followed by a weakening of the monsoon until 11,600 cal B.P., when it strengthened again (Lachniet et al. 2013). Similarly, in the Central Balsas watershed on the interior side of the Sierra Madre del Sur, the late glacial period presented similar patterns of temperature and moisture change as the TMVB (Piperno et al. 2007). Between 13,000 and 10,000 cal B.P. this area experienced substantial increases in temperature and precipitation that resulted in an expansion of lowland tropical forests and refilled lake beds, which became natural “magnets” for human and non-human populations (Piperno et al. 2007).

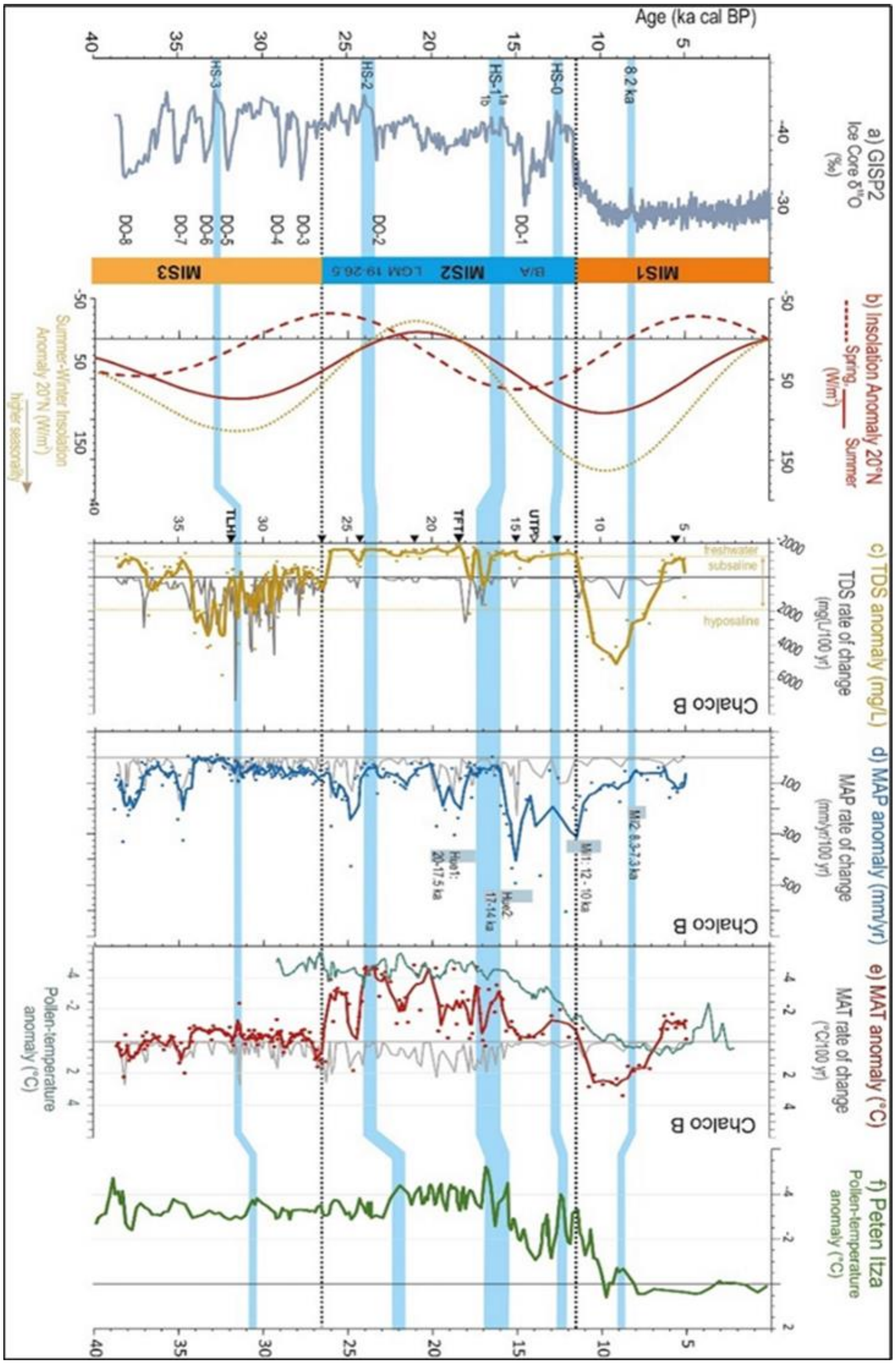

Figure 3.2 Synthesis of relevant climate change proxies for Middle America. A) d18O record from the Greenland Ice Sheet Project (GISP2) Ice core; b) summer-winter insolation anomalies at 20oN latitude; c-e) total dissolved solids (TDS), mean annual precipitation (MAP) and mean annual temperature (MAT) anomalies and rates of change inferred from diatom assemblages analyzed from the Lake Chalco and temperature anomalies inferred from the pollen assemblage at Lake Chalco; f) temperature anomalies inferred from the pollen assemblage from Lake Peten-Itza in Guatemala (Caballero et al. 2019: Figure 7).

Most important for this research study, evidence of fruit bearing trees in the area first appeared approximately 13,600 cal B.P. as part of an expansion of forest extent and diversity in the area. During this time, seasonal dry forests became the dominant ecosystem in the Central Balsas. This study also documented a major shift in vegetation and charcoal content at approximately 7200 cal B.P., interpreted as the onset of widespread anthropogenic landscape modification in the area, including an increase in anthropogenic fire frequency and forest clearing.

Variability in the climates and environments in the highlands also led to the creation of microrefugia throughout the region. In the Central Depression of Chiapas in southeastern Mexico, multi-proxy studies suggest that during the terminal glacial period the vegetational community in the area combined elements from mesophilic, evergreen, and deciduous forests, including fruit-bearing trees from medium and high-altitude forests (Acosta et al. 2018; Eudave 2008; Gonzalez 2015). The Holocene was characterized by a much warmer and drier climate and a vegetational change towards tropical and deciduous forests with much higher levels of biodiversity (Acosta et al. 2018). An analysis of stable carbon and oxygen isotopes from the bones of extinct fauna within various localities in the Villaflores municipality in the Central Depression of Chiapas confirms an open forest-savannah mosaic dominated this area during the Pleistocene-Holocene transition, and may have served as a refugium for megafauna at this time (Gomez-Perez and Carbot-Chanona 2012; Perez-Crespo et al. 2015). Similarly, a review of existing data on extinct equids and mammoths in southern Mexico suggests certain species survived until 12,000 cal B.P. in Chiapas as relict populations in isolated refugia islands created as a result of the expansion of tropical forests in the lowlands (Jimenez-Hidalgo et al. 2019; Perez-Crespo et al. 2012). Much further south, along the Pacific foothills of eastern Panama, paleoecological research suggests that high topographic variability, despite an overall low altitude (<1000m asl) allowed mesic plants, including fruit-bearing trees, to survive in microrefugia, from which they later spread as the climate became warmer and wetter after approximately 11,400 cal B.P. (Piperno and Jones 2003).

Additionally, these studies suggest that the Holocene had a much more variable climate in areas within the highlands with elevations between 2,000-2,500m asl (Caballero-Rodriguez et al. 2018). However, lowland areas with elevations under 2,000m asl likely experienced much higher levels of vegetation turnover following the end of the Pleistocene due to higher species diversity and topographic homogeneity, which led to more widespread change. Areas with elevations between 2,000 and 2,500m, which have a more varied topography, maintained more stable vegetational communities well into the mid-Holocene, which helped modulate the effects of climate change by creating refugia-like conditions (Caballero-Rodriguez et al. 2018). Topographic variability is worth highlighting, given that this is the type of landscape that characterizes the highlands of central and southwestern Honduras, which have high altitudinal variability packed within a limited geographic area.

In contrast to the high environmental variability of the highlands, the lowlands of Middle America experienced widespread climatic and environmental changes at a greater speed and over a much larger spatial extent than in the highlands (Correa-Metrio et al. 2013). A comparison of the Peten-Itza record with that recovered from Lake Chalco in the TMVB suggests temperature changed almost twice as fast in the lowlands than in the highlands (Correa-Metrio et al. 2013). This difference highlights the role of topographic and altitudinal variability in mitigating the impacts of climate change following the end of the Pleistocene, as climate changes in the lowlands were more widespread. Paleoecological and paleoclimatic studies carried out in lacustrine and terrestrial settings across the Yucatan peninsula, for example, shows a general and rapid increase in rainfall and temperature beginning as early as 15,500 cal B.P. which replaced forest-savannah mosaics with the dense tropical forests characteristic of the region today (Anselmetti et al. 2006; Bush et al. 2009; Cohuo et al. 2018, 2020; Correa-Metrio et al. 2012; Escobar et al. 2012; Hoddell et al. 2008; Rosenmeier et al. 2002; Wahl et al. 2014, 2016).

A recent overview of fire frequency in the lowlands of Guatemala (Anderson and Wahl 2016) suggests the early and middle Holocene was characterized by high fire frequencies in the closed canopy forests of this area. However, the authors highlight the fact that naturally occurring and anthropogenic fires cannot be differentiated in these records given their size and extent was not large enough to result in vegetation change. A separate review of charcoal records from across the neotropics (Power et al. 2010) indicates fire activity is correlated with high climate variability in lowland ecosystems, including high seasonality. This study suggested fire activity increased following the onset of Holocene warming but was much higher in seasonally dry forests (characteristic of highland areas) than in moist tropical forests (such as those in the lowlands), which experienced much less fire activity at this time. This is believed to be caused by higher and more constant levels of moisture in the lowlands than the semi-arid highlands, leading to fires with a limited spatial extent. In contrast, highland areas of Middle America tend to be much more seasonal in their rainfall patterns, leading to somewhat predictable patterns of fuel production and burning that are correlated with the rainy and dry seasons, respectively (Power et al. 2010).

To summarize, the paleoenvironmental and paleoclimatic data of Middle America challenges the stereotypical view that tropical regions are unchanging, static, and immutable to past climate change (Piperno and Pearsall 1998: 91). Rather, these data point to a dynamic and changing landscape on the eve of human arrival, with animal and plant populations with no modern analogs. In fact, Piperno and Pearsall (1998) argue that this regional diversity, which included both tropical forests and open areas with grassy, thorn, or shrub vegetation, resulted in a highly productive landscape, and hence an attractive one to human populations moving south across this region. A number of recent studies (Arroyo-Cabrales et al. 2003, 2007; Ceballos et al. 2010; Islebe and Hooghiemstra 1997; McDonald and Davila 2017; Piperno and Jones 2003) have reconstructed Late Pleistocene biogeographic corridors throughout Middle America that can be used to infer the distribution and movement of mammals across the region (Figure 3.3). These corridors were developed by integrating information on morphotectonic provinces (i.e., differentiated based on geomorphology and geological history) with information about the distribution of mammals (including extinct fauna) in Mexico. It has been argued that these corridors were likely used by both human and non-human species as routes of migration and dispersal. For the purposes of this dissertation, these corridors serve as heuristic devices for inferring the environmental knowledge the inhabitants of El Gigante accumulated as they migrated south across the isthmus, as well as the likely habitats and resources available to them in the highlands of southwestern Honduras.

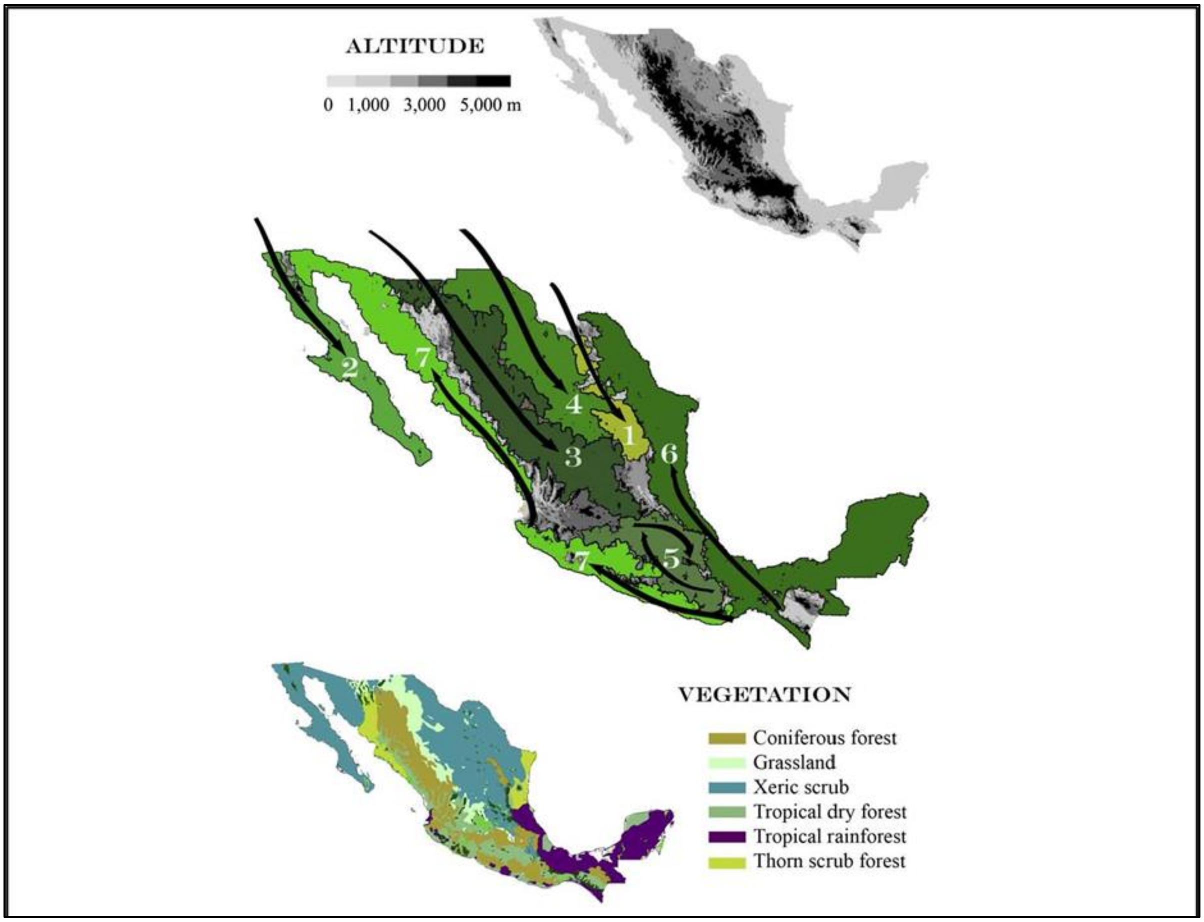

Figure 3.3 Major biogeographic corridors in Mexico during the Pleistocene as inferred from topographic data (top), potential vegetation (bottom), and the distribution of mammalian populations with known habitat and temperature tolerances. (Ceballos et al. 2010: Figure 6).

3.2 The past and present physical and ecological landscape of southwestern Honduras

An Early Holocene lake record from Lake Yojoa is the only paleoenvironmental record available from Honduras that dates to the Pleistocene-Holocene transition (Mehringer 2010; Mehringer et al. 2005). Cores recovered from the lake have a basal date of 13,000 cal B.P. and suggest a cold and dry forested environment at this time. By 9000 cal B.P. tropical species adapted to warmer and wetter conditions dominate the assemblage, a pattern that correlates with what is known from the lowlands of Guatemala and southern Mexico.

The defining physiographic feature of much of central and southwestern Honduras are the mountains of the Central American volcanic arc, which rivers have downcut and divided into a series of mountain ranges and discrete river valleys (Molina Garza et al. 2012; Williams and McBirney 1969). The bedrock of the southwestern highlands, where the El Gigante rockshelter is located, is composed of the Padre Miguel Group, a geological unit formed by ignimbrite from Miocene and Pliocene eruptions, which are highly alkaline in nature (Barberi et al. 2013). The physiography of the highlands offers limited flat terrain and is not conducive to agriculture beyond the household scale, thus leading some to characterize it as a "marginal" environment (Scheffler 2008: 322). Elevations here range from 800-2000 m asl, often within a very narrow area, creating a highly heterogeneous terrain. In addition, this area contains a large number of caves and rockshelters with over 40 having been recorded by surveys in an area of approximately 350km^2 (see Figueroa 2006, 2014; Scheffler 1999). Some of these caves are volcanic in origin, including extinct lava tubes, while others are located near the streams and rivers that formed them and, in some cases, continue to run through them.

The El Gigante rockshelter sits at an elevation of 1300m asl and is located on the toeslope of the Cerro Verde mountain 150m west of the La Estanzuela River, a tributary of the Lempa River that drains towards the Pacific Ocean. The shelter itself is a very large and open gap carved out of the ignimbrite tuff bedrock by the Estanzuela River, which stopped flowing through the shelter well before the earliest dated occupation here. The shelter opening is 12m high, with an entrance that is over 40m across, and an interior area of just under 360m^2. Most importantly, the interior of the shelter has been dry for millennia, creating a sediment sink for the dust resulting from the breakdown of its walls of ignimbrite tuff, which has created excellent preservation conditions within the site.

Modern ecological work in the area surrounding El Gigante has classified it as a, "tropical evergreen seasonal montane forest" (Vreugdenhil et al. 2002: 51), with a high degree of biodiversity given its diverse herbaceous understory and relatively intact watercourses (House et al. 2002). Pedestrian surveys of the area conducted by Scheffler (1999) and myself (Figueroa 2006, 2014) recorded moderate to strong topographic relief, shallow volcanic soils, large swaths of exposed bedrock, and a highly marked seasonal rain cycle, all of these are conducive to both dense and relatively patchy tropical and subtropical forests (Castellanos et al. 1962), depending on disturbance regimes.

El Gigante's mountainous landscape is home to a wide variety of animal species, and the nearby Estanzuela River and its watershed are habitats favorable to fish, reptiles, amphibians, birds, and invertebrates, some of which were presumably available to foraging populations in the past as indicated by preliminary analyses of the site's faunal assemblage (Scheffler 2008; Scheffler et al. 2012). The potential prey listed in Table 3.1 are animal species that have been recorded and identified near El Gigante and similar habitats in central and western Honduras, specifically mountainous areas above 800m asl with seasonal evergreen and/or needleleaf forests (Goodwin 1942; Marineros et al. 1998). These prey types are ranked according to their average liveweight, which is a rough but reliable measure of a resource's return rate (Broughton et al. 2011, though see Lupo et al. 2020; Lupo and Schmitt 2016; Stiner et al. 2000). But, body-size as measured by weight can sometimes be complicated by predator defense mechanisms, mobility patterns, and available hunting technology (see Bird et al. 2009). In this area, white-tailed deer (*Odocoileus virginianus*) would have been the largest and presumably highest-ranked prey. These species prefer early successional environments (Whitaker 2009: 99), such as those promoted by disturbances, have very restricted and predictable home ranges, and their populations are sensitive to both predation and environmental change, all of which figure prominently in studies of human responses to resource depression (Broughton et al. 2010; Wolverton et al. 2008; Wolverton et al. 2012).

Table 3.1 List of animal prey possibly available near El Gigante.

Rank	**Species**	**Common name**	**Ave. Body size (kg)**
1	*Odocoileus virginianus*	White-tailed deer	49
2	*Puma concolor*	Cougar	39
3	*Leopardus pardalis*	Ocelot	30
4	*Pecari tajacu*	Collared peccary	17.05
5	*Mazama americana*	Red brocket deer	14
6	*Canis latrans*	Coyote	13
7	*Procyon lotor*	Northern raccoon	9.2
8	*Agouti paca*	Paca	9
9	*Herpailurus yaguarondi*	Jaguarundi	7
10	*Ateles geoffroyi*	Spider monkey	6.6
11	*Meleagris gallopavo*	Turkey	5.9
12	*Didelphis sp.*	Opossum	5
13	*Nasua narica*	Coatimundi	4.5
14	*Tamandua mexicana*	Lesser anteater	4.3
15	*Dasypus novemcinctus*	Nine-banded armadillo	4
16	*Urocyon cinereoargenteus*	Gray fox	4
17	*Mephitis macroura*	Hooded skunk	2.7
18	*Conepatus mesoleucus*	Western hog-nosed skunk	2.7
19	*Potos flavus*	Kinkajou	2.7
20	*Dasyprocta punctata*	Agouti	2.52
21	*Testudinata sp.*	Turtle	2.4
22	*Bassariscus sumichrasti*	Cacomistle	1.6
23	*Iguana iguana*	Iguana	1.4
24	*Sylvilagus floridanus*	Cottontail rabbit	1
25	*Sciurus variegatoides*	Variegated squirrel	1
26	Various	Bats	0.01

Based on the review of existing paleoenvironmental and paleoclimatic research elsewhere in Middle America, as well as what is known about the highlands of southwestern Honduras, some inferences can be made regarding the landscape of El Gigante during the Pleistocene-Holocene transition. First, the area's altitudinal gradient and present seasonal dry forest vegetation suggests it might have served as a climate refugia for plant and animal species, as has been seen elsewhere in the region, leading to a high biodiversity and overall environmental stability throughout the warming Holocene (Caballero-Rodriguez et al. 2018; Correa-Metrio et al. 2013, 2014; Piperno and Jones 2003). It is likely that, similar to other seasonally dry forests in highland areas north and south, the landscape at El Gigante remained relatively unchanged since the terminal Pleistocene. With the onset of warmer and wetter conditions during the Holocene, small basins in the highlands of southwestern Honduras filled in, creating water sources that served to maintain large mammal populations in this area. The area's high topographic variability and seasonality was possibly also conducive to the growth and expansion of mesic plants, namely fruit-bearing trees, which might have also served to attract browsers as well as human populations here, similar to the Balsas region of Mexico (Piperno et al. 2007) and the highlands of central Panama (Piperno and Jones 2003). The recovery of an incredibly rich paleobotanical assemblage from El Gigante supports this hypothesis and will be described further in Section 3.4.

Second, the southwestern highlands are a mere 90km from the nearest inlet of the Pacific ocean in the Bay of Fonseca and the lowlands at the foot of the mountains, an area which was probably characterized by open grassland-forest mosaics during the terminal Pleistocene and which served as a natural corridor for large herbivores (Arroyo-Cabrales et al. 2003, 2007; Ceballos et al. 2010; McDonald and Davila 2017). These herbivores likely made their way into the southwestern highlands, where it is possible relict populations survived well into the earliest Holocene. This is a distinct possibility given the identification of *Glyptodon* sp. and

Euceratherium sp. in the lowest (i.e., predating human occupation) levels of El Gigante, though these have yet to be dated. The presence of these two species suggests a relatively open landscape in this area sometime in the Late Pleistocene. While *Glyptodon* are mixed feeders, the shrub ox (*Euceratherium* sp.) is often associated with grassy habitats and a grazer diet, though mixed diets have also been suggested (Kropf et al. 2007). The presence of a possible grazer suggests the environment at El Gigante was more open than forested, a pattern which is common to this day (Owen-Smith 2013). This might also suggest an open savannah corridor existed between the coastal lowlands and the southwestern highlands.

What is known of southwestern Honduras' natural and cultural history and context poses an interesting scenario. While it remains largely untenable for agriculture and large-scale settlements to this day, evidence suggests this has been a topographically and environmentally diverse ecosystem since at least the Late Pleistocene and might have been very attractive to foraging populations. These ecological and environmental characteristics are similar to those of other landscapes inhabited early in the prehistory of Middle America and whose archaeological sites have yielded data on subsistence and mobility relevant to the study of the adaptive changes that took place during the PHT in the region.

3.3 The Paleoindian and Early Archaic Record of Middle America

Current knowledge of the Paleoindian and Early Archaic periods (ca. 13,000-7000 cal B.P.) in Middle America is minimal when compared to that of its geographic neighbors. However, a recent revival of Paleoindian research beginning in the late 1990s highlighted the fact that several potential sites from this period were identified half a century ago, but never reinvestigated using modern techniques (i.e. Lohse et al. 2021; Lohse et al. 2006 Sanchez 2001;

Zeitlin and Zeitlin 2000). At the same time, more detailed understandings of this time period, afforded by well-preserved materials from deeply buried contexts with robust chronological models, suggest that the study of these periods in Middle America can and should be informed by research elsewhere, but ultimately needs to be evaluated by models developed using local processes and circumstances (Borrero 2006, 2016).

In the broadest terms, the Paleoindian period in Middle America is defined in its northern border by artifactual and behavioral patterns similar to those observed across most of North America and in its southern limit with materials and behaviors from South America. This is of course hardly surprising given the arbitrary boundaries that separate these three regions. In northernmost Mexico, reliable associations between classic Paleoindian projectile points such as Clovis and Folsom and extinct fauna such as mammoths and gomphotheres are found throughout the Sierra Madre Occidental (Gaines et al. 2009; Prado et al. 2012; Sanchez 2001; Sanchez and Carpenter 2012; Sanchez et al. 2014). Research in the state of Sonora recovered the full spectrum of the Clovis technocomplex, associated with fauna that are currently extinct or not present in the area including gomphotheres, horses, camels, bison, and pronghorn (Gaines et al. 2009; Sanchez and Carpenter 2012; Sanchez-Morales 2018). Interestingly, the vast majority of lithic materials were locally obtained, suggestive of foraging ranges that were much more reduced when compared to those of Paleoindian groups further north. This indicates that in the northernmost parts of Middle America behavioral patterns were already different from those in North America, where rapid colonization of the continent is believed to have occurred (e.g., Kelly and Todd 1988; Meltzer 2009; Moreno-Mayar et al. 2018; Saleeby 2010).

Researchers focused on the earliest inhabitants of the tropics of South America have argued for the examination of the local archaeological record on its own terms and separated from the biases introduced by earlier North American researchers (Borrero 2006, 2016). This process included examining Paleoindian archaeological materials within the context of local models, typologies, and absolute chronologies given a general absence of diagnostic elements such as fluted projectile points throughout most of Middle and South America. For example, despite a paucity of sites dating to before 13,000 cal B.P., the existing records show diets were broad and had a substantial plant-based component that included palms, fruits, nuts, seeds, and roots (Aceituno et al. 2013; Aceituno and Loaiza 2014, 2018; Dickau et al. 2015; Piperno 2011a; Piperno et al. 2017). Archaeological and paleoecological work in Colombia recovered evidence of plant use, plant transplantation and landscape modification through burning and clearing dated as early as 13,000 cal B.P. (see Aceituno and Loaiza 2018, Piperno et al. 2017 for a review of these studies). The earliest sites identified in northwest South America are located in the intermontane valleys and highlands of central Colombia, which were likely inhabited a variety of plant and animal species, including megafauna (Aceituno et al. 2013; Delgado-Burbano et al. 2015).

By 11,500 cal B.P., foraging groups inhabiting the South American tropics greatly reduced their foraging radii and began exploiting exclusively local sources of stone (in some instances utilizing roof spall from the very shelters they inhabited to make their stone tools; e.g., Kipniss 2002: 134). This led to the development of highly localized lithic traditions and an apparent widespread decrease in residential mobility among many of these groups, and perhaps the beginnings of *in situ* genetic divergence (i.e., Reich et al. 2012).

While some of the behavioral patterns characteristic of the Paleoindian and Early Archaic periods in North and South American have been previously identified in Middle America (e.g., Acosta 2008; Flannery 2009; Scheffler 2008; Scheffler et al. 2012), research shows that subsistence and mobility strategies in this region were highly conditioned by local circumstances. This work indicates that the earliest occupants of the region (ca.13,000-12,000 cal B.P.) were drawn to resource-rich areas such as coasts, lake basins, and river valleys (e.g., Chatters et al. 2017; Gonzalez et al. 2006; MacDonald et al. 2020; Ranere et al. 2009; Stinnesbeck et al. 2017). The geographic circumscription and heterogeneity of this region encouraged subsequent colonizing populations (either new arrivals or groups broken off existing populations) to remain highly mobile and continue exploiting nearby ecosystems. These earliest populations had diverse lithic toolkits that also included specialized technologies such as projectile points, indicative of narrow diets focused on the acquisition of a few resources, which is consistent with the Paleoindian record in North America. However, and as Paleoindian research in North America has also demonstrated (e.g., Cannon and Meltzer 2004, 2008; DeAngelis and Lyman 2016), diets were already broad and included a great number of plant and animal species.

Between 12,000-10,000 cal B.P., and shortly after the beginning of the Holocene, populations throughout Middle America began to reduce their residential mobility and foraging radii and developed highly localized technologies, including the use of regionally diagnostic lithic toolkits or, in the majority of cases, transitioned towards wholly expedient and generalized technologies. Research in southern Belize identified a number of stemmed and basally thinned bifacial projectile points (Lohse 2020; Lohse et al. 2006; Stemp et al. 2016, 2018), with the earliest of these, the Lowe point, securely dated to 10,200-9300 cal B.P. (Prufer et al. 2019). This and other associated points represent some of the earliest lithic traditions unique to Middle America and probably represent the relatively early territorial circumscription of populations in the region (Lohse 2020).

During this time there is also a partitioning of subsistence strategies centered around habitat composition. Those parts of the continent that were rich in readily available and predictable resources (e.g., coasts, river valleys, lake basins) allowed for early reductions in residential mobility for Paleoindian and Early Archaic populations. Early reduced mobility has been observed in northwest Mexico along the Sierra Madre Occidental (Gaines et al. 2009; Prado et al. 2012; Sanchez 2001; Sanchez and Carpenter 2012; Sanchez et al. 2014), the Basin of Mexico (Acosta 2008; Aveleyra 1955, 1956, 1967; Aveleyra and Maldonado-Koerdell 1953; Ranere 2006), and the Pacific coast of Chiapas (Kennett and Voorhies 1996; Kennett et al. 2006; Voorhies 2004; Voorhies and Gose 2007; Voorhies et al. 2002). Parts of the region that experienced higher degrees of seasonality following the start of the Holocene, on the other hand, are characterized by a subsistence system where groups aggregated in resource-rich refugia during the winter or rainy season and dispersed towards peripheral parts of the landscape during the less productive dry season, following the model identified in the Tehuacan Valley by MacNeish (1964). This dual subsistence pattern is identified in the Tehuacan Valley (Byers 1967, 1972; Flannery 1967, 1968; Hardy 1993, 1996, 1999; Hole 1986; MacNeish 1964, 1972, 1976), Oaxaca Valley (Flannery 1986; Flannery and Spores 1983; Flannery et al. 1981; Marcus and Flannery 1996; Smith 2000), and the Central Depression of Chiapas (Acosta 2008, 2012, 2013, 2017; Acosta et al. 2011, 2018; García-Bárcena 1980, 1982; García-Bárcena and Santamaría 1982, 1984; MacNeish and Peterson 1962; Santamaría 1981).

The following period, between 10,000-7000 cal B.P. defined as the Early Archaic (Lohse et al. 2006) is when there were further changes in lifeways that began earlier in the region. There is evidence for a larger number and variety of sites located in a greater diversity of ecological settings, suggesting population sizes had increased and demographic circumscription was beginning to occur as groups began settling down in marginal (i.e., less productive) environments (Rosenswig et al. 2015; Voorhies and Lohse 2012). The earliest known burials in the region appeared at this time in the Tehuacan Valley (MacNeish 1964), the Pacific coast of Chiapas (Blake et al. 1992, 1995; Chisholm and Blake 2006; Voorhies 2004), and southern Belize (Posth et al. 2018; Prufer et al. 2019) and indicate increasing levels of territoriality as populations began staking their claims on the landscape by physically placing themselves and their deceased family members within it. The earliest domesticates in the region, squash and maize, were introduced into an already diverse diet, though their role remained secondary to wild resources (Piperno 2011; Piperno et al. 2009; Smith 2000). Use of milling technologies also increased at this time, and purposeful clearing and burning of landscape became more common in the region (Acosta 2008, 2010, 2012; Cooke and Ranere 1992; Piperno and Pearsall 1998).

Research into the Late Pleistocene and Early Holocene in Middle America thus far suggests that foraging groups utilized and occupied rockshelters throughout the region and used these sites as central places in the landscape from which to exploit a variety of different habitats and resources. Many of these groups had specialized and geographically circumscribed projectile point technologies during the Paleoindian that were quickly replaced by more expedient and generalized technologies by approximately 9000 cal B.P. Lastly, it appears these groups modified the landscape through periodic burning and clearing, though this has not yet been investigated in enough detail (though see Kennett et al. 2010; Piperno et al. 2007, 2017).

Studies of the PHT in Middle America (e.g., Acosta 2017; Flannery 2009, 2019; Piperno 2006, 2011; Piperno and Pearsall 1998; Piperno et al. 2017) have developed a series of expectations regarding the natural and behavioral changes that took place. First, they predict environmental degradation took place in the form of decreased habitat productivity (indicated by a decrease in the amount of animal prey and carbohydrate-rich plants; see Piperno and Pearsall 1998), which led to increased variability in the distribution and predictability of resources. They also predict demographic expansion and increased presence of populations in marginal environments with less dependable and predictable resources. Lastly, they predict the adoption of foraging strategies to decrease risk, improve resource unpredictability, and reduce extreme environmental variation, including the diversification of the diet, the development of storage technologies, and the modification of the landscape via clearing and burning as well as transplantation of desirable species to improve their distribution and predictability, all of which are inferred to have reduced the level of residential mobility in foraging populations. The archaeological record of the Middle American Preceramic period largely supports these expectations. However, a review of the existing literature highlights the fact that these changes did not occur in all places, and that they took place at different rates and different times, depending on both social and environmental factors. More importantly, the ecological knowledge acquired by populations over their interaction with the landscapes and resources of the region meant that the behavioral changes associated with the PHT took place over long periods of time, and that behaviors such as the domestication of species were “processes rather than events” (Voorhies and Lohse 2012: 342).

One key missing component of existing hypotheses that seek to explain the adaptive changes taking place during the PHT in Middle America is detailed evidence for loss of habitat productivity and resource depression taking place during the early Preceramic, and more specifically evidence of a decrease in encounter rates with high-ranked resources. Plenty of evidence has been amassed to indicate a broadening of the diet over the span of the Preceramic across most of the region, including a shift in subsistence technologies from specialized and standardized projectile points toward more general-purpose expedient toolkits. However, the recovery and analysis of dated zooarchaeological assemblages required to evaluate this proposition is limited to three cases: the Tehuacan Valley (Flannery 1986; Flannery and Hole 2019), the Central Depression of Chiapas (Acosta 2008; Eudave 2008; Solis-Torres et al. 2020), and Mayahak Cab Pek cave in Belize (Orsini 2016). All three cases, however, present only limited analyses of small faunal assemblages with only very broad chronological assignations.

The analysis of the zooarcheological collection recovered from the El Gigante rockshelter that forms the core of this dissertation will make a substantial contribution to the study of this critical transition in Middle America and beyond, because the faunal assemblage is very large and well-preserved. The site was occupied throughout the Paleoindian and Early Archaic periods and has a relatively well understood chronology. In the following section I summarize what we currently know about the Preceramic occupations of El Gigante from analyses conducted on its lithic, macrobotanical, and stratigraphic datasets.

3.4 The PHT in southwestern Honduras

The PHT in Honduras has been examined by four research projects, all of which have taken place in the highlands of central western Honduras, part of the Cordillera Central or Central American Continental Divide (Figure 3.4). This area is defined by the numerous caves and rockshelters that dot the landscape. It can be argued that the prevalence of natural shelters in this region, which are highly visible and reliable landmarks, would have been a major factor affecting the settlement and subsistence of human populations encountering and adapting to new landscapes and resources. For example, rockshelters and caves could provide protection from the risks associated with exposure to the elements and could serve as central places from which to obtain knowledge of local resource distributions over space and time (i.e., seasonality).

In the 1960s, Bullen and Plowden (1963) conducted a surface survey of preceramic sites near the city of La Esperanza. Because the majority of sites they encountered were found in high elevations (1500-2000m asl), the authors suggested that human groups might have restricted their movement and subsistence to environments similar to those first encountered in North America, namely highland forests (Bullen and Plowden 1963: 384). In addition, among the artifacts recovered during this survey was the fluted base of a biface, described by some as a possible Clovis-like point (Sheets et al. 1990: 145). Despite the interesting possibilities raised by this study, it lacked absolute dates and sufficient knowledge of the distribution of local lithic materials (Scheffler et al. 2012: 600).

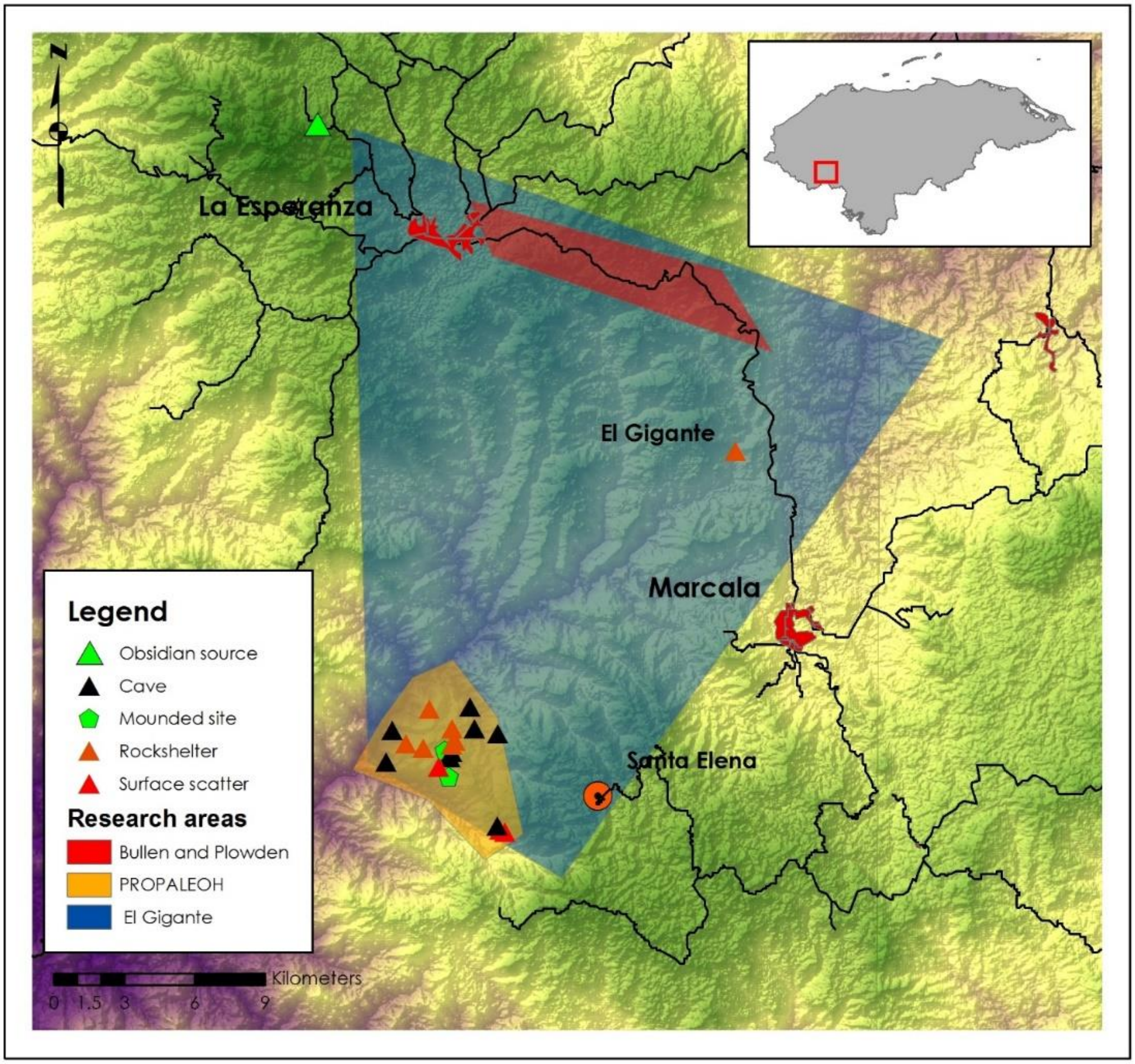

Figure 3.4 The highlands of southwestern Honduras, including the areas examined by various research projects and key sites mentioned in the text.

Scheffler (1999: 255) identified 12 caves and nine shelters during a survey conducted in the early stages of the El Gigante project. He carried out test excavations at other rockshelters in the area with potential stratigraphy but these yielded mixed contexts or strata with relatively late dates (Scheffler 1999). The 2005-2006 season of the Honduran Rock Art Project (PARUP) also carried out a survey of archaeological sites in an area approximately 15km southwest of El

Gigante in the municipality of Santa Elena. This location has a similar geology and topography as the area surrounding El Gigante and had been previously surveyed by Scheffler (1999). The PARUP survey recorded and mapped the location of three caves and five rockshelters, four of which contained rock art, and received reports from local inhabitants for dozens of other similar sites (Figueroa 2006, 2014).

