

Akrotiri *Aetokremnos* and the Cypriot Pygmy Hippopotamus:  
An Interdisciplinary Look at a Late Pleistocene Large Mammal Extinction

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**Abstract**

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The cause for large mammal extinctions in the Late Pleistocene has been debated for decades, with two main factors constantly discussed—human hunting and climatic change. The Cypriot pygmy hippopotamus represents a case study of one such extinction event. The last appearance of this species is at the archaeological site Akrotiri *Aetokremnos* (~12,000 cal. B.P.), the oldest well-dated site on Cyprus. This dissertation represents interdisciplinary analyses surrounding the faunal remains of the Cypriot pygmy hippopotamus at this site, in an attempt to create a more holistic picture of the dynamics of this event and parse out the potential relative impacts of climate change and humans. First, a morphological comparison between other extinct and extant hippopotamids allows the inferences of the behavior and subsistence strategies of the Cypriot pygmy hippopotamus. This is then correlated with the Late Pleistocene climatic change, and documented through stable isotope studies from the Cypriot pygmy hippopotamus remains, showing that this species would have been susceptible to such dramatic change. After the discussion of this paleoecological context, the archaeological site is evaluated for any evidence of post-depositional taphonomic processes which could potentially skew the representation of

faunal remains—creating biases. Next, comparing the demographic profiles at Akrotiri *Aetokremnos* to theoretical and ecological profiles shows compelling evidence that humans hunted this species. With this in mind, a detailed assessment of the skeletal representation at the site allows the inference of human behavior—attempting to identify how humans may have procured and/or utilized this species. Overall, this work sheds light on this species’ dynamics, the nature of accumulation at this particular site, and begins the discussion of how the earliest Cypriots may have procured and interacted with the species.

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## Chapter 1: Introduction

Throughout prehistory and history, the colonization of island environments by humans has frequently led to vertebrate extinctions (Grayson and Meltzer 2002; Grayson 2001; Martin and Steadman 1999; Simmons 2014; Steadman and Martin 2003). As Turvey (2010) notes, the human colonization of islands was followed by vertebrate extinctions in the Mediterranean, West Indies, Madagascar and the Pacific. The arrival of humans to New Zealand led to the extinction of at least nine genera of Moa, the large flightless bird that once thrived on the islands (Baker 2005; Grayson 2001; Holdaway and Jacomb 2000; Worthy 1999). Many of these extinctions were extremely fast, taking as little as 100 years, showing the devastating effects of human hunting on naïve fauna coupled with such indirect anthropogenic effects as large-scale burning and introduction of invasive species (Holdaway and Jacomb 2000). Following the arrival of humans to the Mediterranean island of Mallorca, two small mammals (*Eliomys morpheus* and *Asoriculus hidalgoi*) quickly became extinct as a result of the introduction of competing species, an indirect anthropogenic effect (Bover and Alcover 2008). Steadman's (1995, 2006) work on the Pacific Islands estimates the loss of as many as 2000 species of birds resulting from anthropogenic impacts. The examples of vertebrate extinctions following human colonization are abundant and compelling. In a number of prehistoric settings, however, initial colonization was not followed by rapid extinction, and in some cases was not followed by extinction at all (Turvey 2010).

As more work has been done, it has become apparent that at least in a few cases human colonization was not met with rapid extinction events, but with long periods of coexistence. Turvey et al. (2007) show that the large heptaxodontid rodent, *Elasmodontomys obliquus*, survived the initial human colonization of Puerto Rico and coexisted with humans for over 2000 years. Turvey (2010) suggests that on many Caribbean Islands other small and medium-sized rodents did not face extinction until European arrival, showing significant overlap with human occupation. On the Mediterranean island of Mallorca and surrounding islets, the highly modified dwarf caprine, *Myotragus balearicus*, became extinct late in the Holocene after an overlap with humans of 1000 years or more (Bover and Alcover 2003; Strydomck et al. 2005). The large flightless sea duck, *Chendytes lawi*, coexisted with humans for over 8000 years (Jones et al. 2008; Grayson 2008). These examples show that while island faunas are susceptible to anthropogenic effects, one cannot assume that human colonization causes vertebrate extinctions.

It is also important to note that island extinctions have occurred in the absence of any anthropogenic impacts. Mammoths on St. Paul and Wrangel Island survived well into the Holocene (Boeskorov 2006; Guthrie 2004, 2006). On St. Paul Island, and possibly Wrangel Island, the species eventually became extinct without human presence (Boeskorov 2006; Guthrie 2004, 2006). For these reasons, island extinction events must be evaluated on a case-by-case basis to assess the impacts humans may have had on vertebrate species, rather than assuming human occupation leads to the decline of endemic species.

In addition, most studies of island faunas are Holocene in age, deal with avian species, not mammals, and/or have poor chronological control (Alcover 1999; Jones 2008; Simmons 2014; Slikas 2003; Steadman 2005, 2006; Steadman and Martin 1999; Turvey and Risley 2006; Turvey 2010; Vigne 1999; Wroe et al. 2006). In the Holocene, humans began to impact their

environments in more varied and drastic ways, making particular anthropogenic effects more complicated to determine (Didham et al. 2007; Grayson and Meltzer 2002; Tylianakis et al. 2008). As a result, human colonization of an island environment in the Holocene implies a different intensity and quality of anthropogenic impacts, including larger population sizes, the introduction of a more substantial suite of foreign flora and fauna to the ecosystem, and often more intensive technologies and landscape altering land use practices (e.g. Turvey 2010). While it is often obvious that there are anthropogenic effects leading to extinction, determining the degree of direct and indirect effects becomes increasingly difficult (Grayson and Meltzer 2001).

Island birds are at high risk for decline due to their small population sizes, small and tightly bounded ranges that are susceptible to rapid environmental change and the loss of mechanisms meant to deal with predators and competitors (Blackburn et al. 2004; Boyer 2010; Grayson 2001; Karels et al. 2008; Steadman 1997; Trevino et al. 2007). While it is assumed that island mammals face similar disadvantages, the ecological response of mammals to changing environments is significantly different than birds (eg: Hadly et al. 2003; LoGiudice 2006; VanGils et al. 2007). Despite the overwhelming evidence for vertebrate extinctions following initial human colonization on islands, there are very few cases where it has been shown that large mammals have become extinct in such settings. Possible anthropogenic large mammal extinctions include the pygmy mammoths, *Mammuthus exilis*, of the Channel Islands, the pygmy hippopotamus, *Phanourios minutus*, from Cyprus and several pygmy hippopotami, *H. lemerlei*, and *H. madagascariensis*, from Madagascar (Burney et al. 2003; Crowley 2010; Erlandson et al. 2004; Simmons 1999, 2014). These large mammal extinction events are poorly understood, however. The argument for an anthropogenic cause relies heavily on the assumed correlation of timing between human arrival and the extinction event, and on using non-mammal island

extinction events as models (Agenbroad et al. 2005; Turvey 2010). These assumptions call for a succinct chronology of both human arrival and the extinction event (Bover and Alcover 2008; MacPhee 1999). Unfortunately, most of these studies have poor chronological control over the initial human colonization or the disappearance of the large island mammals, or both (Bover and Alcover 2003; Burney 2003). The pygmy hippo of Cyprus and the pygmy mammoth of the Channel Islands provide distinct exceptions to this situation.

The island endemic pygmy hippopotamus, *Phanourios minutus*, of Cyprus provides a case study for evaluating a late Pleistocene island extinction of a large mammal with excellent chronological control. The timing of the extinction event is well documented in the archaeological site Akrotiri *Aetokremnos*, which contains the earliest evidence of human colonization on Cyprus at ~12,000 cal. B.P., as well as over 300,000 bones of this extinct large mammal (Simmons 1999, 2014). This site is critical to the interpretation of the species' extinction event and key to understanding any anthropogenic involvement in its disappearance. Furthermore, this case study has the potential to improve drawing analogies for other Late Pleistocene, and/or island endemic, large mammal extinctions through the comparison of a more physiologically similar species.

Despite the abundance of *Phanourios* remains throughout the paleontological record of the Pleistocene, the species disappeared from Cyprus abruptly at or soon after the period represented at *Aetokremnos* (Reese 1996; Simmons 1996; Simmons et al. 1999; Strasser 1996). This correlation between the earliest archaeological site and the latest pygmy hippopotamus remains has led to the hypothesis that human hunting, at least in part, may have contributed to the species' extinction (Simmons 1999, 2014). The hypothesis that human hunting played a role in the extinction of the pygmy hippo is based largely on the overlap of artifacts and features with

pygmy hippo bones at *Aetokremnos* (Reese 1996; Simmons 1996, 1999, 2004, 2014; Simmons and Mandel 2007). This hypothesis is contentious, however, and previous critiques of this interpretation note that the differences between strata at the site may lead to the interpretation of an earlier natural accumulation followed by a later human occupation (Ammerman and Noller 2005; Ammerman et al. 2007; Binford 2000; Bunimowitz and Barkai 1996; Grayson 2000).