The most recent effort to study the Paleoindian and Archaic periods in Honduras was the Honduran Paleoindian Project (PROPALEOH), which I undertook in 2013 (Figueroa 2014). I returned to Santa Elena with the goal of identifying additional sites dated to the Paleoindian and Archaic. This included conducting test excavations at sites previously recorded by the El Gigante and PARUP projects and to conduct surface survey in search of additional sites reported by local informants. I did not identify any other sites with reliable subsurface components. However, I recovered a projectile point similar to those identified for the Paleoindian occupation at El Gigante (Figure 3.5) from the surface of the La Sierpe rockshelter, located 17km southwest of El Gigante, indicating that other sites dated to these periods are likely present in the area.

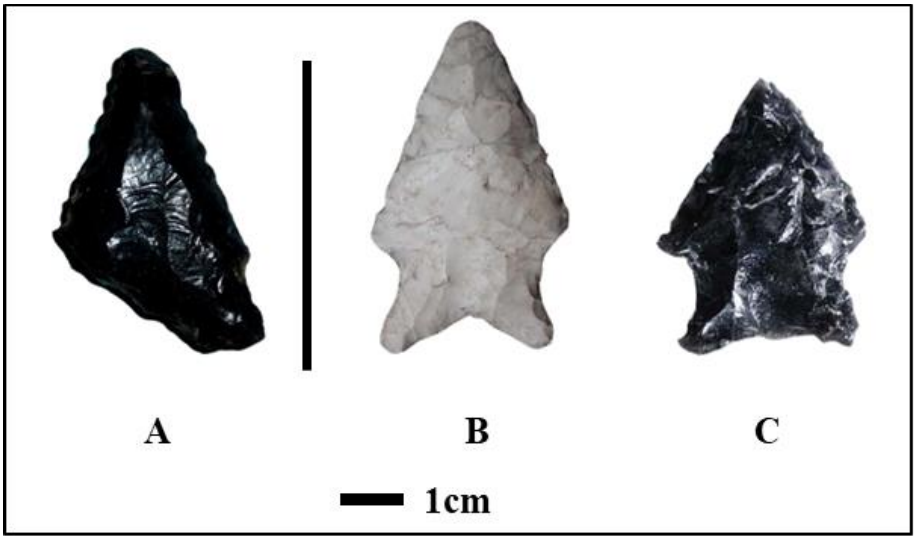

Figure 3.5 Diagnostic projectile points from La Sierpe (A) and El Gigante (B-C; photos of El Gigante points from Scheffler 2008: Figures 28-29).

The research conducted by Bullen and Plowden (1963) led archaeologist George Hasemann of the Honduran Institute of Anthropology and History (IHAH) to return to the area in the early 1990s after hearing reports of a rockshelter with large densities of archaeological materials. This site, the El Gigante rockshelter, is located 15km southeast of the area surveyed by Bullen and Plowden (Scheffler 2008; Scheffler et al. 2012).

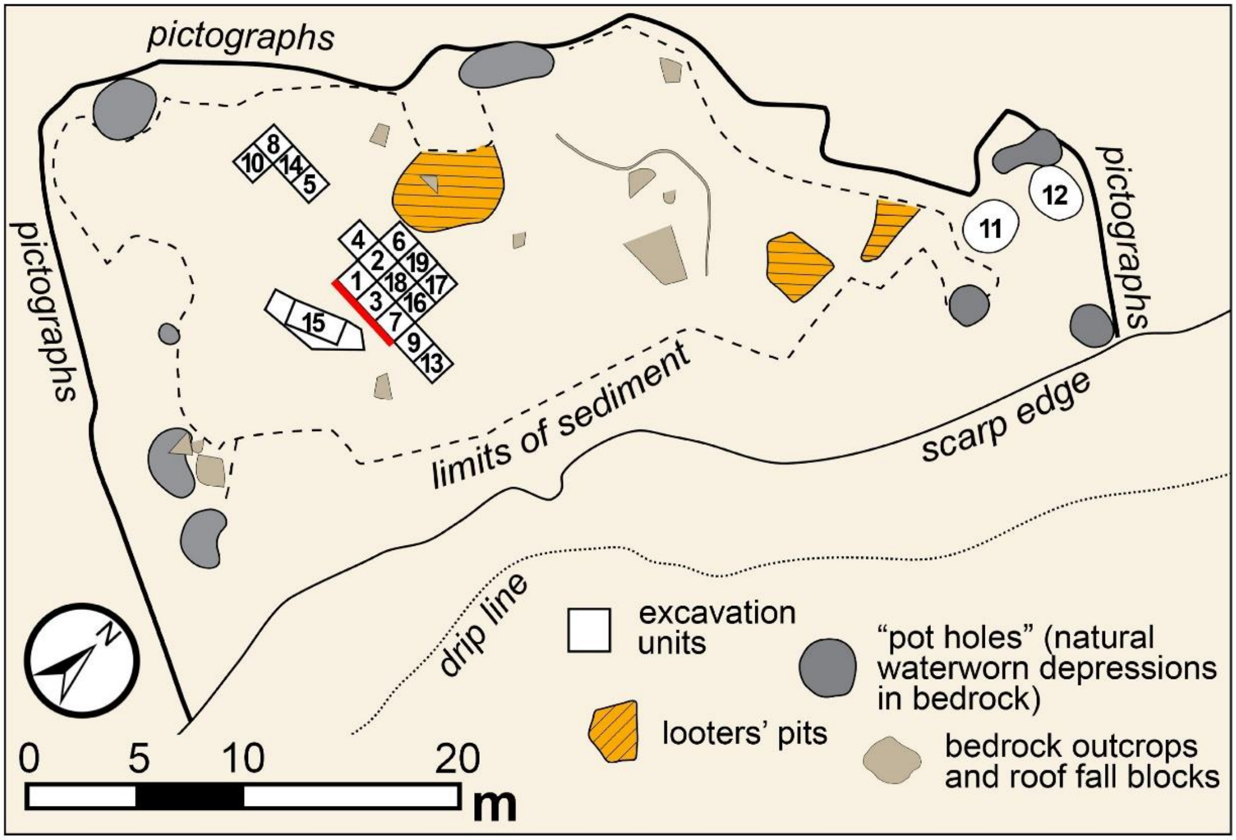

Figure 3.6 Floor plan of El Gigante (Kennett et al. 2017: Figure S1).

The shelter was first excavated in 1993 by Hasemann. This work recovered lithics, ceramics dated to the Middle and Late Formative periods, as well as a large number of macrobotanical remains, which attested to the unique preservation conditions of the site. Hasemann excavated the site again in 1994 and identified over two meters of clearly stratified deposits whose bottom levels lacked ceramics and yielded a possible Fishtail point. A radiocarbon date obtained from materials associated with this point indicated it was deposited between 10,000-9000 cal B.P. (Scheffler 2008). Unfortunately, no official report exists for these initial excavations at the site, and the materials excavated – including faunal, botanical, and lithic specimens – have not been analyzed and remain in storage at the IHAH offices in Tegucigalpa.

More intensive excavations were carried out by Scheffler in 2000 and 2001. Work during the 2000 season involved the excavation of two 1x1m test units in an undisturbed area of the shelter. These units were placed adjacent to the 1994 excavation in order to use its profile as a reference for excavating these units in natural stratigraphic levels (Scheffler 2008). These excavations were meant to provide a rapid and preliminary overview of the stratigraphy at the site and determine the location of intact stratigraphic sequences at the site.

In 2001, Scheffler excavated an additional seventeen 1x1m units across the southern portions of the shelter. All materials excavated in both the 2000 and 2001 seasons were dry screened through a 1/8" mesh, which means the remains of some small mammals are likely to be missing, a fact supported by analyses of a sediment block recovered during these excavations. The main block of excavation was placed perpendicular to the shelter's orientation, and consisted of 12 units (1-4, 6, 7, 9, 13, 16, 17, 18, and 19), which were excavated sequentially in order to expose strata and guide future excavations (Scheffler 2008: 51). Units were also placed near the westernmost wall of the shelter, which had the deepest deposits, and atop two of the site's natural bedrock depressions on the north side of the shelter, all of which had highly disturbed contexts and deposits. The main block of excavations, however, has been found to yield the best-preserved deposits, and its excavation revealed that geogenic sedimentation was slow and the result of long-term grain by grain accumulation of degraded tuffs as well as occasional roof fall

(Scheffler 2008). This suggests the site's sedimentary matrix has a significant anthropogenic component, which geoarchaeological analyses conducted as part of this dissertation verify (see Chapter 5, section 5.6).

Despite their limited scope, these excavations generated a very large material assemblage. Lithic materials recovered from the site (n = 15,669) include artifacts fashioned of obsidian, rhyolite, andesite, chert, and basalt. Analyses of some of these materials (Figueroa 2014; Iceland and Hirth 2021; Scheffler 2008; Scheffler et al. 2012) indicated that the obsidian was procured from the La Esperanza source, located approximately 22km northwest of El Gigante, while the other lithic materials were likely locally obtained. The faunal collection (n > 60,000), which is the subject of detailed analysis in this dissertation, includes the remains of a wide variety of mammals, amphibians, reptiles, birds, fishes, and invertebrates. Macrobotanical remains (n = 31,001) include seeds, rinds, stems, nuts, leaves, and maize cobs. Additionally, partial stratigraphic soil columns were obtained from the south wall of Unit 3, the east wall of Unit 2 and the west wall of Unit 6, all within the main block of excavations, for the purposes of palynological and charcoal analysis.

Based on preliminary analyses of the various material remains preserved at the site, Scheffler (2008: 339) argued that El Gigante's inhabitants had a "home range" pattern of spatial organization during the Paleoindian period, defined by little mobility, limited territoriality, and ranges that likely overlap with those of other nearby populations. Scheffler (2008: 338) used the following lines of evidence to support this hypothesis: (1) paucity of food storage facilities; (2) extensive use of fire within the shelter; (3) low percentages of cortical lithic debitage; (4) expedient and multi-purpose tools; (5) dominance of large game (i.e., deer) in the faunal assemblage; (6) a very diverse botanical assemblage dominated by seasonal plants, and; (7) the absence of any indicators of territoriality. Despite the detailed data used to support this hypothesis, Scheffler (2008: 350) acknowledged that it needed to be tested and refined against data from El Gigante's surrounding landscape.

A recent intensive radiocarbon dating program (N = 141) has begun to clarify the El Gigante's occupation history and has improved the site's potential to inform on the timing and rate of behavioral changes recorded in its stratigraphic record (Kennett et al. 2017). These dates are derived from charred and uncharred botanical specimens and dispersed charcoal, the latter of which might have tenuous chronological relationships with the recovery context, and the stratigraphy and concordance for the dated samples and artifact collections are not yet fully resolved. Owing to the lack of bone collagen preservation at the site, none of the archaeological bone has been dated. Despite these limitations, a probability distribution of these dates shows that El Gigante's occupation was not continuous but episodic (Figure 3.7). Most relevant to the proposed study, this chronological work has revealed a clear Preceramic occupation at the site that spans the Early Holocene (11,010-7430 cal B.P.). This dissertation will focus solely on the treatment and analysis of a sample of the faunal remains from the four earliest occupational phases of occupation at the site: Early and Late Esperanza, and Early and Middle Marcala.

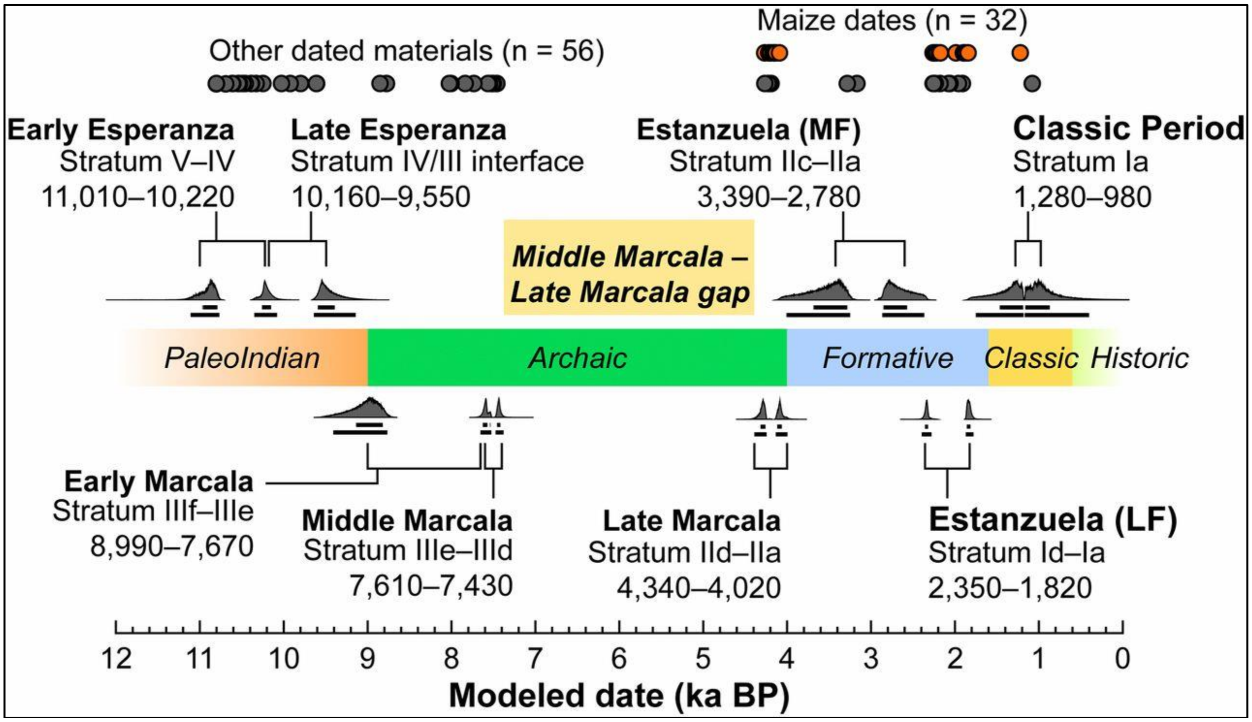

Figure 3.7 14C chronology for El Gigante with modeled occupational phases using local and Mesoamerican nomenclature. (Kennett et al. 2017: Figure 2).

Flaked stone lithics artifacts and debitage have been analyzed by Hirth and Iceland at the Mesoamerican Archaeology Laboratory of the Pennsylvania State University (PSU; Hirth et al. 2018; Iceland and Hirth 2021). These analyses focused on identifying toolkit composition, diversity, and complexity using a technological approach. Of the total assemblage, 6,438 pieces of flaked stone date to the Early and Late Esperanza and Early and Middle Marcala. During the Esperanza phase, the vast majority of flaked lithics (>91%) are expedient flakes produced by nodule and core reduction. Most importantly, these analyses have identified a highly standardized projectile point complex during the Esperanza phase characterized by straight lateral edges, barbed shoulders, corner notching, expanding stems, and basal fluting.

The majority of the flaked tools and tool fragments recovered belonging to this complex suggest intensive levels of fragmentation, reworking, and reuse. This level of reworking is often indicative of the importance of curating these types of artifacts and suggests the inhabitants at El Gigante did not regularly travel often to raw material sources to refresh their inventories, which might in turn indicate a modest level of sedentism. The abundance of point fragments, especially ears, indicates that these points broke on impact following a hunt and were recovered during butchering, which in turn tells us that prey were being hunted not too far away from the site.

In contrast to the Esperanza phase, the flaked stone assemblage from the Early Marcala period only has minimal evidence of formalized tools. In addition, while the majority of flaked stone materials from the Esperanza phases were made out of obsidian, all of which was procured from the nearby La Esperanza source 23 km northwest of El Gigante (Sheets et al. 1990; Sorensen and Hirth 1984), Marcala phase flaked lithics are mostly made out of locally available fine and medium textured tuff (Hirth et al. 2018). This indicates populations at the site were staying near El Gigante for longer periods of time.

The groundstone assemblage recovered from El Gigante is relatively small (n=89) but is also informative of changes in behavioral patterns throughout the Preceramic. There is an increase in the number of groundstone implements from the Esperanza to the Early Marcala phases, which corresponds to a decrease in the number and proportion of flaked stone tools, indicating a stronger reliance on the processing of plant materials.

El Gigante's large botanical assemblage was partially analyzed by Newsom as part of Scheffler's (2008) dissertation research. A systematic analysis of this assemblage is currently under way (Hirth et al. 2018). Initial results show the inhabitants of El Gigante consumed a variety of plant resources during the Early Esperanza phase including arboreal fruits, maguey, wild beans, and squash. The Late Esperanza occupation showed an increase in the consumption of tree species and maguey, which then generally decreased in abundance and ubiquity in the

Early Marcala. However, during the Early Marcala these populations consumed more of certain arboreal fruits, namely avocado and *Sapotaceae*. Perhaps not coincidentally, previous morphological analyses of avocado remains from the site – which are currently ongoing – suggest the directional selection of this species over time, as indicated by increases in rind thickness and decreases in seed size and which are correlated to overall increases in the amount of flesh (Figueroa and Scheffler 2021; Scheffler 2008, 2014).

Existing and ongoing analyses of the lithic, botanical, and faunal materials as well as feature density show a general diversification of the diet and loss of residential mobility between the Early Esperanza and Middle Marcala phases at El Gigante (Figueroa and Scheffler 2021; Scheffler 2008, 2014; Scheffler et al. 2012). These inferences are based on the following archaeological observations: (1) increased abundance of food storage facilities over time; (2) increased use of fire over time, as indicated by an increase in macroscopic charcoal content (see Scheffler 2008); (3) a technological shift from highly curated and resharpened projectile points towards more expedient and multi-purpose tools; (4) increased use of locally available lithic materials over time; (5) increased abundance of smaller game in the faunal assemblage, and; (6) increased diversity and representation of seasonal resources in the botanical assemblage. Most relevant to the proposed study, a preliminary Abundance Index (AI) of the ratio of large mammal to small mammal remains indicated a decline in large game and increased fragmentation of large mammal remains over time (Scheffler 2008: 140-142), both suggesting resource depression, although this remains to be accurately evaluated with more detailed analyses of identified archaeofaunas.

Despite the unique potential of El Gigante's material record to refine our understanding of the adaptive changes taking place during the Early Holocene in the American neotropics, the site’s large and well-preserved faunal assemblage collected during excavation remains unstudied. This dissertation provides essential information regarding the timing and rate of subsistence and mobility changes among local foragers. Moreover, integration of the faunal assemblage with data derived from lithic and macrobotanical analyses sheds further light on the natural and cultural contexts of the episodic occupation of El Gigante during the Preceramic. Critically, this dissertation presents the first systematic evaluation of whether loss of habitat productivity and resource depression took place in the region during the Early Holocene, and the order and timing in which natural and behavioral changes took place in the highlands, with the overarching goal of providing a baseline with which to evaluate the archaeological record of other sites in the region and beyond.

CHAPTER 4:

METHODOLOGY

In this chapter I present the zooarchaeological and geoarchaeological methods and procedures undertaken in this research to evaluate my hypotheses. I conducted faunal analyses on a sample (ca. 24%) of the approximately 60,000 faunal specimens recovered from excavations at El Gigante. This sample was chosen from units within the main block of excavations at the shelter that is stratigraphically intact, as supported by extensive radiocarbon dating. The sample was divided into four assemblages, corresponding to the four phases of Preceramic occupation identified at the site (Table 4.1; Kennett et al. 2017; Scheffler 2008; Scheffler et al. 2012). Despite its large size and excellent state of preservation, the El Gigante faunal assemblage is extremely fragmented (mean greatest length <2 cm), and analytical procedures were chosen with this in mind. Taphonomic characteristics such as carbonate concretions, burning and heat alteration, evidence of acid digestion by non-human predators, and weathering were also recorded in order to evaluate the various anthropogenic and natural processes that impacted the assemblage both chronologically and spatially. Faunal specimens were identified by taxon with the aid of physical and digital comparative collections. Diagnostic zones were used to determine the portions of bones being identified (*sensu* Cohen and Serjeantson 1996; Dobney and Rielly 1988; Knusel and Outram 2004; Watson 1979), which allowed for a more accurate identification of individuals (MNI). Bone size was measured on all identified specimens (greatest length and breadth), and unidentified specimens were grouped into various size classes. All specimens larger than 40mm were analyzed in order to determine the Fracture Freshness Index (FFI; Outram 1998, 2001, 2002), which I used to systematically evaluate the degree to which bones were broken while fresh, thus indicating purposeful breakage as opposed to breakage caused by post-depositional factors such as trampling. I used these raw data to quantify the assemblage over time using both the Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI). These two units of analysis helped me determine the diversity of the assemblage through species richness and evenness (Jones 2004), which I calculated using the total number of taxa (∑TAXA) and the inverse of Simpson's diversity index (SI; Simpson 1949), respectively.

Table 4.1 Preceramic occupations identified at El Gigante examined in this dissertation (based on Kennett et al. 2017: Figure 2).

Date Range (cal B.P.)	**Cultural Horizon - EG**	**Cutural Horizon - Mesoamerica**
11,010-10,220	Early Esperanza	Paleoindian
10,160-9550	Late Esperanza	Paleoindian
8990-7670	Early Marcala	Paleoindian-Archaic
7610-7430	Middle Marcala	Archaic

Using these basic measures of assemblage composition and diversity I developed a procedure to evaluate the major environmental and behavioral expectations of the PHT (Flannery 2009, 2017; Piperno and Pearsall 1998; Piperno et al. 2017). Three different measures were used to examine resource depression: (1) the Artiodactyl Index (after Bayham 1979, 1982; Broughton 1994a, 1994b), which examines the abundance of the highest-ranked prey in the area (deer) relative to all other taxa in the assemblage; (2) changes in carcass exploitation patterns, including changes in mean FFI scores and body part profiles (Manne 2014; Manne et al. 2012; Stiner 2002, 2004), and; (3) changes in the age or mortality profiles of deer as indicators of deer population health and composition (Broughton 2002; Stiner 1990; Wolverton et al. 2008). I examined changes in diet breadth by examining variations in ∑TAXA and the Inverse of Simpson's Diversity Index (SI) over time.

I also carried out a limited geoarchaeological study of sediment samples obtained during excavation to examine intensity of occupation in the shelter (sensu Marwick 2005) and to better understand the taphonomic processes acting upon the archaeological materials from the site, including and especially bone. Previous attempts to obtain radiocarbon dates and DNA from the organic components of bone (i.e., collagen) have not been successful despite the degree of preservation of these materials and have suggested that this might be due to the chemical alteration. I examined the intensity of occupation of the shelter through Mehlich II-extractable phosphorus concentrations measured using molybdate colorimetry (Terry et al. 2000), which is a proxy for the intensity of deposition of organic wastes in the shelter. Bulk magnetic susceptibility and loss-on-ignition offered independent but related proxies for the intensity of occupation that are sensitive to both the deposition of organic wastes and the deposition of hearth byproducts, including ash (Ball 1964; Oldfield and Crowther 2007; Roos and Nolan 2012; Viberg et al. 2013). The geoarchaeological component of this research should be viewed as preliminary given the scarcity of available samples and the unique geochemistry of the site, as I expand upon in section 4.6 below. The protocol used in the collection of faunal data is presented in Appendix A.

4.1 The Faunal Assemblage

The faunal assemblage recovered from El Gigante (ca. 60,000 specimens) is the largest yet recovered from a multi-component site dated to the Paleoindian and Archaic periods in Middle

America. The conditions under which the assemblage was recovered and then stored indicate that post-depositional physical alteration that might affect the results of my analysis is minimal. All materials excavated from the shelter in 2000 and 2001 were dry screened through 1/8” mesh, placed into commercially available zip bags in the field and exported for analysis at the Pennsylvania State University (PSU), where they are currently housed. At PSU, these bagged materials were placed in acid-free museum-quality boxes and kept inside the collections room of the Anthropology Department. Scheffler (2008) pre-sorted and counted the faunal remains recovered from excavation Units 1 and 2 for his dissertation. Subsequently, the remains from Units 17, 18, and 19 were pre-sorted and quantified by Sarah McClure and a number of graduate and undergraduate students at PSU (McClure, personal communication 2017). McClure and Claire Ebert (McClure, personal communication 2017) analyzed 18 bone samples from Units 18 and 19 in 2011 for stable carbon isotopes, which involved their identification and breakage for analysis, and their identifications have been included in my dataset. To my knowledge, no other analyses have been conducted on these remains. I did not wash any of the faunal remains because of their delicate condition and only a few were mechanically cleaned using a soft-bristled brush in order to expose diagnostic landmarks. Post-depositional and post-collection (i.e., recent) breakage in the bone was minimal and was accounted for in the FFI analysis of specimens larger than 40mm. Given the large size of the faunal assemblage, I only examined the remains recovered from Units 1, 2, 18, and 19 (see Figure 3.5 above). Dating and concordance work suggests these units are the most stratigraphically intact at the site (Kennett et al. 2017; Hirth, personal communication, 2017).

4.2 Chronology and Stratigraphy

Faunal remains were divided into assemblages corresponding to the four major Preceramic occupational phases identified by Kennett and colleagues (2017; see Figure 3.6): Early Esperanza (11,010-10,220 cal B.P.), Late Esperanza (10,160-9550 cal B.P.), Early Marcala (8990-7670 cal B.P.), and Middle Marcala (7610-7430 cal B.P.). The number of specimens recorded for each of these strata are listed in Table 4.2.

Table 4.2 Preceramic occupational phases at El Gigante with total number of bones recovered.

Phase	**N total bones**
Early Esperanza	4712
Late Esperanza	3858
Early Marcala	3763
Middle Marcala	2095

The stratigraphy at El Gigante, like that of most rockshelters, represents a palimpsest of activities carried out over a timespan of over 11,000 years. As a result, the stratigraphy is complex and, in some cases, mixed or disturbed by subsequent processes such as rockfalls and intrusive pits and features into earlier strata. This complexity requires a well-defined chronological model and a detailed understanding of the various cultural layers and their vertical and horizontal boundaries. To do this, the existing Bayesian chronological model for the site (Kennett et al. 2017) was complemented by a detailed analysis of the stratigraphy conducted by Hirth (personal communication, 2017). This allowed for the determination of the chronological placement of most of the excavated levels I analyzed for this dissertation (Table 4.3). This is fundamental for understanding the sequence and timing of the broad behavioral changes that took place during the Preceramic period at the site.

Table 4.3 Chronological placement of levels and strata from El Gigante analyzed in this study. EE – Early Esperanza; LE – Late Esperanza; EM – Early Marcala; MM – Middle Marcala. Row shaded in pink indicates intrusive strata (LM – Late Marcala).

Unit 1			**Unit 2**			**Unit 18**			**Unit 19**		
Lvl	**Str.**	**Phase**	**Lvl**	**Str.**	**Phase**	**Lvl**	**Str.**	**Phase**	**Lvl**	**Str.**	**Phase**
15	IVb	LE	16a	III	MM	23	IIIc2	MM	23	III	MM
16a	IV	LE	16b	III	MM	24	IIId3	MM	24	IIId2	MM
16b	IV	LE	17a	IIIe	MM	25	IIIc4	MM	25	IIIe	MM
16c	Ivb	LE	17b	III	MM	26	IIId3.3	MM	26	II/III	LM
			18b	III	MM	27	IIId3.3	MM	27	III	MM
17a	Ivb	EE							31	IIIf2	MM
17b	Ivb	EE	18a	IV	EM	28	IIIe	EM			
17c	Ivb	EE				29	IIIe	EM	28	III	EM
17d	Ivb	EE	18c	III/IV	LE	30	IIIf	EM	29	IIIe	EM
18	Va	EE	19a	Ivb	LE	31	III	EM	30	IIIf2	EM
19	VI	EE	19b	IV	LE	32a	III	EM	32	IIIf2	EM
						32b	III	EM	33	IIIf2	EM
			20	Ivb	EE	32c	III	EM	34	IIIf2	EM
			21a	Va	EE						
			21b	Va	EE	33a	IIIf-IV	EE	35	Ivb	LE
						33b	IIIf	EE	36	Ivb	LE
						34	Ivb	EE			
						35	V	EE	37	Vb	EE
						36	V	EE	38	Ivb	EE
						37	V-VI	EE	39	Vb	EE
						38	Va	EE	40	VI	EE
						39	Va	EE	41	VI	EE
									42	VIIa	EE

4.3 Identification Methods

Identification of the faunal assemblage took place at two different zooarchaeology laboratories with extensive comparative collections. I analyzed Units 18 and 19 at the PSU Zooarchaeology Laboratory and Units 1 and 2 at the Zooarchaeology Laboratory of the University of Missouri. Additionally, I borrowed a complete adult peccary skeleton (*Pecari tajacu*) from the Illinois State Museum and relied on the Florida Museum of Natural History's

Environmental Archaeology Image Gallery (https://www.floridamuseum.ufl.edu/envarch-gallery/) for the identification of other tropical species not represented in the comparative collections. Several skeletal anatomy guides including *Mammalian Osteology* (Gilbert 1980), *Human and Nonhuman Bone Identification: A Color Atlas* (France 2009), *Teeth: Second Edition* (Hillson 2005), *Mammal Bones and Teeth* (Hillson 1992), and *An Osteology of Some Maya Mammals* (Olsen 1982) also provided guidance.

Faunal specimens were identified to the most specific taxonomic level possible using diagnostic features and landmarks. Some elements and fragments were classified to the level of genera, although the majority were only classified to class (e.g., bird, reptile, rodent) or not classified at all. Because the faunal remains recovered from El Gigante are small and highly fragmented (77% of specimens measure <2cm), I used diagnostic zones to identify each specimen, whenever possible. This method divides the major bones of animals into standardized morphologically distinct zones (Figure 4.1; Cohen and Serjeantson 1996; Dobney and Rielly 1988; Knusel and Outram 2004; Watson 1979). This method has the benefit of accurately and systematically quantifying the segments of particular elements that are present in an assemblage irrespective of taxon, which in turn makes the quantification of specimens and individuals simpler and less subjective. The usage of diagnostic zones also allowed for accurate recording of the presence and location of evidence of cultural and natural damage on each bone without using subjective descriptions. For the purposes of this analysis I relied on the diagnostic zones defined by Dobney and Rielly (1988) for most post-cranial elements. I utilized the diagnostic zones defined by Knusel and Outram (2004) for the cranium, and those of Cohen and Serjeantson (1996) for avian bones. Specimens that included fragments (or were themselves fragments) not identified by these sources were assigned a separate zone and a note was made as to what this zone represented.

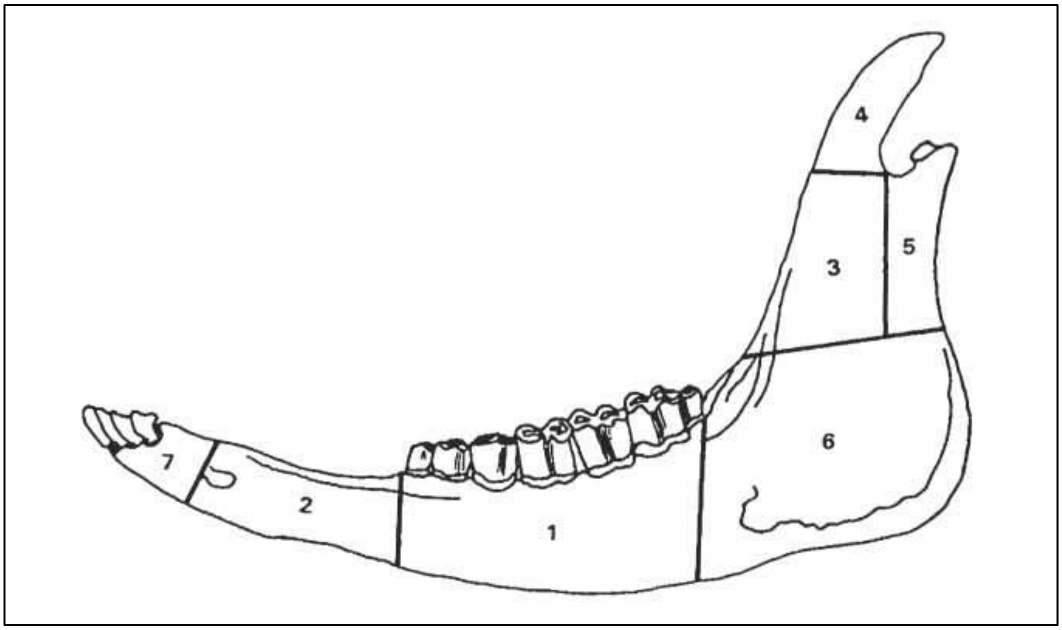

Figure 4.1 Example of diagnostic zones on a cervid mandible. Zones: 1 – tooth row; 2 – diastema including mental foramen; 3 – coronoid process; 4 – anterior portion of ascending ramus; 5 – condyle and neck; 6 – ascending ramus; 7 – corpus mandibulae Dobney and Rielly 1998: Figure 7).

Besides identifying any cultural and natural damage on each specimen I also recorded the specimen side and inferred age, including the criteria used for determining age. Three age categories were used (adult, juvenile, and neonate) and their assignation was based on bone size, epiphyseal closure, and patterns in tooth eruption and wear (the latter following Purdue 1983; Severinghaus 1949). Sex was not a variable I was able to record given the extremely fragmentary nature of the El Gigante faunal remains. Taphonomic factors such as burning, weathering, and carnivore damage were also recorded for each specimen (Lyman 1994).

Evidence of burning and heat alteration on bone was recorded using three different categories based on those proposed by Stiner and colleagues (1995) using specimen color and appearance (Table 4.4). Whenever possible, burning was also identified to a particular diagnostic zone in a specimen.

Table 4.4 Categories of burning damage based on specimen color and appearance.

Category	**Category Name**	**Description**
0	Unburned	No modification.
1	Burned	Red-brown, dark brown, some surface cracking.
2	Carbonized	Blue-black to pure black, some surface spalling.
3	Calcined	Blue-white to pure white, powdery and friable.

One taphonomic process unique to El Gigante is the presence of crystalline and calcium carbonate ($CaCO_3$) concretions, which are present on a large number (ca. 28%) of the analyzed specimens (Figure 4.2). We do not know how these concretions are forming or have formed. These concretions are difficult to remove mechanically without damaging the bone, and only dissolved after bone samples were pre-treated with hydrochloric acid in the course of other analyses carried out as part of this study, which suggests these concretions are made of calcium carbonate. As a result, concretions were not removed as part of my analyses. In addition, and most importantly for my analyses, these concretions often obscured other taphonomic evidence as well as diagnostic landmarks on bone. Specimen weight was not recorded because of the degree to which faunal specimens were differentially and unpredictably affected by infiltration of calcium carbonates and other concretions.

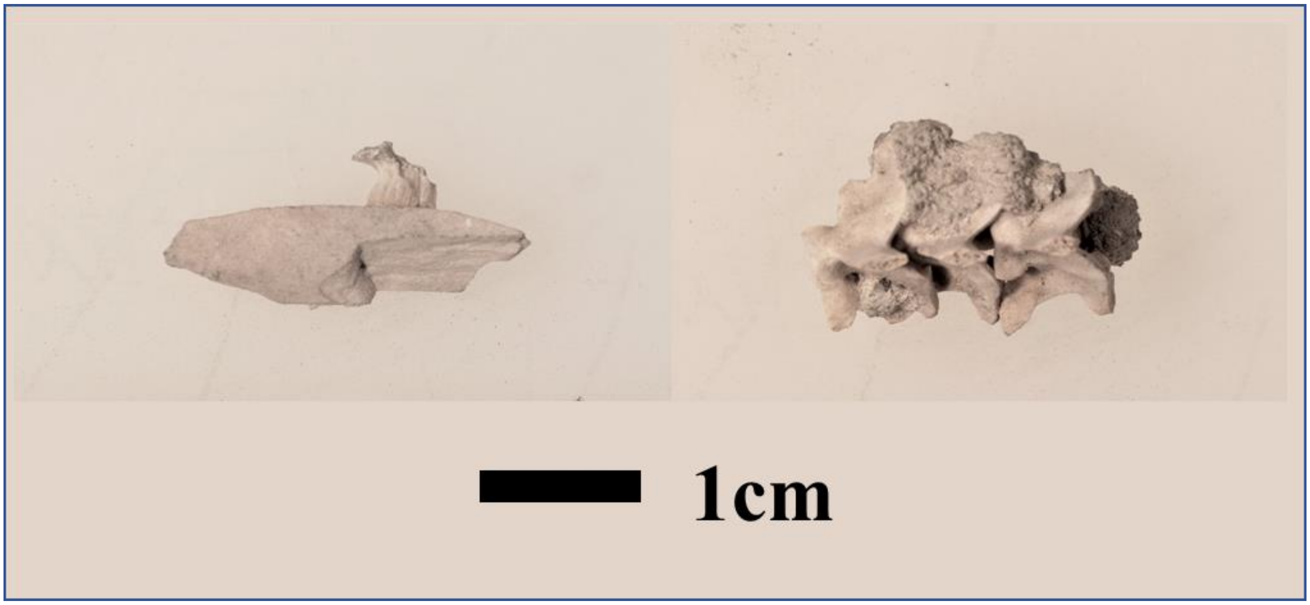

Figure 4.2 Bone fragments with crystalline concretions. Left: unidentified bone. Right: serpent (Colubridae) vertebrae fused by concretion.

Several variables were also recorded to identify and control for the degree of fragmentation of the assemblage. First, greatest length (GL) and greatest breadth (GB) were measured for each identified specimen using a digital caliper with 0.01mm accuracy. Greatest length and specimen area have both been shown to correlate well with the degree of fragmentation of an assemblage (Cannon 2013: 416). Specimens that were not identified to a particular taxon were quantified according to seven size classes: <10mm, 10-15mm, 15-20mm, 20-30mm, 30-40mm, 40-50mm, and >50mm (Table 4.5). Specimens in the <10mm class were quantified according to whether they were burned or not; burning in this case being determined by specimen color and appearance (see Outram 1998: 165).

Table 4.5 Greatest length of bone (GL) by occupational phase.

Size range (mm)	**EE**	**EM**	**LE**	**MM**	**Totals**
<10	856	1055	354	245	2510
10-15	1139	1118	1092	448	3797
15-20	1185	811	1058	407	3461
20-30	859	504	652	275	2290
30-40	209	90	118	47	464
40-50	53	17	42	17	129
50+	17	8	10	3	38
Totals	4318	3603	3326	1442	**12689**

Unidentified specimens in all other size classes were quantified according to four categories: axial ends (e.g., condyles), cancellous bone fragments, and burned and unburned shaft fragments. All bones larger than 40mm (both identified and unidentified to taxon) were analyzed for fracture patterns in order to determine whether these fractures were intentional or post-depositional in nature following the procedure outlined by Outram (1998, 2001, 2002). This approach assigns a score of 0, 1 or 2 to three different criteria related to the processes and contexts that affect fractures: fracture outline or shape, fracture angle relative to cortical surface, and fracture texture or roughness. Lower scores suggest the fracture of a fresh bone, and thus intentionally caused, while higher scores suggest a fracture that occurred once the bone was dry, or post-depositionally. Tallied together, these three scores compose the Fracture Freshness Index (FFI). FFI scores of 0-2 suggest fresh breaks, scores of 3-5 are indicative of fractures occurring on moderately fresh bones or on bones that were first fractured while fresh and then later, and a score of 6 denotes bones with no evidence of fresh fractures.

4.4 Assemblage Quantification Methods

The principal method used to quantify the faunal remains was the Number of Individual Specimens (NISP; Grayson 1984; Lyman 2008; Reitz and Wing 2008). This quantitative unit of analysis is often thought to be the most accurate reflection of the actual number of individuals (ANI) in an assemblage, particularly in large and diverse assemblages such as the one recovered from El Gigante (Lyman 2018, 2019). Refits within the same level were counted as a single specimen. Isolated teeth were counted as single specimens, while teeth found in mandibles and maxillae were counted together as a single specimen. Because the faunal remains were highly fragmented and often covered by carbonate concretions (see below), and because of the size overlap in many of the species available in the area, the quantification of faunal remains was overall very conservative and avoided the use of ambiguous categories such as “large mammal” (see Driver 2011 for a critical review of such terms). Fragments that were too ambiguous to be securely identified to a particular element were quantified as axial, cancellous, and shaft fragments, as stated above.

The minimum number of individuals (MNI; Grayson 1979, 1984) was also calculated for each of the chronological assemblages as a separate measure of assemblage diversity and to examine changes in population structures over time for the purposes of identifying resource depression (Wolverton et al. 2012). MNI was determined by taking into account element side, age, size, and taphonomy.

4.5 Descriptive Summary of Identified Taxa

A total of 3388 faunal specimens were identified to element or portion, which yielded an MNI of 214 individuals from 25 different taxa (Table 4.6). In the following pages, I describe each of the taxa identified and provide relevant information on their natural history, biology, and ethology. I then briefly review the ethnographic and archaeological literature in order to examine the ways in which these animals might have been procured and processed by El Gigate's inhabitants.

Table 4.6 NISP and MNI values for all identified taxa at El Gigante per occupational phase.

	Occupational Phase									
	EE		**LE**		**EM**		**MM**		**Total**	
Scientific name	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**	**NISP**	**MNI**
Didelphidae	1	1	0	0	4	2	1	1	6	4
Chiroptera	0	0	0	0	2	1	4	2	6	3
Dasypus novemcinctus	222	2	170	2	232	3	279	4	903	11
Sylvilagus sp.	25	4	1	1	6	1	0	0	32	6
Lepus sp.	0	0	0	0	2	1	0	0	2	1
Sciurus sp.	0	0	1	1	0	0	0	0	1	1
Neotominae	0	0	0	0	1	1	1	1	2	2
Sigmodontinae	1	1	3	2	4	2	1	1	9	6
Cuniculus paca	0	0	2	1	0	0	0	0	2	1
Rodentia	49	10	20	3	98	11	116	13	283	37
Canidae	2	1	0	0	7	2	0	0	9	3
Procyon lotor	0	0	0	0	2	1	0	0	2	1
Mephitidae	0	0	0	0	4	2	3	1	7	3
Felidae, small	0	0	0	0	1	1	0	0	1	1
Felidae, large	0	0	0	0	1	1	0	0	1	1
Carnivora	0	0	0	0	4	1	2	1	6	2
Tayassuidae	2	1	7	1	0	0	0	0	9	2
Mazama sp.	4	1	4	1	1	1	1	1	10	4
Odocoileus virginianus	394	7	298	5	257	4	129	4	1078	20
Mammalia	15	0	10	0	44	0	198	0	267	0
Aves	4	2	2	1	6	2	11	1	23	6
Testudines	1	1	0	0	0	0	0	0	1	1
Iguanidae	0	0	2	1	2	1	0	0	4	2
Serpentes	16	1	10	1	2	1	0	0	28	3
Reptilia	6	1	3	1	4	1	0	0	13	3
Decapoda	231	26	135	34	257	22	60	8	683	90
Totals	**973**	**59**	**668**	**55**	**941**	**62**	**806**	**38**	**3388**	**214**

Didelphidae (NISP: 6, MNI: 4)

Material: 5 mandible fragments, 1 cranium fragment.

Eight species of New World opossums (Order Didelphidae) have been identified in Honduras (Marineros et al. 1998). These are opportunistically omnivorous mammals that occupy a range of habitats neotropics including pine and oak forests such as those near El Gigante. The largest species and consequently those most commonly hunted by groups today and in recent prehistory are the common opossum (*Didelphis marsupialis*) and Virginia opossum (*Didelphis virginianus*) (Fridberg 2015; Marineros et al. 1998). These species are nocturnal and are slow and easy to hunt, usually with the help of dogs and a source of light (Marineros et al. 1998). They thrive in areas occupied and disturbed by humans and are resilient to high levels of predation because of their high fecundity (Fridberg 2015).

Dasypus novemcinctus **(NISP: 903, MNI: 11)**

Material: 1 mandible fragment, 4 scapula fragments, 793 scutes, 1 proximal humerus, 1 humerus, 4 radii, 2 proximal radius fragments, 2 radius shaft fragments, 4 distal radius fragments, 5 ulnae, 9 proximal ulna fragments, 3 distal ulna fragments, 7 rib fragments, 26 vertebra fragments, 1 femur, 1 femoral head, 3 distal femur fragments, 1 patella, 1 proximal tibia fragment, 2 astragali, 1 astragalus fragment, 3 calcanei, 1 calcaneus fragment, 19 first phalanges, 5 second phalanges, 2 third phalanges.

Nine-banded armadillos are nocturnal scavengers that thrive in edge and disturbed environments, particularly those impacted by human activity (Escamilla et al. 2000; Stahl 2006, 2008; Stahl and Pearsall 2012). They live in burrows often in the vicinity of settlements or recently cleared fields (Linares 1976). They have high reproductive rates and but research suggests they are susceptible to the effects of overhunting (Hill et al. 2003). However, these effects are ameliorated in areas that remain disturbed by humans for agriculture and horticulture (Emery and Brown 2012; Koster 2009). Armadillos are not very fast and can be easily pursued though they often retreat to their burrows. Highly skilled hunters are able to find these burrows through tracking – or, if they hunt only occasionally, with the help of dogs (Koster 2008)– and then proceed to dig them out with simple tools (Hill et al. 1984). These animals are also captured with traps set against the openings of their burrows (Smith 2003), although the Aché in South America dig armadillos out of their burrows using sticks and capture and kill them by hand (Hill et al. 1984). Recent research shows the communal hunting armadillos increases the return rate for those involved (Janssen and Hill 2014).

***Sylvilagus* sp. (NISP: 7, MNI: 1)**

Material: 2 mandible fragments, 2 maxilla fragments, 2 scapula fragments, 1 proximal humerus fragment, 3 distal humerus fragments, 4 innominate fragments, 2 vertebrae fragments, 1 femur, 4 distal femur fragments, 2 calcanei, 5 first phalanges, 2 phalanx fragments, 1 metatarsal, 2 metatarsal fragments.

Two species of cottontail rabbits are found in Middle America: the eastern cottontail (*Sylvilagus floridanus*) and the forest cottontail (*Sylvilagus brasiliensis*) (Marineros et al. 1998). Both species are similar in size, weight and are largely indistinguishable in terms of their postcranial skeletal morphology (Ruedas et al. 2017). Eastern cottontails are usually found in drier areas while forest cottontail prefer habitats with higher precipitation and humidity (Marineros et al. 1998; Reid 2009). Both species prefer to inhabit forest edges and are usually attracted to disturbed landscapes, particularly anthropogenic ones (Reid 2009; Stahl 2009).

However, forest cottontails prefer to inhabit deciduous or secondary forests (de Sousa e Silva Junior et al. 2015). Both species also prefer flat land over rugged terrain because the latter impedes their movement and speed, which are their main mechanism for predator avoidance (Glebskiy et al. 2018). Because of their exceptionally high fecundity, cottontails can withstand high levels of hunting and predation. Their main method of predator avoidance is speed, and hunting these animals requires the identification of burrows and their capture using nets, traps or by hand (Godinez Guevara and Vasquez Garcia 2003). Research suggests hunting and capturing cottontails using dogs also occurs among some indigenous groups but this is a recent development (Greaves 1997).

***Lepus* sp. (NISP: 2, MNI: 1)**

Material: 2 premolars

Jackrabbits are larger than cottontails and are adapted to more open and arid areas. In Mesoamerica, the majority of these species inhabit the desert scrublands of central and northern Mexico (Flannery 1967), though there are two species, the Tehuantepec jackrabbit (*Lepus flavigularis*) and the white-sided jackrabbit (*Lepus callotis*) that live in tropical and subtropical grasslands and savannahs as far south as Oaxaca (Brown et al. 2018). Similar to cottontails, jackrabbits are captured using nets or traps and sometimes with the help of dogs (Flannery 1966, 1967). Communal jackrabbit drives have also been proposed as a highly effective capture mechanism, this based on ethnographic data from North America and the archaeological record of the arid parts of Mesoamerica, though there is no evidence for this behavior in the tropical areas of the region (see Flannery 1966, 1967).

***Sciurus* sp. (NISP: 1, MNI: 1)**

Material: 1 proximal femur fragment.

Two species of squirrel have been identified in Honduras thus far, the variegated squirrel (*Sciurus variegatoides*) and Deppe's squirrel (*Sciurus deppei*; Marineros et al. 1998). These small arboreal rodents inhabit a wide variety of habitats throughout the continent, though prefer sparsely forested and mountainous area. There is some evidence for squirrel hunting in the archaeological record of semiarid and tropical deciduous forests of northern South America (see Piperno and Pearsall 1998: 187). Ethnographic research in Honduras has also documented squirrel hunting in dense lowland tropical forests (Marineros et al. 1998: 154).

***Cuniculus paca* (NISP: 2, MNI: 1)**

Material: 1 mandible fragment, 1 upper molar fragment.

Pacas are large rodents that inhabit mature and disturbed neotropical forests (Reid 2009). They are primarily vegetarian and are particularly abundant in areas with fruit-bearing trees (Marineros et al. 1998; Martinez-Ceceñas et al. 2020; Perez 1992). They are found in a variety of lowland and highland environments, but prefer to live near permanent sources of water, which they use as a route of escape when pursued (Beck-King et al. 1999; Marineros et al. 1998; Perez 1992). Although pacas prefer primary forest environments (Perez 1992), they also occupy secondary vegetation and agricultural fields, where they do considerable damage (Gallina et al. 2012). Pacas are particularly sought after by hunters in neotropical forests today because of the high yield and quality of their meat (Escamilla et al. 2000; Hill and Hawkes 1983; Koster 2009). Traditionally, pacas are hunted by locating their burrows, blocking hidden exits with obstacles or traps, and then by forcing the animal to escape the burrow (Gallina et al. 2012; Hill and Hawkes

1983; Smith 2003). This form of hunting/trapping is best done collaboratively in groups, which increases the return rate of this particular species (Janssen and Hill 2014). More recently, likely due to a loss of traditional knowledge related to tracking (see Gallina et al. 2012, dogs are used to help hunters locate burrows and chase the prey (Koster 2009). Pacas are hunted year-round by contemporary populations, though hunters prefer to hunt them during the dry season, when these animals gather near sources of water and are easier to pursue (Gallina et al. 2012).

***Procyon lotor* (NISP: 2, MNI: 1)**

Material: 1 cranium fragment, 1 lower molar fragment.

Raccoons are small carnivores found in a number of habitats throughout the Americas. In Middle America they are more often found along watercourses and in wooded areas (Marineros et al. 1998). In neotropical forests these animals have a very restricted geographic distribution and often occur in very low densities (Arita et al. 1990), consequently they are rarely hunted in the region (Escamilla et al. 2000). But raccoons prefer anthropogenically disturbed landscapes, such as garden or field plots, where they do considerable damage. Among contemporary populations, they are often are often killed but rarely consumed (see Koster 2007; Godinez and Vazquez 2003).

Tayassuidae (NISP: 9, MNI: 2)

Material: 1 canine, 3 vertebrae fragments, 1 proximal metapodial fragment, 1 tarsal fragment, 1 first phalanx, 1 second phalanx, 1 third phalanx.

There are two species of peccary in the neotropics, the collared peccary (*Pecari tajacu*) and the white-lipped peccary (*Tayassu pecari*). They inhabit a wide variety of ecosystems including tropical forests and savannahs, but prefer those with abundant fruit-bearing trees whose seeds they help disperse (Beck et al. 2005). White-lipped peccaries are much larger than collared peccaries, and have an average weight of 25-30kg vs. 15-20kg, respectively (see Escamilla et al. 2000; Hill et al. 2003). White-lipped peccaries are more sensitive to and avoid ecosystems disturbed or occupied by humans, while collared peccaries generally thrive in these areas (Daily et al. 2003). The meat of both of these species is highly desired by hunters, but the meat of the white-lipped peccary is often preferred because of its flavor (Altrichter 1999; Koster 2008). Peccaries travel in herds and leave trails that are easy to follow (Hill and Hawkes 1983). However, white-lipped peccaries travel in much larger herds and are much more aggressive than collared peccaries (Cullen et al. 2001). Hunting either species of peccary requires large groups (Koster 2007), though individuals can also be captured with traps (Koster 2009).

***Odocoileus virginianus* (NISP: 1078, MNI: 20)**

Material: 4 antler fragments, 77 cranium fragments, 20 mandible fragments, 12 tooth fragments, 2 scapula fragments, 1 humeral head, 4 proximal humerus fragments, 8 humerus shaft fragments, 13 distal humerus fragments, 30 proximal radius fragments, 7 radius shaft fragments, 11 distal radius fragments, 10 proximal ulna fragments, 3 distal ulna fragments, 132 rib fragments, 229 vertebra fragments, 12 innominate fragments, 12 femoral heads, 5 proximal femur fragments, 7 femur shaft fragments, 19 distal femur fragments, 3 patellae, 5 patella fragments, 9 proximal tibia fragments, 2 tibia shaft fragments, 7 distal tibia fragments, 4 proximal fibula fragments, 212 metapodial fragments, 72 first phalanx fragments, 41 second phalanx fragments, 26 third phalanx fragments, 3 phalanx shaft fragments, 3 astragali, 5 astragalus fragments, 2 calcanei, 10 calcaneus fragments, 55 tarsal/carpal fragments.

There are currently three deer species present in Middle America: white-tailed deer (WTD; *Odocoileus virginianus*), Yucatan brocket deer (*Mazama pandora*) and red brocket deer (*Mazama temama*). All three species have considerable morphological (Cantryll-Stewart 2017) and genetic (Araujo et al. 2016; Escobedo-Morales et al. 2016; Gutierrez et al. 2017) overlap, making their zooarchaeological identification difficult. Moreover, the taxonomy of American deer is currently in flux because phylogenetic studies are revising existing genera and species that have been defined almost exclusively by morphological traits (see Escobedo-Morales et al. 2016; Gutierrez et al. 2017). However, given that these revisions are still in progress, I will use existing classifications throughout the dissertation. WTD are the largest mammal in the region and are often the top ranked species in studies of human subsistence (Emery and Brown 2012). WTD are highly adaptable and inhabit a wide variety of ecosystems. They prefer mosaics of forests and open areas with clearings ideally comprising no more than 60% of the total area in dry subhumid zones and low levels of brush canopy cover and density (Fulbright and Taylor 2001; Mandujano 2016; Ortega-S et al. 2011). WTD are particularly attracted to disturbed landscapes, especially those influenced and managed by humans. Studies of traditional vegetation management systems suggest that they help deer populations recover from overhunting and maintain healthy populations (Mandujano 2016).

Changes in environmental productivity and levels of predation directly affect the body size and mortality profiles of WTD populations (Fulbright and Ortega 2006; Lopez-Arevalo et al. 2011; Wolverton 2008). Specifically, a decline in environmental productivity is expected to cause a decline in amount of available food, resulting in smaller body sizes, but individuals appear to have a greater chance of surviving to an older age than under normal foraging conditions (Wolverton 2008). Increased hunting of WTD, on the other hand, decreases population densities, resulting in improved forage conditions for surviving individuals and results in an increase in body size. At the same time, increased harvest pressure leads hunters to pursue and hunt younger individuals (i.e., of sub-prime age), resulting in younger age profiles (Wolverton 2008).

Hunting deer requires mechanisms that counter the animal's ability to escape and avoid predation and involves driving them to strategic locations on the landscape (rivers, cliffs, walls) or capturing them by surprise from a blind, either during the day or at night (e.g., Koster 2007; Mandujano 2016; Velarde and Cruz 2015). Ethnographic studies of indigenous deer hunting in Middle America indicate that hunters often capture one deer per foray and that larger adult males are preferred over females and juveniles (Koster 2007, 2008, 2009; Mandujano 2016).

***Mazama* sp. (NISP: 10, MNI: 4)**

Material: 1 antler fragment, 1 cranium fragment, 2 calcanei, 2 astragali, 4 naviculocuboids, 2 naviculocuboid fragments.

Brocket deer, unlike WTD, prefer to forage in densely forested habitats, and while they are more often found in the lowlands (Marineros et al. 1998; Perez-Crespo et al. 2012). Recent studies show these species inhabit the mountainous highlands of Middle America as well (see Perez-Solano and Mandujano 2013). Brocket deer prefer mature forests and are highly averse to human disturbance, making them more difficult to hunt (Koster 2009; et al. 2016; Marineros et al. 1998).

Although Brocket deer are generally smaller than WTD, modern specimens of both genera overlap in size (Cantryll-Steward 2017; James 2013). Brocket deer species are difficult to differentiate skeletally, and in this research I only identified specimens to genus (*Mazama* sp.) by using metric and non-metric methods for identifying each of these species, though none of these have been evaluated systematically. Some of the existing techniques rely on the presence of nearly complete and complete specimens such as carpals, tarsals, and metatarsals and rely on size as the method for distinguishing different species (Cantryll-Stewart 2017; James 2013; von den Driesch 1976). To help with identifications, I compiled metric data on the elements mentioned above from published literature (Cantryll-Stewart 2017; Densmore 2009; Purdue 1989) and an online photographic archive (Florida Museum of Natural History Environmental Archaeology Image Search; FLMNH 2020) and compared these with complete specimens from the El Gigante assemblage. Based on the complete specimens from El Gigante available for measurement, I used the following measurements (following von den Driesch 1976 and Purdue 1989): astragalus greatest length (GLl) and greatest medial and lateral depth (Dm, Dl); calcaneus greatest length (GL) and greatest depth (GD, also known as greatest width or W; see Densmore 2009); and naviculo-cuboid width (W) and depth (D). All measurements from the FLMNH were estimated based on the image scale and are thus less than precise. But the compiled data show a clear separation of size between WTD and brocket deer. Some of the El Gigante specimens fall in between the species, in which case they were classified as cervidae.

Astragali measurements suggest two of the five whole astragali recovered from El Gigante were likely from brocket deer (Table 4.7, Figure 4.3). One likely belongs to a WTD. The remaining two specimens straddle the size of both species and I have designated them as cervidae.

Table 4.7 Skeletal measurements of astragali from existing literature and El Gigante specimens. GLl – astragalus greatest length, Dm/Dl/ASLD – astragalus greatest medial and lateral depth. References: Cantryll-Stewart 2017: Table 8-1, Figure 6-1; Florida Museum of Natural History Environmental Archaeology Image Gallery.

Specimen(s)	**Species**	**GLl**	**Dm/Dl/ASLD**
EG 18.34.41	Brocket deer	25.68	18.90
EG 1.16c.6	Brocket deer	27.56	17.32
EG 1.15.2	Cervidae	30.30	21.12
EG 2.21b.6	Cervidae	30.40	21.41
EG 1.16c.5	White-tailed deer	33.84	19.69
Modern	White-tailed-deer	33.98	18.26
Modern	White-tailed-deer	37.09	19.69
Modern	White-tailed-deer	35.5	19.43
Modern	White-tailed-deer	39.59	22.09
El Mirador Preclassic	White-tailed-deer	40.39	23.33
El Mirador Early Classic	White-tailed-deer	40.48	22.69
El Mirador Early Classic	White-tailed-deer	37.9	18.75
Illinois males (mean)	White-tailed-deer	42.91	23.85
Illinois females (mean)	White-tailed-deer	40.08	22.3
FLMNH modern 4573	White-tailed-deer	37	N/A
FLMNH modern 1556	Brocket deer	26	N/A
FLMNH modern 8851	Brocket deer	26	N/A
Guatemala	Brocket deer	20	14.5
Guatemala	Brocket deer	20.8	15
Trinidad Island	Brocket deer	23.7	19.7
Trinidad Island	Brocket deer	25.2	19
Trinidad Island	Brocket deer	26	18.8

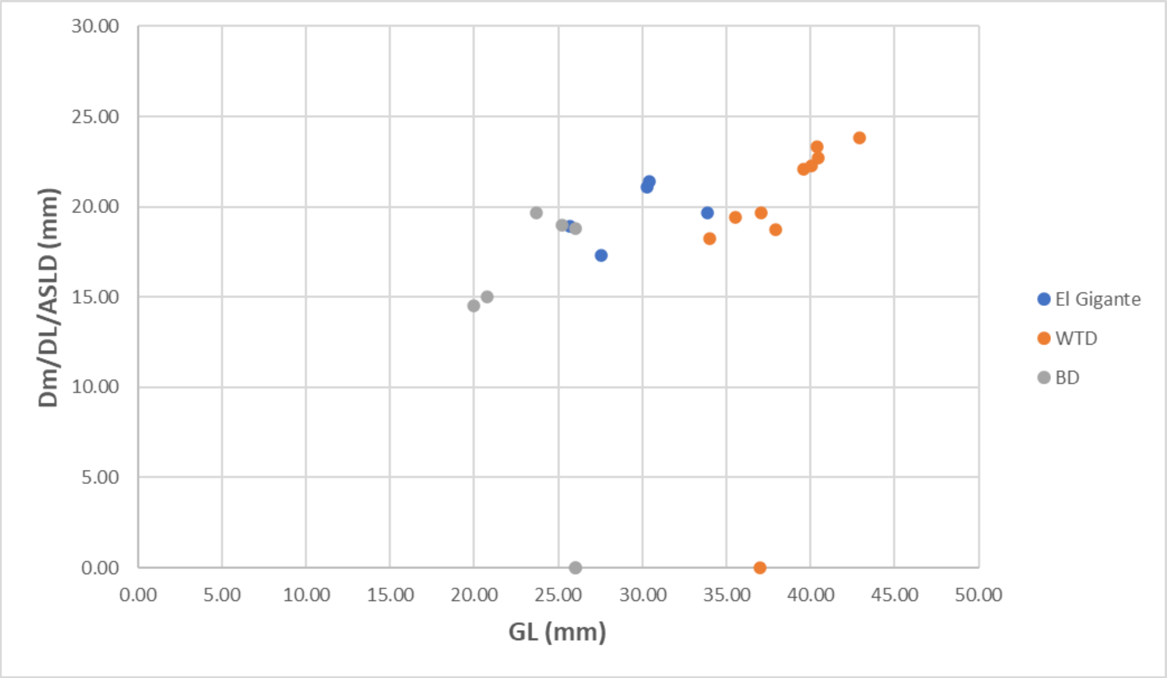

Figure 4.3 Greatest length (mm) and greated depth of astragali from published sources and El Gigante.

Of the four whole calcanei measured from El Gigante, two likely represent WTD and two brocket deer, without any significant overlap in size (Table 4.8, Figure 4.4).

Table 4.8 Skeletal measurements of calcanei from existing literature and El Gigante specimens. GL – greatest length, GD – greatest depth. References: Cantryll-Stewart 2017: Figure 7-9; Densmore 2009: Table 10; Florida Museum of Natural History Environmental Archaeology Image Gallery.

Specimen(s)	**Species**	**GL**	**GD**
EG 1.17b.1	White-tailed deer	70.34	20.83
EG 18.35.25	White-tailed deer	73.55	21.83
EG 1.16c.8	Brocket deer	56.74	20.81
EG 1.15.3	Brocket deer	58.70	20.44
Modern	White-tailed-deer	76	25.5
Modern	White-tailed-deer	80.6	27
Modern	White-tailed-deer	81.6	27.3
Modern	White-tailed-deer	89	29.5
Historic	White-tailed-deer	81	26.3
Historic	White-tailed-deer	82.5	28.5
Ft. Hood males (mean)	White-tailed-deer	84.33	28.58
Ft. Hood females (mean)	White-tailed-deer	79.46	27.38
Austin males (mean)	White-tailed-deer	82.13	27.93
Austin females (mean)	White-tailed-deer	77.88	26.97
FLMNH modern 1556	Brocket deer	54.5	N/A
FLMNH modern 8851	Brocket deer	57	N/A

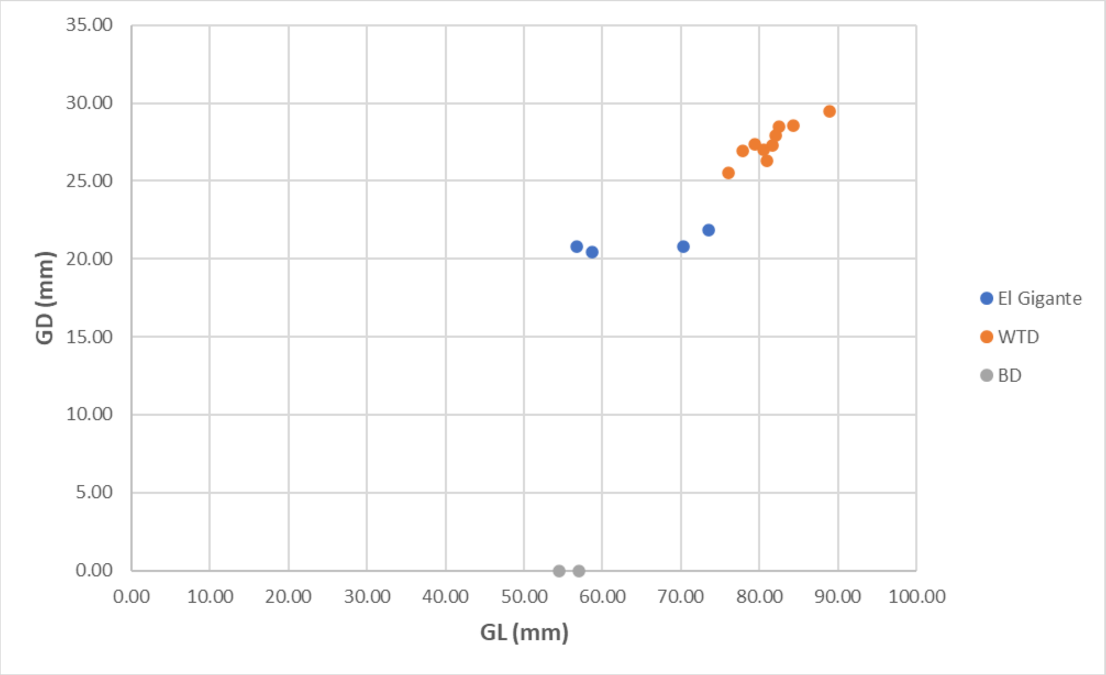

Figure 4.4 Greatest length (mm) and greatest depth of calcanei from published sources and El Gigante.

Of the six naviculo-cuboids measured from El Gigante, four are smaller than the brocket deer specimens from the literature, while two fall in between both species, though are closer to the WTD measurements and were assigned as such (Table 4.9, Figure 4.5). Two of these specimens are fragments of a single element and are circled in red in Figure 4.5.

Table 4.9 Skeletal measurements of naviculo-cuboids from existing literature and El Gigante specimens. W – width, D – depth. References: Densmore 2009: Table 10; Florida Museum of Natural History Environmental Archaeology Image Gallery.

Specimen(s)	**Species**	**W**	**D**
EG 18.26.1	Brocket deer	17.84	14.57
EG 1.15.13	White-tailed-deer	18.97	20.71
EG 1.17b.2	White-tailed-deer	19.37	20.60
EG 1.17c.12	Brocket deer	21.20	15.09
EG 1.17c.13	Brocket deer	24.63	13.09
EG 18.35.35	Brocket deer	25.71	9.70
Ft. Hood males (mean)	White-tailed-deer	30.59	26.39
Ft. Hood females (mean)	White-tailed-deer	28.59	24.53
Austin females (mean)	White-tailed-deer	28.63	24.3
FLMNH modern 4573	White-tailed-deer	29	22
FLMNH modern 1556	Brocket deer	22	19
FLMNH modern 8851	Brocket deer	21	16

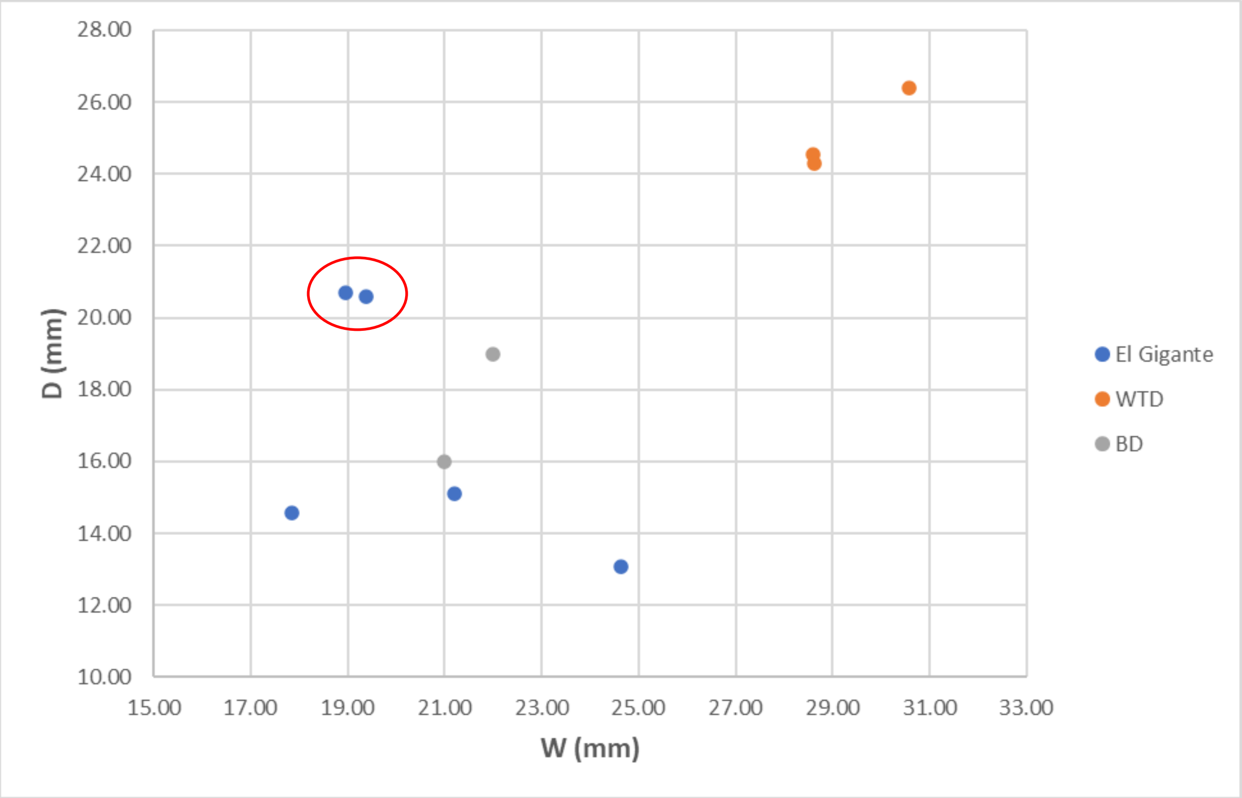

Figure 4.5 Width (mm) and depth (mm) of naviculo-cuboids from published sources and El Gigante. Specimens circled in red are two halves cut from the same bone.

Pseudothelphusidae (NISP: 683, MNI: 90)

Material: 176 chela fragments, 507 carapace fragments (carapace remains were too fragmented to identify individual elements).

The remains of crabs, the third most abundant taxon in the assemblage, have tentatively been identified as belonging to the Pseudothelphusidae family of freshwater crabs common to the highlands of the neotropics (John Christy and Javier Luque, personal communication). This family of crabs inhabit low-velocity creeks and rivers with angular rocky substrates and abundant shade, such as the nearby Estanzuela River, though some species are also adapted to living in caves (Cumberlidge et al. 2014; Rólier-Lara et al. 2013). Pseudothelphusid crabs prefer to inhabit the edges of water bodied and hide under rocks and fallen vegetation (Alvarez et al.

2012). Decapods such as pseudothelphusid crabs are considered a delicacy among Yanomami foragers in Brazil (Magalhães et al. 2006). These crabs are captured using basket sieves if found underwater and by hand if on land, after which they are immobilized and transported to camp for consumption. Once captured, crabs are roasted – either directly on coals or wrapped in leaves if large quantities are available – then consumed (Magalhães et al. 2006).

4.6 Habitat Fidelity Analysis

Habitat fidelity analysis identifies the various habitats represented within a faunal assemblage based on an understanding of species ecology, with the goal of evaluating patterns in the use of different habitats by the human populations who created the assemblage (Emery and Thornton 2008). This analysis is based on the quantification of habitat fidelity values for taxa inhabiting five different habitats: mature or closed-canopy forest, secondary or disturbed forest, rivers, wetlands and swamps, open habitats with scattered trees, and zones of human residential occupation. These values were determined using modern ecological data from neotropical species (Emery and Thornton 2008: Table 3). Only specimens identified to at least the level of taxonomic family are included in the analysis, which at El Gigante corresponds to 11 taxa (Table 4.10). The only taxon whose habitat fidelity values were added for this study was the pseudothelphusidae freshwater crab family, whose members strictly inhabit riverine and shoreline habitats.

Table 4.10 Habitat fidelity values of identified taxa at El Gigante. Habitats include: mature/closed canopy forest (MF), secondary/disturbed forest (SEC), riverine/lacustrine and shoreline habitats (RIV), wetland/swamp habitats (WET), habitats with low or scattered arboreal vegetation (including agricultural fields and savannas) (AGR), and cleared habitats around human habitation areas (RES).

Scientific name	**MF**	**SEC**	**RIV**	**WET**	**AG**	**RES**
Didelphidae	0.1	0.5	0.2			0.2
Dasypus novemcinctus	0.2	0.4			0.4	
Sylvilagus sp.		0.5			0.5	
Sciurus sp.	0.5	0.5				
Cuniculus paca	0.25	0.25	0.2	0.2	0.1	
Procyon lotor	0.1	0.15	0.25	0.25	0.1	0.15
Mephitidae		0.6	0.1	0.1	0.2	
Tayassuidae	0.6	0.2			0.2	
Mazama sp.	0.6	0.3		0.1		
Odocoileus virginianus	0.1	0.45			0.45	
Pseudothelphusidae			1			

The index of the relative representation of a particular habitat (H_i) in an assemblage is calculated using the following formula:

$$H_i = \sum(NISP_x \times f_{Hx})$$

Where $NISP_x$ refers to the number of identified specimens of taxon *x* and f_{Hx} refers to the fidelity value for that particular taxon in that particular habitat.

4.7 Geoarchaeological Methods

A subset of the sediment samples collected by previous excavations at El Gigante (n = 15, see Table 4.11) was analyzed using a suite of geoarchaeological, geochemical, and magnetic prospecting methods in order to infer the depositional context for the faunal remains and to determine if it was feasible to examine occupational intensity using these materials. These sediment samples all come from a column removed from the south wall of Unit 3 and corresponding to the strata later excavated from Unit 18 (Scheffler 2008: 50). The column measured 5x5 cm and samples were bagged according to observed strata, though strata thicker than 5cm were bagged separately. The analyses I conduced were a pilot study meant to inform future geoarchaeological research at the site, and only a small subset of samples was selected for analysis. While other sediment columns were also extracted during excavation of the shelter, these have already undergone charcoal and pollen analysis and can no longer be feasibly analyzed for the purposes of this dissertation. All analyses were conducted at the Environmental Archaeology Laboratory at Southern Methodist University. Aliquots of each sample were then taken to determine soil pH, phosphorus concentrations, organic carbon and charcoal concentrations, and magnetic susceptibility. Soil pH was measured by creating a 1:1 sediment to deionized water slurry and analyzing it with an Oakton Eco Tester pH 2 meter. pH in this case allowed for an examination of the depositional context of the faunal assemblage, though high pH values are also associated with the deposition of ash (Barba 2007; Barba and Denis 1983; Barba et al. 1995).

Table 4.11 Sediment samples analyzed as part of this dissertation.

Sample	**Sample weight (g)**
18-8	19.9
18-13a	29.3
18-16	19.9
18-18	22.3
18-23	30.2
18-24	30.6
18-27	19
18-30	21
18-31	20.7
18-32b	21.7
18-34	25
18-36	24.6
18-38	24.1

Phosphorus concentrations were extracted by adding a 20 mL of 10% Mehlich II weak-acid solution to 2 g of powdered sample and were measured using molybdate colorimetry following the procedure developed by Terry and colleagues (2000). Phosphorus concentrations have been widely used for the study of living surfaces in Mesoamerica (e.g., Fulton 2015; Fulton et al. 2013; Lamoureux-St-Hilaire et al. 2019; Middleton et al. 2010; Mixter 2016; Wells 2003; Wells et al. 2007, 2017) and elsewhere (e.g., Roos and Nolan 2012) to infer variation in the intensity of deposition of organic wastes as a proxy for the intensity of occupation and the identification of activity areas.

Percent organic carbon (% OC) and charcoal concentration are related but independent proxies for the intensity of occupation that are sensitive to both the deposition of organic wastes and the deposition of hearth byproducts, including ash (Ball 1964; Roos and Nolan 2012; Viberg et al. 2013). % OC and charcoal concentration were determined using a variant of the acid digestion and loss-on-ignition (LOI) protocol described by Winkler (1985) and developed by

Roos (n.d.). This method estimates both burned and unburned organic matter gravimetrically following chemical digestion of a sample in hydrochloric (HCl) and concentrated nitric acid (HNO_3) followed by LOI.

4.8 Summary of Methodology and Procedure

The zooarchaeological methods and procedures outlined in this chapter aim to provide the data necessary to evaluate the major components of the BSR hypothesis in the neotropics from the unique faunal assemblage from El Gigante. Previous studies of Preceramic subsistence patterns in the region suggest Preceramic groups throughout Middle America already had diverse a diet early in the period that broadened over time, presumably as a response to resource depression (Flannery and Wheeler 1985; Piperno and Pearsall 1998). However, these studies have relied on small and in some cases chronologically limited (i.e., Guilá Naquitz, see Chapter 3) assemblages, given the preservation conditions across the neotropics. As a result, these studies have been largely descriptive, and have not addressed the tenets of this hypothesis, much less how these have been revised by more recent approaches that apply some of the expectations of Niche Construction Theory. The size and state of preservation of the El Gigante faunal assemblage require a robust methodology that can examine changes in subsistence and mobility patterns over time as well as changes in the local landscape, all while controlling for the taphonomic processes that conditioned the preservation of this assemblage.

CHAPTER 5:

ZOOARCHEOLOGICAL AND GEOARCHAEOLOGICAL RESULTS

I analyzed a total of 14,429 specimens from four different excavation units at El Gigante, representative of the four Preceramic strata identified at the site (Kennett et al. 2017). This number includes all identified and unidentified specimens. The analyzed sample represents approximately 24% of the ca. 60,000 recovered specimens recovered from all excavated strata at the shelter (Scheffler 2008). El Gigante’s faunal assemblage is well-preserved despite the impact of a number of taphonomic processes on the assemblage. My results of analyses presented here suggest that the collection of data from these specimens was unimpeded by taphonomic degradation.

The quantities of specimens recovered varied vertically and horizontally, which suggests variability in the use of rockshelter space over time and space. A refit analysis of the faunal materials recovered from one of the four excavation units indicates that present understanding of the site’s chronology is generally robust, although stratigraphic mixing as a result of human and non-human factors is present, as indicated by previous research (Kennett et al. 2017; Scheffler 2008; Scheffler et al. 2012). Significant noncultural taphonomic processes at the site are chemical rather than physical, though these impact the bone only at the molecular level.

Extensive purposeful fragmentation of even the most robust skeletal elements (i.e. phalanges), as indicated by fresh breaks in the bone, was the largest impediment for the identification and analysis of the faunal remains from El Gigante. Only 23.5% of all analyzed specimens were identified to taxon (NISP = 3,388). Most of the identified assemblage belongs to a limited number of taxa, which supports the role of El Gigante as one of several sites/areas utilized by foragers inhabiting the highlands of southwestern Honduras (Scheffler 2008; Scheffler et al. 2012). The largest of the taxa identified was white-tailed deer (WTD; *Odocoileus virginianus*) and it would appear El Gigante was largely used for processing deer carcasses and working on the tools necessary to capture this prey (see Iceland and Hirth 2021).

Most pertinent to this dissertation and to the examination of the adaptive changes taking place during the Preceramic in Middle America, my analyses suggest resource depression of deer and a loss of foraging efficiency occurred periodically at El Gigante, though these changes did not always result in a broadening of the diet, a process that occurred gradually throughout the Preceramic occupation of the site irrespective of prey abundances. Related to this, faunal and geoarchaeological data collected in this project suggest a general increase in the intensity of use of the rockshelter over time, leading up to a long period of abandonment during the Late Archaic (ca. 7100-4200 cal B.P.).

5.1 Distribution of the Faunal Assemblage

Faunal remains accumulated at a lower rate in older, deeper strata and increased over time (Table 5.1, Figure 5.1), suggesting that more animals were consumed during later occupations of the shelter. This correlates well with the results of my geoarchaeological analyses (see Section 5.5 below) that indicate an increase in the intensity of human occupation of the shelter over time via increased charcoal and phosphorus input (see Barba 2007; Marwick 2005; Oldfield and Crowther 2007; Roos and Nolan 2012; Rosendahl et al. 2014).