The work presented here is an attempt to provide an evaluation of human impact in this Late Pleistocene, large mammal extinction event. Through a series of four papers, I give a multifaceted picture of this species, the faunal remains represented at the archaeological site Akrotiri *Aetokremnos*, and evidence for human impact that may have influenced the extinction of the Cypriot pygmy hippopotamus. By examining the relationship between humans and the pygmy hippopotamus at the archaeological site Akrotiri *Aetokremnos*, we can begin to move beyond temporal correlation and discuss the ways in which humans may have contributed to the species decline during this time—if at all. It is only after understanding this relationship that we can step back and address the ultimate cause(s) of the disappearance of this species.

### **Cyprus and *Phanourios minutus***

Cyprus is the most biogeographically isolated island in the Mediterranean (Hadjisterkotis et al. 2000). The last period of connection with any other land mass was during the Messinian salinity crisis, approximately 5.3 mya, when the Mediterranean was sealed and the sea evaporated (Cita 1982). Due to the island's isolation by the Mediterranean Sea, and by large impassable salt deserts present during the Messinian salinity crisis, Cypriot vertebrate faunas have long been unique in composition. This makes the island an excellent location to study mammalian extinction for several reasons: (1) with limited immigrations, any drastic effects of an invading species should be apparent; (2) species are likely highly specialized to island

environments, amplifying the effects of negative stressors (such as change in climate or introduction of competitors); and (3) one can assume limited (or no) gene flow between island and mainland populations. Akrotiri *Aetokremnos* provides both the earliest archaeological site on the island and the latest assemblage of *Phanourios minutus* remains (Reese 1996; Simmons 1996; Simmons 1999; Strasser 1996). The site is located on the southern tip of the island on the Akrotiri Peninsula atop a steep cliff, and at present it sits approximately 40 meters above the Mediterranean Sea (Simmons, 1999). *Aetokremnos* was first excavated between 1987 and 1990 by Alan Simmons (Simmons 1999). Due to imminent erosion, a small team, including myself, returned to finish the excavation in June 2009.

Despite the abundance of *Phanourios* remains throughout the paleontological record, the species disappeared from Cyprus abruptly at or soon after the period represented at *Aetokremnos* (Reese 1996; Simmons 1996; Simmons et al. 1999; Strasser 1996). This correlation between the earliest artifacts and the latest pygmy hippopotamus remains is largely responsible for the proposal that human hunting contributed to the species' extinction (Simmons 1999). However, the debate over the pygmy hippo assemblage arose due to the differences in the contents of the strata of which the site is composed.

Akrotiri *Aetokremnos* is a small collapsed rock shelter with well-preserved stratigraphy. The deposits consist of four distinct strata, two of which are seen as major occupation layers (strata 2 and 4) and have thus been the focus of analysis. Stratum 1 consists of crushed/burnt shell and a small portion of bone. Stratum 2 contains 88% of the cultural material recovered, including nine of the eleven identified archaeological features (Simmons 1999; Knapp 2010). Stratum 3 is an intermittent sterile layer consisting of wind-blown sediment. In contrast, Stratum 4 contains 80% of the pygmy hippopotamus remains and two archaeological features, both of

which are concentrations of burnt hippopotamus bones. The radiocarbon dates for layers 2 and 4 suggest a difference of a few hundred years, such a short time span that it is undetectable by current dating methods (Simmons 1999). Due to this short time lapse between layers 2 and 4, many have interpreted *Aetokremnos* as a processing site, and hypothesize that the extinction of *Phanourios* was at least partially the result of human hunting (Simmons 1999, 2004). However, the imbalance of bone and artifacts between these layers has led to other explanations arguing for an early accumulation of bone followed by a later human occupation (Ammerman and Noller 2005; Ammerman 2007; Binford 2000; Bunimowitz and Barkai 1996). Temporal control at *Aetokremnos* is strong. Timing of the extinction event appears to be known and correlation with human arrival seems clear. Nonetheless, there has been no agreement as to whether the two are causally related.

The following research attempts to resolve this issue and assess the relationship between humans and the pygmy hippopotamus at Akrotiri *Aetokremnos*. This is accomplished by first addressing the issues surrounding the nature of accumulation in the lower strata of Akrotiri *Aetokremnos* and determining whether humans are responsible for the creation of this lower layer. Then the site is evaluated for evidence of humans hunting this species. Finally, this discussion is placed within the context of Late Pleistocene climate change and the subsistence strategies and habitat preference of the pygmy hippopotamus—in order to identify additional stressors outside of direct anthropogenic ones.

### **Potential Impact of Climate Change and Human Influence at Akrotiri *Aetokremnos***

A shift in climate can drastically affect the stability of island ecosystems, where highly specialized plants and animals may have limited ability to adapt to rapid change (e.g. Chung

2007; Mortreux and Barnett 2009; Smith et al. 2001). On the mainland, species may migrate to more favorable conditions; in an isolated island environment this is not an option and endemic faunas can suffer severe consequences (e.g. Duncan and Blackburn 2004; Rijdsdijk et al. 2011). Akrotiri *Aetokremnos* was created during a time of dramatic global climate change—the Younger Dryas. The effects of this climatic change is well understood at the higher latitudes, but becomes much more variable in the equatorial regions.

In addition to climate change, island endemic faunas are extremely vulnerable to the introduction of novel species. Novel species can add competitive pressure causing a decline in already limited resources and have a dramatic effect on the success of endemic populations (e.g., Blackburn 2004; Boyer 2010; Case and Bolger 1991; Karels 2008; Trevino 2007; Simberloff 2000). The extinction of the pygmy hippopotamus occurred during both a period of global climate change and following the introduction of a potential competitor—the wild boar, *Sus scrofa* (Chlachula 2010; Harrison 2010; Rosenbaum et al. 1996; Sima et al. 2004; Simmons 1999; Vigne 2009).

*Aetokremnos* contains the most recent pygmy hippo remains and the first remains of the wild boar, *Sus scrofa*, on Cyprus (Simmons 1999; Vigne 2009). The species appears to be a dwarfed version of its mainland counterpart (Vigne 2009). The presence of dwarfing and the inability of the wild boar to access the island by other means have led to the hypothesis that humans are the cause for this species' introduction (Vigne 2009). Vigne et al. (2009) argue that this species was first introduced 11,400-11,700 cal. years ago. The fact that the species is the only recognized novel competitor on the island at this time, combined with the short overlap of the two species, suggests that this introduction may have contributed to the decline of the hippos. While the scope of this research does not fully address the potential impacts of this competitor, it

is critical to note that the wild boar was present and should be factored into future work and consideration of indirect anthropogenic impacts. This work, however, will focus on the potential roles of human hunting and climate change in this extinction event.

### **Approach to the Problem:**

Before fully addressing the nature of the pygmy hippopotamus extinction, there are several issues that need to be resolved. **First**, we need to discuss the subsistence strategy and habitat preference of this species and the potential impact climate change may have had on the vulnerability of the population. **Second**, we need to evaluate potential taphonomic factors that may have impacted the composition of the faunal assemblage at the site— which have potentially created misleading patterns. **Third**, we need to address whether this entire site is anthropogenic in nature, or whether it is a combination of a lower natural accumulation followed by a cultural accumulation as some suggest. Finally, **fourth**, if this site is anthropogenic in nature we need to identify what information about human procurement and processing of these species is available by looking at the faunal assemblage. Only after these steps can we begin to discuss the potential impact humans may have had on leading to the extinction of the Cypriot pygmy hippopotamus.

Chapter 2, “**Inferring behavior and subsistence of the Cypriot pygmy hippopotamus through skeletal morphology and stable isotopes,**” is aimed at identifying the subsistence strategies and habitat preference of the Cypriot pygmy hippopotamus, and infer the behavior of the species. This paper combines a long-term, adaptive look at habitat selection and subsistence based on the skeletal and tooth morphology. Comparisons to extant and extinct species of hippopotami are utilized to infer behavior. Behavior is then correlated with evidence for shifting

climate on the mainland during the Late Pleistocene. Change in subsistence of this species at this time of climate change is then inferred through stable nitrogen and oxygen isotopes. Overall, this paper works to parse the potential significance that Late Pleistocene climate change may have had on the survivability of this species.

Chapter 3, “**Evaluating post-depositional taphonomic processes on the Cypriot pygmy hippopotamus assemblage at Akrotiri *Aetokremnos* (ca. 12,000 cal. B.P.)**”, first reiterates the geoarchaeology of the site noting evidence for intact deposits. It then examines the post-depositional taphonomic factors potentially present at Akrotiri *Aetokremnos* that may have altered the composition of the skeletal assemblage. This paper specifically addresses the most likely taphonomic processes present at this site, based on previous geoarchaeological work: density mediated attrition and fragmentation. Fragmentation is discussed as being the potential result of either roof fall or extensive burning—both of which are prevalent at the site. Ultimately, this paper attempts to identify biases that may impact analysis of the faunal assemblage that may need to be taken into consideration when evaluating potential human impact.

Chapter 4, “**Demographic evidence of human hunting and procurement of the extinct Cypriot pygmy hippopotamus**” takes a close look at the demographic profiles of the Cypriot pygmy hippopotami that comprise the site—identifying whether the nature of accumulation is anthropogenic or natural. Using a modified ternary graph, the age structure of the faunal assemblage is compared to ecological studies where accumulation methods are well documented such as culling projects or ecological survey. This chapter provides evidence for human hunting in the absence of direct evidence such as cutmarks and/or impact fractures.