Table 5.1 Total number of specimens (NSP) non-standardized and standardized per century, by occupational phase (EE-Early Esperanza, LE-Late Esperanza, EM-Early Marcala, MM-Middle Marcala).

	EE	**LE**	**EM**	**MM**
Phase duration (years)	790	610	1320	180
NSP	4,761	3,805	3,889	1,974
Std NSP	602.66	623.77	294.62	1,096.67

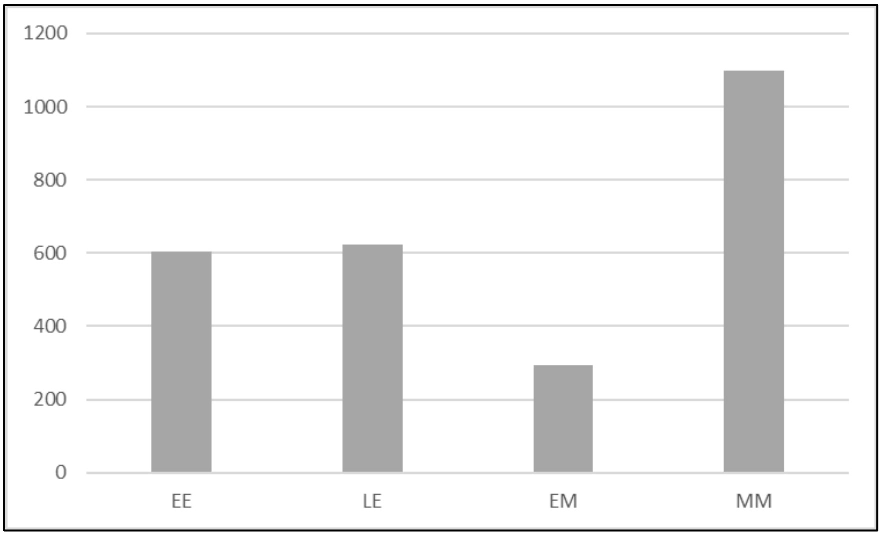

Figure 5.1 Distribution of all analyzed faunal specimens (NSP standardized per century) by occupational phase.

The spatial distribution of bone according to excavation unit is highly uneven (Table 5.2). Units 1 and 2 contain markedly less bone than units 18 and 19. This difference is due in large part to the volume of sediment excavated from each excavation unit. While a detailed spatial analysis of the excavated strata is pending (Hirth, personal communication, 2018), I estimated the volume of the sediments excavated from the preceramic levels of these four units using excavation depths (Scheffler 2008). These estimates show units 18 and 19 had almost twice the volume of excavated sediment than units 1 and 2. However, when NSP counts are standardized per cubic meter of excavated sediment, Unit 1 has the densest amount of material followed by units 18 and

19, with unit 2 having the lowest density of faunal materials. An examination of excavation profile drawings (Scheffler 2008: Appendix B) shows the Preceramic strata are thinnest in Unit 2 and thickest in Unit 1. Given that these units are adjacent to each other, these differences in thickness might be due to the spatial segregation of activity patterns. For example, no features were identified during the excavation of the preceramic strata of Unit 1, while Unit 2 contains a large and deep pit feature (Feature 3) dated to the Middle Marcala dug into Early Marcala and Late Esperanza levels, as well as a living floor surface dated to the Early Marcala phase (Scheffler 2008). Units 18 and 19 also contained traces of this living floor and evidence for small, shallow pit features (Features 14 and 15; see Scheffler 2008: 101).

Table 5.2 Stratigraphic and faunal assemblage information for each excavation unit analyzed for this dissertation.

	Unit 1	**Unit 2**	**Unit 18**	**Unit 19**
Levels analyzed	15-19	16a-22	23-39	23-42
Avg starting depth (cm)	88.4	81	51	72
Avg ending depth (cm)	109	112.6	105	128.6
Avg volume of excavated strata (m^3)	0.21	0.32	0.54	0.57
NSP	2,476	1,527	5,303	5,123
NSP/m^3	12,019.42	4,832.28	9,820.37	9,051.24

The El Gigante occupational chronology is well established (see Chapter 2; Kennett et al. 2017; Scheffler et al. 2012). Finer-grained stratigraphic concordance work is ongoing and requires additional dates as well as a detailed evaluation of excavation records and material remains, both of which are outside the goals of this dissertation. Stratigraphic mixing is a common occurrence in rockshelters with archaeological remains, particularly those with fine-grained sediments such as El Gigante (Collins 1991; Walthall 1998). I conducted a refit analysis of the specimens identified in Unit 18 (n=1592 or 11% of the analyzed assemblage) to explore the stratigraphic integrity of El Gigante. There were refits between levels 23-24, 24-25-29, 25-29, and 38-39. Two of these refits, corresponding to conjoins of an armadillo ulna and radius between units 24/25-29, suggest stratigraphic mixing between these levels, which have been dated to the Middle and Early Marcala, respectively, and are 6cm apart in depth (Scheffler 2008: 429). Stratigraphic mixing has also been identified by radiocarbon dating at the site (Kennett et al. 2017), though this is largely limited to the upper strata at the site, which have been impacted by later period human activities such as burials and recent looting (Scheffler 2008). The Preceramic strata are largely intact and what mixing occurs can largely be explained by pit features from later time periods excavated into underlying strata (see Scheffler 2008). Even so, the overall chronology at El Gigante remains robust and well constrained, particularly when viewed from a broad temporal perspective, such as the one I employ in this dissertation, which focuses on examining behavioral changes across identified Preceramic occupational phases.

5.2 Taphonomy of the El Gigante Faunal Assemblage

Excellent preservation conditions within the El Gigante rockshelter have allowed for the recovery of organic remains beyond the fauna including textiles, fibers, and macrobotanical remains. The unique geochemistry of the El Gigante depositional matrix and the environmental conditions at the site – very stable humidity and temperature levels – have permitted this preservation. In addition, the highly alkaline nature of the shelter's matrix (mean pH = 9, see Section 5.6 below) likely prevented bacterial growth and the consequent demineralization of bone (see Child 1995), and significant bioturbation of the deposits. Both of these are taphonomic processes that negatively impact neotropical faunal assemblages, particularly those recovered from caves and rockshelters. However, taphonomic processes unique to El Gigante did affect the faunal assemblage. In this section, I summarize these processes and how they impacted the assemblage. This section begins by describing the impacts of various taphonomic processes identified at El Gigante including deposited or precipitated carbonates, weathering, burning, and non-human bone damage. I then examine the fragmentation of the assemblage, which influenced and hindered taxonomic and taphonomic identification.

5.2.1 Presence and impacts of carbonate concretions on bone

The geochemistry of the El Gigante matrix led to the precipitation of calcium carbonate ($CaCO_3$) on many of the faunal specimens recovered (see Figure 4.2). A large number of the bones from the analyzed occupational phases have concretions (n=594, 17.5%). Unit 1 has the highest counts of bones with concretions, while Unit 19 has the fewest (Table 5.3). Chronologically, bones have more concretions in younger than older strata, with the exception of the Late Esperanza contexts (Table 5.4).

A contingency table analysis was used to evaluate differences in the distribution of bones with concretions across excavation units and chronological phases, standardized per century and excavated volume. Results suggest there are statistically significant differences between excavation units (G = 491.593, *p*=.000) but not between occupational phases (G = 13.999, *p*=.122). Freeman-Tukey deviates reveal that bones with concretions are significantly overrepresented in strata from Unit 1 and underrepresented in Unit 18 and 19 contexts. Unit 1 also has the thinnest Preceramic deposits in terms of excavated volume, and the abundance of carbonate concretions in this unit might be related to *in situ* chemical weathering, whereby ash carbonates dissolved and were translocated to and precipitated on bone. This would simultaneously increase the rate of concretions and decrease sediment volume. Although there are no statistically significant differences between occupational phases, Late Esperanza strata contain a much larger number of bones with concretions (28.3%), followed by bones in Middle Marcala contexts (19.7%). While existing data cannot explain the high incidence of concretions in Late Esperanza strata, my data and other datasets analyzed from the shelter (macrobotanical remains and lithic artifacts) suggest occupations were longer and more intensive during the Middle Marcala (Scheffler 2008; Scheffler et al. 2012). Longer and more intensive occupations likely resulted in higher amounts of ash being deposited, leading to more carbonate precipitation in bones. However, these interpretations need to be evaluated further, especially with geoarchaeological and geochemical data that are presently unavailable for the site.

Table 5.3 Faunal specimens (NISP) with concretions by excavation unit by number and percentage, as well as standardized per volume of excavated sediment (m^3). Freeman-Tukey deviates are in parentheses and bolded values are significant at *p*=.05 (± 1.47).

Unit	**NISP with concretions**	**% of identified bones with concretions**	**NISP with concretions, standardized**	**Total NISP**
1	185	34.39	898.06 **(12.89)**	538
2	74	22.56	234.18 (0.95)	328
18	252	15.83	466.67 **(-6.76)**	1592
19	83	8.92	146.64 **(-13.04)**	930

Table 5.4 Faunal specimens with concretions by occupational phase by number and percentage, as well as standardized per century. Freeman-Tukey deviates are in parentheses and bolded values are significant at *p*=.05 (± 1.47).

Phase	**NISP with concretions**	**% of identified bones with concretions**	**NISP with concretions, standardized**	**Total NISP**
EE	94	9.65	11.9 **(-2.66)**	974
LE	189	28.34	30.98 **(2.06)**	667
EM	152	16.17	11.52 (-0.35)	940
MM	159	19.70	88.33 (0.32)	807

5.2.2 Evidence of bone weathering

Evidence of weathering on bone can be used as a relative measure indicating how long the specimen was exposed before being buried. Weathering is the deterioration of the bone through cracking, splitting, splintering, and eventually spalling off of bone as a result of this exposure (Stiner et al. 1995). It should be noted that weathering varies geographically and cannot be used as a precise indicator of time of exposure. Further, because the bones discussed here were in a rockshelter, which provided some cover from the elements, and weathering might have been reduced. Weathering was recorded using a 0-3 point scale, with a higher number indicating increased weathering of the specimens (Table 5.5).

Table 5.5 Weathering scale used in this study.

Weathering scale	Description
0	Greasy, no cracking or flaking. Perhaps with skin or ligament/soft tissue attached.
1	Cracking parallel to fibre structure (longitudinal). Articular surfaces with mosaic cracking of covering tissue and bone.
2	Flaking of outer surface (exfoliation). Cracks are present and edge is angular.
3	Rough, homogenously altered compact bone resulting in fibrous texture. Weathering penetrates 1 - 1.5 mm maximum. Crack edges are rounded.

Most specimens (79%) present little to moderate weathering (weathering scale 0-1) and the most common damage is in the form of incipient longitudinal and mosaic cracking on the surface of the bone (Figure 5.2, Tables 5.6 and 5.7). Approximately 18.6% have some cortical bone flaking on the surface, along with some cracking (weathering scale 2). This might be due to the dry conditions of the cave, which also affected the degree of fragmentation of the remains. A contingency table analysis indicates that there are statistically significant differences in the degree of bone weathering across excavation units (G=502.305, *p*=.000) but not across occupational phases (G=11.869, *p*=.221). Freeman-Tukey deviates show heavily weathered specimens (weathering scale 3) and non-weathered specimens (w = 0) are significantly overrepresented in Unit 18 strata, though heavily weathered specimens are still a very small percentage (3.96) of the total.

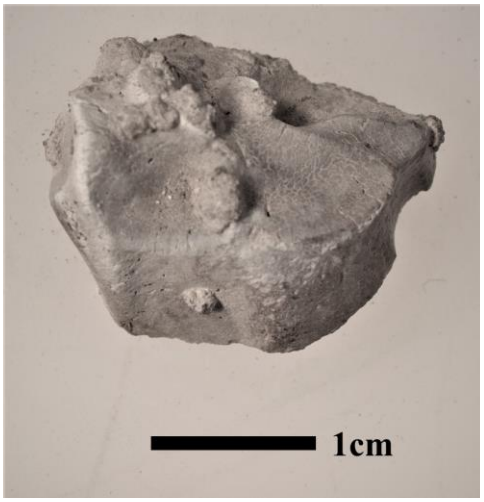

Figure 5.2 Deer astragalus showing calcium carbonate concretions and mosaic cracking on the surface (weathering scale 1).

Table 5.6 Degree of weathering of faunal specimens by excavation unit. Raw and standardized data per excavated volume in m^3 are presented. Freeman-Tukey deviates are in parentheses and bolded values are significant at *p*=.05 (± 1.47).

	0		**1**		**2**		**3**	
Unit	**n**	**n std.**	**n**	**n std.**	**n**	**n std.**	**n**	**n std.**
1	145 26.95%	703.88 **(-12.65)**	267 49.63%	1,296.12 **(9.63)**	122 22.68%	592.23 **(3.63)**	4 0.74%	19.42 **(-5.49)**
2	138 42.07%	436.71 (0.36)	125 38.11%	395.57 (0.46)	61 18.6%	193.04 (-0.61)	4 1.22%	12.66 **(-1.72)**
18	782 49.12%	1,448.15 **(6.27)**	458 28.77%	848.15 **(-8.03)**	289 18.15%	535.19 **(-1.59)**	63 3.96%	116.67 **(6.47)**
19	464 49.89%	819.79 **(5.14)**	300 32.26%	530.04 **(-3.42)**	159 17.1%	280.92 **(-2.19)**	7 0.75%	12.37 **(-4.31)**

Table 5.7 Degree of weathering of faunal specimens by occupational phase. Raw and standardized data per excavated volume in m^3 are presented. Freeman-Tukey deviates are in parentheses and bolded values are significant at *p*=.05 (± 1.47).

Phase	**0**		**1**		**2**		**3**	
	n	**n std.**	**n**	**n std.**	**n**	**n std.**	**n**	**n std.**
EE	430 44.15%	54.43 (-0.24)	346 35.52%	43.8 (-0.17)	174 17.86%	22.03 (0.64)	24 2.46%	3.04 (0.54)
LE	282 42.28%	46.23 (-0.49)	256 38.38%	41.97 (0.32)	124 18.59%	20.33 (0.72)	5 0.75%	0.82 (-0.61)
EM	439 46.7%	33.26 (0.16)	238 25.32%	18.03 **(-1.68)**	226 24.04%	17.12 **(1.61)**	37 3.94%	2.8 (1.22)
MM	376 46.59%	208.89 (0.36)	312 38.66%	173.33 (0.62)	107 13.26%	59.44 (-1.38)	12 1.49%	6.67 (-0.39)

5.2.3 Evidence of burning and heat alteration

Analysis of the exposure of skeletal remains to fire can inform on both taphonomic and behavioral processes that created and impacted a faunal assemblage (Shipman et al. 1984; Stiner et al. 1995). Conditions such as the state of the bone prior to its exposure to fire, the temperature of the fire, and whether exposure to it was intentional or incidental and brief or prolonged must be taken into account in order to infer what process(es) produced burned bone (Lyman 1994). Exposure of bone to fire causes macroscopic changes such as changes in color, texture, and size as well as microscopic changes as bone mineral recrystallizes and even melts at high temperatures (>645°C; see Shipman et al. 1984). A number of experimental studies conducted in the past four decades has identified how exposure to fire affects bone at various scales of analysis and has guided archaeologists in identifying the markers of these processes. Of particular relevance to this dissertation, three stages of burning have been identified: (1) superficial burning or roasting as a result of short-term exposure to low-temperature fires (<220°C); (2) carbonization resulting from the prolonged (ca. 25 minutes) exposure of bone to fires burning at between 360-525°C, and; (3) calcination, whereby bones are directly exposed to high temperature fires (above 450-500°C) for long periods of time (ca. 6 hours), which causes the black carbon in bone to oxidize and become white, powdery, and friable (David 1990; Shipman et al. 1984, Stiner et al. 1995; though see Lyman 1994 for a critical discussion of these stages and their indicators). Experiments by Stiner and colleagues (1995) show that carbonization can also occur in bones that were buried between 1-15cm below the surface of a campfire.

In this dissertation, evidence of burning and heat alteration on bone was recorded on identified specimens (NISP = 3,388) using a 0-3 category scale modified from Stiner and colleagues (1995) and based on the stages summarized above (see Table 4.4). The majority of bones (76.9%) were not burned (burning scale 0). Of the bones that were burned, the majority (65.3%) were calcined (burning scale 3). A contingency table analysis of these data standardized per cubic meter of excavated volume (for excavations units) and century (for occupational phase) indicates that there are statistically significant differences in how the degree of burning is distributed across units (Table 5.8, Figure 5.2; G=193.647, *p*=.000) and occupational phases (Table 5.9, Figure 5.3; G=117.411, *p*=.000), indicating both temporal and spatial patterns. Freeman-Tukey deviates show an increase in burning activity and the temperature at which bones were exposed over time at the site.

Burned bones are overrepresented in Early Esperanza strata, suggesting there is more evidence of burning as a result of cooking activities at this time than during any other occupational phase. Calcined bones still make up the largest proportion of burned bone during this phase (13.45%), indicating the direct exposure of bone to fire at this time. Calcined bones are sometimes the result of the deliberate discarding of bones into a fire in order to avoid foul smells and pests and thus maintain a clean living space (e.g., Aplin et al. 2016; Gifford Gonzalez

1989). Because calcination requires bones to have some organic matter, the presence of calcined bones during the Early Esperanza suggests that occupations of the shelter at this time were long enough to require these types of activities.

Carbonized bones are overrepresented during the Early Marcala, suggesting this burning pattern may be the result of shelter cleanup activities taking place at this time. This possibility is supported by preliminary geoarchaeological data obtained as part of this study (see section 5.6), as well as by the presence of a living floor dated to this occupational phase (Scheffler 2008). Alternatively, Early Marcala bones could have become carbonized following post-depositional burning from hearth fires taking place during the subsequent Middle Marcala phase. This possibility is corroborated by the fact that calcined bones are overrepresented during the Middle Marcala, which perhaps indicate a larger number of high-temperature fires were built at this time, something that is also corroborated by the geoarchaeological data, which show higher levels of wood ash being produced at this time. The dominance of calcined bones during the Middle Marcala (20% of all identified specimens) suggests possible shelter clean-up activities at this time were larger and more frequent, and might in turn suggest longer and/or more intensive occupations of the rockshelter.

Calcined and carbonized bones are also overrepresented in Unit 18 strata, which contain a number of small pit features identified during excavation. The purpose of the features is yet to be defined (Scheffler 2008; Hirth, personal communication, 2020).

Table 5.8 Evidence of burning in faunal specimens by unit. Raw and standardized counts per excavated volume in m^3 are presented. Freeman-Tukey deviates are in parentheses and bolded values are significant at *p*=.05 (± 1.47).

	Unburned		**Burned**		**Carbonized**		**Calcined**	
Unit	**n**	**n std.**	**n**	**n std.**	**n**	**n std.**	**n**	**n std.**
1	414 76.95%	2,009.71 (0.04)	36 6.69%	174.76 (1.02)	1 0.19%	4.85 **(-4.83)**	87 16.17%	422.33 (0.65)
2	243 74.09%	768.99 (-0.56)	47 14.33%	148.73 **(5.13)**	0 0%	0 **(-4.69)**	38 11.59%	120.25 (-1.71)
18	1178 73.99%	2,181.48 **(-1.31)**	47 2.95%	87.04 **(-5.19)**	79 4.96%	146.3 **(5.45)**	288 18.09%	533.33 **(2.93)**
19	769 82.69%	1,358.66 **(2.00)**	61 6.56%	107.77 (1.17)	1 0.11%	1.77 **(-7.07)**	99 10.65%	174.91 **(-3.78)**

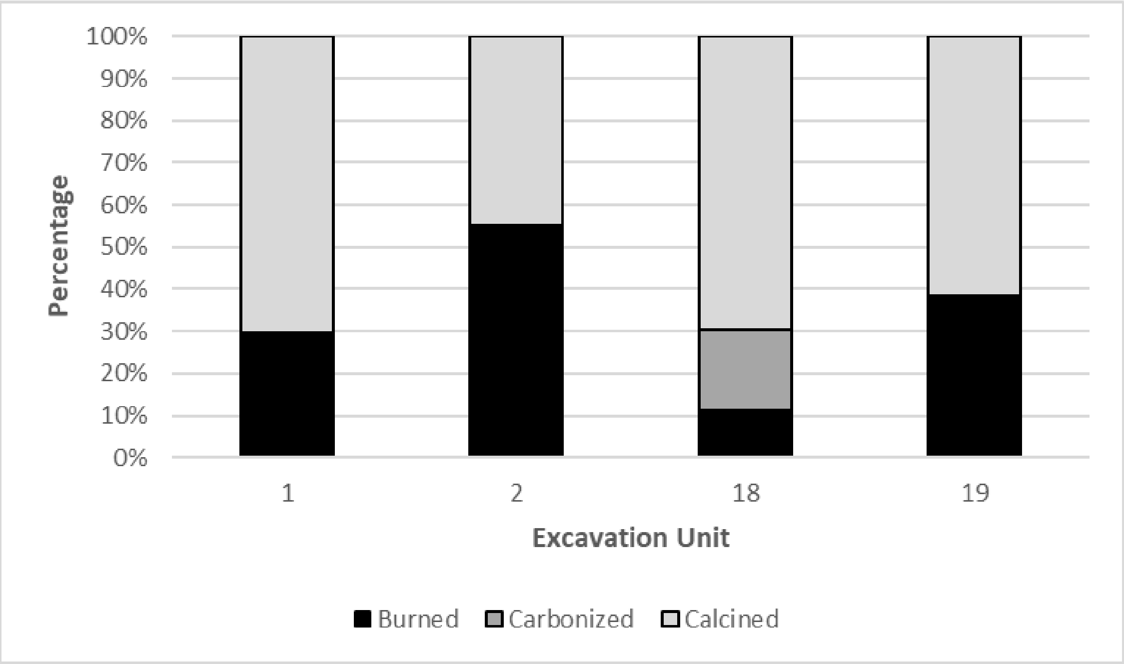

Figure 5.3 Degree of burning by excavation unit.

Table 5.9 Evidence of burning in faunal specimens by occupational phase. Raw and standardized counts per century are presented. Freeman-Tukey deviates are in parentheses and bolded values are significant at *p*=.05 (± 1.47).

Phase	**Unburned**		**Burned**		**Carbonized**		**Calcined**	
	n	**n std.**	**n**	**n std.**	**n**	**n std.**	**n**	**n std.**
EE	745 76.49%	94.3 (-0.12)	86 8.83%	10.89 **(3.75)**	12 1.23%	1.52 **(-2.63)**	131 13.45%	16.58 (-1.35)
LE	568 85.16%	93.11 **(2.39)**	30 4.5%	4.92 (-1.26)	1 0.15%	0.16 **(-5.63)**	68 10.19%	11.15 **(-3.55)**
EM	700 74.47%	53.03 (-0.83)	36 3.83%	2.73 **(-2.51)**	52 5.53%	3.94 **(4.96)**	152 16.17%	11.52 (0.84)
MM	591 73.23%	328.33 (-1.18)	39 4.83%	21.67 (-0.96)	16 1.98%	8.89 (-0.72)	161 19.95%	89.44 **(3.31)**

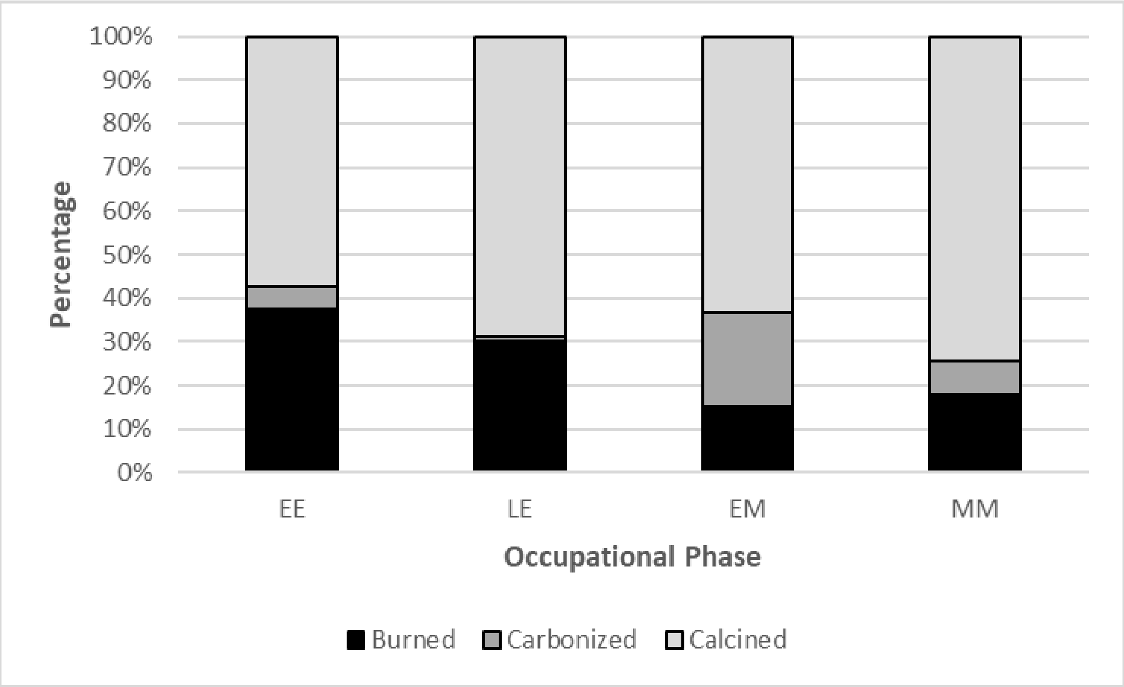

Figure 5.4 Degree of burning of all faunal remains (NISP) by occupational phase.

There are also statistically significant differences in the distribution of burned bone according to taxon (G=828.311, *p* = .000; Table 5.10). Freeman-Tukey deviates show that burned bones are overrepresented in the remains of artiodactyls, rodents, and cottontails and carbonized bones are overrepresented in reptiles and rodents. Calcined bones are overrepresented among canids, artiodactyls, and undifferentiated reptiles. Nearly all burning categories are significantly overrepresented in the remains of artiodactyls which at El Gigante include white-tailed deer (WTD; *Odocoileus virginianus*), brocket deer (*Mazama* sp.), and peccaries (Tayassuidae).

If indeed calcined bones at El Gigante are representative of purposeful clean-up activities, then the high levels of calcination of artiodactyl remains is not surprising given that it was the most abundant taxon in the assemblage. This pattern of burning of artiodactyl remains indicates these animals were consumed and discarded inside the shelter since its earliest phase of occupation.

Table 5.10 Burned bones by taxon and burn class. Only statistically significant results are presented. Freeman-Tukey deviates are in parentheses and bolded values are significant at *p*=.05 (± 1.80).

Taxon	**Unburned**	**Burned**	**Carbonized**	**Calcined**
Aves	15 (-0.67)	3 (1.19)	0 (-0.72)	5 (1)
Canidae	4 (-1.16)	0 (-0.77)	1 (1.09)	4 **(1.80)**
Carnivora	3 (-0.71)	0 (-0.56)	0 (-0.23)	3 **(1.66)**
Chiroptera	5 (0.61)	0 (-0.48)	0 (-0.19)	0 (-0.93)
Cuniculus paca	2 (0.45)	0 (-0.22)	0 (-0.08)	0 (-0.45)
Dasypus novemcinctus	829 **(4.44)**	20 **(-5.65)**	0 **(-7.8)**	54 **(-7.51)**
Decapoda	681 **(5.97)**	0 **(-11.80)**	0 **(-6.67)**	2 **(-16.23)**
Didelphidae	3 (-0.71)	1 (0.86)	0 (-0.23)	2 (1.07)
Felidae	1 (-0.28)	0 (-0.22)	0 (-0.08)	1 (0.97)
Iguanidae	4 (0.56)	0 (-0.4)	0 (-0.16)	0 (-0.79)
Mephitidae	0 **(-4.1)**	0 (-0.7)	0 (-0.29)	8 (3.51)
Artiodactyla	670 **(-6.81)**	114 **(5.20)**	26 (0.61)	287 **(9.36)**
Procyon lotor	2 (0.45)	0 (-0.22)	0 (-0.08)	0 (-0.45)
Reptilia	5 **(-1.77)**	1 (0.39)	2 **(1.7)**	5 **(1.83)**
Rodentia	177 **(-3.7)**	35 **(3.49)**	37 **(7.16)**	45 (0.75)
Serpentes	23 (-0.04)	0 **(-1.85)**	0 (-0.88)	7 (1.3)
***Sylvilagus* sp.**	17 **(-2)**	12 **(4.05)**	0 (-0.97)	5 (0.25)
Testudines	1 (0.38)	0 (-0.11)	0 (-0.04)	0 (-0.24)

I also noted the presence or absence of burning on the unidentifiable specimens from the El Gigante faunal assemblage (n=11,041). A contingency table analysis of these data shows there is a statistically significant relation between burning, bone size, and phase of occupation (G=598.311, *p*=.000). Freeman-Tukey deviates show burned bones are significantly overrepresented during the Early Esperanza and Middle Marcala phase. During the Early Esperanza phase bones in the size rage of 20-40mm are most often burned, whereas during the Middle Marcala almost all size classes exhibit evidence of burning (Table 5.11). This agrees with the conclusion of longer, more frequent and/or more intense use of fire within the shelter at this time.

To further examine whether patterns of burning in bone were related to clean-up activities being conducted within the shelter (e.g., Lupo et al. 2021) I examined whether bones of animals of different sizes were burned at the same time as part of mass cleaning episodes, as follows. I carried out a Spearman's rank correlation (r_s)between the proportion of burned bones from artiodactyls and rodents, and these data are not correlated (r_s=0, *p*=1). I also compared the distribution of burned bones to geoarchaeological proxies for fire such as pH and charcoal content (mg/g) on a sample of the excavated levels of Unit 18 carried out as part of the geoarchaeological analyses (see section 5.6). Importantly, the quantity of burned bone and amount of charcoal in the sediment matrix are correlated (r_s=0.683, *p*=0.042), which suggests at least some of the bones deposited in Unit 18 were burned through processes that involved burning large sections of the shelter floor at one once as part of mass cleaning activities. However, these data remain preliminary until a more systematic study of the shelter's sedimentary matrix can be carried out.

Table 5.11 Evidence of burning in unidentifiable bone from the El Gigante assemblage. Freeman-Tukey deviates are in parentheses and bolded values are significant at *p*=.05 (± 1.63).

Phase	**<10mm**		**10-15mm**		**15-20mm**		**20-30mm**	
	UB	**B**	**UB**	**B**	**UB**	**B**	**UB**	**B**
EE	449 (0.28)	367 (0.91)	566 **(-4.2)**	439 **(-1.82)**	672 (0.16)	380 (0.13)	436 (0.47)	268 **(3.35)**
LE	211 **(-8.07)**	132 **(-10)**	614 **(3.87)**	383 (0.57)	638 **(4.93)**	315 (1.22)	409 **(4.02)**	128 **(-3.29)**
EM	551 **(8.64)**	412 **(6.56)**	591 (1.49)	393 (-0.14)	444 **(-4.88)**	263 **(-2.92)**	263 **(-5.13)**	141 **(-2.99)**
MM	81 **(-5.35)**	109 (0.13)	184 (-1.61)	179 **(2.49)**	193 (-0.9)	143 **(2.35)**	135 (0.32)	93 **(2.98)**

Phase	**30-40mm**		**40-50mm**		**50+mm**	
	UB	**B**	**UB**	**B**	**UB**	**B**
EE	99 **(1.81)**	64 **(3.35)**	31 (1.37)	10 (1.28)	5 **(1.65)**	2 (-0.31)
LE	78 **(1.71)**	10 **(-4.74)**	24 (1.19)	3 (-0.88)	0 **(-1.72)**	3 (0.64)
EM	45 **(-3.02)**	24 **(-1.68)**	6 **(-3.88)**	0 **(-3.75)**	1 (-0.38)	3 (0.56)
MM	17 **(-1.74)**	19 **(1.72)**	9 (0.63)	6 **(2.09)**	0 (-0.88)	0 (-1.09)

5.2.4 Non-human bone damage

Evidence of non-human bone accumulation or modification resulting from carnivorous animals is quite limited. Of the 3,388 identified specimens (NISP), only five (all belonging to birds and/or large mammals) display evidence of non-human damage in the form of rodent or carnivore gnaw marks. It is possible other faunal remains contain these markings but these were obscured by high levels of fragmentation and calcium carbonate concretions. Importantly, all of the large mammal remains found at El Gigante have an anthropogenic origin, given that there is no evidence of the shelter being used or disturbed by large non-human predators such as canids and felids. Large predators would not have access to the interior of the shelter because to enter the shelter one must climb a vertical scarp approximately 4m in height (Figure 5.5). The identified remains of at least one undifferentiated canid in the assemblage suggests the possibility that the inhabitants of the rockshelter could have had domesticated dogs (C*anis familiaris*) which gnawed on bones already deposited on the site, creating the gnaw marks mentioned above.

Contrary to the evidence for large predators using the shelter, there is sufficient evidence to indicate small predators used El Gigante over time and likely deposited faunal remains into the shelter's deposits. Excavations at the site recovered four regurgigated raptor pellets both on the surface and buried within the strata. A detailed analysis of these pellets is forthcoming and beyond the scope of the present dissertation. However, a preliminary assessment of these pellets was made to better inform these analyses

Figure 5.5 Entrance into the El Gigante rockshelter.

The first of these pellets was recovered on the surface and is the largest of the four, measuring approximately 8x6x3cm (Figure 5.6). It appears to originally have been bones encased within a pouch of hair and fibers, but the majority of the bones became disaggregated. Given its size, this pellet was likely regurgitated by a large owl species such as the great horned owl (*Bubo virginianus*). This species is prevalent along the Pacific slope of Honduras (Mejia 2012). Bones within this pellet present some amount of damage due to breakage and acid digestion, which is common for larger species of owls such as the great horned (Montalvo et al. 2016). However, the overall degree of breakage and damage by acid digestion is minimal, and some of the smaller bones are still articulated. Because owls tend to decapitate then swallow their prey whole, bone breakage is often minimal, as is damage by digestive acids (Andrews 1990).

Figure 5.6 Large owl pellet recovered from the surface of the El Gigante rockshelter.

The other three pellets were found buried in the more recent strata of the shelter likely dating to the Classic Period (AD 250-1000) and are much smaller in size than the pellet described above.

Most of these are likely fragments of much larger pellets (Figure 5.7). The largest of these pellets measures just over 2cm in length and is composed of several fragmented long bones, some smaller bone, all within a dry but soft fabric-like matrix. Because these pellets appear to be fragments of much larger specimens, we cannot be sure of the raptor species that produced them. However, most of the visible bones appear unbroken, present little to no visible acid damage, and in the case of the pellet recovered from Unit 3, some of the bones are still partially articulated (Figure 5.7c). The size of some of the bones visible in these pellets suggest that if disaggregated small animal remains digested by avian predators were present in other layers of the site, these were likely not recovered during excavation given the size of the screens used (1/8") in excavation.

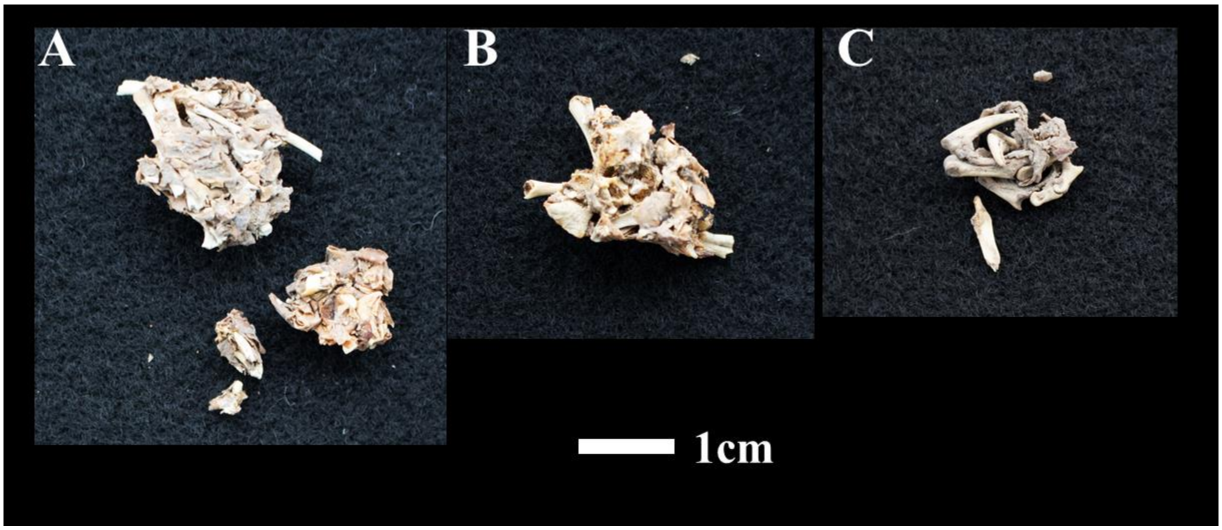

Figure 5.7 Owl pellets recovered from excavated strata at El Gigante. A: recovered from Unit 1, Level 2. B: Recovered from Unit 2, Level 3a. C: recovered from Unit 3, Level 4.

It is possible, however, that some of the rodent bones in the site were deposited by non-humans. Although a large percentage (40%) of the rodent remains recovered from El Gigante display evidence of burning, no rodent (or other small animal) remains were found with indications of human use (such as cutmarks). Nevertheless, foragers also readily consume rodents, so one cannot assume that these remains do not represent food bone.

In order to identify the agents that deposited rodent remains within the shelter I used a number of taphonomic analyses following the methodology developed by Andrews (1990). I first calculated the relative abundance of skeletal elements, which are an indicator of the dietary preferences of different predators such as large felids (i.e., Pumas, *Puma concolor*), the black-chested buzzard-eagle (*Buteo melanoleucus*), variable hawk (*Geranoaetus polyosoma*), great horned owl (*Bubo virginianus*), and the barn owl (*Tyto alba*). The relative abundance of skeletal elements indicative of each of these taxa obtained from a list compiled by Lopez (2020). Relative abundance is calculated using the following formula:

$$\frac{MNEi}{Ei\ x\ MNI}\ x\ 100$$

Where MNEi corresponds the minimum number of elements (MNE) identified in an assemblage (i.e., each occupational phase at El Gigante), Ei corresponds to the expected number of each element within the skeleton of a single individual, and MNI is the minimum number of individuals identified in the assemblage. I also calculated three other indices, also based on MNE, to infer the degree to which different components of the skeleton (cranial, postcranial, distal proximal) are represented in an assemblage. First, the postcrania/crania index (pc/c), which is calculated as follows:

$$\frac{8\ x\ (femora + tibiae + humeri + radii + ulnae)}{5\ x\ (mandibles + maxillae + isolated\ molars)}$$

A similar index is generated with the following formula:

$$\frac{femora + humeri}{mandibles + maxillae}$$

If values for both of these indices are lower than 1, then cranial elements are better represented in the assemblage, whereas values higher than 1 indicate postcranial elements are more common (Andrews 1990). The distal:proximal index helps identify the degree to which distal and proximal parts of the skeleton are represented and is calculated a follows:

$$\frac{tibiae + ulnae[or\ radii]}{femora + humeri}$$

Values lower than 1 in this index indicate better representation of proximal elements and values higher than 1 indicate that distal elements are better represented.

All rodent assemblages at El Gigante exhibit low average values of relative abundance of skeletal elements (<20%; see Table 5.12). With the exception of the Late Esperanza phase rodent assemblage, lower limb long bones were often well represented (>50%), whereas smaller elements such as metapodials, phalanges, and vertebrae are rarely present. This pattern is likely the result of the recovery methods used during excavation, namely screen size. `The cranial:postcranial skeletal indices (Table 5.13) show postcranial elements dominate the rodent assemblage across all occupational phases but particularly during the Early Esperanza. The distal:proximal index data show that during the Early Esperanza proximal elements are better represented, but that during the other occupational phases representation of proximal and distal elements is roughly the same.

Table 5.12 Minimum number of elements (MNE) and relative abundance (RA) of rodent skeletal elements at El Gigante, by occupational phase. Numbers in parenthesis indicate minimum number of individuals (MNI) identified for each phase.

	EE (9)		**LE (4)**		**EM (11)**		**MM (13)**	
Element	**MNE**	**RA**	**MNE**	**RA**	**MNE**	**RA**	**MNE**	**RA**
Maxillae	1	5.56	0	0.00	2	9.09	0	0.00
Mandibles	2	11.11	5	62.50	8	36.36	6	23.08
Isolated incisors	0	0.00	0	0.00	2	4.55	0	0.00
Isolated molars	1	0.93	0	0.00	2	1.52	0	0.00
Vertebrae	3	0.61	1	0.45	12	1.98	3	0.42
Ribs	2	0.89	3	3.00	6	2.18	1	0.31
Scapulae	1	5.56	0	0.00	0	0.00	1	3.85
Humeri	8	44.44	1	12.50	7	31.82	8	30.77
Ulnae	1	5.56	0	0.00	2	9.09	1	3.85
Radii	2	11.11	0	0.00	0	0.00	0	0.00
Pelvis	2	11.11	1	12.50	5	22.73	4	15.38
Femora	11	61.11	4	50.00	15	68.18	14	53.85
Tibiae	9	50.00	4	50.00	15	68.18	25	96.15
Metapodials	0	0.00	0	0.00	1	0.45	3	1.15
Calcanea	1	5.56	0	0.00	1	4.55	1	3.85
Astragali	0	0.00	0	0.00	0	0.00	0	0.00
Phalanges	1	0.20	0	0.00	1	0.16	1	0.14
Mean RA		12.57		11.23		15.34		13.69

Table 5.13 Taphonomic values for the El Gigante rodent assemblage following indices developed by Andrews (1990).

Index	**EE**	**LE**	**EM**	**MM**
Postcranial/cranial (pc/c)	12.40	2.88	5.20	12.80
Postcranial/cranial (f+h/md+mx)	6.33	1.00	2.20	3.67
Distal/proximal (t+u/f+h)	0.53	0.80	0.77	1.18

When examined together, the above indices only sometimes match those expected in rodent assemblages created by owls (Table 5.14; Lopez 2020; Lopez and Chiavazza 2020). These values sometimes are closer to those of other birds of prey such as hawks and eagles (e.g., Lopez et al. 2017). However, unlike eagles and hawks, the bones and teeth of animals consumed by owls do not exhibit signs of acid digestion. Rodent remains from El Gigante do not exhibit any signs of digestion damage, indicating they accumulated within the rockshelter as a result of owls, human predation, or the natural death of individuals living within the shelter's matrix, though the latter is unlikely given that no burrowing features were identified during excavation.

Table 5.14 Taphonomic values for various predators following indices developed by Andrews (1990). From Lopez 2020: Table S6.

Common name	**Scientific name**	**pc/c index**	**f+h/md+mx index**	**distal/proximal index**
Puma	*Puma concolor*	0.5063	0.708	0.247
Pampas cat/Geoffroy's cat/Jaguarundí	*Leopardus colocolo/ Leopardus geoffroyi/Puma yagouaroundi*	0.81	0.68	0.52
Chaco owl	*Strix chacoensis*	2.99	0.7877	0.9696
Black-chested Buzzard-eagle	*Geranoaetus melanoleucus*	1,103	0.303	1,783
Variable hawk	*Geranoaetus polyosoma*	0.655	0.649	0.66
Burrowing owl	*Athene cunicularia*	2.01	0.6464	0.6302
Burrowing owl	*Athene cunicularia*	3.31	0.8795	0.6867
Burrowing owl	*Athene cunicularia*	4.04	1.08	0.9438
Great horned owl	*Bubo virginianus magellanicus*	3,106	0.95	0.9474
Barn owl	*Tyto furcata*	1.95	1	0.93
Barn owl	*Tyto furcata*	2.99	1.03	0.95
Barn owl	*Tyto furcata*	3.98	1,057	1,003
Barn owl	*Tyto furcata*	3.31	0.86	0.98
Barn owl	*Tyto furcata*	2.37	0.9119	0.7955
Barn owl	*Tyto alba*	2.25	1,088	0.91
Barn owl	*Tyto alba*	no data	0.52	0.908
Barn owl	*Tyto alba*	2.51	0.93	1.05

Although human consumption of rodents in Mesoamerica has been documented (e.g., Flannery 1986; Widmer and Storey 2016), it is often associated with the mass capture and consumption of these taxa, and the small quantity of rodent remains identified at El Gigante (NISP = 93, MNI = 37) does not support this interpretation. What is perhaps more likely is that the actions of a number of different agents, some human and some not, were responsible for the accumulation of the rodent remains at El Gigante, and additional analyses are needed before a firmer interpretation can be made, including analyses of the coprolites recovered during excavation, which will yield more direct evidence of the species consumed by the site's inhabitants.

5.2.5 Bone size and fragmentation processes

The fragmentation of faunal remains results in their "analytical absence" (Lyman and O'Brien 1987:493) and must therefore be evaluated in order to understand the parameters of other analyses conducted on that assemblage. Two measurements, greatest length (GL) and greatest breadth (GB), were taken from every bone identified to a particular taxon. A brief examination of both measures (Figures 5.8, 5.9) shows bones recovered from El Gigante were skewed to relatively small sizes (mean GL = 19mm, mean GB = 10mm).

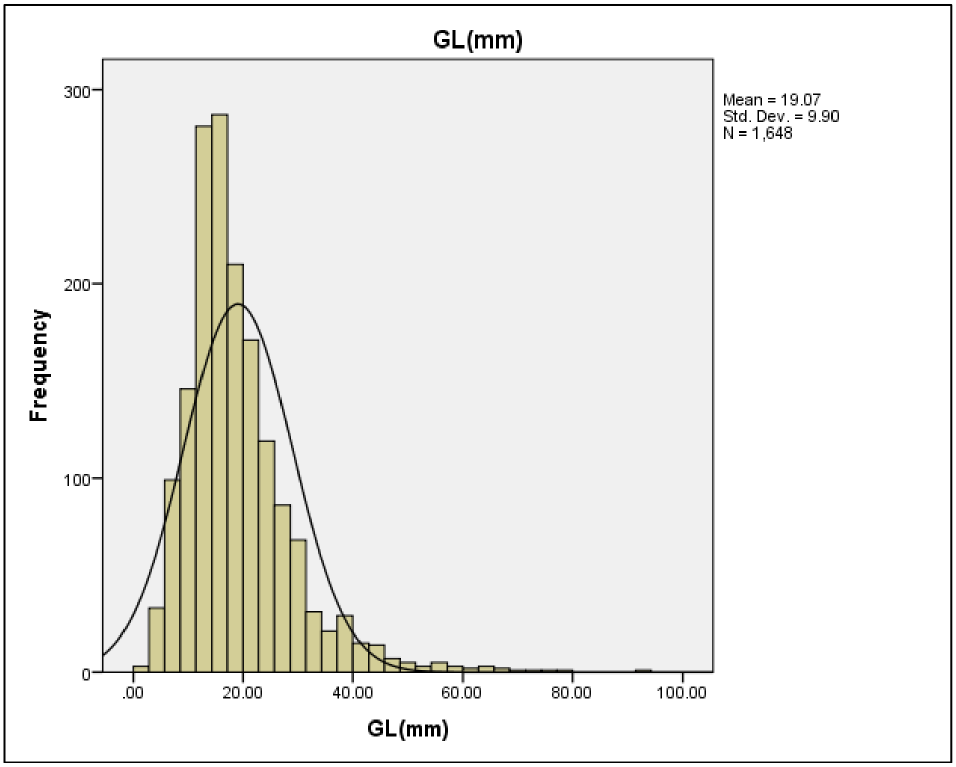

Figure 5.8 Distribution of greatest length (GL) measurements at El Gigante.

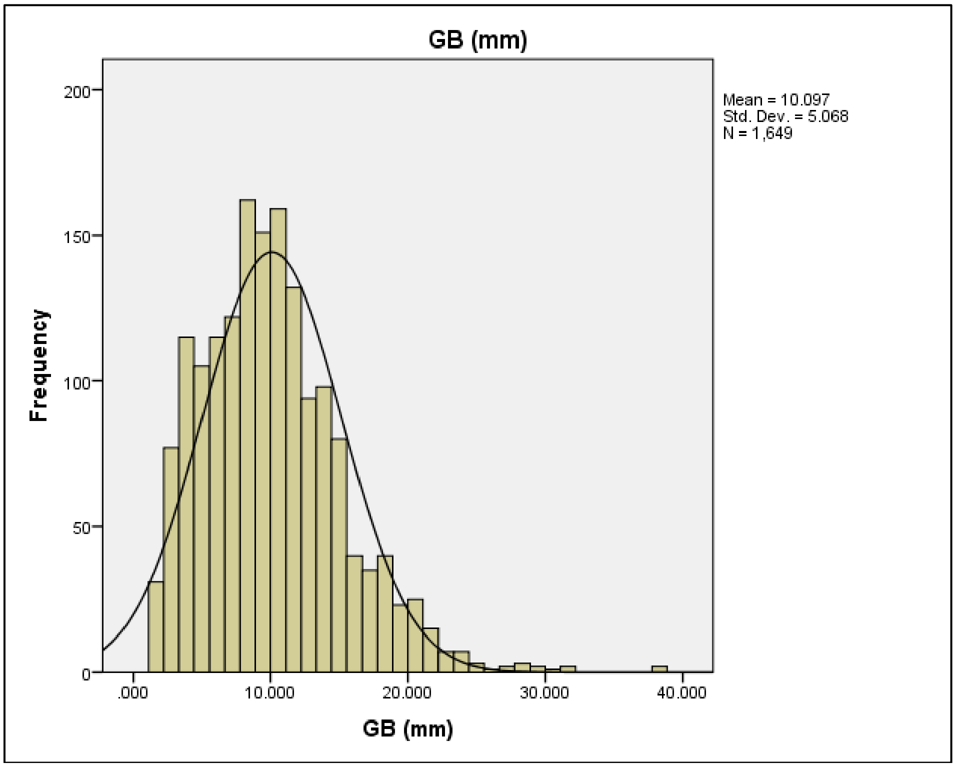

Figure 5.9 Distribution of greatest breadth (GB) measurements at El Gigante.

Because these measurement data are not normally distributed, I used a contingency table analysis to determine whether there are significant differences in bone size across the different excavation units and occupational phases at El Gigante, standardizing the data according to cubic meters of excavated volume and century (Tables 5.15 and 5.16). These tests determined that there are statistically significant differences in how GL and GB are distributed across units (G=2662.242, *p*=.000) and occupational phases (G=61.955, *p*=.000). Freeman-Tukey deviates indicate bones smaller than 10mm are significantly overrepresented in Unit 18 and Early Marcala strata while larger bones (>40mm) are significantly overrepresented in Unit 1. Freeman-Tukey deviates also indicate that bones ranging from 30-40mm, which are larger than the mean of the analyzed sample, are significantly overrepresented during the Early Esperanza phase, while smaller bone sizes are overrepresented in the Late Esperanza (10-15mm) and Early Marcala (<10mm). These results show a general decrease in bone size over time, which in turn suggests bone size is not negatively associated with depth and thus fracturing due to sediment overburden is minimal or nonexistent (Figure 5.10).

Table 5.15 Greatest length of bone (GL) by excavation unit. Raw and standardized counts per m^3 of excavated sediment are presented. Freeman-Tukey deviates are in parentheses and bolded values are significant at *p*=.05 (± 1.57).

			Unit				
			1	**2**	**18**	**19**	**Totals**
Size Class (mm)	**0-10**	**n**	480	276	2338	930	4024
		n std.	2285.71 **(-14.49)**	873.42 **(-11.43)**	4329.63 **(31.05)**	1643.11 **(-15.45)**	
	10-15	**n**	665	431	1320	1509	3925
		n std.	3166.67 (-0.59)	1363.92 (1.4)	2444.44 **(-4.44)**	2666.08 **(4.1)**	
	15-20	**n**	650	374	938	1554	3516
		n std.	3095.24 **(3.4)**	1183.54 (-0.26)	1737.04 **(-15.13)**	2745.58 **(10.26)**	
	20-30	**n**	510	344	563	911	2328
		n std.	2428.57 **(8.05)**	1088.61 **(8.03)**	1042.59 **(-18.06)**	1609.54 (0.91)	
	30-40	**n**	119	80	106	163	468
		n std.	566.67 **(6.02)**	253.16 **(5.17)**	196.3 **(-9.97)**	287.99 **(-2.52)**	
	40-50	**n**	34	18	32	46	130
		n std.	161.9 **(3.64)**	56.96 (1.15)	59.26 **(-4.54)**	81.27 (-1.11)	
	<50	**n**	16	4	8	10	38
		n std.	76.19 **(4.73)**	12.66 (-0.87)	14.81 **(-3.79)**	17.67 **(-2.6)**	

Table 5.16 Greatest length of bone (GL) by occupational phase. Raw and standardized counts per century are presented. Freeman-Tukey deviates are in parentheses and bolded values are significant at *p*=.05 (± 1.57).

			Phase				
			EE	**LE**	**EM**	**MM**	**Totals**
Size Class (mm)	**0-10**	**n**	1286	639	1515	584	4024
		n std.	162.78 (-0.03)	104.75 **(-4.89)**	114.77 **(3.14)**	324.44 (1.49)	
	10-15	**n**	1144	1092	1132	557	3925
		n std.	144.81 **(-1.69)**	179.02 (1.15)	85.76 (0.09)	309.44 (0.36)	
	15-20	**n**	1188	1060	811	457	3516
		n std.	150.38 (0.19)	173.77 **(2.24)**	61.44 **(-1.77)**	253.89 (-0.93)	
	20-30	**n**	864	654	506	304	2328
		n std.	109.37 (1.11)	107.21 (1.05)	38.33 **(-1.8)**	168.89 (-0.68)	
	30-40	**n**	209	119	89	51	468
		n std.	26.46 **(1.58)**	19.51 (0.39)	6.74 (-0.81)	28.33 (-1.05)	
	40-50	**n**	53	42	17	18	130
		n std.	6.71 (0.56)	6.89 (0.59)	1.29 (-1.17)	10 (-0.09)	
	<50	**n**	17	10	8	3	38
		n std.	2.15 (0.41)	1.64 (0.43)	0.61 (0.33)	1.67 (-0.43)	

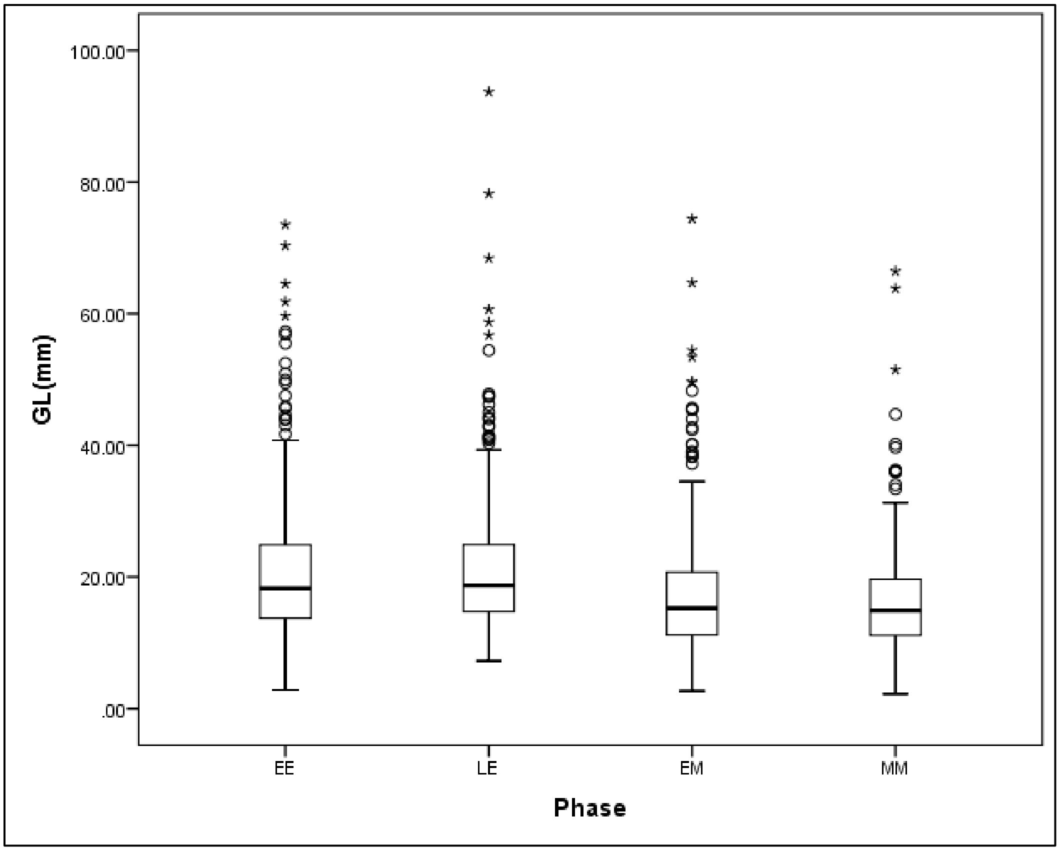

Figure 5.10 Greatest length of bone (GL) by occupational phase.

5.3 Identification of the assemblage

I quantified the abundance of species within the analyzed sample of the El Gigante faunal assemblage using Number of Individual Specimens (NISP) and Minimum Number of Individuals (MNI). Identified specimens were rather evenly distributed among the various occupational phases of the site (Figure 5.11). The earliest phase, Early Esperanza, contains the most identified specimens (n=973). However, when standardized to account for variability in the duration of each of the phases, many more identifiable specimens were recovered from Middle Marcala strata per century of occupation. This matches the pattern found in total specimen count (NSP) dated to this occupational phase (see Table 5.1 above) and is indicative of longer stays in the shelter – or, alternatively, more intensive hunting episodes – that produced a higher accumulation rates for the faunal assemblage.

Mammals were overwhelmingly the most represented class of vertebrates, followed by reptiles and birds (Table 5.17). Amphibians are by far the least common class of animals identified at the site. Crabs were the only invertebrate taxa recovered at the site.

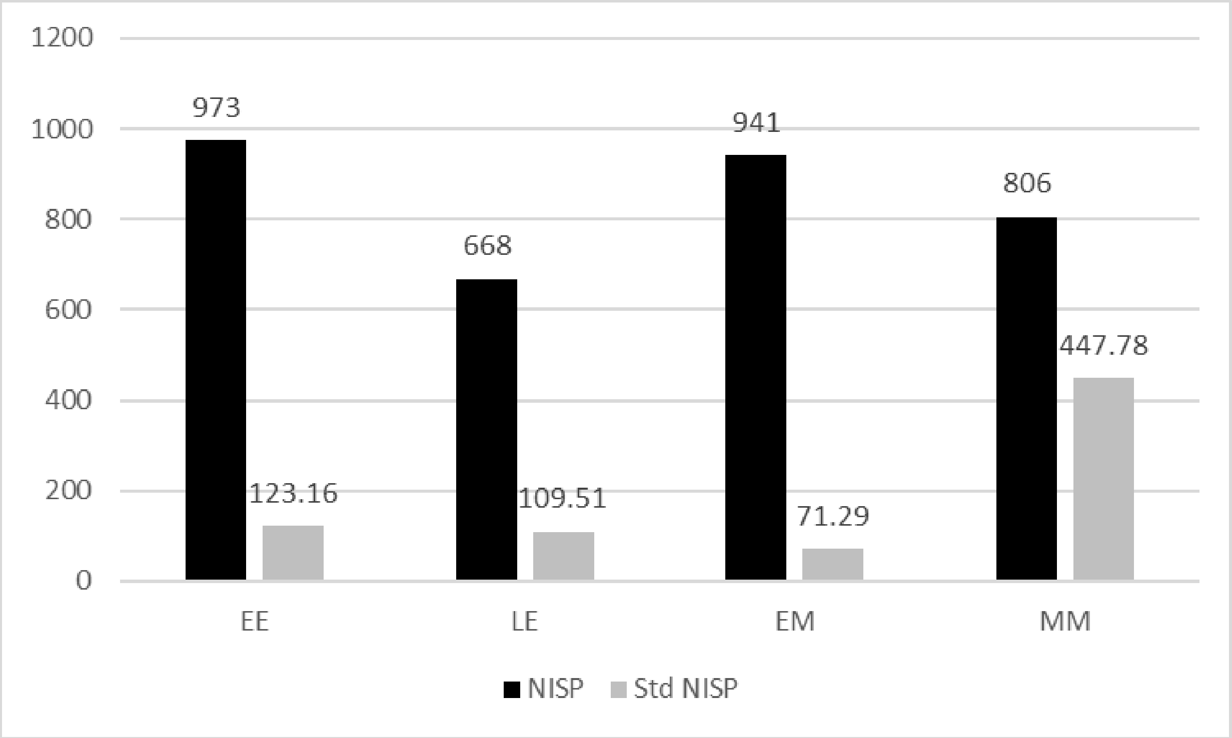

Figure 5.11 Number of identified specimen (NISP) counts by occupational phase, including raw counts and counts standardized per century.

Table 5.17 Number of identified specimen (NISP) by identified class for the entire analyzed assemblage.

Class	NISP	%
Mammals	2,636	77.80
Birds	23	0.68
Reptiles	45	1.33
Amphibians	1	0.03
Invertebrates	683	20.16

5.3.1 Number of Identified Specimens (NISP) at El Gigante

Most specimens were identified to genus, followed by order and species (Table 5.18). 1985 specimens (58.6%) were identified to species level. However, approximately 40% of these specimens (n=793) correspond to armadillo (*Dasypus novemcinctus*) scutes, which artificially inflate these figures. These patterns are again related to the high degree of fragmentation of the assemblage, which impacts the identification of small and medium-sized fauna to a higher degree than large-sized fauna, such as deer.

Table 5.18 NISP by level of taxonomic identification for all phases.

Taxonomic level	NISP	%
Class	303	8.94
Order	1,007	29.72
Family	48	1.42
Genus	45	1.33
Species	1,985	58.59

Most of the specimens identified to genus belong to deer (n=1,078, 96%). When standardized per century, cervids are the most abundant taxa in all occupational phases, followed by armadillos, crabs, then rodents (Figure 5.12; Table 5.19). The cervid category includes the remains of white-tailed (WTD, *Odocoileus virginianus*) and brocket deer (*Mazama* sp.). The highly fragmentary nature of the assemblage made the separation of these two species particularly difficult, and only a few specimens securely belonging to brocket deer were identified (n=10). Cervids, particularly WTD, are the largest taxon identified in the assemblage, and was likely the highest-ranked resource of Preceramic foraging groups inhabiting the neotropics of Middle America (see Chapter 4; Piperno and Pearsall 1998).

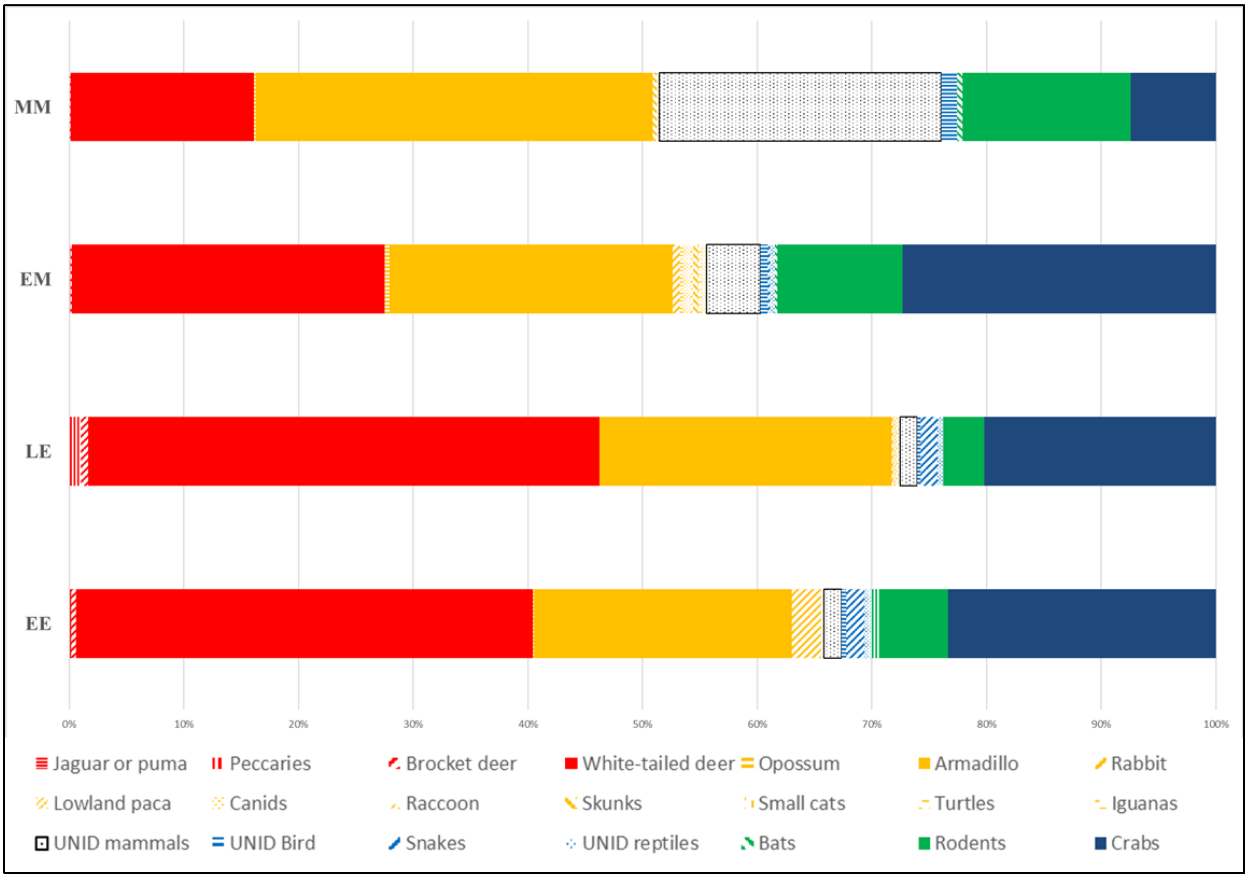

Figure 5.12 Percentage of NISP (standardized per century) by taxon and occupational phase. Mammals are color coded by size (red – large, orange – medium, green – small), blue bars represent crabs and hashed black and white bars represent unidentified specimens.

Table 5.19 NISP values (raw and standardized per century) by occupational phase. Freeman-Tukey deviates are in parentheses and bolded values are significant at *p*=.05 (± 1.66).

Taxon	**Occupational Phase**							
	EE		**LE**		**EM**		**MM**	
Scientific name	**n**	**Std. n**	**n**	**Std. n**	**n**	**Std. n**	**n**	**Std. n**
Didelphidae	1	0.13 (-0.29)	0	0 (-0.26)	4	0.3 (-0.17)	1	0.56 (0.57)
Chiroptera	0	0 (-0.52)	0	0 (-0.47)	2	0.15 (-0.31)	4	2.22 (0.74)
Dasypus novemcintus	222	28.1 (-1.65)	170	27.87 (-0.87)	232	17.58 (-0.52)	279	155 (1.45)
Sylvilagus sp.	25	3.16 **(2.01)**	1	0.16 (-0.65)	6	0.45 (-0.44)	0	0 **(-1.87)**
Lepus sp.	0	0 (0)	0	0 (0)	2	0.15 (0)	0	0 (0)
Sciurus sp.	0	0 (0)	1	0.16 (0)	0	0 (0)	0	0 (0)
Neotominae	0	0 (-0.29)	0	0 (-0.26)	1	0.08 (-0.17)	1	0.56 (0.57)
Sigmodontinae	1	0.13 (-0.29)	3	0.49 (-0.26)	4	0.3 (-0.17)	1	0.56 (0.57)
Cuniculus paca	0	0 (0)	2	0.33 (0)	0	0 (0)	0	0 (0)
Rodentia	49	6.2 **(-2.23)**	20	3.28 **(-3.14)**	98	7.42 (0.02)	116	64.44 **(2.16)**
Canidae	2	0.25 (-0.29)	0	0 (-0.26)	7	0.53 (1.25)	0	0 (-0.85)
Procyon lotor	0	0 (0)	0	0 (0)	2	0.15 (0)	0	0 (0)
Mephitidae	0	0 (-0.52)	0	0 (-0.47)	4	0.3 (-0.31)	3	1.67 (0.74)
Felidae, small	0	0 (0)	0	0 (0)	1	0.08 (0)	0	0 (0)
Felidae, large	0	0 (0)	0	0 (0)	1	0.08 (0)	0	0 (0)
Carnivora	0	0 (-0.29)	0	0 (-0.26)	4	0.3 (-0.17)	2	1.11 (0.57)
Tayassuidae	2	0.25 (-0.29)	7	1.15 (1.16)	0	0 (-0.17)	0	0 (-0.85)
Mazama sp.	4	0.51 (0.69)	4	0.66 (0.76)	1	0.08 (-0.44)	1	0.56 (-0.45)

Odocoileus virginianus	394	49.87 **(2.98)**	298	48.85 **(3.54)**	257	19.47 (0.51)	129	71.67 **(-4.37)**
Mammalia	15	1.9 **(-5.69)**	10	1.64 **(-5.14)**	44	3.33 **(-2.82)**	198	110 **(4.22)**
Aves	4	0.51 (0.05)	2	0.33 (-1.25)	6	0.45 (-0.87)	11	6.11 (0.87)
Testudines	1	0.13 (0)	0	0 (0)	0	0 (0)	0	0 (0)
Iguanidae	0	0 (0)	2	0.33 (0)	2	0.15 (0)	0	0 (0)
Serpentes	16	2.03 (1.24)	10	1.64 (1.33)	2	0.15 (-0.56)	0	0 **(-2.26)**
Reptilia	6	0.76 (1.13)	3	0.49 (-0.26)	4	0.3 (-0.17)	0	0 (-0.85)
Decapoda	231	29.24 **(2.57)**	135	22.13 **(1.7)**	257	19.47 **(2.67)**	60	33.33 **(-4.19)**

When standardized per century, rates of cervid deposition (NISP) remained relatively steady throughout the 1,400-year long Esperanza phase, declined significantly during the Early Marcala, and increased to its highest rate during the Middle Marcala, indicating an increase in occupational intensity during this latter phase. However, despite their abundance, deer became a less significant component of the diet at this time when considered in proportion to the remains of other taxa, something I examine in greater detail in section 5.4 below. A contingency table analysis reveals that there are statistically significant differences in NISP rate across phases at El Gigante (G=220.043, *p*=.000). Freeman-Tukey deviates show that cervid remains are significantly overrepresented in Early and Late Esperanza contexts and significantly underrepresented in Middle Marcala strata. Freeman-Tukey deviates also suggest rodents generally increase in representation over time and are significantly overrepresented in Early and Middle Marcala strata and significantly underrepresented during the Early and Late Esperanza phases. An increase in commensal taxa such as rodents might indicate an increase in human activity at the shelter over time, including the presence of a more disturbed landscape in this area (see Stahl 2006, 2008; Stahl and Pearsall 2012).

Freshwater crabs are significantly overrepresented during the Early and Late Esperanza and Early Marcala and significantly underrepresented during the Middle Marcala, despite their abundance in the latter faunal assemblage. This indicates that the shelter's inhabitants were collecting more crabs during the Middle Marcala than during earlier periods, though these figures were overshadowed by the collection of a wider variety of taxa at this time such as armadillos and birds, as well as an increased abundance of WTD. Cottontail rabbits (*Sylvilagus* sp.) are also overrepresented in Early Esperanza strata and underrepresented during the Middle Marcala phases, where they are entirely absent. Cottontails are often found in open grasslands or areas with some presence of herbaceous and woody that are not heavily wooded and also in anthropogenically disturbed environments (see Chapman and Ceballos 1990; Chapman et al. 1980; Emery and Thornton 2008; Reid 2009; Stahl 2009). Their complete absence from the Middle Marcala assemblage is curious given that the presence of other disturbance-loving taxa and an increase in plant taxa that require human propagation (i.e., avocados; see Figueroa and Scheffler 2021; Scheffler 2008) suggest the landscape at this time was disturbed. Low abundances of cottontail rabbits during the Middle Assemblage might instead suggest is that anthropogenic impacts in the area surrounding El Gigante focused on propagating certain species of fruit trees (which are abundant in the macrobotanical assemblage; see Figueroa and Scheffler 2021; Scheffler 2008) rather than on creating openings in the forest by burning or clearing vegetation, which has been recorded elsewhere in the region (e.g., Aceituno and Loaiza 2018; Acosta 2008; Piperno et al. 2017). However, this needs to be evaluated using independent paleoenvironmental data.

5.3.2 Minimum Number of Individuals (MNI) at El Gigante

NISP counts were used to calculate the Minimum Number of Individuals (MNI) following the procedure I outlined in Chapter 4. Overall MNI counts for the El Gigante assemblage are small (Table 5.20). A contingency table analysis of MNI counts standardized per century shows there are no statistically significant differences in how MNI are distributed across occupational phases (G=26.279, *p*=1.000). However, this might be due to the small sample size. An exploration of the data shows a steady decline in the abundance of deer over time, an abundance of leporids during the Early Esperanza and crabs during the Late Esperanza.

Table 5.20 MNI values (raw and standardized per century) by occupational phase.

Taxon	**Occupational Phase**								
Scientific name	**EE**		**LE**		**EM**		**MM**		**Total MNI**
	n	**Std. n**	**n**	**Std. n**	**n**	**Std. n**	**n**	**Std. n**	
Didelphidae	1	0.13	0	0	2	0.15	1	0.56	4
Chiroptera	0	0	0	0	1	0.08	2	1.11	3
Dasypus novemcintus	2	0.25	2	0.33	3	0.23	4	2.22	11
Sylvilagus sp.	4	0.51	1	0.16	1	0.08	0	0	6
Lepus sp.	0	0	0	0.00	1	0.08	0	0	1
Sciurus sp.	0	0	1	0.16	0	0	0	0	1
Neotominae	0	0	0	0	1	0.08	1	0.56	2
Sigmodontinae	1	0.13	2	0.33	2	0.15	1	0.56	6
Cuniculus paca	0	0.00	1	0.16	0	0	0	0.00	1
Rodentia	10	1.27	3	0.49	11	0.83	13	7.22	37
Canidae	1	0.13	0	0	2	0.15	0	0	3
Procyon lotor	0	0	0	0	1	0.08	0	0	1
Mephitidae	0	0	0	0	2	0.15	1	0.56	3
Felidae, small	0	0	0	0	1	0.08	0	0	1
Felidae, large	0	0	0	0	1	0.08	0	0	1
Carnivora	0	0	0	0	1	0.08	1	0.56	2
Tayassuidae	1	0.13	1	0.16	0	0	0	0	2
Mazama sp.	1	0.13	1	0.16	1	0.08	1	0.56	4
Odocoileus virginianus	7	0.89	5	0.82	4	0.30	4	2.22	20
Mammalia	0	0	0	0	0	0	0	0	0
Aves	2	0.25	1	0.16	2	0.15	1	0.56	6
Testudines	1	0.13	0	0	0	0	0	0	1
Iguanidae	0	0	1	0.16	1	0.08	0	0	2
Serpentes	1	0.13	1	0.16	1	0.08	0	0	3
Reptilia	1	0.13	1	0.16	1	0.08	0	0	3
Decapoda	26	3.29	34	5.57	22	1.67	8	4.44	90
Totals	**59**		**55**		**62**		**38**		**214**

5.3.3 The Composition of the Preceramic Faunal Assemblage at El Gigante

An examination of the NISP and MNI data shows how changes in the abundance of particular taxa over time are related to the choices made by the Preceramic inhabitants of El Gigante. In general, MNI data are so small across the identified taxa as to be uninformative given the highly fragmented nature of the assemblage, and I focus the following summary on NISP counts alone.

First, deer remains are the most abundant at the site across all occupational phases except the Middle Marcala, when armadillo remains are most abundant. This highlights the importance of this taxon to the inhabitants of El Gigante and also suggests that the site was used for processing and consuming deer. Only a few of the cervid remains were identified as belonging to Brocket deer (*Mazama* sp., NISP = 10, MNI = 4), the second-largest species available in the area, though this number is likely greater given the size of the cervid assemblage and the difficulty in differentiating between brocket and WTD.

Armadillos (*Dasypus novemcinctus*) are the second most abundant at the site once by accumulation rate. However, the vast majority of armadillo specimens (n=793, 87.8%) are scutes, with each individual animal having hundreds of these. Therefore, the high NISP and accumulation rate for armadillo may be misleading about their relative importance in the diet.

The majority of crab specimens (n = 507, 74%) were small (<10mm) undifferentiated shell fragments. Despite the abundance of crab remains in the assemblage, other riverine species including amphibians, fish, and other invertebrates (i.e., snails), are notably absent despite their ubiquity in other Preceramic zooarchaeological assemblages from the region (Eudave 2008; Flannery and Wheeler 1985; Orsini 2016). This absence is interesting given the proximity of El Gigante to the nearby Estanzuela River (~100m). An examination of the ethnographic and ethnohistoric literature for the area indicates that the Lenca who inhabited the highlands of central and southwestern Honduras since at least Prehistoric times do not consume many freshwater snails (i.e., Pachychilus spp.), a practice that is common among groups inhabiting valleys and lowlands (Gómez Zúñiga 2011). The fish most consumed by the highland Lenca are locally known as *olominas*, a generic term referring to small livebearers from a number of species, especially mollies (*Poecilia* sp.; Matamoros et al. 2009). Ethnohistoric accounts from other highland areas of Mesoamerica (Acuña 1982) indicate groups near sources of water focused on collecting crabs and *olominas*, which is similar to the assemblage from El Gigante. Ethnohistoric and ethnographic accounts from southwestern Honduras suggest *olominas* were and are still mass captured using nets and baskets, dried, and consumed whole (Carias et al. 1998; Chapman 1992; Gómez Zúñiga 2011). These consumption patterns and the small size of these fish (<10cm) suggests their remains would not have been recovered by excavations at El Gigante. However, it might be possible to detect their consumption through the analysis of coprolites recovered from the site, which is pending (Scheffler 2008).

Rodents are the fourth most abundant taxa in the assemblage. The presence of owl pellets on the surface and buried strata of the shelter suggest some of these remains were likely brought into the shelter by non-human predators. Additionally, it is possible rodents lived and died within the strata at the site, given some degree of bioturbation identified in the course of excavations (Scheffler 2008: 89). However, no large burrows were identified during excavation, which suggests numbers of burrowing animals at the site was low, resulting in relatively minor bioturbation of the site's strata. Despite the above, the majority of rodent bones (40%) are burned, which is often interpreted as being a sign of their consumption (see Flannery 1986; Widmer and Storey 2016). Given that this proportion of burned rodent remains is much higher than the average for the analyzed assemblage (ca. 23%), it is quite probable that some of the rodents identified in the assemblage were being consumed by El Gigante's inhabitants.

Somewhat surprisingly, canid remains are absent from the assemblage, given the importance of these animals to later cultures of the region (Valadez Azua et al. 2013). In addition, only two specimens were securely identified to belonging to felids: a distal radius belonging to a small-bodied felid, and a first phalanx belonging to a large-bodied specimen, possibly a puma (*Puma concolor*) or jaguar (*Panthera onca*), both from Early Marcala strata. The phalanx was found complete – a rare occurrence at El Gigante, which might suggest its purposeful curation. Only a few remains of bats (Chiroptera) were recovered and identified. Most of these were recovered from sorted bulk sediment samples and not in the sample of faunal remains recovered during excavation, which indicates these remains were too small to be recovered by the size of the screens used in the excavations (1/8"). Their small number might also be due to the large size of the opening of the shelter, which creates lighting and humidity conditions that are not preferred by bats, especially given the prevalence of more suitable caves elsewhere in this area.

Peccary (Tayassuidae) remains are uncommon in the assemblage. Because they are highly social animals, peccaries prefer large unbroken stretches of mature forests and avoid disturbed and open areas (Meyer et al. 2019). The current landscape of the highlands of southwestern Honduras does not include many such areas, which might explain the relative absence of this species in the faunal assemblage, and would suggest that relatively open environments characterized the El Gigante landscape even after the onset of the Holocene.

Leporid remains correspond to just under 2% of the total assemblage NISP. At least a few specimens were identified as belonging to cottontail rabbits (*Sylvilagus* sp.), though some specimens belonged to larger individuals, suggesting perhaps the presence of leporid species not present in the area today such as jackrabbits (*Lepus* sp.), which prefer drier and more open habitats. The remains of rabbits were particularly abundant during the Early and Late Esperanza phases, a pattern I examine in the next section.