Finally, in Chapter 5, “**Direct human modification and relative skeletal abundance of the Cypriot pygmy hippopotamus at Akrotiri *Aetokremnos***”, the faunal assemblage is

carefully evaluated for evidence of butchery, and the skeletal composition of the species used to infer potential human behavior associated with the procurement and use of the pygmy hippopotamus. This chapter focuses on identifying different strategies between strata and discusses potential explanations for the variability of skeletal elements within strata and species richness between strata. Within the context of the previous analyses, the relative skeletal abundance (RSA) of this species provides valuable insight into the strategies employed by the earliest Cypriots—a group of people about whom we have limited information to date.

This dissertation is a compilation of four papers in various stages of publication. As a result, each chapter represents a stand-alone paper, and when taken as a single document here can be repetitive regarding background information that provides context for each individual analysis. To date, chapters two and five have been submitted for publication and are out for review. Chapters three and four have been submitted and have been requested for “review and resubmit”. All data collected is available as open access on Zenodo.org (Wopschall 2015).

As a collection, the following four papers identify the potential impacts of a dramatically changing climate and humans on the Cypriot pygmy hippopotamus extinction. It is through a more detailed understanding of this species’ paleoecological context, further evidence for human interaction with this species, and a clear context of the climate and habitat changes happening on the island at this time period that we are able to paint a more complete picture of this large mammal extinction.

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## **Chapter 2: Inferring behavior and subsistence of the Cypriot pygmy hippopotamus through skeletal morphology**

### **Abstract**

The pygmy hippopotamus of Cyprus, *Phanourios minutus*, became extinct near the end of the Late Pleistocene (~12,000 cal. B.P.), during a period of dramatic climate change and about the time of first human presence on the island. In order to discuss the potential impacts of both climate and humans on this extinction event, we need to better understand the paleoecological context of this species. Here, I evaluate the skeletal morphology of *Phanourios minutus* in comparison with two extant hippopotami (*H. amphibius* and *C. liberiensis*; the modern hippo and modern pygmy hippo) and two extinct pygmy hippopotami from Madagascar (*H. lemerlei* and *H. madagascariensis*) to infer the paleoecological context and subsistence strategy of the insular Cypriot species as it evolved on the island. Showing that the Cypriot pygmy hippopotamus was adapted to terrestrial browsing in closed environments. I then evaluate the stable carbon and nitrogen isotopes of the faunal remains at Akrotiri *Aetokremnos*, the earliest well-dated archaeological site on the island and the latest well-dated occurrence of this species. Through the isotopic studies, I infer subsistence and, by proxy, climate and habitat selection of the Cypriot pygmy hippopotamus near the time of extinction—suggesting that diet is shifting in a way that reflects increasing aridity in the region. This adaptive morphological view, combined with the isotopic data near the timing of the species extinction, is then placed within the larger context of regional climate change during the Late Pleistocene. Overall, this evidence shows climatic change in the Late Pleistocene may have dramatically impacted the survivability of the Cypriot pygmy hippopotamus.

### **Introduction**

The Late Pleistocene is marked by a noticeable increase in global large mammal extinctions (Barnosky et al. 2004; Faith et al. 2009; Grayson 2007; Haynes 2009; MacPhee 1999). For decades the debate over the cause of this global extinction event has focused largely on two causal factors: humans and climate change (Bulte et al. 2006; Field & Wroe 2012; Meltzer 1986; Metcalfe et al. 2011; Nikolskiy et al. 2011; Surovell et al. 2005; Turney et al. 2008). Parsing out the relative impact of humans and climate change on these events has proven difficult largely because these events often correlate temporally with each other.

Many attempts have been made to explain the Late Pleistocene mammal extinctions as a large scale event, where all taxa are assumed to have succumbed to the same ultimate cause of extinction (Alroy 2001; Faith et al. 2009; Martin 2005; Martin & Klein 1984). While this approach is appealing in that it would explain a large scale phenomenon, it often overlooks the behavioral and ecological dynamics of the variety of species that went extinct at this time period (Grayson 1991, 2007; Grayson & Meltzer 2002, 2003). In order to address the ultimate cause/s of extinction in the Late Pleistocene, a species-level approach needs to be employed. An approach that evaluates the dynamics of each extinction event after which, if appropriate, large-scale trends and patterns can be explained between species. This species-level approach should aim to evaluate the relative impacts of human activity (including both direct influences such as human hunting and indirect ones such as habitat alteration) and climate change on each species studied.

In order to gain a complete picture of the relative importance of anthropogenic and environmental stressors on the long-term sustainability of fauna, the paleobiology of each species needs to be fully explored—focusing on a more complete understandings of each's evolutionary history, environmental adaptations, subsistence strategies, and other behaviors. However, this task can prove difficult when evaluating extinct species for which there are few or no modern correlates, when limited climatic proxies are available, and/or when complex ecosystem dynamics with multiple variables need to be considered.

Here I attempt to address this issue with an extinct island-endemic large mammal species, the Cypriot pygmy hippopotamus *Phanourios minutus*. The Cypriot pygmy hippo provides an excellent case study for evaluating the correlation between behavior, paleobiology, and climatic change. It characterizes a Late Pleistocene extinction event that coincides with both the Younger

Dryas (YD) climatic event and with the first arrival of humans to Cyprus (Simmons 1999; Vigne et al. 2009). Furthermore, as an endemic island species, the Cypriot pygmy hippo is assumed to be highly specialized for the restricted ecological diversity of Cyprus when compared to the mainland. These restricted ecological conditions allow for better control of potential confounding variables. In addition, interspecific relationships between Late Pleistocene Cypriot fauna were very 'unbalanced,' lacking large, carnivorous predators, and exhibited insular adaptations to the island landscape, potentially making them more susceptible to climatic changes and the resulting habitat fluxuations (Reese 1996; Simmons 1999). This assemblage also affords an opportunity to compare the morphology of *Phanourios minutus*, to date a poorly understood species, to several living correlates (the modern hippopotamus and modern pygmy hippopotamus) as well as to two extinct species of island-endemic dwarfed hippopotami from the island of Madagascar, and to infer behavioral similarities and differences from these species' various morphological adaptations.

Through a morphological comparison of the cranial and dental adaptations of these five species (two extant, three extinct), I reconstruct the subsistence strategies and habitat preference of *Phanourios minutus* and, by proxy, the climate and environment of Cyprus over an longer time scale in which this species adapted to its island environment. Using stable carbon and nitrogen isotope data from the archaeological site Akrotiri *Aetokremnos*, I make inferences about the environment and diet of the individuals represented at this site, the last documented site bearing remains of the species on the island and presumably antecedent to the species' extinction by only a short time. In combination, the long-term adaptive analyses shown through comparative morphology and the short-term behavioral patterns inferred from isotope analyses for the single population at *Aetokremnos* allow us to evaluate the dynamics of this species and to

gain an understanding of how the Younger Dryas may have impacted the species survivability.

### ***Phanourios minutus* and the Hippopotamid Taxon**

While at present only two species of hippos remain (*Hippopotamus amphibius* and *Choeropsis liberiensis*), this taxon was once robust and complex (for an extensive review of hippopotamid evolution, see Boisserie et.al. 2011). Hippopotamids first appeared in the early Miocene (Boisserie et al. 2011; Orliac et. al. 2010), and while the fossil record for this group still requires further clarification (O'Leary & Gatesy 2008; Theodor 2004; van Tuinen & Hadly 2004), this taxon clearly had great success throughout the Miocene and into the Pliocene, when the taxon/family began a widespread process of endemism (Boisserie et al. 2011). Focused in African regions, this increased endemism is likely related to the taxon's/family's semiaquatic habitat preference, entailing limited dispersal possibilities and leading to a notable, high degree of geographical isolation between hippopotamid populations based on patchy water availability (Boisserie et al. 2011). In the early Pleistocene, there was a notable expansion of Hippopotamids throughout most African basins and then into Europe and western Asia often attributed to increasing water availability and the expansion of many lake and river systems (Boisserie et al. 2011). Despite the robust collection of species within the larger hippopotamid taxon, those belonging to the group *Hippopotamus* appear to have been the most common to cross major bodies of salt water and inhabit islands (Boisserie et al. 2011). Several islands were inhabited at various stages by *Hippopotamus* spp. and are universally interpreted to have undergone at least two major adaptations to their respective insular island habitats: reduced body size and increased terrestrialization (Boisserie et al. 2011). While a good deal of work has been undertaken

exploring the relationship between morphology and behavior of the two dwarfed hippopotamus species of Madagascar (Burney et al. 2004; Stuenes 1989, 1991), little has been conducted regarding the morphology of the pygmy hippopotamus of Cyprus, *Phanourios minutus*.

The Cypriot pygmy hippo, *Phanourios minutus*, is well known throughout the paleontological record of the Eastern Mediterranean island of Cyprus and is assumed to have been present on the island since the early Pleistocene (Boekschoten & Sondaar 1972; Boisserie et al. 2011; Sondaar 1986). The species' extinction at the end of the Pleistocene appears to coincide with the first documented presence of humans on the island (Knapp & Blake 2008; Simmons 1999; Vigne et al. 2009), as attested by the archaeological site Akrotiri *Aetokremnos*, a collapsed rock shelter on the southern tip of the Akrotiri Peninsula. *Aetokremnos* has excellent chronological control and represents two occupational layers spanning several hundred years around approximately 12,000 cal B.P. (Knapp & Blake 2008; Simmons 1999, 2004; Vigne et al. 2009). Because of the temporal correlation between pygmy hippo extinction and initial human occupation of the island, this extinction has been frequently discussed as anthropogenic (e.g. Simmons 1999). However, even if humans hunted and/or utilized this species it does not imply that they impacted their extinction. Understanding the relative impact either of humans or of climate change on the extinction of the species is not possible without first understanding the ecological context of this species and consequently how it might have responded to the changing climate of the Late Pleistocene.

## **Methods and Materials**

To provide a more complete picture of *Phanourios minutus* and of the factors that led to its extinction, I evaluate its biogeography through isotope and morphological analyses of the fossil remains of the Cypriot pygmy hippopotamus (craniomorphology and the hypsodonty

index). This analysis is extended through comparison between the Cypriot pygmy hippopotamus and modern hippopotamus (*Hippopotamus amphibius*), extant pygmy hippopotamus (*Hexaprotodont liberiensis*), and the two extinct pygmy hippopotami of Madagascar (*H. lemerlei* and *H. madagascariensis*). Identifying functional connections between the morphological adaptations and known behaviors of extant species or inferred behaviors of extinct species affords an opportunity to interpret the behaviors of *Phanourios minutus* by allowing analogies to be drawn between comparable morphologies of these various hippopotamus species. Such morphological comparisons provide an evolutionary understanding of the species' behavior, emphasizing its long-term adaptations. In contrast, stable carbon and nitrogen isotope analyses are used to interpret the behavior and paleoecology of the species on a short time scale, near the time of the species' extinction. These data are placed within the context of known climatic change in the Eastern Mediterranean at the end of the Pleistocene, specifically during the Younger Dryas event, when the archaeological site *Aetokremnos* was occupied. The combination of these analyses provides clearer insight on the relative impact of climatic change on this extinction event.

All Cypriot pygmy hippopotamus remains used for this analysis were recovered from the archaeological deposits at Akrotiri *Aetokremnos*, which includes over 300,000 individual hippopotamus fragments representing over 300 individual hippopotami. These remains were analyzed and evaluated at the Episkopi Museum in Episkopi, Cyprus, where they are curated. Data for other species considered here were collected from previously published sources. Isotope analyses on Cypriot pygmy hippo remains were performed at the University of Washington's ISO Lab.

## Comparative Morphology

Previous work suggests that those hippo species/populations that colonized islands show an increased trend toward terrestrialization (Boisserie et al. 2001; Eltringham 1999; Sondaar 1986). This inference is based primarily on three morphological comparisons: limb, cranial, and tooth morphology. For example, published comparisons of the two extinct hippo species of Madagascar have demonstrated morphological differences between the more terrestrial *H. madagascariensis* and the semi-aquatic *H. lemerlei*, these behavioral interpretations being reinforced by fossil locations (Stuenes 1991). Unfortunately, little of this comparative work has included a consideration of Cypriot pygmy hippo behavior, and that which has been done has produced conflicting results (Boisserie et al. 2011; Caloi & Palombo 1994; Houtemaker & Sondaar 1979). Limb morphology of the Cypriot pygmy hippo suggests increased terrestrialization through limb stabilization and a more unguligrade foot (rising on one toe similar to a deer) (Boisserie et al. 2001; Eltringham 1999; Sondaar 1986). On the other hand, some scholars note that this species retained high eye orbits—a feature commonly associated with semi-aquatic habitats (Boekschoten & Sondaar 1972; Simmons 1999; Sondaar 1986). Here I revisit and attempt to resolve these conflicting behavioral interpretations by subjecting the Cypriot pygmy hippopotamus to a quantitative morphological comparison with the two extinct dwarfed hippos from Madagascar, the extant modern hippo, and the extant pygmy hippo. In particular, I attempt to identify two major behaviors of the Cypriot pygmy hippo through comparison of cranial and tooth morphology: habitat selection (e.g. aquatic versus terrestrial, open versus closed) and feeding strategies (e.g. browsing versus grazing).

The comparison of the cranial morphologies of the five hippopotamus species considered here are used to decipher habitat selection, and by proxy the paleobiogeography of Cyprus. In

addition, tooth morphology of *Phanourios minutus* is evaluated to both identify the hippopotamus' feeding strategy and infer the biogeography of the species over their evolutionary history on the island.

### **SKELETAL MORPHOLOGY AND INFERRED BEHAVIOR**

In general, the clade *Hippopotamidae* is characterized by a semi-aquatic habitat selection and is considered a grazer relying largely on aquatic plant materials (Eltringham 1999). Yet, while hippopotamids are characterized as preferential grazers, they also demonstrate some flexibility in food acquisition. In times of stress, they are capable of adopting a more browser-like foraging strategy, incorporating more variable plants into their diet (Boisserie et al. 2005; Souron et al. 2012).

The common ancestor of *H. amphibius* and *P. minutus* is assumed to be *Hippopotamus antiquus*, a species that evolved in Africa and radiated outward to cover a considerable range including the northern shores of the Mediterranean (Boisserie 2005; Boisserie et al. 2011; Orliac et al. 2010). Both of Madagascar's endemic dwarfed hippos are assumed to be descendants of *H. amphibius*, who likely swam or floated to the island (Eltringham 1999). The extant pygmy hippopotamus, *Hexaprotodon liberiensis*, is not a part of the *Hippopotamidae* clade but shares a common ancestor with all hippopotami. Despite their phylogenetically distant relationship with the extinct species discussed here, their small size and terrestrial habitat preference provide a good analogue for inferring the habitat selection of dwarfed hippopotamid species based on skeletal morphology.

Comparison of *H. amphibius* and *Hex. liberiensis* indicates key morphological differences between terrestrial and aquatic species (Table 2.1). Relative to *H. amphibius*, the

terrestrial *Hex. liberiensis* has lower eye orbits, a thin suborbital region, and forward-facing eyes (Boisserie 2005). Conversely, the aquatic *H. amphibius*'s elevated eye orbits, thick suborbital region, and laterally placed eyes are seen as adaptations for spending large amounts of time in the water (Stuenes 1989). Raised eye orbits position the eyes much higher on the head, allowing aquatic species to be submerged underwater while maintaining sight of their surroundings above the surface.

**Table 2.1 Comparison of Species with aquatic and terrestrial traits**

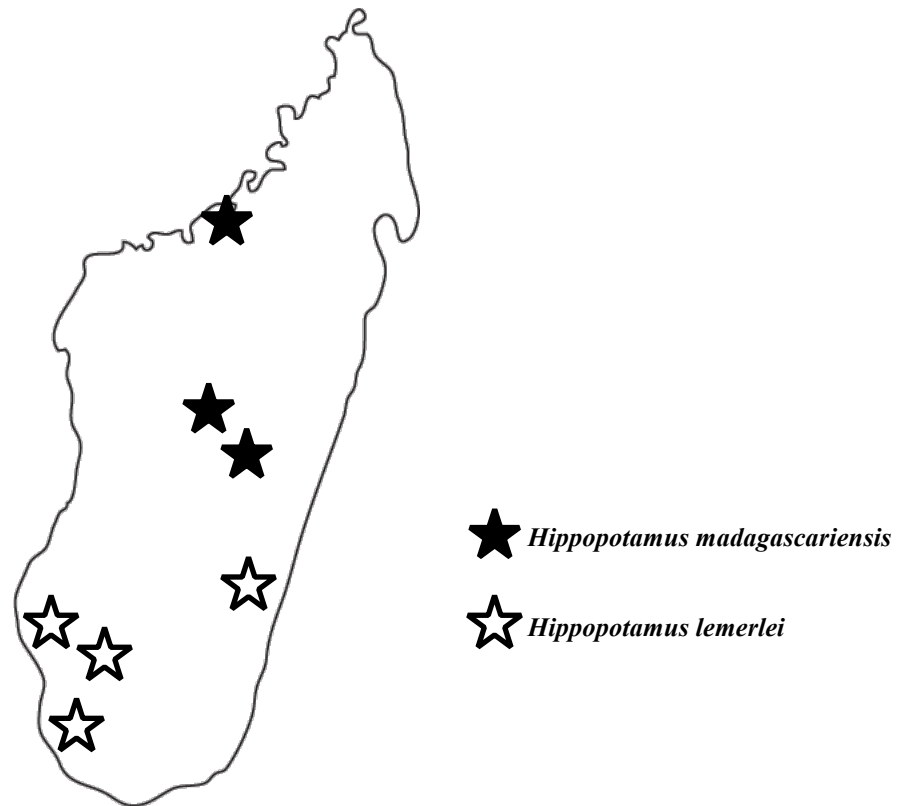
Species	Aquatic Traits					Terrestrial Traits				
	Elevated eye orbits	Long facial region and short postorbital part of skull	Thick suborbital region	More lateral view	Plantigrade	Lower eye orbits	Equivalent facial region and postorbital skull	Thin suborbital region	Frontal view	Unguligrade
<i>H. amphibius</i>	X	X	X	X	X					
<i>Hex. liberiensis</i>						X	X	X	X	
<i>H. lemerlei</i>	X	X	X	X						
<i>H. madagascariensis</i>						X	X	X	X	
<i>P. minutus</i>						X	X	X		X