5.4 Diversity of the El Gigante Preceramic Faunal Assemblage

In order to evaluate whether or not resource depression occurred at El Gigante and to determine whether resource depression was caused by environmental changes or human predation, I employed a methodological procedure based on the protocol developed by Wolverton and colleagues (Wolverton 2002, 2008; Wolverton et al. 2008, 2012). This methodology determines whether resource depression took place and then seeks to identify whether it was caused by environmental or anthropogenic changes. This is particularly useful because it was developed using the life-history and ecology of WTD, which as stated above is the highest-ranked species in the area and is well-represented in the El Gigante faunal assemblage.

For the purposes of this dissertation, I assume foraging efficiency to mean the overall net return rate associated with a hunting strategy whereby prey rank is determined generally by size but with caveats previously noted (Broughton 1994; Broughton et al. 2011; Piperno and Pearsall 1998; though see Lupo et al. 2020 for a discussion of other forms of ranking). In the case of El Gigante, the relative abundance of artiodactyls (WTD) to other smaller prey, also known as the Abundance or Artiodactyl Index (AI), will provide a measure of the relative proportion of different prey exploited at the site. The expectation is that a higher AI reflects a higher proportion of high-ranked species (WTD) and thus a higher level of foraging efficiency (Bayham

1979, 1982; Broughton 1994a, 1994b). As originally formulated using taxa in North American assemblages, AI is calculated by comparing the proportion (NISP) of artiodactyls to that of lagomorphs – both of which are abundant in North American faunal assemblages. However, given the small sample size of lagomorphs identified in the El Gigante assemblage, I calculated AI using the following formula, which is based on the comparison of artiodactyl NISP to the NISP of the entire assemblage (see Wolverton et al. 2012 for a discussion of this particular formula):

$$\mathrm{AI} = \frac{\sum \text{artiodactyls}}{\sum \text{artiodactyls} + \sum \text{NISP}}$$

Changes in assemblage diversity have been used by zooarchaeologists to infer encounter rates with prey and consequently estimate the diet breadth of a particular group, with the assumption that changes in the encounter rate of high-ranked prey will result in changes in overall foraging efficiency, and thus changes in their representation in an assemblage (Jones 2004; Lupo 2007; Wolverton et al. 2012). Assemblage diversity (a proxy for diet breadth) is most commonly determined by measurements of assemblage richness and evenness. Richness, also known as ∑TAXA, refers to the total number of different taxa in a particular assemblage and is heavily influenced by sample size. Evenness, on the other hand, quantifies how evenly different taxa are represented in an assemblage. In this dissertation I use the reciprocal or inverse of Simpson’s Index (SI; Simpson 1949), which quantifies both the evenness and richness of prey in a diet (Stiner 2001; Stiner and Munro 2011). This index places particular importance on the most abundant taxon in a sample, making it less sensitive to species richness and thus more appropriate for archaeological assemblages than other diversity indices (i.e., Shannon-Weaver index; see Jones 2004: 310). In addition, this particular index is also less sensitive to different sample sizes, though a sample size (NISP) of 99 has been deemed a minimum threshold for this particular index analysis (Stiner and Munro 2011: 622). The formula for calculating this index is as follows:

$$\mathrm{SI} = \frac{1}{\sum({p_i}^2)}$$

Where p_i represents the proportion of each taxon (measured in this case by the NISP) within an assemblage. In this study, I follow Stiner and Munro (2011) and only include specimens identified to at least the taxonomic level of family in the determination of this index, in order to better reconstruct dietary patterns. For this particular index, low SI values represent a narrow diet breadth and high SI values are indicative of a diverse diet. For example, in an assemblage that contains 20 possible taxa, an index value of 20 would signify all possible taxa are equally represented in the assemblage, indicating the most possible diverse diet given available resources; on the other hand, an index value of 1 would suggest the diet is centered around a very limited number of taxa and is thus narrower (Stiner 2001).

Two measurements of carcass exploitation patterns were calculated to determine the extent and types of fragmentation of the assemblage and help identify taphonomic processes and behavioral patterns. First, standardized body part profiles helped determine differences in the representation of body parts in the assemblage, which served as a proxy for prey processing and transport decisions made by El Gigante’s inhabitants (Manne 2014; Manne et al. 2012; Stiner 2002, 2004). Second, the FFI, which determines the intensity to which bones were fragmented, will be used to evaluate the occurrence of grease and marrow extraction practices (Outram 1998, 2001, 2005). I determined that the FFI approach was the most appropriate measure of fragmentation, when compared to others (i.e., NISP:MNE, NSP:NISP) given the highly fragmented El Gigante assemblage (see Outram 1998: 141 and Lyman 1994: 294 for reviews of other fragmentation measures).

Changes in mortality profiles (i.e., age structures) and body size in WTD were used to evaluate whether resource depression was caused by hunting pressures or environmental change (Broughton 2002; Lupo 2007; Stiner 1990; Wolverton 2008). The small sample size available (MNI = 20 WTD across all occupational phases) does not permit more than a qualitative examination of these patterns. Age and body size provide paleoenvironmental proxies that are directly correlated to the faunal assemblage and reflect physiological changes resulting from the WTD’s unique life-history and ontogeny (Fulbright and Ortega 2006; Lopez-Arevalo et al. 2011; Wolverton 2008).

The methodology outlined above requires that I first identify whether or not resource depression occurred on the landscape of El Gigante. I then examine what factors led to this change in the availability of high-ranked prey (i.e., deer). As noted, I used two different measures of assemblage diversity to examine changes in the diet of the inhabitants of El Gigante: the artiodactyl index (AI) and Inverse of Simpson’s Index (SI). Both of these indices reflect foraging efficiency, or the rate at which foraging groups at this site encountered and hunted high-ranked prey, specifically white-tailed and brocket deer. Table 5.21 and Figures 5.13-5.14 show both of these indices across the different occupational phases of El Gigante.

Table 5.21 Measures of assemblage diversity over time. NISP counts used to calculate these measures only include specimens identified to the family level.

Measure	**Occupational Phase**			
	EE	**LE**	**EM**	**MM**
NISP	931	643	879	591
Richness	14	14	21	12
Inverse of Simpson	3.322	3.031	3.949	3.131
Artiodactyl Index	0.427	0.470	0.294	0.220

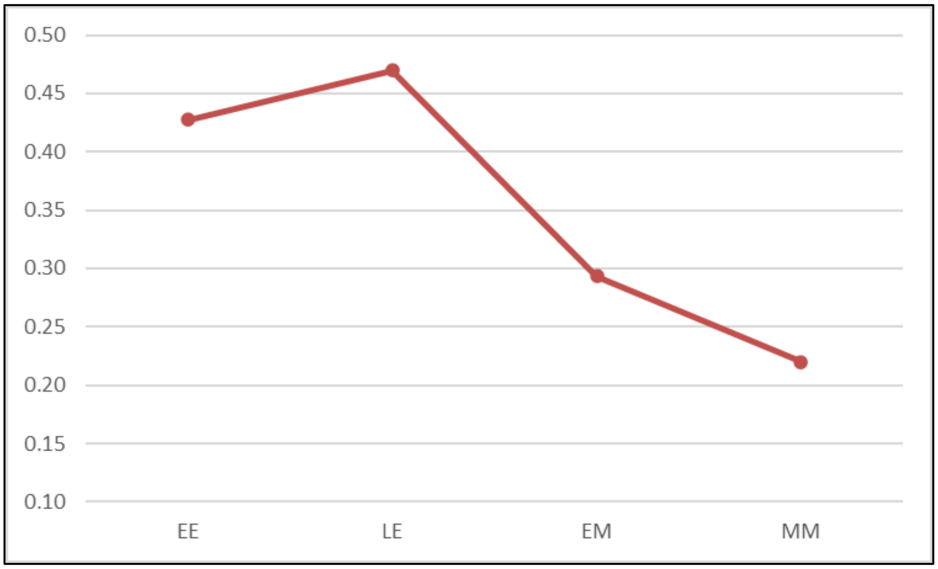

Figure 5.13 Artiodactyl index by occupational phase.

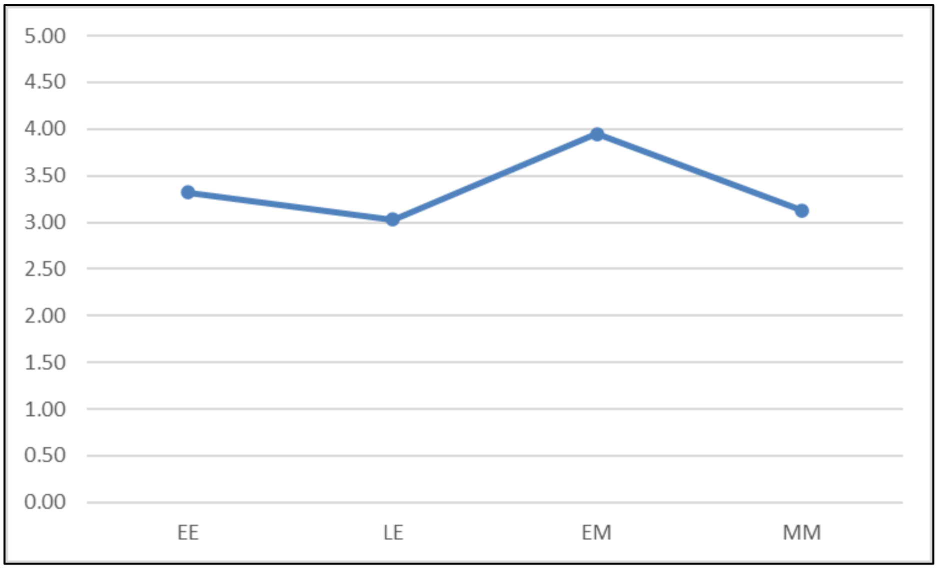

Figure 5.14 The inverse of Simpson's index by occupational phase.

These data suggest a decline in foraging efficiency over time and little if any change in species richness or diet breadth. A general decrease in AI following the end of the Esperanza Phase suggests cervid remains were less dominant in later assemblages. The SI values are overall very low (<4) considering 19 different taxa were used to calculate the index. This indicates that the diet breadth of El Gigante's inhabitants remained relatively narrow throughout the entire Preceramic and was dominated by a limited number of species, namely WTD, as indicated by the NISP counts presented above. However, diet breadth is expected to increase in response to a decline in foraging efficiency (MacArthur and Pianka 1966; Stephens and Krebs 1986; Winterhalder and Smith 2000). This discrepancy might be explained by the very high number of unidentified mammals in the Middle Marcala assemblage (NISP = 198), which account for 74% of all unidentified mammal specimens in the analyzed assemblage. When standardized per century, bones during this phase are generally smaller than in the other phases (<15mm), making their identification difficult and skewing the diversity indices presented above.

Something else notable about both of these indices is that they both do not shift significantly until after the Late Esperanza phase, which suggests a period of ca. 1,400 years during which groups utilizing this landscape changed their subsistence very little. This merits additional examination because according to some existing research on the Preceramic (Flannery 1986; Piperno and Pearsall 1998; Piperno et al. 2017) changes in diet breadth are expected to occur relatively early in the Holocene, following what is assumed to be widespread environmental change. This long period of behavioral and possibly environmental stability is followed by a similarly long span of time (the Early Marcala, ~1300 years) during which the diet was highly diverse. Other lines of evidence reviewed above indicate occupations of the shelter were short and likely limited to a very narrow set of activities.

One additional line of evidence for evaluating a decrease in foraging efficiency is carcass exploitation patterns. Briefly, more effort put into the processing of a carcass by deliberately breaking the bone to obtain marrow and/or fat is sometimes assumed to indicate a drop in foraging efficiency that required maximizing the nutrients obtained from captured prey (Church and Lyman 2003; Lupo and Schmitt 1997; Lyman 1994; Outram 2001, 2002, 2004).

Bones that were not identified to a particular taxon were classified into seven different size classes and four different categories, as described in Chapter 4 (see Table 5.22). A contingency table analysis reveals that there are statistically significant differences in bone fragment categories across size classes at El Gigante (G=519.253, *p*=.000). Importantly, Freeman-Tukey deviates show that cancellous bone fragments are significantly overrepresented in the 10-20mm size classes and that unburned shaft fragments are significantly overrepresented in the larger size classes (20-50mm). This fragmentation pattern is indicative of purposeful fragmentation of bone for the extraction of both fat and marrow, whereby diaphyses are splintered while fresh and cancellous bone is comminuted and often smaller in size following breakage and boiling (see Outram 2001). I examined the proportion of purposeful breakage using other indices, described below.

Table 5.22 Unidentified bone fragments by size class and bone category. Freeman-Tukey deviates are in parentheses and bolded values are significant at p=.05 (± 1.64).

	Size Class (mm)							
Bone type	**0-10**	**10-15**	**15-20**	**20-30**	**30-40**	**40-50**	**50+**	**Totals**
Axial	0 **(-9.68)**	58 **(2.46)**	72 **(4.78)**	4 **(-5.39)**	1 **(-1.88)**	0 (-1.31)	0 (-0.3)	135
Cancellous	0 **(-17.67)**	238 **(8.43)**	124 (0.89)	52 **(-2.32)**	0 **(-6.38)**	1 (-1.38)	0 (-0.76)	415
Shaft – unburned	1292 (-0.19)	1659 **(-5.29)**	1751 (0.93)	1187 **(4.03)**	238 **(2.58)**	69 **(2.49)**	8 (0.13)	6204
Shaft – burned	1020 **(3.96)**	1394 **(2.56)**	1101 **(-2.43)**	630 **(-3.72)**	117 **(-1.86)**	19 **(-2.97)**	6 (0.33)	4287
Totals	2312	3349	3048	1873	356	89	14	11041

Burned bone fragments comprise 38.8% of the total unidentified bone assemblage (n=4,287). Figure 5.15 shows the chronological distribution of burned and unburned bone as percentages of the assemblage of each occupational phase. A contingency table analysis of these data shows there are statistically significant differences in how bone fragment categories and size classes are distributed across occupational phases at El Gigante (G=658.389, *p*=.000). Freeman-Tukey deviates (Table 5.23) indicate that some of the smallest bones analyzed (<20mm) are significantly underrepresented in Early Esperanza deposits but tend to be significantly overrepresented in Early and Middle Marcala contexts. This suggests bones were more intensively broken during later phases of occupation of the shelter, particularly the during the Early Marcala phase. Interestingly, large bones (i.e., 30-50mm) are significantly overrepresented during the Middle Marcala, indicating within-bone nutrient extraction during this time were variable. Other data described above suggest the Early Marcala was marked by short-duration occupations of the shelter, perhaps as a result of localized faunal resource depression, a pattern which would require the maximization of within-bone nutrient extraction (see Outram 2001).

Table 5.23 Distribution of unidentified bone fragments by size class, bone category, and occupational phase. Freeman-Tukey deviates are in parentheses and bolded values are significant at *p*=.05 (± 1.66).

Phase		**EE**	**LE**	**EM**	**MM**
<10mm	**UB**	449 (0.28)	211 **(-8.07)**	551 **(8.64)**	81 **(-5.35)**
	B	367 (0.91)	132 **(-10)**	412 **(6.56)**	109 (0.13)
10-15mm	**Axial**	26 (1.32)	12 (-0.86)	19 (0.65)	1 **(-2.64**)
	Canc.	64 **(-2.04)**	89 **(2.95)**	68 (0.08)	17 **(-1.72)**
	Shaft - B	439 **(-1.82)**	383 (0.57)	393 (-0.14)	179 **(2.49)**
	Shaft - UB	476 **(-4.07)**	513 **(3.22**)	504 (1.49)	166 (-0.71)
15-20mm	**Axial**	27 (0.5)	18 (-0.22)	27 (1.39)	0 **(-4.61)**
	Canc.	46 (0.55)	50 **(2.66)**	21 **(-2.64)**	7 **(-1.84**)
	Shaft - B	380 (0.13)	315 (1.22)	263 **(-2.92)**	143 **(2.35)**
	Shaft - UB	599 (-0.06)	570 **(4.51)**	396 **(-4.8)**	186 (0.07)
20-30mm	**Axial**	3 (1.18)	1 (0.12)	0 (-1.35)	0 (-0.64)
	Canc.	16 (-0.38)	21 **(1.75)**	12 (-0.68)	3 (-1.06)
	Shaft - B	268 **(3.35)**	128 **(-3.29)**	141 **(-2.99**)	93 **(2.98)**
	Shaft - UB	417 (0.49)	387 **(3.75)**	251 **(-5.03)**	132 (0.59)
30-40mm	**Axial**	1 (0.87)	0 (-0.44)	0 (-0.46)	0 (-0.19)
	Canc.	0 (0)	0 (0)	0 (0)	0 (0)
	Shaft - B	64 **(3.35)**	10 **(-4.74)**	24 **(-1.68)**	19 **(1.72)**
	Shaft - UB	98 **(1.75)**	78 **(1.75)**	45 **(-2.99)**	17 **(-1.72)**

40-50mm	**Axial**	0 (0)	0 (0)	0 (0)	0 (0)
	Canc.	0 (-0.54)	0 (-0.44)	0 (-0.46)	1 (1.22)
	Shaft - B	10 (1.28)	3 (-0.88)	0 **(-3.75)**	6 **(2.09)**
	Shaft - UB	31 (1.44)	24 (1.26)	6 **(-3.82)**	8 (0.33)
50+mm	**Axial**	0 (0)	0 (0)	0 (0)	0 (0)
	Canc.	0 (0)	0 (0)	0 (0)	0 (0)
	Shaft - B	2 (-0.31)	3 (0.64)	3 (0.56)	0 (-1.09)
	Shaft - UB	5 (1.65)	0 **(-1.72)**	1 (-0.38)	0 (-0.88)

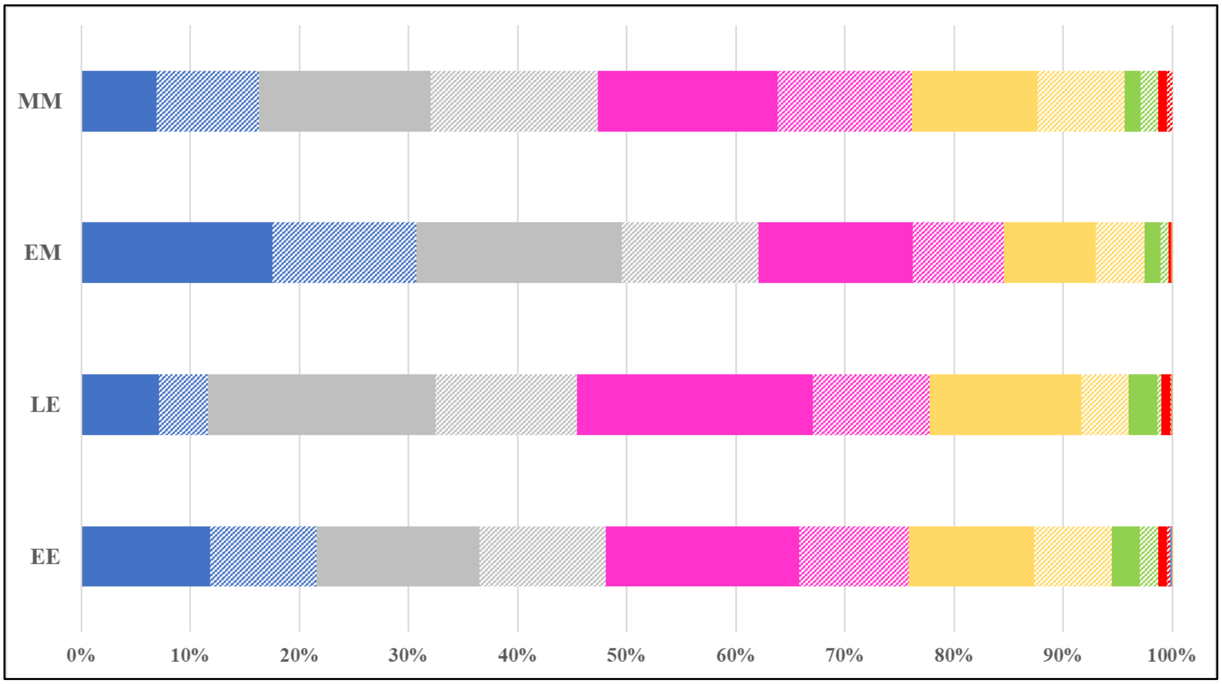

Figure 5.15 Burned (solid) and unburned (hashed) unidentified bone fragment size classes. Blue: <10mm, Grey: 10-15mm, Pink: 15-20mm, Yellow: 20-30mm, Green: 30-40mm, Red: 40+mm.

Fracture Freshness Index (FFI) scores were assigned to 445 bone fragments larger than 40mm (Table 5.24, Figure 5.16). This number includes bones that were identified to particular taxa larger than 40mm. FFI scores of 0-6 are calculated based on three criteria: fracture outline or shape, fracture angle relative to cortical surface, and fracture texture or roughness, with lower scores indicating fresher bones were broken (Outram 1998, 2001, 2002). There is a general drop in FFI score over time (Table 5.25, Figure 5.17), with a very sudden drop during the Middle Marcala, which is indicative of a higher proportion of bones being broken while fresh.

Table 5.24 FFI score counts and percentages by occupational phase.

Phase		**EE**	**LE**	**EM**	**MM**	**Totals**
FFI Score	**0**	95 (49.74%)	73 (52.14%)	17 (29.82%)	42 (73.68%)	227 (51.01%)
	1	19 (9.95%)	14 (10.00%)	11 (19.30%)	4 (7.02%)	48 (10.79%)
	2	14 (7.33%)	17 (12.14%)	11 (19.30%)	3 (5.26%)	45 (10.11%)
	3	19 (9.95%)	8 (5.71%)	9 (15.79%)	4 (7.02%)	40 (8.99%)
	4	9 (4.71%)	4 (2.86%)	5 (8.77%)	2 (3.51%)	20 (4.49%)
	5	5 (2.62%)	4 (2.86%)	2 (3.51%)	(0.00%)	11 (2.47%)
	6	30 (15.71%)	20 (14.29%)	2 (3.51%)	2 (3.51%)	54 (12.13%)
Totals		**191 (42.92%)**	**140 (31.46%)**	**57 (12.81%)**	**57 (12.81%)**	**445**

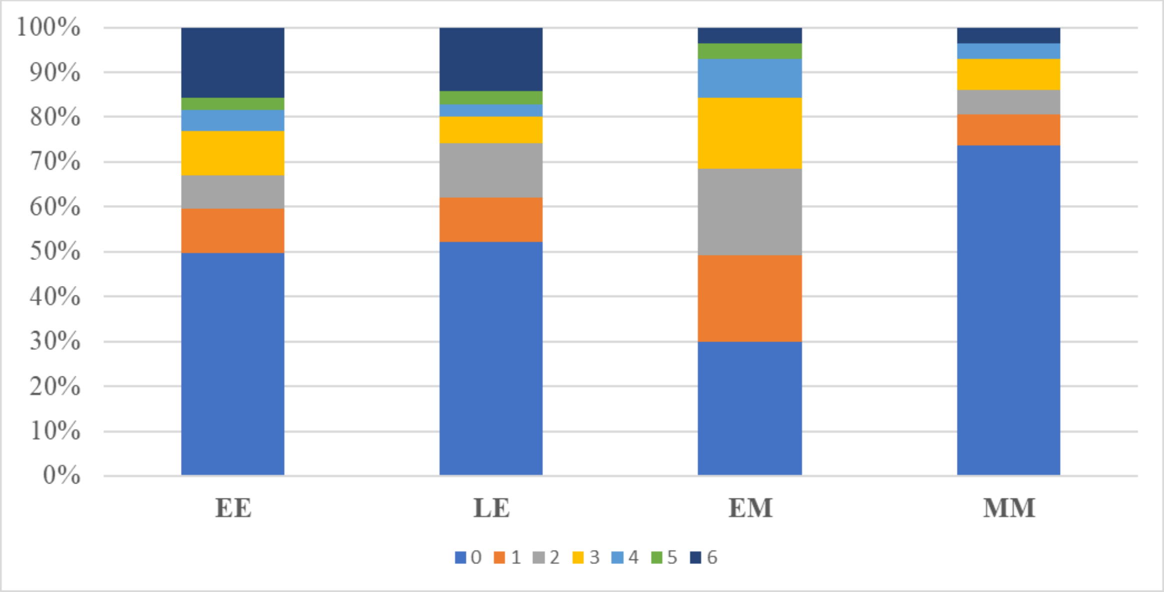

Figure 5.16 Distribution of FFI scores by occupational phase.

Table 5.25 Mean FFI score by occupational phase.

Phase	**Mean FFI**
EE	1.81
LE	1.63
EM	1.79
MM	0.74

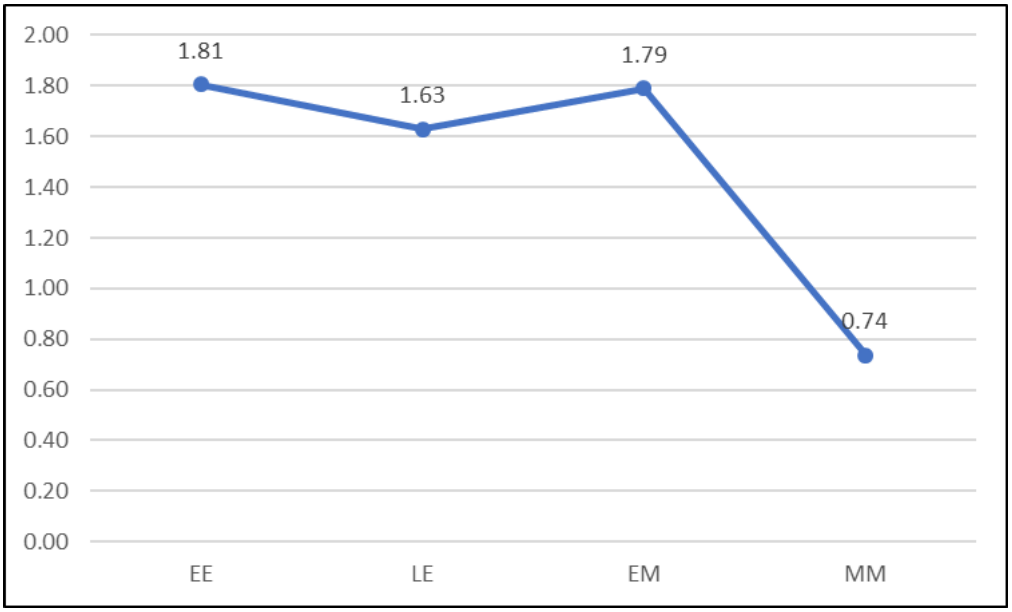

Figure 5.17 Mean FFI score by occupational phase.

A contingency table analysis indicates that there are statistically significant differences in how FFI scores are distributed in each occupational phase (G=45.619, *p*=.000). Freeman-Tukey deviates (Table 5.26) indicate bones with FFI scores of 0 are significantly overrepresented during the Middle Marcala strata, while scores of 1-2 are overrepresented in the Early Marcala. Bones with FFI scores of 6 are significantly underrepresented in both of these phases. These patterns imply that during later Preceramic occupations of the site bones were fractured while fresh, indicating their purposeful breakage for the extraction of marrow or grease (Outram 1998, 2001). A visual examination of FFI scores, however, shows that deliberate breaking of fresh bone was a common practice at El Gigante from its earliest occupation, though it became more dominant later on in time. This indicates marrow and grease extraction practices increased in intensity over time, which further supports a decline in foraging efficiency over time at the site. Alternatively, this might indicate that El Gigante was occupied during a different season towards the end of the Preceramic, perhaps the dry season during which animal prey are scarce and must be processed more intensively.

Table 5.26 FFI score counts by occupational phase. Freeman-Tukey deviates are in parentheses and bolded values are significant at p=.05 (± 1.57).

	FFI Score						
	0	**1**	**2**	**3**	**4**	**5**	**6**
EE	95 (-0.22)	19 (-0.3)	14 (-1.23)	19 (0.48)	9 (0.22)	5 (0.23)	30 (1.36)
LE	73 (0.22)	14 (-0.22)	17 (0.77)	8 (-1.34)	4 (-0.88)	4 (0.38)	20 (0.75)
EM	17 **(-2.47)**	11 **(1.72)**	11 **(1.88)**	9 (1.53)	5 (1.33)	2 (0.57)	2 **(-2.21)**
MM	42 **(2.21)**	4 (-0.82)	3 (-1.17)	4 (-0.40)	2 (-0.21)	0 **(-1.58)**	2 **(-2.21)**

Now that I have determined that a decrease in foraging efficiency occurred in the El Gigante landscape, I can examine whether this was driven by environmental or anthropogenic (i.e. demographic) factors. Unfortunately, the examination of changes in cervid body size is currently not possible because only three complete calcanei and three complete astragali are present in the analyzed sample, and these only represent the two earliest occupational phases at the site. Accordingly, I do this analysis by examining the age structures of cervid individuals identified in the assemblage, as described in Chapter 4. My sample size for the evaluation of age structures is too small for a robust analysis, and I am thus limited to a qualitative interpretation of these data.

An examination of the ages of the 24 individual cervid remains identified in my analyses (Table 5.27, Figure 5.18) shows a preference for adult animals during the Early Esperanza. During the Late Esperanza the number of adult individuals captured decreased, a pattern which continued into the Early and Middle Marcala. Neonate individuals (fawns) are present in earlier assemblages but disappear by the Middle Marcala. Overall, the individuals being captured by El Gigante's inhabitants were younger over time, which is indicative of increased harvest pressure over time, which results in fewer individuals surviving to an older age (Wolverton 2008).

Table 5.27 Cervid age groups by occupational phase.

Phase	**Adult**	**Juvenile**	**Neonate**	**MNI**
EE	4	2	1	7
LE	2	2	1	5
EM	1	2	1	4
MM	1	3	0	4

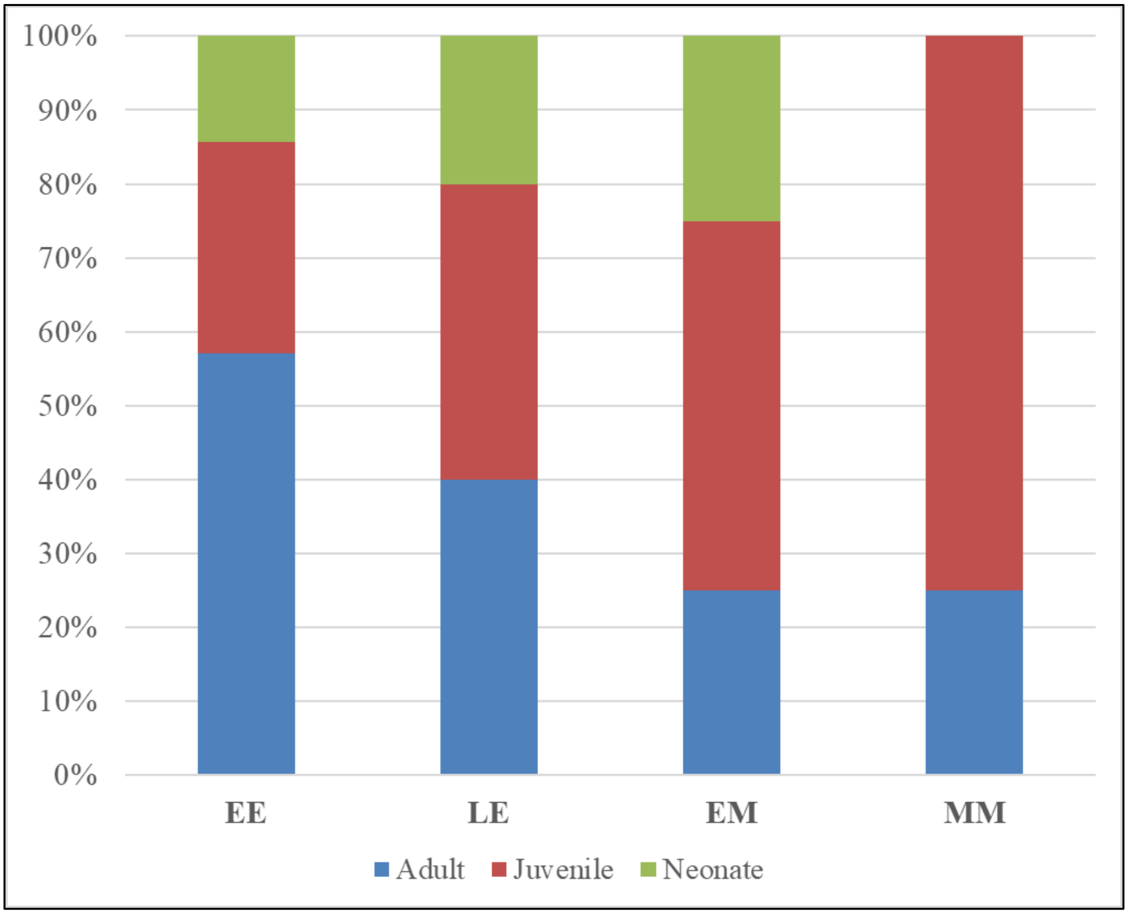

Figure 5.18 Distribution of cervid age classes by occupational phase.

5.5 Habitat representation at El Gigante during the Preceramic

Table 5.28 and Figure 5.19 show the results of the habitat fidelity analysis conducted on the El Gigante Preceramic faunal assemblage. A contingency table analysis of these data indicates there are no statistically significant differences in how these habitats are represented in each occupational phase (G=13.499, *p*=0.564). However, a visual examination of the data show that taxa from secondary forests, open habitats, and riverine and shoreline habitats dominate the assemblage. This is not surprising given that the most common taxa in the assemblage are deer, armadillos, and crabs, which are the species that best represent these habitats. The representation of secondary forests and open habitats changes in tandem throughout the Preceramic, increasing slightly in dominance over time. Both of these habitats have been associated with anthropogenically managed landscapes or “forest gardens” (Emery and Thornton 2008: 170). It is interesting to note, however, that there is a drop in the representation of mature forests, secondary forests, and open habitats during the Early Marcala phase but an increase in the dominance of taxa from riverine environments in the assemblage, namely crabs. This phase overlaps with the 8.2 ka climate anomaly characterized by cold and dry conditions across Middle America, which would have slowed or contracted the expansion of tropical forests between ca. 8300-8000 cal B.P. (e.g., Caballero et al. 2019; Wahl et al. 2016). The representation of taxa from mature forests also increases over time, which would be expected given the expansion of these habitats across Middle America during the Early and Middle Holocene.

Table 5.28 Proportionate representation of different habitats (%) by occupational phase at El Gigante.

	Mature Forest	**Secondary Forest**	**Riverine and shoreline**	**Wetlands**	**Open habitats**	**Human habitation areas**
EE	9.95	31.93	26.35	0.05	31.70	0.02
LE	11.55	33.37	22.14	0.13	32.82	0.00
EM	9.61	28.37	33.91	0.13	27.84	0.14
MM	14.67	36.42	12.79	0.08	35.99	0.04

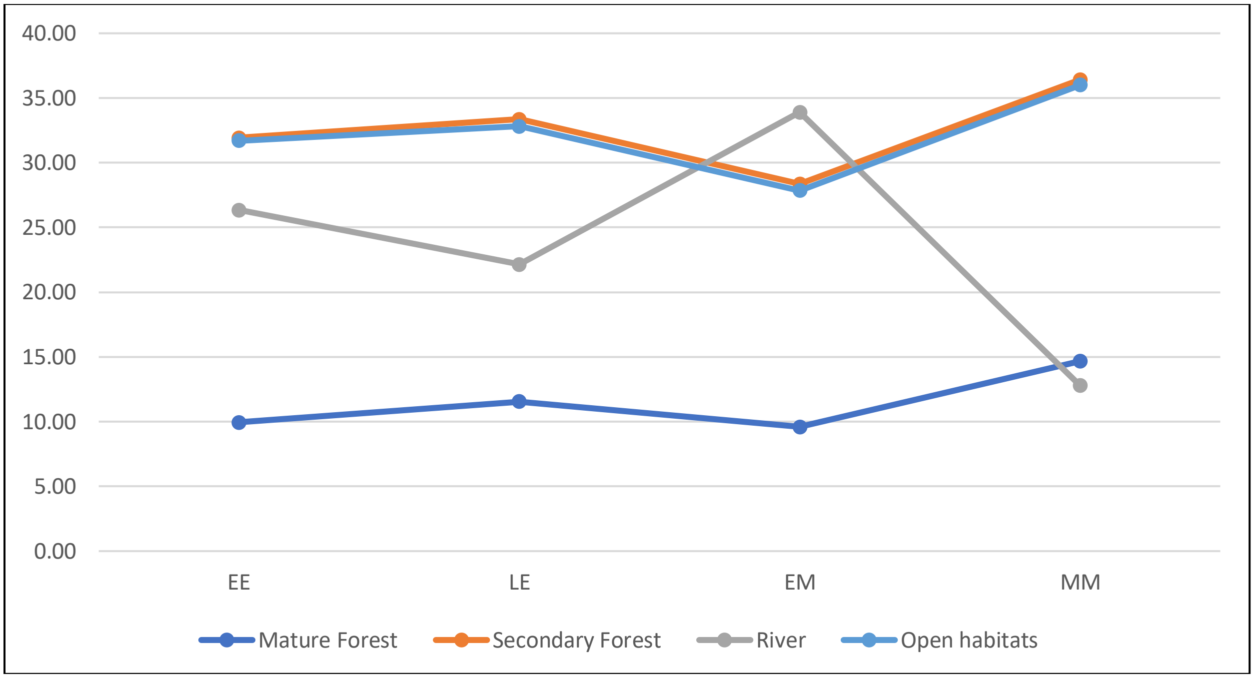

Figure 5.19 Variability in the relative representation of the four most common habitat types at El Gigante by occupational phase.

5.6 Geoarchaeological data

A limited number of sediment samples (n = 11) from Unit 18 were analyzed using a variety of geoarchaeological and geochemical methods used to infer intensity of occupation over time (Table 5.29, Figure 5.20). These methods included soil pH, soil organic matter, charcoal and phosphorus concentrations, and magnetic susceptibility (see Section 4.7 above). Unfortunately, no Late Esperanza strata were present in Unit 18 and this occupational phase is not represented by the data. Despite the small sample size and the limited spatial extent they represent, a contingency table analysis test shows there are statistically significant differences in the distribution of geochemical and magnetic susceptibility data within Unit 18 when the strata are divided by phase (G=2196.030, *p*=.000). First, Freeman-Tukey deviates indicate higher pH levels are overrepresented during the Early and Middle Marcala phases and underrepresented in some of the Early Esperanza strata. Results show that pH steadily increases upwards across the analyzed strata from a mean of 7.05 in the Early Esperanza to a mean of 9.5 during the Middle Marcala. Ethnoarchaeological research in Mesoamerica (e.g., Barba 2007; Barba and Denis 1983; Barba et al. 1995) has found pH levels are indicative of the presence of wood ash in living surfaces. This suggests higher inputs of wood ash over time at the site, which in turn implies greater intensity of use or longer occupations of the rockshelter over time. This interpretation is supported by the charcoal data, which for the most part matches well with changes in pH values. This interpretation is also bolstered by higher densities of bone being deposited at the site during later periods (see above) and an increase in local sources of chipped stone at the site (Hirth et al. 2018; Scheffler 2008).

Freeman-Tukey Deviates also show high levels of charcoal are overrepresented in the Early and Middle Marcala and are underrepresented in the Early Esperanza strata. pH levels and magnetic susceptibility change in tandem, the latter also supporting an increase in the deposition of ash, and thus a more intensive use of the rockshelter (see Marwick 2005; Oldfield and Crowther 2007; Roos and Nolan 2012; Rosendahl et al. 2014), between the Early Esperanza and the Early Marcala and a slight decrease during the Middle Marcala. A correlation analysis (Table 5.30) shows a strong correlation (r=.91) between these two variables and between charcoal and LOI. The amount of unburned soil organic matter (SOM) also generally increases over time. Freeman-Tukey Deviates show higher SOM is overrepresented during the Middle Marcala and underrepresented in the Early Esperanza strata, but the overall results show this percentage varies over time, with some Early Esperanza strata showing percentages almost as high as those during the Middle Marcala.

Table 5.29 Summary of geoarchaeological data obtained from Unit 18 sediment samples (P-amount of phosphorus, χfd – frequency-dependent magnetic susceptibility, SOM-soil organic matter) by occupational phase.