The fact that these distinct morphological traits appear to correspond with habitat differences inferred for the two extinct Madagascar dwarfed hippos, *H. lemerlei* and *H. madagascariensis*, strengthens the argument for their general association with habitat selection. While these two dwarfed hippos share a common ancestor (*H. amphibius*), they show several striking morphological differences in cranial morphology. *H. madagascariensis* has a thin suborbital region and similar craniomorphology to that of *Hex. liberiensis*, suggesting a terrestrial habitat selection (Figure 2.1). This assumption is further supported by the highland recovery location of fossils of this species (Figure 2.2). *H. lemerlei*, conversely shows many

similarities to that of *H. amphibius*, including a thick suborbital region, elevated eye sockets, and a long facial region with short postorbital skull (Table 2.1). The majority of fossils identified as *H. lemerlei* were recovered from the island's lowlands and coastal regions, further supporting the aquatic habitat selection.



Figure 2.1 Top to bottom: *H. lemerlei* showing high eye orbits with thick orbital crest; *P. minutus* showing relatively low eye orbits and thin orbital crest; *H. madagascariensis* showing low eye orbits and thin suborbital crest



**Figure 2.2** Map showing the approximate distribution of pygmy hippopotami on the island of Madagascar.

Placing *P. minutus* within this terrestrial versus aquatic habitat framework, the species' skeletal morphology strongly suggest that it was fully terrestrial. In addition to having a lowered eye orbit, a facial region-to-postorbital cranium ratio close to 1, and a frontal view, *P. minutus* also has an unguligrade foot morphology unique within the *Hippopotamidae* clade, its toes being more similar to those of bovids and deer rather than those of plantigrade walkers like *H. amphibius*. This limb morphology suggests that *P. minutus* was well-adapted to climbing and walking on rugged terrain, but likely not a good runner (van der Geer 2010).

## TOOTH MORPHOLOGY: HYPHODONTY INDEX (HI), JAW LENGTH, AND MUZZLE WIDTH

Analysis of dental morphology, including both tooth shape and wear, provides additional information on the behaviors of these species regarding both their habitat selection and subsistence strategies. The molars of *H. antiquus* (the assumed ancestor of *H. amphibus* and potentially of *P. minutus*) suggest a grazing subsistence strategy, which is reflected in both *H. amphibus* and the dwarfed hippo from Madagascar, *H. lemerlei*. Conversely, *P. minutus* shows a marked shift toward a more lophodont state. This would suggest a return to browsing and is considered a more 'primitive' foraging strategy for *Hippopotamidae*. Previous studies have noted that the Cypriot pygmy hippo molars appear to have a lower crown height relative to their grazing ancestors (Boisserie 2005; van der Geer 2010). Grazers tend to have a highly abrasive diet, due in part to silica content in plant material and in part to sediment consumed with acquired resources, requiring constant grinding action and quickly wearing the grazer's teeth down (Mendoza & Palmqvist 2008). Having a high crown height accommodates this highly abrasive diet and feeding strategy and is seen throughout the obligate grazers of the animal kingdom (Mendoza et al. 2002; Mendoza & Palmqvist 2008).

To test the hypothesis that *P. minutus* shifted from a grazing and toward a browsing subsistence strategy, I calculated the hypsodonty index (HI) for *P. minutus* and compared it to the HI and other cranial morphology of the other five hippo species considered here. The HI is a measure of the molar crown height relative to the occlusal width. HI has been used as a stand-alone measure for evaluating grazing versus browsing strategies frequently in paleontology, archaeology and ecology, and is frequently interpreted as an indicator of feeding preferences and habitat selection in ungulates (Mendoza et al. 2002; Mendoza & Palmqvist 2008). As a result, the HI is commonly used as a proxy for paleodiet and paleoenvironment reconstruction (Feranec

2003; Janis et al. 2002; Jernvall 2002; Mendoza et al. 2002; Mendoza & Palmqvist 2008; Palmqvist et al. 2003).

Mendoza & Palmqvist (2008) evaluated the functional significance of HI values in their analysis of the diet and habitat choice of modern ungulates. Their study of 134 extant ungulate species, from two orders (Artiodactyla and Perissodactyla) and 13 families, showed that it is possible to discriminate between closed and mixed or open environments by comparing the HI to the anterior jaw length (JLB; Mendoza & Palmqvist 2008). Similarly, comparing the HI and muzzle width (MZW; Mendoza & Palmqvist 2008) allows grazers to be distinguished from browsers.

HI was calculated for seventeen *P. minutus* specimens from Akrotiri *Aetokremnos* from unworn lower third molars by dividing crown height by occlusal width (Janis et al. 2002; Table 2.2). Molars used to calculate the index were randomly selected from throughout all units at the site. MZW was calculated for three specimens that could be confidently associated with three of the lower molars used to calculate HI values, all from prime aged individuals. MZW was measured from the outer junction of the boundary between the maxilla and premaxilla (Mendoza et al. 2002). JLB was calculated for these same three individuals, measuring from the base of the third incisor to the first premolar (Mendoza et al. 2002). Values for MZW and JLB were size-adjusted by dividing each by the lower molar tooth row length, measured along the base of the teeth (Palmqvist & Mendoza 2006, 2007).

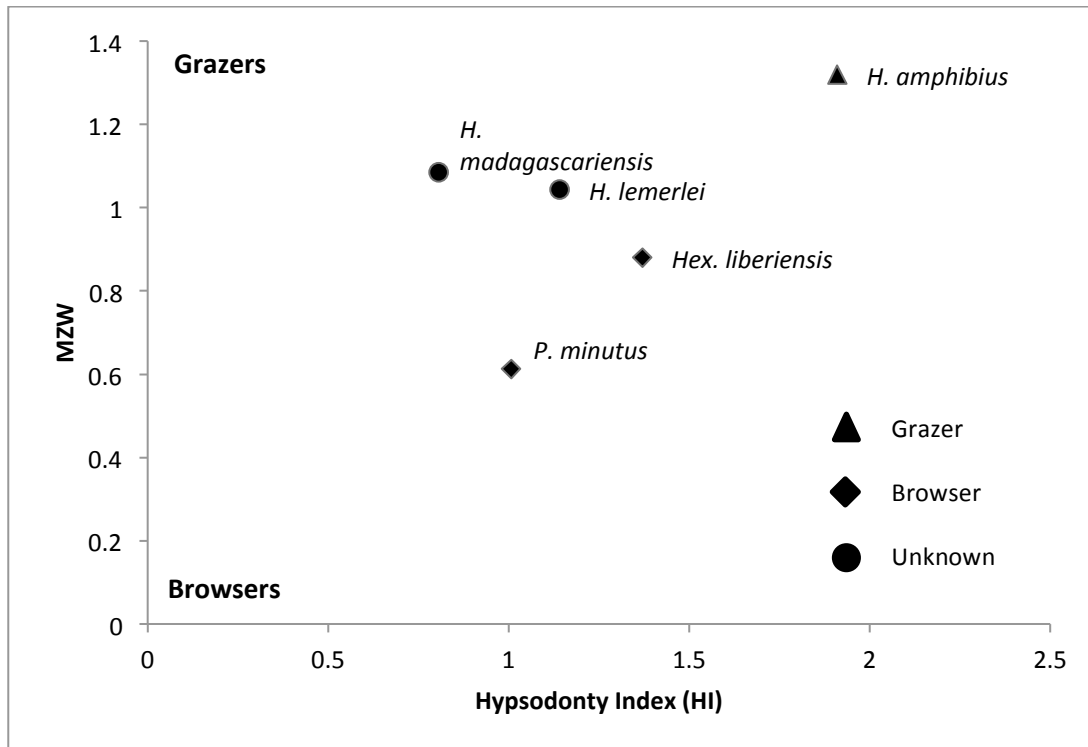
**Table 2.2 Measured crown height, occlusal width and calculated HI for Cypriot pygmy hippos at Akrotiri *Aetokremnos*.**

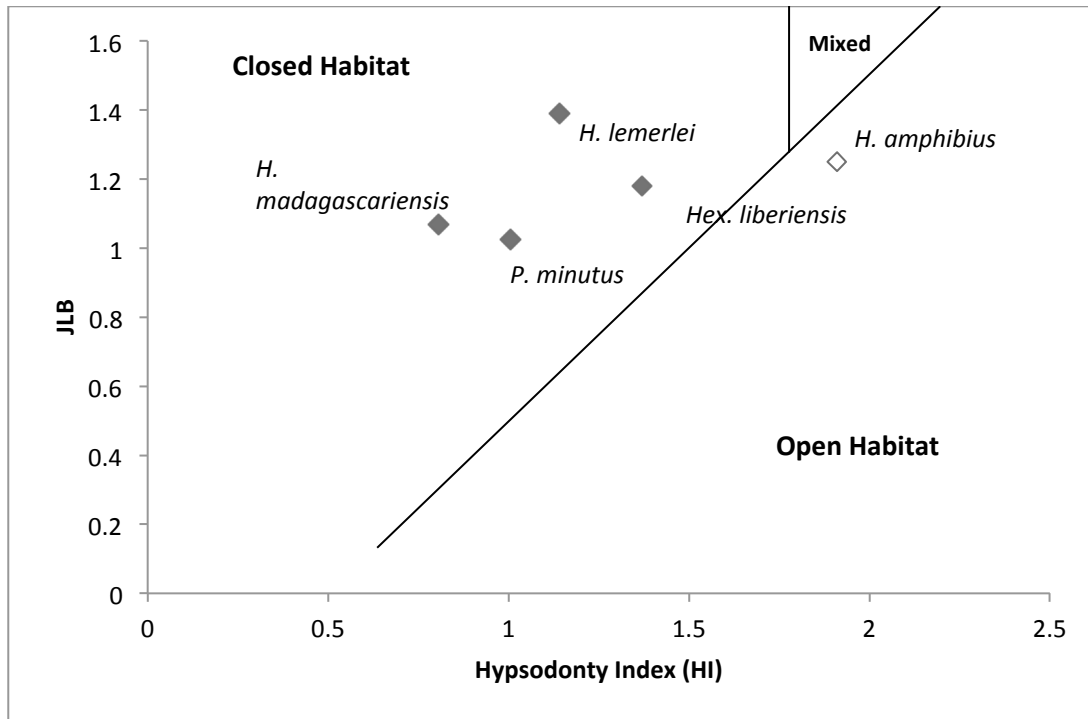
<b>Crown Height</b>	<b>Occlusal Width</b>	<b>Hypsodonty Index (HI)</b>
20.21	20.09	1.006
19.07	19.01	1.003
20.27	20.01	1.013
20.03	19.89	1.007
19.45	19.31	1.007
19.77	19.64	1.007
19.91	19.7	1.011
20.3	20.05	1.012
20.11	20.05	1.003
20.14	20.07	1.003
19.87	19.81	1.003
20.25	20.09	1.008
20.42	20.37	1.002
20.2	20.04	1.008
20.11	20.01	1.005
19.83	19.71	1.006
19.97	19.9	1.004
	<b>Average</b>	<b>1.006 ± .0033</b>

Plotting both MZW and JLB against HI for the Cypriot and extinct Madagascar pygmy hippopotami, along with artiodactyls analyzed in Mendoza and Palmqvist (2008), suggests that the Cypriot pygmy hippopotamus was a browser in a closed habitat (Table 2.3; Figure 2.3).

**Table 2.3 Comparison of diet, habitat, hypsodonty index (HI), anterior jaw length (JLB), and muzzle width (MZW) of two extant and three extinct species of Hippopotamid.**

Species	Diet	Habitat	HI	JLB	MZW	References
<i>Hexaprotodon liberiensis</i>	Br	CH	1.37	1.18	0.88	Mendoza & Palmqvist 2007, Tobler 1991, White, L. 1986, Eltringham 1993
<i>Hippopotamus amphibius</i>	FG	OH	1.91	1.25	1.32	Mendoza & Palmqvist 2007, Owen-Smith 1988, Kingdon 1979
<i>Phanourios minutus</i>	-	-	1.01	1.02	0.61	
<i>Hippopotamus madagascariensis</i>			0.81	1.07	1.09	Stuenes 1989
<i>Hippopotamus lemerlei</i>			1.14	1.39	1.04	Stuenes 1989





**Figure 2.3 Comparison of the Cypriot pygmy hippopotamus (*P. minutus*) to *H. amphibius*, *H. madagascariensis*, *H. lemerlei*, *H. liberiensis***

Overall, the preceding morphological comparisons not only confirm that the Cypriot pygmy hippopotamus was a terrestrial browser but also suggest that this species may have evolved in a closed environment consisting of trees and shrubs. These data provide an adaptive look at the subsistence strategies and paleoecology of this species. To address the question of whether shifts in their subsistence options or their environment impacted their survivability, we must turn our attention away from this adaptive analysis and toward measuring their diet and behavior near the time of their extinction.

### **Stable Isotopes as Diet and Paleoclimate Proxies**

Stable isotope signatures in tissues of organisms are used to reconstruct diet, local environmental conditions, and migration, as well as to measure prehistoric population health in a

wide variety of fields, including paleoecology and archaeology (Casey & Post 2011; Cerling et al. 2008; Harris et al. 2008; Szpak et al. 2010, 2012, 2013). The composition of consumer tissues are directly related to the carbon and nitrogen isotope composition of the foods they consume and can provide valuable insight into paleodiets and climate, after trophic level enrichment has been accounted for (Szpak et al. 2010). Carbon isotopes in ungulates are often used to determine the relative dietary importance of browsed and grazed foods, both for individuals and species, because grazing diets are typically much higher in C<sub>4</sub> plants, which modulates  $\delta^{13}\text{C}$  upward in the tissues of herbivorous consumers (Passey et al. 2005; Szpak et al. 2013). For terrestrial plants, variation in  $\delta^{13}\text{C}$  values is largely dependent on the photosynthetic pathway that they employ for carbon fixation, with C<sub>4</sub> plants fixing more <sup>13</sup>C relative to <sup>12</sup>C than do C<sub>3</sub> plants (Clements et al. 2009; O'Leary 1987). Nitrogen isotope values, on the other hand, can serve as proxies for paleoclimatic conditions, as the ratio of <sup>15</sup>N to <sup>14</sup>N in plant tissues is strongly influenced by environmental factors, showing a positive correlation with mean annual temperature and a negative correlation with precipitation or water availability (Szpak et al. 2013).

Assays of carbon and nitrogen isotope ratios on the remains of Cypriot pygmy hippopotami provides valuable insight into both the diet and climatic conditions of this species leading up to its extinction at the end of the Pleistocene, when compared to carbon and isotope signatures of the well-studied modern hippo (*H. amphibius*), late Miocene aged hippopotami, and other ungulates.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were calculated for the enamel of 12 *Phanourios minutus* teeth, all prime adults based on Laws (1968) classification. All lab work was completed by the University of Washington's IsoLab following their standard protocol for solid  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis ([www.isolab.ess.washington.edu](http://www.isolab.ess.washington.edu)).

Bulk samples from selected teeth were collected to analyze solid  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Individual teeth were selected based on a random selection of field numbers (associated with location within site) and quality of preservation/completeness of each specimen. The UW IsoLab used elemental analysis to combust, convert and purify solid materials into  $\text{CO}_2$  and  $\text{N}_2$  for the analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  using a Costech elemental analyzer coupled to a Thermo MAT253 isotope mass spectrometer. Samples were flash combusted at 1000 °C with excess oxygen in a Costech ECS 4010 Elemental Analyzer (EA) equipped with a zero-blank autosampler. The combustion column was packed with cobaltous oxide for a combustion aid and silvered cobaltous oxide to scrub sulfur compounds. A helium carrier set to 80 mL / min moved combustion products through a 650 °C reduced copper column to ensure complete reduction of  $\text{NO}_x$  compounds to  $\text{N}_2$  and also to absorb all excess oxygen. Sample gases were then carried through a magnesium perchlorate trap to absorb all water and then through a 3 m gas chromatography column to separate  $\text{N}_2$  from  $\text{CO}_2$ . The EA effluent flows into a ThermoFinnigan Conflo III where the stream is split to reduce the flow rate from 80 mL/min to 2 mL/min. The reduced flow rate then flows through an open split with excess helium via fused silica capillary tubing. A pressure differential between the ThermoFinnigan MAT253 isotope ratio mass spectrometer and the Conflo III along fused silica capillary tubing allows helium and sample gas to move into the electron bombardment source for subsequent ionization, acceleration, focusing, separation, and measurement of masses 28, 29 for  $\delta^{15}\text{N}$  and 44, 45, 46 for  $\delta^{13}\text{C}$ . Internal laboratory reference materials are interspersed with samples for a two point calibration which allows for blank correction and conversion to the  $\delta^{15}\text{N}$  Air- $\text{N}_2$  and the  $\delta^{13}\text{C}$  VPDB scales.

The IsoDat software provided  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values relative to the respective reference gas cylinders (along with all other selected data) were imported into a matlab script for data reduction. A linear regression was completed, independently for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , using the raw  $\delta$  values and the accepted values of the internal reference materials. All data are corrected to the Air-N<sub>2</sub> scale, for  $\delta^{15}\text{N}$ , and to the VPDB scale, for  $\delta^{13}\text{C}$  using these respective linear equations. Precision and accuracy are estimated for each run using a third internal reference material that is treated as an unknown. Reference materials are chosen to flank the sample range in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values. All data from this isotope analysis is available on Zonodo.org (Wopschall 2015).