Level	**Phase**	**pH**	**Charcoal (mg/g)**	**Xfd**	**SOM**	**P (mg/kg)**	**% LOI OC**
23	MM	10.7 **(2.89)**	44.64 **(-4.53)**	12.28 **(3.94)**	21.05 **(5.11)**	956.81 (0.15)	4.04 (-0.95)
24	MM	9.2 (1.65)	177.07 **(5.56)**	5.74 (1.48)	5.66 (0.26)	1225.76 **(-2.21)**	13.58 (1.58)
27	MM	8.7 (0.62)	262.55 **(6.35)**	5.96 (0.67)	12.18 (1.13)	1890.8 **(-2.54)**	27.19 **(3.04)**
30	EM	9.5 **(1.76)**	291.31 **(12.01)**	5.9 (1.31)	5.39 (-0.38)	1251.84 **(-5.07)**	21.38 **(2.94)**
31	EM	9 (1.29)	333.44 **(13.64)**	4.85 (0.78)	8.37 (0.6)	1310.52 **(-5.99)**	27.57 **(4.14)**
32	EM	8.9 (0.86)	362.11 **(13.12)**	4.9 (0.45)	9.45 (0.48)	1610.44 **(-5.28)**	20.78 **(2.15)**
34	EE	9.5 (1.15)	215.94 **(4.34)**	8.02 (1.57)	21.41 **(3.56)**	1766.92 **(-1.93)**	15.57 (0.97)
36	EE	7.4 **(-3.65)**	173.91 **(-17.04)**	2.6 **(-3.51)**	10.43 **(-3.33)**	5916.9 **(4.79)**	9.53 **(-5.84)**
38	EE	7.9 (-0.47)	279.07 **(3.65)**	3.75 (-0.78)	8.42 (-0.93)	2549.32 (-1.15)	25.71 **(1.82)**

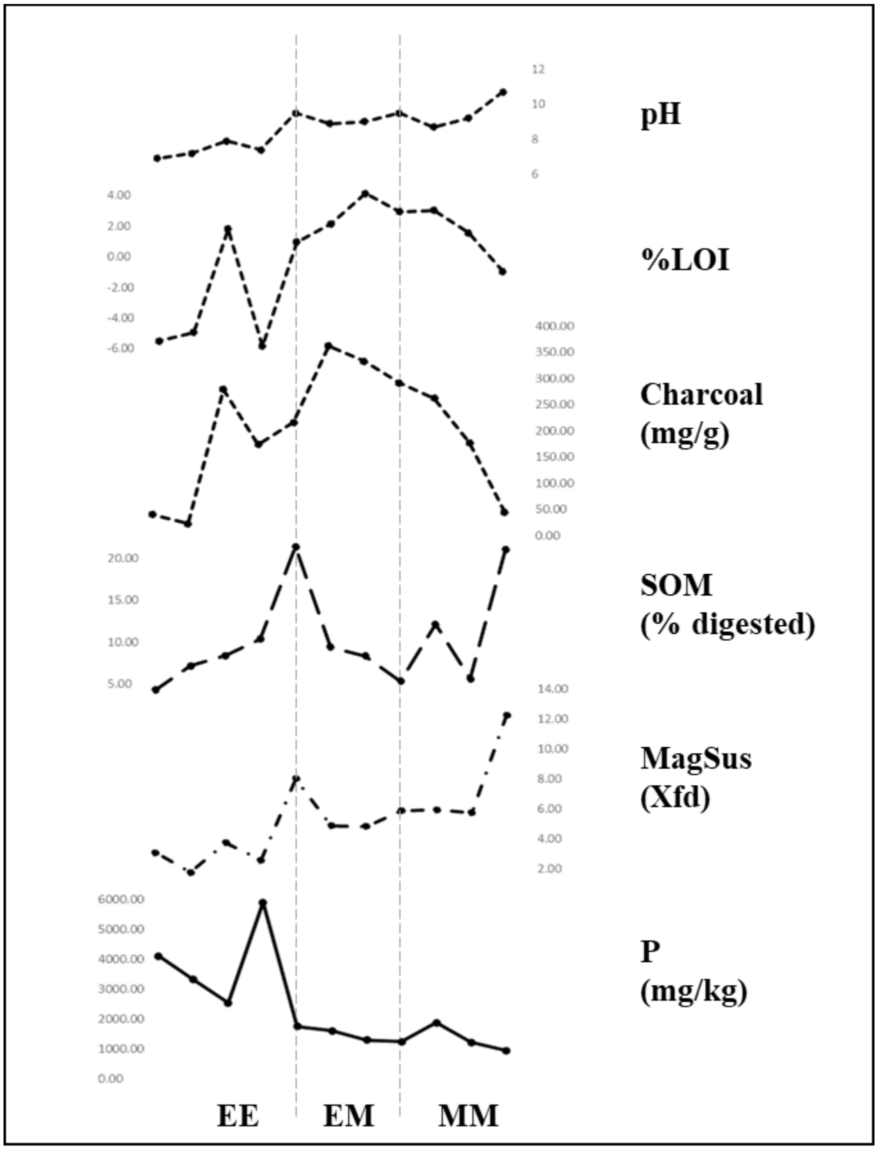

Figure 5.20 Summary of geoarchaeological data obtained from Unit 18 sediment samples by occupational phase.

Phosphorus results contradict the trends summarized above. Phosphorus concentrations decrease over time, with higher levels being overrepresented in the Early Esperanza strata. Higher phosphorus levels are inferred to be indicative of higher levels of deposition of organic waste and thus a greater intensity in the use of a particular space (Terry et al. 2000, 2004; Viberg et al. 2013; Wells et al. 2000). The phosphorus data presented here are contradictory to all other geoarchaeological and geochemical datasets and instead suggest a decrease in the use of the shelter over time. Something important to mention here is that the level of detectable phosphate in all the samples analyzed were extremely high, which required the samples to be diluted, in some cases down to 0.1%, thus making these results less precise. One possible interpretation of this pattern is that phosphorus leached down the sediment column at El Gigante. Unfortunately, all available sediment samples from El Gigante were analyzed as part of this study and additional excavation and coring are necessary to evaluate this.

Table 5.30 Results of a correlation analysis between the various geoarchaeological data collected from El Gigante. Strong positive and negative correlations are shaded.

	pH	**Charcoal (mg/g)**	**Xfd**	**HNO3 Digestion**	**P (mg/kg)**	**% LOI OC**
pH	1					
Charcoal (mg/g)	0.258	1				
Xfd	0.911	-0.044	1			
HNO3 Digestion	0.593	-0.109	0.761	1		
P (mg/kg)	-0.823	-0.373	-0.659	-0.252	1	
% LOI OC	0.207	0.917	-0.043	-0.124	-0.420	1

CHAPTER 6:

DISCUSSION

In this dissertation I aim to contribute to our understanding of the human-environment dynamics taking place during the Early Holocene in Middle America, a period of intense climatic, ecological, and behavioral change. To do so, I integrated the results of my analyses of a sample of the Preceramic period (11,010-7430 cal B.P.) faunal remains and sedimentary records recovered from the El Gigante rockshelter in southwestern Honduras with existing analyses of the site's lithic and macrobotanical assemblages to identify and examine the interplay of four major processes taking place during this critical transition in prehistory: climatic and ecological change, resource depression and concomitant loss of foraging efficiency, behavioral change (i.e., changes in subsistence and mobility), and anthropogenic landscape modification. Previous research suggests each of these processes occurred sometime during the Preceramic across the neotropics (Aceituno and Loaiza 2018; Aceituno et al. 2013; Acosta et al. 2018; Dickau et al. 2015; Flannery 1986; Lohse et al. 2006; Prufer et al. 2019) including at El Gigante (Scheffler 2008; Scheffler et al. 2012). However, a lack of adequate assemblages has not permitted a thorough examination of the environmental and behavioral changes that took place at this time and the processes that contextualized them. Existing research has developed a series of hypotheses and questions needed to be evaluated using archaeological and paleoenvironmental data from this time period.

The Broad-Spectrum Revolution hypothesis (BSR; Flannery 1969, 1986) and the plant food production hypothesis (PFP; Piperno 2006, 2011; Piperno and Pearsall 1998; Piperno et al. 2017) make the following predictions regarding how these processes unfolded following the Pleistocene-Holocene Transition (PHT): (1) environmental degradation took place following the end of the Pleistocene, causing a decline in the size and abundance of higher-ranked prey (i.e., resource depression of megafauna and large fauna such as deer); (2) these circumstances led foragers to adopt a more diverse diet, reduced residential mobility, and the modification of the landscape. The niche construction hypothesis (NCT; Smith 2015, 2016; Zeder 2012, 2016) suggests that reduced mobility, increased diet breadth, and landscape modification occurred before or independent of environmental degradation and resource depression and were instead proactive actions taken by highly knowledgeable populations taking advantage of resource-rich landscapes occupied persistently for long periods of time.

The data I collected and synthesized from El Gigante suggest the four processes listed above occurred during the Preceramic, though not in the order predicted by the hypotheses summarized above. Some caveats apply to my interpretations and discussion of my data. There is no evidence as of yet of a Late Pleistocene occupation (>11,000 cal B.P.) of El Gigante, and I can only make inferences about ecological and behavioral changes that took place during the earliest Holocene, the period after which megafauna were already extinct in the region (see Piperno et al. 2017 for a review of the relevant literature). Related to this, my interpretations are based on a sample of faunal materials recovered from the central portion of the shelter and might not be – and likely are not – representative of the entire array of activities carried out within the shelter. Ethnographic research has shown groups use the back wall, central, drip line, and exterior areas of caves for different purposes (see Walthall 1998 for a review of this literature), and I can only assume the behaviors I observe in the central portion of the shelter are but a small part of a much broader subsistence and settlement system. Third, the faunal remains deposited at El Gigante were impacted by two significant taphonomic processes: the precipitation of calcium carbonate on the surface of bone and a high degree of fragmentation. However, I argue that much of the latter is due to intentional breakage of bones for the extraction of within-bone nutrients. Fourth and finally, the distribution of human activities over space and time impacted the vertical and horizontal distribution of bone and ash. Ash within the shelter presumably originated from anthropogenic fire, given that this is a closed system, and I believe is the source of the calcium carbonate precipitated on bone.

Despite these limitations and the resulting small size of the identified sample, my analyses of the Preceramic faunal assemblage from El Gigante provides some novel insights into a key period of transition in the prehistory of Middle America about which we still know precious little. Specifically, the Early Holocene at El Gigante appears to have been characterized by a relatively open landscape with an abundance of a unique suite of resources, namely deer and fruit trees. Foraging populations returned to this site over the course of the Preceramic and stayed longer every time despite decreasing returns from the area’s animal resources. To compensate for this, these populations began pursuing a wider variety of prey and processed what prey was captured to extract marrow and fat. More importantly, these populations began to devote more time and effort to gathering and processing plant resources, which they continued to exploit more intensively during the next few hundred years. However, following this period of intense plant consumption it appears that the shelter was left unused for nearly three thousand years, suggesting these strategies were not enough to warrant occupation of El Gigante and its surroundings until the development of maize agriculture during the Middle and Late Holocene, when the site was re-occupied (Kennett et al. 2017; Scheffler 2008; Scheffler et al. 2012).

The Preceramic faunal remains from El Gigante highlight the entangled nature of subsistence and mobility decisions among foragers and how multiple lines of evidence are necessary for reconstructing these and the environmental and anthropogenic processes that informed them. Though the research presented in this dissertation has started to evaluate existing hypotheses aimed at explaining the various changes taking place during the Preceramic in Middle America, it poses more questions than it answers, at various scales. How intensively were the highlands of southwestern Honduras occupied and possibly impacted by foraging groups during the Early Holocene? Were other sites in this area – including other caves and shelters – used for similar purposes? Did populations inhabiting this area interact with those inhabiting other biogeographic zones, namely the lowland valleys to the east and north? More broadly, did foraging groups inhabiting other seasonal tropical forests and highland mountainous areas of Middle America behave in similar ways to the inhabitants of El Gigante, returning to these environments despite decreasing returns from animal resources? Lastly, if plant resources were central to the diets of foragers since the Early Holocene, what material indicators might we look for in the archaeological record, given that we are still heavily biased towards identifying diagnostic artifacts made and used in human-animal interactions (i.e., projectile points)?

6.1 Evaluating the PHT in Middle America

Over half a century has passed since Flannery (1969, 1986) first defined the Broad-Spectrum Revolution (BSR) hypothesis to explain the ways in which foraging populations experienced and responded to the climatic and environmental changes taking place during the

PHT. Following this transition a foraging way of life gave way to sedentism and cultivation and culminated with the development of domestication and agriculture. Flannery modified this model – which had originally been based on Old World archaeological sequences –using data he and others had gathered in Mesoamerica, which unlike the Old World had not experienced large demographic growth following the end of the Pleistocene and where animal domestication was largely absent. Despite this revision, Flannery's model still relied on demographic pressures driving populations towards "marginal" environments with higher degrees of resource unpredictability, requiring populations to expand their diet and reduce their residential mobility in order to ameliorate this.

The expectations set forth by the BSR hypothesis were highly adaptable to models developed out of Optimal Foraging Theory, which predict changes in diet and mobility following changes in resource rank and availability (Charnov 1976; Charnov et al. 1976; Kelly 1992, 2007; MacArthur and Pianka 1966; Stephens and Krebs 1986; Surovell 2009; Winterhalder and Smith 2000). Piperno and Pearsall (1998; Piperno 2006, 2011; Piperno et al. 2017) utilized the expectations of OFT to develop their own hypothesis – which I term the plant food production (PFP) hypothesis – regarding the environmental and behavioral changes taking place during the PHT. Specifically, they argue that the climatic and environmental changes taking place at the end of the Pleistocene resulted in the replacement of open landscapes by dense tropical forests, causing the depression and ultimately extinction of megafauna and most large fauna from the neotropics. They further argue that populations previously specializing in hunting big game (as indicated by the specialized toolkits recovered throughout the region) had to broaden their diet and reduce their residential mobility in response to their drastically changing surroundings. Lastly, and in response to the BSR hypothesis, they argue that population growth during the PHT did not play a role in the adaptive changes taking place at this time but instead occurred after these behaviors were already in place.

More recently, Smith (2011a, 2011b, 2015, 2016) and Zeder (2012, 2016) pushed back against the PFP hypothesis by arguing that the behavioral adaptations of the PHT are not responses to resource depression but resource abundance. They argue that areas with abundant and predictable resources made early reduced residential mobility more advantageous (as posited by the patch choice model; Stephens and Krebs 1986). Long-term occupations of these environments led to increasingly modified landscapes and eventual demographic growth, necessitating the broadening of the diet and intensification of anthropogenic niche construction behaviors.

Research on the Preceramic in Middle America and the broader neotropics has both supported and contradicted various components of the hypotheses outlined above. First, while there is evidence for ecological and climatic change taking place during the terminal Pleistocene, these changes were neither homogeneous nor synchronous across the region (e.g. Caballero-Rodriguez et al. 2018; Correa-Metrio et al. 2013). Second, evidence for the hunting of megafauna is limited to a few sites in central and northern Mexico and northern south America (e.g., Aceituno et al. 2013; Acosta et al. 2018; Gonzalez et al. 2016; Sanchez-Morales 2018). Third, research indicates demographic growth took place during the PHT at and near El Gigante, supporting one of the major expectations of the BSR hypothesis. This matches evidence elsewhere in the region showing the reduction of foraging radii and the development of certain territorial behaviors approximately at 11,000-9500 cal B.P. as indicated by the presence of locally distinctive projectile point types such as lanceolate, fishtail, and bifacial points in the Balsas, Tehuacan, and Oaxaca valleys of southern Mexico (Flannery 1986; Hole 1986;

MacNeish 1976; Ranere et al. 2009), the Central Depression of Chiapas (Acosta et al. 2018; García-Bárcena and Santamaría 1982, 1984), southern Belize (Lohse 2020; Prufer et al. 2019), El Gigante in Honduras (Iceland and Hirth 2021), and Costa Rica and Panama (Pearson 2002, 2003, 2004; Ranere 2000, 2006). A decrease in residential mobility – and concurrent development of these distinct lithic traditions – is predicted by the patch choice model to be the result of either demographic packing of the landscape or of populations taking advantage of stable patches with predictable and easily identified resources, the latter also predicted by gene-culture coevolutionary theory (Boyd and Richerson 1985).

Existing research and the hypotheses derived from it have relied heavily on macro and microbotanical and lithic assemblages, and much less so on faunal remains, which are fundamental for evaluating whether resource depression occurred here or not, what mechanisms drove it, and what role thes resources played before, during, and after its onset. This work has also not been sufficiently delimited chronologically given the dearth of adequate datasets to do so and we have lacked contexts where we can examine the interplay between these processes and how they unfolded over time.

6.2 Preceramic Human-environment Dynamics at El Gigante

The El Gigante zooarchaeological assemblage is roughly an order of magnitude larger than the next largest recovered from Middle America, at the Mayahak Cab Pek cave in Belize (Orsini 2016; Prufer et al. 2019). Unfortunately, the El Gigante faunal specimens are highly fragmented, limiting their potential for identification and analysis. Bone specimens from the site have a mean greatest length of approximately 2cm even when only taking into account the bones identified as belonging to cervids (n=1078), which comprise the vast majority of the analyzed materials. In addition, the high accumulation of ash within the shelter – most likely the product of wood ash deposited as a result of anthropogenic activity (Scheffler 2008) – has caused the precipitation of calcium carbonate concretions on a large number of bones (28%), compounding the difficulty of identifying highly fragmented specimens. The exposure of bones to sources of high heat has also affected a similarly high proportion of the assemblage (23.1%). Despite these analytical challenges, the systematic study of these taphonomic processes has identified their impacts on the faunal remains and aided in the study of the history of use of the rockshelter.

The chronological model developed for the occupation of El Gigante indicates that it was used discontinuously throughout the Terminal Pleistocene and Early Holocene (Kennett et al. 2017; Scheffler 2008; Scheffler et al. 2012). In addition, existing and ongoing analyses of the site's macrobotanical remains indicate the site was used primarily during the rainy season, which today corresponds to the months of July to September (Scheffler 2008; Scheffler et al. 2012). This implies that this site was likely one of many utilized by foragers inhabiting the highlands of southwestern Honduras over the course of a seasonal round. Four datapoints can help us pinpoint the foraging radius for these populations. First, all of the obsidian artifacts recovered from the site have been sourced to the La Esperanza source, located 23km northwest of El Gigante (Hirth et al. 2018; Iceland and Hirth 2021; Sorensen and Hirth 1984). Second, a decline in the abundance of obsidian in the flaked stone assemblage over time in favor of locally available materials such as chert, chalcedony, and silicified pumice suggests only limited forays to La Esperanza and thus a foraging radius of under 23km. Third, archaeological surveys of the area (Figueroa 2014) recovered a projectile point with a similar morphology to the points found in the earliest levels of El Gigante (Hirth, personal communication, 2018) from the surface of a site 17km southwest of the shelter (Figure 3.5 above). Lastly, one of the few mollusk specimens recovered from the site and the only one dated to the Preceramic strata, is the shell of a bivalve, possibly a species of clam (Figure 6.1). This specimen comes from Unit 1, Level 22b, located just below Feature 5. Radiocarbon dating of a charcoal sample from this feature returned a date of 11,012-10,696 cal B.P. (Kennett et al. 2017; Scheffler 2008; Scheffler et al. 2012), meaning this marine shell was likely procured by the shelter's inhabitants and left at the site. Though more research is needed to verify this, it would appear that the inhabitants of El Gigante traveled between the mountains and the coast – or interacted with coastal groups – as part of their seasonal round. In the following pages I present a phase-by-phase account of the human-environment dynamics taking place at El Gigante as reconstructed from the available data.

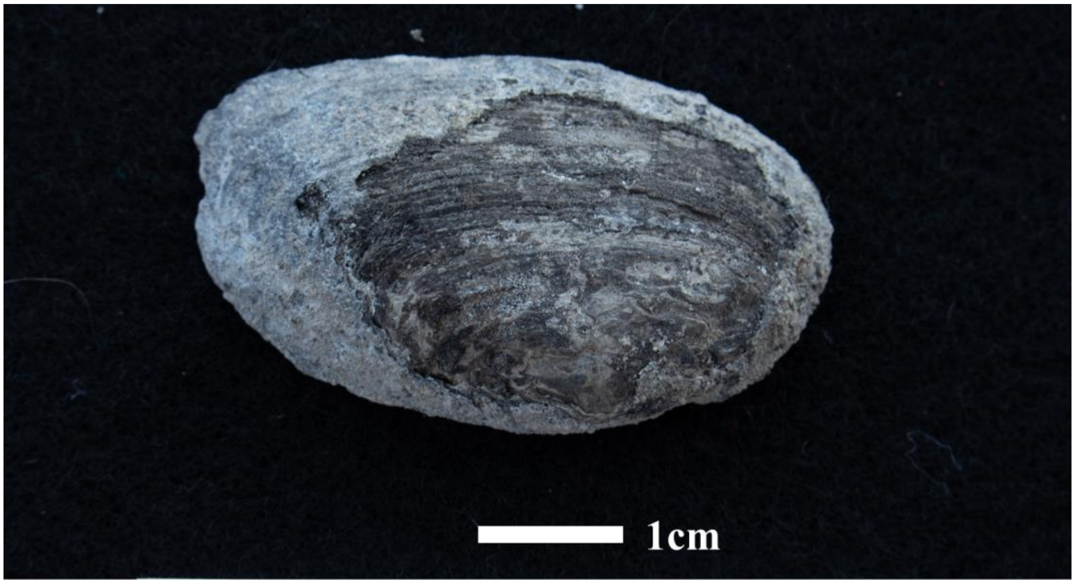

Figure 6.1 Marine bivalve specimen recovered from the earliest occupation of El Gigante.

6.2.1 The Early Esperanza Phase (11,010-10,220 cal B.P.)

The earliest occupation at the site, during the Early Esperanza phase, might best be characterized as a series of short-term occupations focused on the acquisition of deer and complemented by the collection of a wide variety of plant and animal resources. The amount of bone (NSP = 4751, or 602.7 bones per century) and charcoal ($\bar{x}$=146.34 mg/g) deposited at this time are low compared to most other occupational phases, indicating a low intensity of use of the shelter. The lithic assemblage is characterized by a specialized bifacial projectile point toolkit unique to El Gigante. Projectile point fragments, impact scars, and evidence for intense rejuvenation indicate that the shelter was used for processing prey and for repairing and preparing hunting equipment, among other activities (Iceland and Hirth 2021). The majority of the flaked stone utilized by the shelter's inhabitants at this time was acquired from the La Esperanza obsidian source, while only a small percentage was obtained from more local sources, meaning foragers at this time preferred to rely on higher quality materials for fashioning their lithic toolkits. However, high levels of projectile point rejuvenation suggest these groups did not have ready access to this material despite it being located only 22km away.

Evidence for intensive carcass processing, the presence of tree fruits in the diet, and shelter cleaning activities (i.e., calcined bone) during this phase indicate stays at the shelter were longer than a single event and perhaps lasted an entire rainy season, given the availability of some of the plant taxa recovered from these strata, especially tree fruits (Scheffler 2008). A reduction in the degree of residential mobility and an increase in the intensification of use of this landscape would be expected in one of two scenarios: (1) demographic circumscription caused by population packing of the landscape, or; (2) landscape heterogeneity created steeper gradients of productivity and/or predictability that made the El Gigante area more attractive and/or moves to other patches more costly or less productive (Kelly 2007, 2013; Stephens and Krebs 1986). Archaeological surveys of the highlands of southwestern Honduras have not been extensive or systematic enough to evaluate either scenario, though this study and others from El Gigante tentatively support the second scenario.

The identification of the remains of megafauna – a shrub ox (*Euceratherium* sp.) and a glyptodon (*Glyptodon* sp.) – in the pre-occupation levels of the shelter indicate this area was characterized by an open forest-savannah mosaic and could have served as a refugium for these animals (Kropf et al. 2007; Owen-Smith 2013) and other species that prefer open environments, including deer (Wolverton 2008; Wolverton et al. 2012). The topographic and altitudinal gradient of the highlands of southwestern Honduras could have helped buffer the effects of climate and environmental change following the end of the Pleistocene, as has been observed in other highland areas of Middle America (Correa-Metrio et al. 2013). Because of this, areas such as the southwestern highlands likely functioned as diverse refugia for a number of plant and animal species. Related to this, research across the neotropics (e.g., Gallina-Tessaro et al. 2019; Mandujano et al. 2013; Ramos-Robles et al. 2013) shows that seasonally dry tropical forests – such as the El Gigante landscape – have much higher mammalian biomass than wet forests and higher proportions of fruit trees as a result of high soil fertility. Moreover, white-tailed deer inhabiting tropical forests prefer habitats with highly irregular terrain, a well-developed understory and dense stands of fruit trees, including *Sideroxylon capiri* and *Spondias purpurea*, both of which are abundant in the El Gigante macrobotanical assemblage (Scheffler 2008). Thus it can be proposed that the highlands of southwestern Honduras were an attractive landscape to foragers since the earliest Holocene, a time during which tropical forests on the lowland were expanding and becoming denser and less optimal environments for large-bodied prey such as deer.

The faunal component of the diet during this initial phase of occupation of the shelter was narrow and dominated by cervids and to a lesser degree armadillos and crabs. At least eight deer were hunted during this time, most of which were adult individuals (MNI=4), though juveniles and neonates are also present, indicating a large and healthy population on the landscape. This mortality profile is also indicative of low levels of hunting pressure, related either to low human population levels or high levels of mobility, either of which allowed deer populations to recover and live longer (Wolverton 2008). The bones of deer at this time were not often placed in or exposed to sources of high heat, though they were often (ca. 67%) broken while fresh, which indicates processing for the extraction of marrow and grease.

This all suggests El Gigante's inhabitants practiced a "foraging subsistence-settlement system" (Kelly 2013: 86) focused on the acquisition of high-ranked prey (i.e., deer). Groups with such narrow diets that are largely dependent on hunting tend to have larger foraging radii (Kelly 2013: 95) and move often. The patch choice model predicts that once high-ranked resources become scarce within a patch, foragers move to adjacent ones unless they cannot do so or unless these neighboring patches are less productive (Kelly 2013; MacArthur and Pianka 1966; Stephens and Krebs 1986). This appears to have been the case during the Early Esperanza. However, data related to the subsistence of El Gigante's inhabitants during this phase is equivocal. Despite what appear to be high levels of mobility, deer carcasses during this phase were purposefully fragmented in order to gain access to within-bone nutrients. Purposeful, extensive, and non-selective breakage of bones, the type I identified at El Gigante, is often expected to occur in contexts of resource depression and nutritional stress – either behavioral as a result of overhunting or environmental as a result of for example seasonal changes – or due to a lack of mobility, which necessitates more intensive use of existing resources (Bar-Oz and Munro 2007; Lupo et al. 2013; Morgan 2015; O'Brien and Liebert 2014). Most of the evidence I collected seems to suggest the Early Esperanza inhabitants of El Gigante had plenty to eat, more so if we consider the plant component of the diet (Figueroa and Scheffler 2021; Scheffler 2008;

Scheffler et al. 2012). Larger bone fragments (>30mm) are common during this phase, yet phalanges (MNE = 29) were also commonly broken, so much so that not a single complete one was identified. Ethnographic data suggests phalangeal marrow is particularly prized for its flavor and texture, while at the same time being relatively easy to obtain (Jin and Mills 2011). Given the above, it would appear that the processing of bone for the extraction of marrow – at least during this phase – was one of dietary preference and not necessity.

6.2.2 The Late Esperanza Phase (10,160-9550 cal B.P.)

The occupation of El Gigante during the Late Esperanza phase appears to be indicative of a continuation of many of the behavioral patterns observed during the previous phase of occupation. The number of bones deposited in the shelter remained small (NSP = 3,805 or 623.8 bones per century), indicating the length and frequency of stays at the shelter remained relatively stable from the previous phase. The diet remained largely unchanged in terms of the number of taxa represented. Adult deer were less common in the assemblage, possibly indicating that hunting levels were high enough to prevent individuals from living to an older age, though the sample size is too small to make a definitive conclusion (Wolverton et al. 2012). Bone fragmentation remained almost unchanged as well, further supporting the idea that this behavior was related to dietary preferences rather than as a response to nutritional stress.

The lithic assemblage during the Late Esperanza is increasingly dominated by locally available stone more than La Esperanza obsidian, indicating a reduction in the foraging radii of these populations or, alternatively, that hunting was becoming a less dominant subsistence activity at this time. This is supported by a significant decrease in the number of projectile points and fragments during this phase of occupation (Iceland and Hirth 2021). Additionally, there is a significant decrease in the ratio of flaked to groundstone, indicating a more intensive use of plant foods at the shelter. The diet breadth of the shelter's inhabitants remained largely the same as during the Early Esperanza, though tree fruits and maguey became more abundant and there was an increase in the abundance of groundstone in the lithic assemblage, indicative of increased plant processing activities (Figueroa and Scheffler 2021; Scheffler 2008). This is curious because the tree fruit species identified at El Gigante do not require any grinding, which suggests the processing of plants that are available either during the dry season, such as oak acorns (*Quercus* sp.) or species that are available year-round such as palm nuts (*Acrocomia* sp.). Alternatively, root crops such as manioc (*Manihot esculenta*) or grasses such as *Zea* sp., *Setaria* sp., or *Panicum* sp. could have also been ground, though this remains to be determined.

In sum, during the Late Esperanza we see the maintenance of a successful subsistence and mobility system by foragers who appear to have utilized this landscape sporadically and discontinuously during the Early Holocene. El Gigante and its surroundings continued to be an attractive area to return to, presumably because of its abundant plant and animal resources. This behavioral stability might also be related to environmental and climatic stability, suggesting this area remained unchanged throughout this time, a point I explore further in my discussion of the next phase of occupation of the shelter.

6.2.3 The Early Marcala Phase (8990-7670 cal B.P.)

The Early Marcala phase is the longest occupational phase at the site during the Preceramic and is comparable in length to both Esperanza occupations combined. The presence of jackrabbits (*Lepus* sp.) in the assemblage, which are adapted to drier climates and open grassland/savannah environments and are not found in Honduras today, suggests this area remained relatively open up until this time. At least two radiocarbon dates obtained for this phase overlap with the 8.2 ka climatic event (see Kennett et al. 2017:SI). This event is characterized by a global drop in temperatures also identified across Middle America (e.g., Caballero et al. 2019; Hillensheim et al. 2005; Lachniet et al. 2004; Wahl et al. 2016) that would have perhaps helped this landscape remain a climatic refugium up until this time. However, despite this apparent environmental stability, several key behavioral shifts took place during this occupational phase.

The amount of bone deposited in the shelter decreased dramatically (from 623 to 294 bones per century), though the number of discarded plant remains increased slightly (Scheffler 2008). Diagnostic lithic types disappeared from the assemblage and were replaced by more expedient tools fashioned out of mostly local raw materials (Iceland and Hirth 2021). An overall decrease in the abundance of flaked stone is correlated with a dramatic increase in the number of groundstone artifacts, which suggests the continued development of practices for obtaining more nutrients out of plant resources and might be related with longer stays at the shelter for processing plant resources.

The faunal diet breadth during this phase expanded when compared to previous occupational phases. Twenty-one different taxa are present in the assemblage, including the first felids identified at the site, as well as other smaller mammals such as skunks and raccoons. One of the felids identified in this assemblage is likely a puma (*Puma concolor*) or jaguar (*Panthera onca*) and is represented by a complete phalanx (Figure 6.2). This is noteworthy because no other complete phalanges from large mammals were recovered from the analyzed materials, and I argue that the recovery of this complete specimen might be indicative of its purposeful curation. Perhaps not coincidentally, jaguars and other large felids feature prominently in the oral history and rock art of the highlands of southwestern Honduras (Figure 6.3), though this iconography remains undated. While unrelated to subsistence, I suggest that behaviors such as these are indicative of the development of local long-lasting cultural traditions at this time, something which has been observed elsewhere in the region (e.g., Rosenswig et al. 2015; Voorhies and Lohse 2012).

Figure 6.2 First phalanx from a large felid recovered from Early Marcala stratum 19.30.

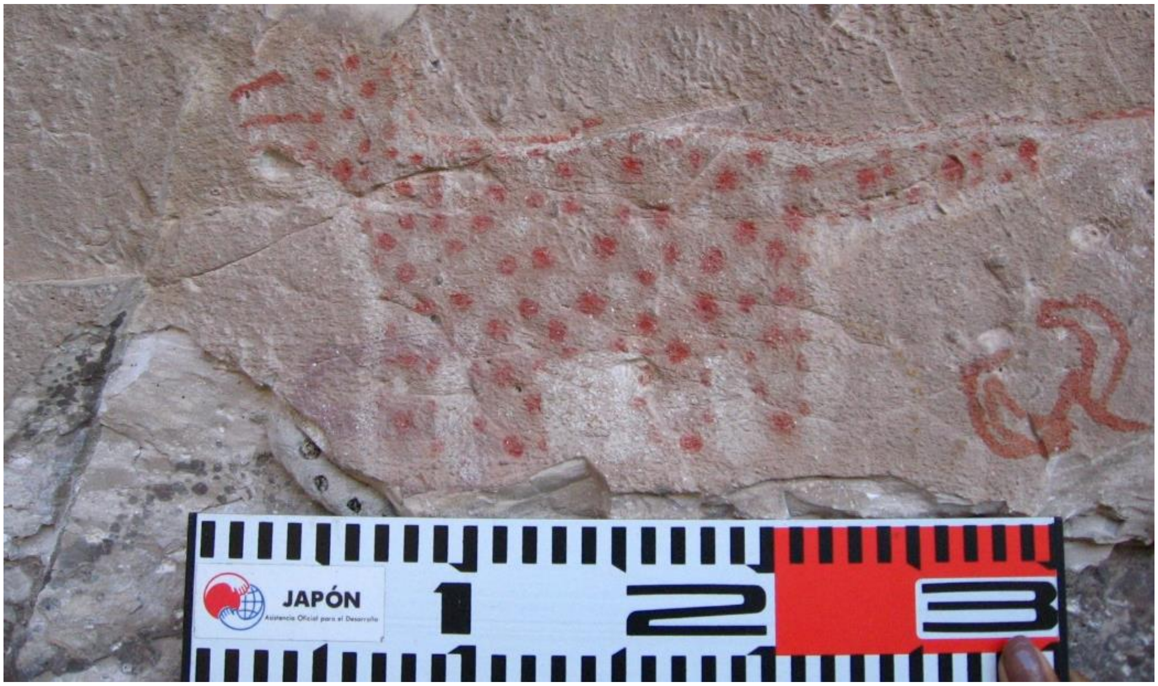

Figure 6.3 Felid pictogram from El Tigre del Nazario site, located 17 km southwest of El Gigante.

Cervids remained the most abundant taxon in the assemblage but their numbers declined considerably. The deer being hunted were also significantly younger, possibly indicating resource depression as a result of overhunting (Wolverton 2008; Wolverton et al. 2012). What deer were hunted were heavily processed for marrow and grease, as indicated by an abundance of small bone fragments (<10mm). Given the above, in addition to the overlap between this occupational phase and the 8.2 ka climatic event, I am currently unable to determine whether resource depression, if it indeed took place in the landscape surrounding El Gigante, was drive n by climatic or anthropogenic forces. Paleoenvironmental data will help elucidate whether this area was indeed affected by the climatic event in question, and the recovery and analysis of a larger faunal assemblage might permit the examination of body size in identified deer specimens, which would allow me to make a stronger inference about this.

It would appear that El Gigante during the Early Marcala phase was a logistical camp only sporadically utilized for a few tasks, the most important being the procurement, processing, and consumption of plant foods. The small amount of materials deposited in the shelter over two millennia suggests the resources being procured near El Gigante were not enough to sustain lengthier occupations, leading these groups to largely abandon this area. However, some occupations during this phase appear to have been much longer than others in the past, as indicated by several lines of evidence. First, this phase is characterized by higher proportions of fruit trees, as well as wild beans, squash, and bottle gourd, the latter of which necessitate human propagation and thus longer occupations (Piperno 2011; Piperno et al. 2009; Smith 2000). Second, a slight increase in the amount of charcoal deposited in the shelter combined with the documentation of a distinct living floor, the only one identified during the Preceramic period at the site, suggests at least one occupation of significant length – enough to create such a surface –

took place at this time (Hirth, personal communication; Scheffler 2008). Third, the inhabitants of the shelter were increasingly using local sources of chipped stone to fashion an expedient toolkit, indicating increased familiarity with the area or perhaps demographic circumscription. These data suggest a shift in mobility and subsistence, as these populations increasingly focused not on hunting but on the propagation, collection, and processing of plant foods. These scenarios, however, are not mutually exclusive and it is entirely possible that the site was used as a logistical camp by different groups that focused on hunting deer or on collecting and processing plants over time. This palimpsest of activities is likely further obscured by the high degree of fragmentation of the faunal materials recovered from this phase, compounded by the length of time it represents.

6.2.4 The Middle Marcala Phase (7610-7430 cal B.P.)

The Middle Marcala phase, the shortest of the Preceramic, represents another major change in how El Gigante and its landscape were utilized by foraging populations. Occupations of the shelter during this time are longer and/or more intensive, as indicated by a substantial increase in the amount of charcoal, bone, and plant remains deposited at the site. The proportion of calcined bones increased significantly during this time, indicating cleaning activities taking place within the shelter and thus the lengthy shelter occupations that required it.

In terms of the surrounding environment, the available data do not tell us much. Taxa from mature, secondary, and open habitats increase in abundance during the Middle Marcala. Mature forests are expected to continue expanding as a function of Holocene climate (e.g., Correa-Metrio et al. 2013), so this trend is not surprising. Secondary forests and open habitats, possibly indicative of managed “forest gardens” might point to a stronger and more impactful anthropogenic presence on the landscape.

The faunal diet breadth contracted at this time, and only 12 taxa are represented in the assemblage. Crabs were but a minor component of the diet at this time, while the proportion of rodent remains increased quite significantly. Deer continued to dominate the assemblage, and those individuals that were captured were slightly older in age than during the previous occupational phase, meaning these populations were allowed to recover, though perhaps this was an unintended result of only sporadic occupation of the area during the preceding occupational phase. What deer were hunted were heavily processed for within-bone nutrients, as indicated by a dramatic decrease in fracture freshness index (FFI) scores and an abundance of small bone fragments.

Importantly, plant resources continued to gain importance in the diet during this time and tree fruits, especially avocado (*Persea* sp.) and Sapotaceae, became much more abundant. Existing and ongoing morphometric research suggests these species were managed in order to increase their abundance and productivity, the latter by increasing the amount of edible flesh produced by each fruit (Figueroa and Scheffler 2021). Groundstone implements also increased in abundance, as did squash remains, suggesting the continued use and likely artificial propagation of this species at this time (Scheffler 2008).

The increased significance of plant resources during the Middle Marcala helps explain some of the changes in the faunal assemblage. First, there is a significant representation of faunal taxa that thrive in disturbed environments, including deer, rodents, and armadillos (Stahl 2006; Stahl and Pearsall 2012), which may indicate that the landscape was modified by human activities. Alternatively, this might indicate a landscape that became more heterogeneous and open as a result of climatic change, though this is unlikely given that regional records suggest the expansion of dense tropical forests over time, not their diminution (Piperno and Pearsall 1998; Piperno et al. 2017). In either case, these are inferences that must be evaluated by future research employing independent paleoenvironmental proxies.

I believe that during the Middle Marcala El Gigante's inhabitants switched from a collector to a forager system of subsistence (Kelly 2013: 78), characterized by an increase in the intensification of use of the site and its surroundings and a focus on the use of residential bases in order to maximize the acquisition of resources (Winterhalder and Kennett 2006). Yet, despite these efforts, the shelter appears to have been abandoned following this phase for nearly 3000 years. However, this interpretation is only tentative given the sampling issues discussed above. What is perhaps most likely is that the behaviors developed during the Preceramic at El Gigante focused on human-animal interactions continued to be elaborated upon during later time periods, as plants continued to take on a more central role of the diet of the groups inhabiting this region.