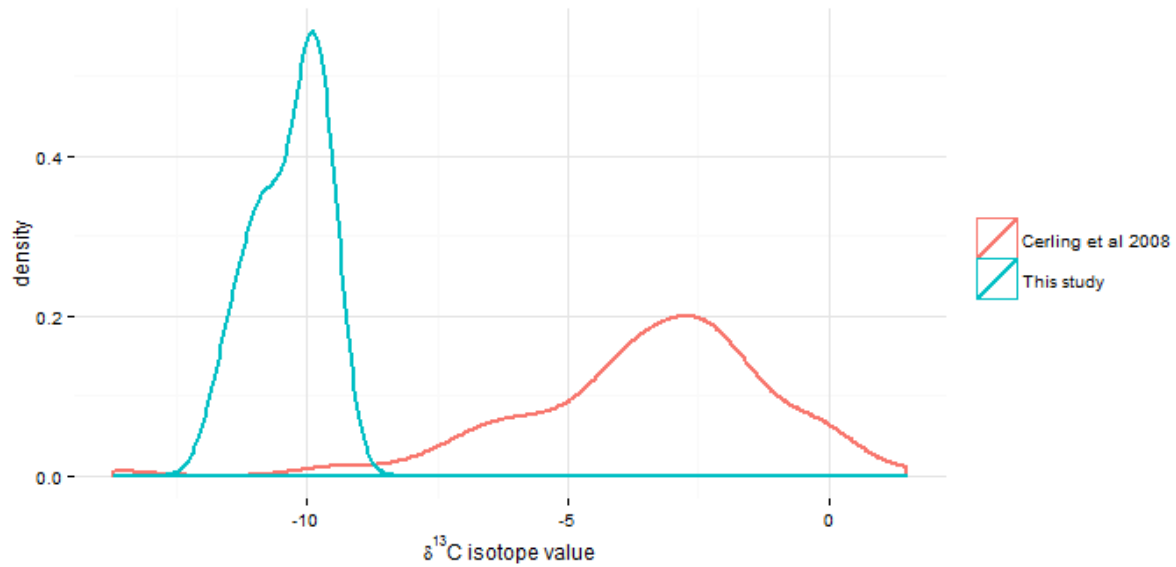
## **CARBON ISOTOPES**

The average value of  $\delta^{13}\text{C}$  in the pygmy hippopotamus is -10.357 (SD= 0.676; n= 12; Table 2.4). Comparison between this value and those measured for obligate grazers and browsers, modern hippos, and elephants from Kenya, suggests that the pygmy hippos of Akrotiri *Aetokremnos* were largely browsers, with minimal C<sub>4</sub> plants in their diet (Cerling et al. 2008) (Table 2.5). While the Cypriot pygmy hippos at *Aetokremnos* appear to have consumed a diet higher in C<sub>3</sub> plants than that of the modern hippo, modern hippos are known to be opportunistic feeders who adapt their feeding behaviors to browsing as needed (Cerling et al. 2008). While modern hippos were once assumed to have a high C<sub>4</sub> diet based on field observations of feeding behaviors, recent isotope studies have shown a much greater input of C<sub>3</sub> vegetation than previously expected (Boisserie 2005; Cerling et al. 2008; Field 1972; Field & Laws 1970; Lewison 2007). Overall, the pygmy hippo of Cyprus show a much more narrow feeding strategy reliant on a large composition of C<sub>4</sub> plants.

**Table 2.4  $\delta^{13}\text{C}$  for Cypriot pygmy hippos at Akrotiri *Aetokremnos*; FN: Field Number**

<b>FN</b>	<b><math>\delta^{13}\text{C}</math></b>
1127	-10.015
490	-9.729
1089	-10.873
684	-11.265
367	-10.180
854	-10.843
459	-9.671
913	-11.609
208	-9.912
270	-9.534
532	-9.973
684	-10.676
<b>Average:</b>	<b>-10.357 <math>\pm</math> .676237</b>

Focusing more on the range of carbon isotope values of the Cypriot pygmy hippo, it becomes clear that it is very narrow compared to that of the modern hippo and elephant. In Cerling et al.'s (2008) analysis, the modern hippo's  $\delta^{13}\text{C}$  values range between a maximum of 1.5 to a minimum of -13.7. In contrast, Cypriot hippo values range between a maximum -9.53 of and minimum of -11.6. While Cerling et al. (2008) had a much larger sample size, this range difference appears to be statistically significant (Figure 2.4). This suggests a much more specific diet range for this species, either as the result of plant availability or species specialization—both scenarios which are likely in an insular island environment.



**Figure 2.4 One-way permutation test based on 9999 Monte-Carlo resampling ( $p < 2.2e^{-16}$ ); showing significantly narrowed range for stable carbon isotope values in the pygmy hippopotamus of Cyprus when compared to the modern hippopotamus.**

**Table 2.5 Comparison of grazers and browsers average  $\delta^{13}\text{C}$  values (Cerling et al. 2008)**

	$\delta^{13}\text{C}$	1 SD
<i>Grazers</i>		
Alcelaphins	1.9	1.2
Buffalo	0.8	1.3
Waterbuck	0.6	1.1
Warthog	-0.5	1.2
Zebra	0.2	1.0
<b>Average Grazer</b>	<b>0.6</b>	
<i>Browsers</i>		
Giraffe	-12.8	1.5
Dikdik	-12.5	1.6
Average browser	-12.7	
Modern Hippo	-3.6	2.5
Elephant	-11.5	2.5
<b>Cypriot Pygmy Hippo</b>	<b>-10.356</b>	<b>.6762</b>

## NITROGEN ISOTOPES

The  $\delta^{15}\text{N}$  values of herbivore body tissue have been shown to correlate positively with annual mean temperature and negatively with rainfall or water availability (Grocke et al. 1997; Hartman 2011; Murphy & Bowman 2009; Pate & Anson 2008). High nitrogen values are typically observed in herbivores that inhabit hot and arid environments, irrespective of elevation (Hartman 2011). Several hypotheses have been posed to explain this phenomenon, focusing on both physiological responses and dietary impact (Ambrose & DeNiro 1986; Murphy & Bowman 2009), although it appears that the main factor causing this correlation is rooted in dietary preferences (Hartman 2011).

The  $\delta^{15}\text{N}$  values measured for the Cypriot pygmy hippopotami at *Aetokremnos* averaged 8.09 (SD= 0.906; Table 2.6). Estimates for the nitrogen enrichment resulting from fractionation for each increase in trophic level ranges from +2‰ to +3.4‰ (Schmidt et al. 1999). Consequently, plants consumed by the pygmy hippopotami of *Aetokremnos* are estimated to have  $\delta^{15}\text{N}$  values ranging between 4.69‰ and 6.09‰, subtracting 2‰ to 3.4‰ from the assemblage average of 8.09. Handley et al.'s (1999) study of global foliar  $\delta^{15}\text{N}$  values suggests that foliar  $\delta^{15}\text{N}$  values falling within or close to this range are associated with a wide distribution of mean annual rainfall (MAR) and habitat types (Table 2.7). However, Handley et al.'s (1999) foliar  $\delta^{15}\text{N}$  sample shows a negative correlation between  $\delta^{15}\text{N}$  and MAR, following the relationship

$$\delta^{15}N_{\text{Foliar}} = 4.39 - 0.003 \times \text{MAR}$$

( $P < 0.00001$ ,  $r = -0.59$ ,  $n = 97$ ). If the Cypriot foliar  $\delta^{15}\text{N}$  value inferred from the mean *Aetokremnos* hippo  $\delta^{15}\text{N}$  values is estimated to lie between 4.69‰ and 6.09‰. Arranging this equation implies arid conditions in Cyprus during the Late Pleistocene.

$$MAR = \frac{4.39 - \delta^{15}\text{N}_{\text{Foliar}}}{3}$$

**Table 2.6  $\delta^{15}\text{N}$  values for the Cypriot pygmy hippopotamus at Akrotiri Aetokremnos**

<b>FN</b>	<b><math>\delta^{15}\text{N}</math></b>
1127	8.797
684	7.670
913	6.549
359	7.334
208	7.162
854	7.492
684	8.837
1089	9.611
367	8.884
459	8.191
684	7.744
1127	8.828
<b>Average:</b>	<b>8.092 ± 0.906</b>

**Table 2.7 Foliar  $\delta^{15}\text{N}$  as it relates to mean annual temp (MAT), mean annual rainfall (MAR), and habitat type. From Handley et al. 1999.**

Foliar $\delta^{15}\text{N}$ (‰)	MAT (°C)	MAR (mm)	Elevation (m)	Latitude	Location	Habitat
+5.8	16	230	350	35.5 S	S. Africa	semi-desert
+5.1	23	570	350	23 S	S. Africa	tall tree savannah
+5	17	30	350	22.5 S	S.E. Africa	dry river plain
+6.0		100	700	22.5 S	S.E. Africa	lowland savannah
+6.1		150	700	22.5 S	S.E. Africa	lowland savannah
+5.1	30	85	140	33.5 N	S.W. USA	mesquite desert
+5.3	16	230	1400	32.5 N	S.W. USA	Desert
+5.6	3.1	452	146	48 N	Inner Mongolia	Steppe
+4.5	14.5	1390	335	36 N	S.E. USA	deciduous forest
+5.0		287	598	24.2 S	N. Australia	
+6.0	11	400	5	36 N	W. USA	coastal scrub

In summary, stable carbon and nitrogen isotope analyses suggest that the pygmy hippopotami of Late Pleistocene Cyprus conformed to a narrow browsing subsistence strategy relative to the opportunistic subsistence strategy demonstrated for modern hippos, and that they encountered an arid environment during this period.