To summarize, analyses of the El Gigante assemblage allow me to partially evaluate the major expectations of existing hypotheses developed to explain the natural and adaptive changes taking place during the PHT. I propose that the end of the Pleistocene created favorable conditions for human and non-human populations in the highlands of southwestern Honduras, including an environment that remained cool and dry up through 8990-7670 cal B.P., especially when compared to the lowlands to the east, north, and south of this area (e.g., Caballero-Rodriguez et al. 2018; Correa-Metrio et al. 2012; Gomez-Perez and Carbot-Chanona 2012; Perez-Crespo et al. 2015; Piperno and Jones 2003). This stable climate maintained high levels of biodiversity while also promoting the growth of plant species with predictable seasonal variations, including fruit-bearing trees (Flannery 1986; Piperno and Jones 2003). This scenario is supported by paleoenvironmental research elsewhere in the region and what little we know of the past and present ecology of the highlands of southwestern Honduras. Specifically, archaeological and paleoenvironmental work conducted in other seasonally dry forests of Middle America (Caballero-Rodriguez et al. 2018; Correa-Metrio et al. 2013, 2014; Piperno and Jones 2003) has consistently shown that areas with high altitudinal heterogeneity minimized the impact of changes in temperature and moisture following the end of the Pleistocene. Additionally, increased seasonality following the end of the Pleistocene made the distribution of resources in these areas much more profitable, especially when compared to more environmentally and seasonally homogeneous habitats, such as the wet tropical forests of the lowlands (Correa-Metrio et al. 2013; Piperno and Pearsall 1998).

The identification of megafauna in the pre-occupation strata of the rockshelter and of jackrabbit remains (*Lepus* sp.) up through the Early Marcala phase also suggests this landscape remained relatively dry and open until at least this time. This heterogeneous landscape thus acted as a climatic and environmental refugium for a variety of plant and animal species. Within this landscape, El Gigante was perfectly positioned at the confluence of a diversity of resource-rich habitats including the Estanzuela River and its tributaries, inter-montane valleys with open pine-oak forests, and patches of open savannah. This site thus became the central place (*sensu* Winterhalder and Kennett 2006) for a successful and stable subsistence system that took full advantage of highly favorable local circumstances. Initially, the site was likely one among many other such central places part of a broader subsistence system centered on the acquisition of large mammals, namely deer. Moreover, and at least during the Early and Late Esperanza, the area around El Gigante was likely more attractive than neighboring landscapes, making longer and more frequent visits advantageous.

Deer became much less abundant on the landscape over time, leading to a loss of foraging efficiency and consequently to higher levels of carcass processing in order to maximize nutrient extraction (Figure 6.4). Deer populations were also affected by overhunting later in time, which led to a younger age structure, particularly during the Early Marcala phase. Interestingly, these behavioral changes didn’t start until late in the occupational sequence of the site, indicating a long (ca. 1,450 years) period of relatively non-intensive use of this landscape despite inferred environmental change for the region (i.e., Piperno and Pearsall 1998; Piperno et al. 2017) and supported by the faunal data presented in this study (Figure 6.5). This pattern is not predicted by existing hypotheses nor previous research in the region (e.g., Aceituno and Loaiza 2018; Acosta 2008; Piperno et al. 2017) and merits additional consideration.

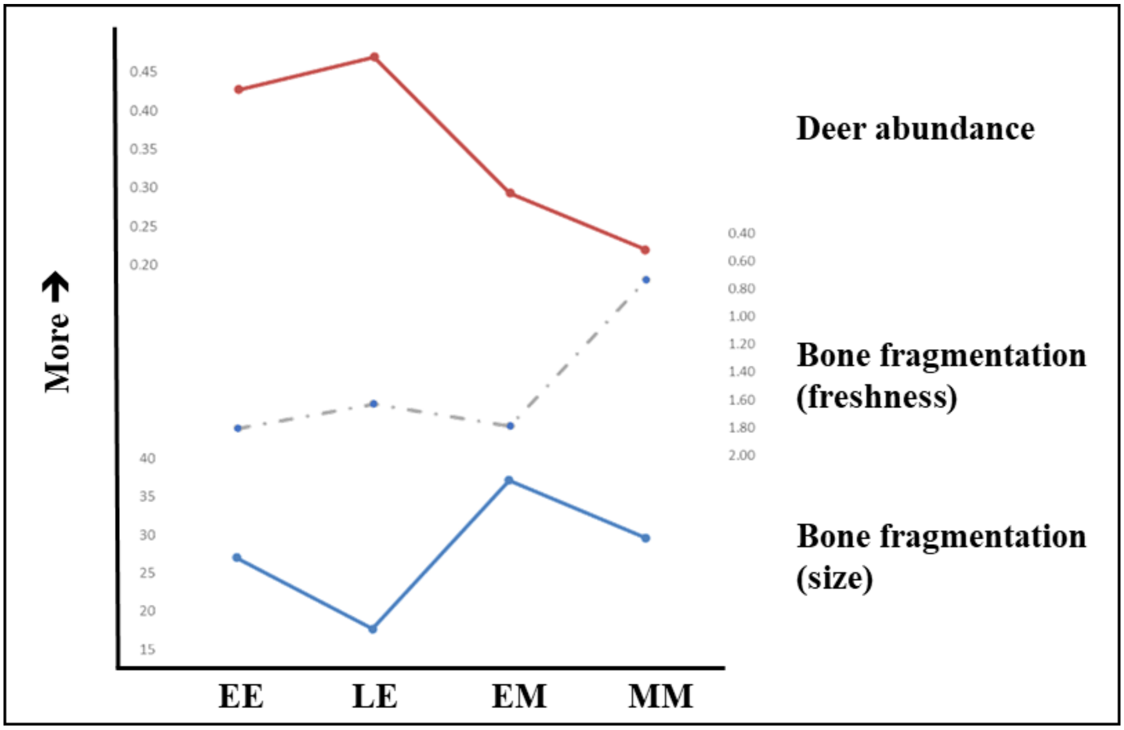

Figure 6.4 Indices of foraging efficiency obtained from El Gigante fauna data by occupational phase (EE-Early Esperanza, LE-Late Esperanza, EM-Early Marcala, MM-Middle Marcala). From top to bottom: deer abundance according to the Artiodactyl Index (AI); average Fracture Freshness Index (FFI) scores as a proxy for bone fragmentation; percentage of bones measuring <10mm as an additional proxy for bone fragmentation.

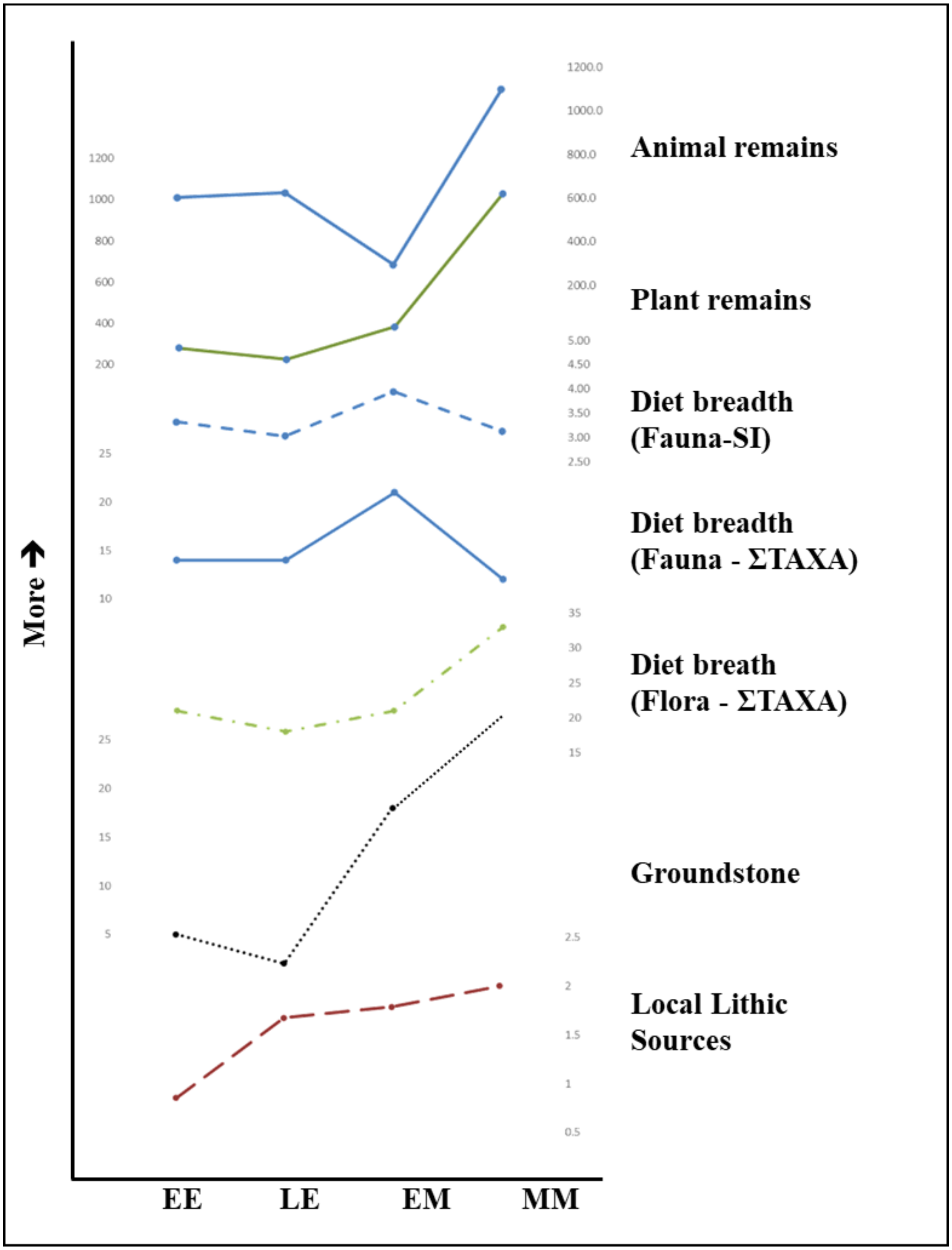

Figure 6.5 Overview of El Gigante datasets by occupational phase. Data (top to bottom): NSP of faunal remains; NSP of macrobotanical remains (from Figueroa and Scheffler 2021); the inverse of Simpson's Diversity Index (SI) as a measure of dietary breadth for fauna; faunal species richness (ΣTAXA) as a separate indicator of diet breadth; ΣTAXA for macrobotanical remains (from Figueroa and Scheffler 2021; Scheffler 2008); number of groundstone tools over time (from Hirth et al. 2018); the ratio of local lithic materials to non-local obsidian as an indicator of abundance of local sources (from Hirth et al. 2018).

The long-term re-occupation of the landscape of El Gigante and the consumption of certain plants could have resulted in some form of landscape modification – both intentionally to improve the distribution of desired species and unintentionally as the result of long-term and persistent use of this landscape (Rindos 1996). The long-term consumption of tree fruits helped their propagation in a variety of deliberate and unintentional ways (Figueroa and Scheffler 2021). A morphometric analysis of avocado remains has identified an increase in the size of seeds and thickness of rinds over time, indicating the directional and artificial selection of specimens with higher amounts of edible flesh, thus indicating the presence of agroforestry practices that date back to the Late Esperanza (Figueroa and Scheffler 2021). The propagation of desired plant species likely helped maintain the area's high biodiversity for a much longer period of time, creating a cycle whereby resources that prefer such disturbed ecosystems (i.e., deer), became more predictably distributed, promoting longer and more frequent stays over time.

The datasets collected as part of this research, when integrated with the lithic and macrobotanical data collected by previous and ongoing studies at the site leads me to develop the following hypothesis: anthropogenic resource depression occurred at El Gigante during the Preceramic period prior to evidence of significant climatic and environmental change and its inhabitants adapted by *initially* moving to other, more productive patches and returning to El Gigante only sporadically (Early Marcala occupation) *and then* by modifying the landscape (Middle Marcala occupation), which improved the distribution and predictability of desired animal resources and made longer and more frequent occupations more energetically efficient. Sometime after 7600 cal B.P., the landscape surrounding El Gigante became more heavily forested and demographic packing of the region surrounding El Gigante pushed foraging groups to return to the shelter to occupy it more intensively and for longer periods of time, resulting in a significant diversification of the diet. Alternatively, it is possible foragers were drawn to occupy and utilize El Gigante and its surroundings more intensively because of prior anthropogenic landscape modification, in this case the propagation of fruit trees and perhaps maguey, which would have made these resources more predictable, abundant, and reliable in an otherwise increasingly challenging environment. Additional research is needed to parse the latter two alternative scenarios, including and especially paleoenvironmental work near the shelter.

The data I collected and integrated into the robust chronological model developed for El Gigante (Kennett et al. 2017) allowed me to begin identifying the sequence and timing of the four key processes taking place during the Preceramic: climatic and environmental change, loss of foraging efficiency, changes in subsistence and mobility, and anthropogenic landscape modification. The scenario suggested by the El Gigante materials supports some of the material expectations of each of the hypotheses developed to explain Preceramic human-environment dynamics, while at the same timing proposing a new sequence of events.

The data presented in this dissertation and those data being gathered by ongoing research at El Gigante suggest we need to revisit the models we have used to interpret the human-environment dynamics that took place during the Pleistocene-Holocene transition. This will minimally require the integration of longitudinal archaeological and paleoenvironmental research that utilizes multiple and independent lines of evidence to identify the degree and timing of landscape modification behaviors and the impact these had on both human and non-human components of the landscape. More importantly, this requires the development of a model that takes into account approaches and expectations of both Optimal Foraging Theory and Niche Construction Theory in order to strike a balance in how we examine changes in human decision-making and their ecological contexts.

CHAPTER 7:

CONCLUSIONS

Key transitions in human prehistory – such as the move away from a foraging way of life and the adoption of plant cultivation – are marked by significant shifts in human-environment dynamics. The Pleistocene-Holocene transition (PHT) in Middle America was a time of widespread ecological and behavioral change that set the stage for later socioeconomic developments such as domestication, agriculture, and sedentism. However, we do not yet understand how these practices developed out of a foraging way of life. This effort requires integrating multiple lines of evidence to reconstruct landscapes and the behaviors of the human societies that inhabited them and how these interacted and changed over long spans of time. It also necessitates a theoretical framework that makes predictions related to human decision-making in different socio-ecological settings at various temporal and spatial scales, requirements that are met by NeoDarwinian theories, namely Optimal Foraging Theory (OFT), Gene-Culture Coevolutionary Theory (GCT), and Niche construction Theory (NCT) (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981; Charnov 1976; Charnov et al. 1976; MacArthur and Pianka 1966; Odling-Smee et al. 2003; Stephens and Krebs 1986). Given its large, well-preserved, and well-dated material assemblage, El Gigante is a “strong analytical case” (Reid and Whittlesey 1982: 18) with which to evaluate the interplay of the key processes taking place throughout the Preceramic period: environmental change, loss of foraging efficiency and concomitant resource depression, changes in forager diet and mobility, and landscape modification. Moreover, a holistic study of the shelter's unique archaeological record – although it represents a single locus of human activity in what was presumably a landscape widely used since the latest Pleistocene (see Figueroa 2014; Figueroa and Scheffler 2021) – highlights the complementary nature of OFT, GCT, and NCT in evaluating human-environment relations during this key adaptive transition. Beyond contributing to substantive and theoretical discussions in archaeology, the research presented in this dissertation contributes to existing studies seeking to understand the origins of biodiversity in the neotropics, whose ultimate goal is to identify strategies to protect it against the impacts of anthropogenically-driven climate change (see Golicher et al. 2012; Rowan et al. 2020; Rull 2011; Stan and Sanchez-Azofeifa 2019; Vegas-Vilarrubía et al. 2012). This and other research shows the potential of archaeology to inform current conservation efforts in the neotropics, where human impacts on the landscape have a long and complex history (Amand et al. 2020; Power et al. 2010; Rick and Sandweiss 2020; Roberts et al. 2017).

The research presented in this dissertation assessed the behavioral and environmental dynamics that took place during the Preceramic period (11,010-7430 cal B.P.) in Middle America. By integrating the analysis of multiple datasets from a unique multi-component site, I was able to make some inferences regarding the interplay between the climatic, environmental, and behavioral changes taking place during the Pleistocene-Holocene transition in the highlands of southwestern Honduras. My results show that El Gigante's Preceramic inhabitants maintained a subsistence system centered on a limited variety of animal prey and an ever-growing inventory of edible plants that allowed them to successfully navigate the impacts of climatic, environmental, and demographic change as well as resource depression occurring throughout the region at this time. These conclusions have implications for the ecology and prehistory of the region and contribute to a better understanding of the processes and mechanisms that shape and are themselves shaped by human-environment interactions over long spans of time. Equally important, this study highlights the value and complementarity of existing models and approaches from Optimal Foraging Theory (OFT), Gene-culture Coevolutionary Theory (GCT), and Niche Construction Theory (NCT) for examining the economic decisions made under particular ecological circumstances at various chronological scales.

Specifically, existing research on the Pleistocene-Holocene transition in Middle America has focused on the identification of short-term "negative" human-environment relations (see Jones and Hurley 2017; Smith 2011a, 2011b; Zeder 2012), namely those based on behavioral responses to climate change, environmental degradation, and resource depression (Flannery 1986; Orsini 2016; Piperno 2011; Piperno and Pearsall 1998; Piperno et al. 2017). These studies have applied models developed under OFT for predicting human-environment interactions (i.e., behavioral responses to changes in patches and resources), and have relied on paleoecological and macrobotanical assemblages and to a smaller degree on small or fragmentary faunal records (e.g., Eudave 2008; Flannery 1986; Orsini 2016) or the association between lithic artifacts and megafauna remains (e.g., Piperno et al. 2017). Despite these important advances, we have lacked the materials and contexts necessary to adequately study the earliest occupations of the region and consequently have not identified the contexts and processes that conditioned these changes later on in time.

My results depart from those of previous studies of the Middle American Preceramic in two significant ways: first, they show that resource depression – in this case referring to a decrease in the availability of deer, the highest-ranked prey in the area – did not occur until more than 2,000 years after the first occupation of the El Gigante rockshelter, which suggests environmental conditions did not deteriorate as much or as widely as previously stated (see Piperno and Pearsall 1998; Piperno et al. 2017). Second, work elsewhere in the neotropics (e.g., Aceituno and Loaiza 2014, 2018; Piperno et al. 2017) has shown anthropogenic landscape modification was one of several behavioral responses to anthropogenically-driven resource depression and also the result of long-term occupation and use of neotropical habitats and their resources. In light of this record, the behavioral changes taking place at El Gigante during the Preceramic period should be viewed both as necessary adaptations forced upon Preceramic foragers by negatively changing demographic and environmental circumstances, as well as purposeful strategies developed by a group of agents with a deep knowledge of their resource-rich surroundings. Equally as important, this study highlights the need to develop theoretical models that are based on local processes and circumstances (i.e., Borrero 2006, 2016).

Paleoenvironmental data are critical for evaluating the hypotheses I explored in this dissertation. These data are lacking for much of Middle America, particularly in seasonal tropical forests such as those that characterize the El Gigante landscape today and likely in the past. Similarly, the suggestion that El Gigante was one of many sites utilized by Preceramic foragers calls attention to the need to conduct systematic surveys of this area, which clearly holds much promise for documenting and understanding the PHT.

7.1 Revising our Approach to the Preceramic in Middle America

The study of the origins of domestication and agriculture in Middle America has rightly emphasized the role and importance of plant resources in subsistence systems, given their central role in the later prehistory of the region (e.g. Flannery 1986; Piperno et al. 2017). This research has also predicted that an increased utilization of plants occurred sometime during the Early

Holocene, when megafauna became extinct and large fauna became scarce on the landscape as a result of post-Pleistocene environmental degradation (Piperno and Pearsall 1998). However, these inferences are based on paleoecological and limited paleontological data and have not been evaluated using archaeological datasets, which remain scarce. This body of research has identified three broad behavioral patterns occurring throughout the region beginning at around 13,000 cal B.P. and becoming widespread by 7000 cal B.P.: 1) an increase in the diversity of the diet and a reduction in residential mobility, often seen in the development of regional dietary and technological traditions, 2) a decrease in foraging radii as populations utilized increasingly local resources such as lithic raw materials and certain plant and animal species, and 3) evidence of intended and unintended long-term modification of the landscape through burning, clearing, and the transplantation and propagation of certain plant species (Aceituno and Loaiza 2018; Acosta 2008, 2010, 2012; Blake et al. 1992, 1995; Chisholm and Blake 2006; Cooke and Ranere 1992; Flannery 1986; MacNeish 1964; Piperno 2006, 2011; Piperno and Pearsall 1998; Piperno et al. 2009, 2017; Posth et al. 2018; Prufer et al. 2019; Rosenswig et al. 2015; Voorhies and Lohse 2012).

I believe existing approaches to the study of the Preceramic period are largely based on previous North American approaches to the study of the PHT that are centered on how human populations responded to demographic expansion and a decline in large animals and megafauna following the end of the Pleistocene by expanding their diet and reducing their mobility (Bousman and Oksanen 2012; Bousman and Vierra 2012; Carr and Adovasio 2012; Yerkes and Koldehoff 2018). However, despite the existence of some sites with secure evidence of human hunting of megafauna in northern Mexico (Gaines et al. 2009; Prado et al. 2012; Sanchez 2001; Sanchez and Carpenter 2012; Sanchez et al. 2014) and Colombia (see Piperno et al. 2017 for an overview of this literature), the hunting of megafauna has not been securely identified in Middle America. In addition, existing paleoecological research shows environmental degradation was not widespread spatially or chronologically in the region (e.g., Caballero et al. 2019; Correa-Metrio et al. 2013; Lachniet et al. 2013; Lozano-Garcia et al. 2015; Metcalfe et al. 2015). These contradictions in our data and our models thus require a revision, which this dissertation calls attention to.

First, this study lends support to existing research that shows that highland regions in Mesoamerica were not the marginal or unproductive environments they were once thought to be (e.g., Caballero-Rodriguez et al. 2018; Correa-Metrio et al. 2013, 2014; Piperno and Jones 2003). The periodic low-intensity use of the shelter and its surroundings during its first two occupational phases indicates this area remained rich in valuable resources, namely cervids and fruit trees, both of which remained abundant for millennia.

This long-term interaction between humans and fruit-bearing trees culminated with the artificial selection of at least one species, avocado (*Persea Americana*), though ongoing research suggests other species were also subject to similar processes (Figueroa and Scheffler 2021; Scheffler 2008). The abundance and predictability of these resources near El Gigante and evidence of the shelter's reoccupation despite decreasing foraging efficiency suggests this particular landscape was ranked higher than others nearby, as predicted by the patch choice model (Stephens and Krebs 1986). It is precisely this higher patch rank that made longer and more intensive stays at El Gigante more advantageous, an inference that is supported by my results.

Over time, longer and more intensive stays at the rockshelter, perhaps combined with decreasing habitat productivity caused by increasing establishment of Holocene climatic conditions by ca. 7000 cal B.P. (see Correa-Metrio et al. 2012, 2013; Hodell et al. 2000, 2008; Markgraf 1989; Schmidt et al. 2004), resulted in the significant reduction of deer on the landscape. Despite this, foraging groups periodically returned to El Gigante and likely continued propagating certain plant species, all while hunting and heavily processing what animal prey they could find.

Based on prior research at El Gigante (Figueroa and Scheffler 2021; Scheffler 2008) and elsewhere in the neotropics (e.g., Aceituno and Loaiza 2014, 2018) landscape modification in this area could have begun as short-term actions intended to improve the distribution of plant resources that had positive, long-term, and unintended consequences for the distribution of animals. However, this particular inference needs to be evaluated using independent paleoenvironmental datasets that examine changes in the El Gigante landscape before and throughout the Preceramic.

While the type and resolution of the data I collected is too coarse to allow me to directly examine anthropogenic niche construction on the El Gigante landscape, tantalizing clues suggest this might have been the case, and need to be evaluated more systematically by additional research. For example, ongoing stable carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope analysis of bone carbonate samples will help examine differences in the ratio of C_3 to C_4 plants consumed by herbivores hunted by El Gigante residents and will be used as a proxy for landscape patchiness and climate (e.g., Graham et al. 2014; Repussard et al. 2014).

Ultimately, this study presents a much more nuanced understanding of the sequence of major behavioral and environmental changes that took place during the Preceramic period in Middle America that informs the study of this major shift in human-environment dynamics. These results enrich our understanding of human agency and subsistence strategies during a pivotal yet poorly understand period in human history by tracing the chronological order in which environmental change, resource depression, and behavioral changes in subsistence, mobility, and niche construction behaviors took place. Just as paleoecological research in the region has highlighted its environmental heterogeneity following the end of the last ice age, this dissertation shows how interactions between plants, animals, and human populations were affected by changing local conditions, challenges, and opportunities. At a broader level, this research shows that the expectations put forth by models developed out of Optimal Foraging Theory (OFT) and Niche Construction Theory (NCT) address the different yet fundamentally intertwined dimensions of human decision-making and its ecological context at different temporal and spatial scales. By combining these complementary theoretical approaches this dissertation provides a unique example of how short-term subsistence and mobility decisions such as overhunting or habitat modification can create new selective pressures that have long-term impacts on future environments and populations (see Broughton et al. 2010; Freeman et al. 2015; Mohlenhoff et al. 2015; Neto and Albuquerque 2018; Piperno et al. 2017; Stiner and Kuhn 2016).

7.2 El Gigante as a Proxy for Climate and Environmental Research

The value of the research presented in this dissertation has the potential to extend beyond the fields of anthropology and archaeology to inform ongoing efforts to understand and help address the impacts of climate change on tropical forests worldwide over long spans of time. Materials and data recovered from archaeological sites have been used to inform the fields of climate research and conservation biology for decades (see Amand et al. 2020, Roberts et al. 2017 for a review of this work). Archaeological and paleoenvironmental research in tropical forests worldwide continues to show these environments are the product of long histories of entanglement between human societies and their socio-natural surroundings (e.g., Lombardo et al. 2020; Roberts et. al 2017). In the neotropics, these studies indicate highland areas have long been hotspots for biodiversity and fundamental to the evolution of species due to their ability to buffer the degree and extent of the impact of climatic change and act as climatic refugia (Caballero-Rodriguez et al. 2018; Correa-Metrio et al. 2013; Gomez-Perez and Carbot-Chanona 2012; Perez-Crespo et al. 2015; Piperno and Jones 2003). Recent work has begun to examine the potential of neotropical highlands to act as biodiversity nurseries in which to carry out biodiversity conservation efforts, with the ultimate goal of undertaking restoration efforts in heavily depleted and degraded areas, namely the lowlands (Golicher et al. 2012; Rull 2011; Sanchez-Ramos et al. 2018). The identification of the El Gigante landscape as a climatic refugium well into the Holocene highlights the need for additional climate and environmental research in this area given its potential to act as a refugium against ongoing and future ecological changes in the region, and can help inform policies designed to protect such areas against negative anthropogenic impacts such as intentional burning and deforestation, which are rampant across the highlands of Honduras today.

APPENDIX A: ZOOARCHAEOLOGICAL DATA COLLECTION PROTOCOL

A1. General guidelines

- Every cell must be filled in. If nothing can be entered for a field write “NA”
- Every bone specimen should be entered on a single line, even if they refit. Refits should be described under the **Notes** column. The only time specimens should be combined is if the breakage can be reliably identified as a result of bagwear

A2. Information on each cell/column

- **Analyst:** 3 initials of analyst
- **Analysis date:** Date of analysis in MM/DD/YY format
- **Unit #**
- **Level:** Level #
- **FS#:** Faunal specimen number. Each bone receives a unique number based on its unit and level of provenience (e.g., FS# 18.1.1 is the first bone analyzed from Level 1 of Unit 18)
- **Context:** Stratum (S#) and/or Feature (F#) number
- **Other provenience:** Any specified provenience that does not fall into the other provenience fields (e.g., triangulations, specific depths, etc.)
- **Taxon:** Specific taxonomic id of specimen
    - Use standardized nomenclature (www.itis.gov and www.zoobank.org)
    - A note on open nomenclature: If the genus level ID is secure but species is not, use cf. (i.e. *Meleagris* cf. *gallopavo*) and be explicit how this identification was made under **ID basis**
    - Specimens that can only be labeled to genus level and could be a number of species should be coded as *Genus* spp. and explained under **ID basis**
    - Non-Linnaen categories, such as “medium mammal,” require a systematic paleontology
- **Element:** Code for element ID. If the specimen is a portion that contains teeth as well, teeth must be listed in the **Other** column. For instance, if you have a mandible with two teeth you enter it as “Mant.” In the **Other** column you enter the codes for the teeth that are present
- **Side:** Code for element side
- **ID basis:** Narrative describing basis for taxonomic ID; Include citations as appropriate
    - Example: “based on comparison with X species”, “based on presence of X feature (sulcus, foramen, etc.)”
- **BZ1-12:** Record present (P) or absent (A) for the bone zones present in the specimen. A zone should only be recorded as present if more than 50% is present to prevent recording the same bone twice. If a zone is not applicable to the element, enter “NA”

- **CT (Cultural taphonomy, Loci, and Cultural characteristic):** There are multiple columns for recording cultural damage because a bone may have cutmarks (or other kinds of damage) in several different places. Damage that is in close proximity (<.50 cm) is recorded as a single act/event. Damage located further apart on the bone is recorded as a separate event
    - **CT (Cultural taphonomy):** Code for cultural modification
    - **CT Loci:** The BZ# for where the modification is located. If it is on multiple zones, list the zones separated by a comma (e.g., 1, 2, 3)
    - **CT characteristic:** Code for orientation on the bone and to other marks within the single event
- **Noncultural taphonomy and NT Loci:** Same as for **Cultural taphonomy**
- **Weathering:** See weathering scale codes
- **Pathology and PathLoci**
    - **Pathology:** Code for the identified palaeopathology. Enter “NA” if none present.
    - **PathLoci:** The BZ# for the pathology identified. If it is on multiple zones, list the zones separated by a common (e.g., 1, 2, 3)
    - **PathNotes:** Additional descriptions and notes about the identified pathology
- **Age:** Age estimate of specimen, see codes.
- **Evidence:** Characteristic that was used to estimate age. See codes.
- **Measurements:** All measurements should be in millimeters (mm) and to the nearest hundredth. Skeletally immature and incomplete specimens should not be measured. Burnt bone should not be measured because dimensions are altered by heat (Von Den Driesch 1976). If the measurement cannot be recorded, enter “NA”.
    - **GL:** greatest length
    - **PB/GB:** proximal breadth or greatest breadth
    - **DB:** distal breadth
    - **MD:** mandibular depth
    - **AL:** alveolar length
- **Notes:** Use this for comments that are not covered by the codes
    - If a refit, mention which FS# this one refits to
    - **Photographs:** Only photograph interesting modifications and bone tools. Information for photography is entered in the photo log

A3. Codes used in data collection

Skeletal Elements

Element	**Code**
Alisphenoid	Alsp
Alveolar bone	Alv
Angular process (mandible)	Mana
Antler	Ant
Auditory bullae	Aub
Auditory meatus	Aum
Periotic	Per
Basioccipital	Baso

Basisphenoid	Bsph
Cornoid process (mandible)	Manp
Cranium frag undiagnostic	Cra
Cranium complete	Crac
Cranium half incomplete	Crahi
Frontal	Fro
Horn core	Hrnc
Horn (detached)	Hrn
Jugal (mid zygomatic arch)	Jug
Interparietal	Ipr
Lacrimal	Lac
Mandible (fra no teeth)	Man
Mandible (frag with teeth)	Manft
Mandible (dmi/half no teeth)	Manf
Mandible (demi with teeth)	Mant
Mandible (complete)	Manc
Mandibular condyle	Mancy
Mastoid process	Mast
Maxilla (frag no teeth)	Max
Maxilla (frag with teeth)	Maxft
Maxilla (demi no teeth)	Maxf
Maxilla (demi with teeth)	Maxt
Nasal	Nas
Nasal turbinate	Nast
Occipital	Occ
Occipital condyles	Occy
Orbit	Orb
Palate	Pal
Parietal	Par
Premaxilla	Prem
Presphenoid	Pres
Pterygoid process	Ptgy
Postorbital process	Porb
Quadrate	Qua
Ramus (mandible)	Ram
Supraorbital process	Sppr
Squamosal	Squ
Temporal	Tem
Tympanic ring	Tym
Vomer	Vom
Zygomatic arch (maxillar arm)	Zygm

Zygomatirc arch (squamosal arm)	Zygs
Petrosal	Pet
Canine (unknown)	C
Deciduous incisor (unknown)	DI
Deciduous canine	Dc
Deciduous premolar	Dp
Lower deciduous incisor (unknown)	Ldi
Lower deciduous incisor (# if known)	Ldi#
Lower deciduous premolar (unknown)	Ldpm
Lower deciduous premolar (# if known)	Ldpm#
Lower canine	Lc
Lower incisor	Li
Lower premolar (unknown)	Lpm
Lower premolar (# if known)	Lpm#
Lower molar (unknown)	Lm
Lower molar (# if known)	Lm#
Upper deciduous incisor (unknown)	Udi
Upper deciduous incisor (# if known)	Udi#
Upper deciduous canine	Udc
Upper deciduous premolar (unknown)	Udpm
Upper deciduous premolar (# if known)	Udpm#
Upper incisor (unknown)	Ui
Upper incisor (# if known)	Ui#
Upper canine	Uc
Upper premolar (unknown)	Upm
Upper premolar (# if known)	Upm#
Upper molar (unknown)	Um
Upper molar (# if known)	Um#
Tooth fragment (unknown)	Tth
Molar fragment (unknown)	M
Premolar fragment (unknown)	Pm
Incisor fragment	I
Lower incisor fragment	Lif
Unknown tooth root fragment	Troo
Acetabulum (detached)	Ace
Atlas	Atl
Axis	Axi
Caudal (# if known)	Cau#
Caudal (unknown)	Cau
Caudal fragment (unknown)	Cauf
Centrum (indeterminate)	Cen

Cervical (# if known)	Cv#
Cervical (unknown)	Cv
Cervical centrum	Cvc
Cervical centrum anterior process (detached)	Ccap
Cervical centrum posterior process (detached)	Ccpp
Cervical vert spinous proucs	Cvs
Cervical vert transverse spine	Cvts
Cervical vert transverse process	Cvtp
Cervical vert fragment	Cvf
Coccygeal vertebra	Ccv
Hyoid	Hyo
Ilium	Ili
Innominate (half of pelvis)	Innh
Innominate fragment	Innf
Innominate fragment (unknown)	Inn
Ischial tuberosity	Ischt
Ischium	Isch
Ischium fragment	Ischf
Lumbar (# if known)	Lv#
Lumbar (unknown)	Lv
Lumbar centrum	Lvc
Lumbar centrum anterior process (detached)	Lcap
Lumbar centrum posterior process (detached)	Lcpp
Lumbar vert spinous process	Lvs
Lumbar vert transverse process	Lvts
Lumbar pedicle	Lvp
Manubrium	Mab
Pubis	Pub
Rib (# if known)	Rib#
Rib (unknown)	Rib
Rib head detached	Ribh
Rib plus attached head/neck	Ribn
Rib plus head, neck, angle	Ribc
Rib tubercle only	Ribt
Rib plus tubercle	Ribst
Rib shaft only	Ribs
Rib, angle, no head, no shaft	Riba
Rib, ventral shaft end below angle	Ribv
Rib shaft plus sternal extremity	Ribstr
Sacral vertebra	Sacv

Sacrum	Sac
Scute	Scu
Sternabrae (# if known)	Stb#
Sternabrae (unknown)	Stb
Sternal/false rib	Srib
Sternum	Ster
Thoracic (# if known)	Tv#
Thoracic (unknown)	Tv
Thoracic centrum	Tvc
Thoracic centrum anterior process (detached)	Tcap
Thoracic centrum posterior process (detached)	Tcpp
Thoracic vert rib facet	Tvr
Thoracic vert spinous process	Tvs
Thoracic vert transverse process	Tvts
Turtle shell	Turt
Unknown vertebra anterior process (detached)	Ucap
Unknown vertebra posterior process (detached)	Ucpp
Unknown vertebra spinous process	Uspi
Unknown vertebra transverse process	Trans
Vertebrae fragment (unknown)	Vert
Xiphoid	Xph
Crab shell	Cshe
Crab pincer	Cpin
Clavicle	Clv
Proximal femur	Pfem
Femur	Fem
Femur head (detached)	Femh
Distal femur	Dfem
Femur shaft	Femsh
Proximal tibia	Ptib
Tibia	Tib
Tibia shaft	Tibsh
Tibial tuberosity (detached)	Tibtu
Distal tibia	Dtib
Distal fibula	Dfib
Proximal fibula	Pfib
Fibula	Fib
Fused tibia and fibula	Tibfib

Tarsal (unknown)	Tars
Astragalus	Ast
Calcaneus	Cal
Lateral malleolus	Latm
Cuboid	Cub
Naviculocuboid	Nvc
Navicular	Nv
Lateral cuneiform	Lcun
Intermediate cuneiform	Icun
Intermediate/lateral cuneiform	Ilcun
Medial cuneiform	Mcun
Proximal metatarsal	Pmtm
Metatarsal	Mtm
Metatarsal shaft	Mtms
Distal metatarsal	Dmtm
Phalange (unknown)	Phaa
Phalange (# if known)	Pha#
Terminal/distal/ungual phalanx	Phat
Phalange fragment	Phaf
Radiale	Brad
Ulnae	Buln
Patella	Pat
Sesamoid	Ses
Scapula	Sca
Scapula blade (no glenoid)	Scab
Glenoid cavity only (detached)	Glen
Scapula fragment	Scaf
Proximal humerus	Phum
Humerus	Hum
Distal humerus	Dhum
Humerus shaft (only)	Hums
Humerus head (detached)	Humh
Proximal radius	Prad
Radius	Rad
Distal radius	Drad
Radius shaft (only)	Rads
Proximal ulna	Puln
Ulna shaft (only)	Ulns
Ulna	Uln
Distal ulna	Duln
Fused radius and ulna	Raduln

Carpal (unknown)	Carp
Lunate	Luna
Scaphoid	Scaph
Scapholunate	Scapl
Magnum	Magn
Unciform	Unci
Cuneiform	Cune
Trapezoid	Trap
Proximal Metacarpal	Pmcm
Metacarpal	Mcm
Metacarpal shaft	Mcms
Distal metacarpal	Dmcm
Proximal metapodial	Pmtp
Metapodial shaft	Mtps
Distal metapodial	Dmtp
Metapodial	Mtp
Indeterminate bone	Ind
Articular surface	Arts
Long bone shaft	Lbn
Not identifiable	NID
Synsacrum	Syn
Carpometacarpus	Cpm
Tarsometatarsus	Taro
Tendinal splints	Tens
Furcula	Fur
Coracoid	Cora
Pygostyle	Pygo
Tibiotarsus	Tibt
Fused thoracic vertebrae (# if known)	Ftv####
Dentary	Dent

Cultural Taphonomy

Taphonomy	**Code**
Cutmark isolated	Cm
Cutmark more than 1	Cm#
Hack isolated	Hck
Hack more than 1	Hck#
Chop isolated (shear fracture)	Ch
Chop more than 1	Ch#

Burnt (partially)	Burn1
Carbonized (partially)	Burn2
Calcined (partially)	Burn3
Burnt (completely)	Burn4
Carbonized (completely)	Burn5
Calcined (completely)	Burn6
Carbonized/calcined (partially)	Burn7
Carbonized/calcined (completely)	Burn8
Burnt (very small amount <1/2 bone)	Burn9
Impact mark/scar	Imp
Flake scar	Flsc
Bipolar damage	Bidm
Incision other	Inc
Spiral fracture	Spf
Fracture (general)	Frac
Chewing	Chw
Use wear	Use
Striations	Stri
Smoothing	Smo

Non-cultural Taphonomy

Taphonomy	**Code**
Stained	Stain
Toothmark isolated	Tooth
Toothmark >1	Tooth#
Tooth puncture isolated	Toothp
Tooth puncture >1	Toothp#
Gnawmarks carnivore	Gnc
Gnawmarks rodent	Gnr
Toothpits	Toothpit
Crushed unknown cause	Crusho
Scratches (unknown)	Scrt
Polished	Poli
Scatological bone	Scat
Rootechtching	Root
Concretions	Conc

Orientation of taphonomic marks

Mark orientation	Code
Angled	Ang
Angled and not parallel	Angn
Angled and parallel	Angp
Longitudinal	Long
Longitudinal and not parallel	Longn
Longitudinal and parallel	Longp
Sagittal	Sa
Sagittal and not parallel	San
Sagittal and parallel	Sap
Transverse	Tr
Transverse and not parallel	Trn
Transverse and parallel	Trp
Circular	Cir

Age Indicators

Age	Code
Juvenile	Juv
Adult	Ad
Unknown	Unk
Old	Old
Possible infant/neonate	Neo

Evidence for Age Determination

Evidence	Code
Dentition erupting	Der
Dentition worn	Dwn
Unfused bones	Unf
Fused bones	Fus
Incomplete cortical bone	Unclco
Woven bone	Wov
Dentition unworn	Dun
Degeneration	Deg
Size	Siz

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