## Conclusions

Considered together, the morphological comparisons and stable isotope analyses of the Late Pleistocene Cypriot pygmy hippo population begin to provide a more complete picture of the stressors that may have contributed to this species' extinction. Reconstruction of the Cypriot pygmy hippo's evolutionary history and insular morphological adaptations suggests that this species was adapted to a terrestrial habitat (as evidenced by the foot/limb, cranial, and tooth morphology) and that it transitioned away from grazing and towards browsing. Cranial morphology furthermore suggests that this species evolved in a close environment consisting of

trees and shrubs. In contrast, while the stable carbon isotope analysis supports a match between the species' evolved foraging strategy and the feeding behaviors of the *Aetokremnos* population, there is evidence that this populations faced a relatively arid environment that was not only incompatible with its evolved adaptation for a closed habitat but potentially also entailed a decline in the availability of C<sub>3</sub> plants.

Currently, no paleoclimate proxy data exist for Late Pleistocene Cyprus, and the regional impact of the Younger Dryas cold period near the equator is assumed to be more highly variable than it appears to have been at northern latitudes (Rutter et al. 2000). The impact of this climatic event on the eastern Mediterranean region and adjacent mainland of the Levant Basin is extensively debated in the archaeological literature, as this period coincides with a dramatic change in land use and mobility throughout the region (Bar-Yosef 1998; Blockley & Pinhasi 2011; Eshed et al. 2010; Haldorsen et al. 2011; Maher et al. 2012). Robinson et al. (2006) have compared multiple climatic proxies throughout the Levant in an attempt to correlate climatic events across this smaller region. Using lake level, paleosol, fluvial sediment, terrestrial paleobotanical, terrestrial geochemical (speleotherm, lacustrine sediment and mollusc), and marine records, they were able to identify a regional signal for the Younger Dryas throughout the Levant. They note that this period is tied to extreme aridity, with annual rainfall less than 150mm and an increase in C<sub>4</sub> vegetation (Robinson et al. 2006). This period was immediately followed in the Levant by a series of marked wet events, likely mirrored by episodes of alluvial fan formation on Cyprus (Robinson et al. 2006). If these proxy data from the Levant and Cyprus are taken to indicate similar paleoenvironments in the two regions following the YD, one could further assume that this similarity extended to the preceding, YD, period. In this case, the main difference between the two regions would then be the island insularity of Cyprus, increasing the

vulnerability of its endemic species to dramatic environmental changes (MacArthur 1967; van der Geer 2010).

Because the Cypriot pygmy hippopotamus appears to have been adapted to a closed environment where they presumably browsed on a narrow diet of C<sub>3</sub> plants, an increasingly arid climate would have had a potentially devastating impact on their survivability. To further address the relative importance of climate change for this extinction event, it will be desirable to explore more direct paleoclimate proxies for Late Pleistocene Cyprus and to conduct a more thorough evaluation of *P. minutus* populations through time. These studies should include morphological comparisons between multiple paleontological sites and ancient DNA analyses that could provide insight into the species' population dynamics leading up to the Late Pleistocene.

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### **Chapter 3: Evaluating post-depositional taphonomic processes on the Cypriot pygmy hippopotamus assemblage at Akrotiri *Aetokremnos* (ca. 12,000 cal. B.P.)**

**Abstract:** Akrotiri *Aetokremnos* is one of the earliest archaeological sites in Cyprus (ca. 12,000 cal. B.P.), as well as one of the largest deposits of the endemic and extinct Cypriot pygmy hippopotamus, *Phanourios minutus*. Initial publications covering the excavations in the 1980s led to the interpretation of this site as an example of direct association between humans and pygmy hippos. This relationship has been extrapolated to suggest a possible influence of human hunting on the extinction event of this species. This proposal became hotly debated on the basis of two main issues: proving direct association/ intact site stratigraphy, and the lack of faunal analysis at a site that is overwhelmingly comprised of faunal remains. Here I provide a geoarchaeological review of the site—reiterating the support for intact stratigraphy and the presences of intact cultural material in the lower stratum. I then evaluate the most likely post-depositional taphonomic factors at this site: density mediated attrition and fragmentation. These analyses show that there is no evidence for density mediated attrition at this site, and that fragmentation is likely not the result of roof fall (dynamic impact) or natural burning, and in at least one feature appears to be the result of anthropogenic burning. Ruling out potential natural biases related to post-depositional taphonomy, will allow us to use the faunal remains in determining the nature of the site and potential human behavior related to the procurement and use of the Cypriot pygmy hippopotamus.

Despite the abundance of Cypriot pygmy hippopotamus, *Phanourios minutus*, remains throughout the paleontological record through the Pleistocene, the species disappeared from Cyprus abruptly at or soon after the period represented at the archaeological site Akrotiri *Aetokremnos* (Reese 1996; Simmons 1996, 1999; Strasser 1996). Akrotiri *Aetokremnos* contains the earliest well documented evidence of human colonization on Cyprus at ~12,000 cal B.P., as well as over 300,000 bones of the extinct pygmy hippo (Simmons 1999, 2014). This correlation between the earliest archaeological site and the latest pygmy hippopotamus remains has led to the hypothesis that human hunting contributed to the species' extinction (Simmons 1999, 2014). The hypothesis that human hunting potentially played a role in the extinction of the pygmy hippo

is based largely on the overlap of artifacts and features with pygmy hippo bones at this site (Reese 1996; Simmons 1996, 1999, 2004, 2014; Simmons & Mandel 2007). However, this hypothesis is contentious, and the differences between strata at the site have led some to interpret the site as an earlier natural accumulation followed by a later human occupation (Ammerman & Noller 2005; Ammerman 2007; Binford 2000; Bunimowitz & Barkai 1996; Grayson 2000). Before addressing human utilization of this species, we must first clear up the nature of the lower bone bed strata and the upper cultural strata—determining if they are both intact cultural deposits, or a natural deposit overlaid by a cultural deposit with mixing.

Simmons and many collaborators (1999) argue for the cultural accumulation of the pygmy hippopotamus based on clear-cut stratigraphy, the large number of specimens, evidence for extensive burning, and artifacts in direct association with faunal remains. This interpretation has been widely debated, with critics citing questionable dating and the lack of a detailed faunal analysis, in addition to a report by taphonomist Olsen (1999) citing no evidence for cutmarks, breakage for marrow extraction and the possibility of explaining the extent of burning by indirect fire (Binford 2000; Grayson 2000; Olsen 1999). All of these critiques lead to the larger question of the nature of the deposits and whether stratigraphy is intact or if extensive post depositional mixing had occurred.

Since publication, the questions regarding the antiquity of *Aetokremnos* and the timing of occupation have been addressed and resolved elsewhere (Ammerman and Noller 2005; Bunimovitz and Barkai 1996; Simmons 1999; Simmons and Mandel 2007; Vigne et al. 2009). The critiques that have not been fully addressed are surrounding the nature of accumulation of the lower strata. In addition, before fully answering questions relating faunal remains to human behavior, we must ensure that post-depositional processes have not significantly altered the

assemblage composition, and as a result mask the patterns potentially present from human alteration. Here I evaluate potential post-depositional taphonomic processes by first reiterating the evidence for stratigraphic integrity at the site which was initially overlooked by critics (also recently discussed in Simmons 2014), and then by evaluating evidence for post-depositional density mediated attrition and fragmentation. Carnivore damage is not discussed here, as there were no predators or scavengers present on the island of Cyprus that may have chewed bone. Through these analyses, I show multiple lines of evidence that suggest post-depositional factors do not significantly alter the composition of pygmy hippopotamus remains at Akrotiri *Aetokremnos* and that the skeletal elements present accurately represent the faunal material at time of deposition. As such, any analyses related to natural or cultural impacts on this species based on the faunal remains does not need to factor in these potential biases.

### **Stratigraphy: A review of the evidence**

Stratigraphic integrity remains one of the most debated topics regarding the nature of cultural influence on Akrotiri *Aetokremnos* despite the issue being addressed with sufficient detail (Mandel 1999; Mandel and Simmons 1997; Simmons and Mandel 2007) and succinctly reiterated by Simmons (2014). Here I offer a brief overview to orient the reader to the site stratigraphy, and discuss some key concerns that have been brought up in previous critiques of the site and the cultural implications of the lower Stratum 4 bone bed.

Akrotiri *Aetokremnos* provides both the earliest archaeological site on the island and the latest assemblage of *Phanourios minutus* remains (Reese 1996; Simmons 1996, 1999, 2014; Strasser 1996). The site is located on the southern tip of the island on the Akrotiri Peninsula atop a steep cliff and, at present, sits approximately 40m above the Mediterranean Sea. It is a

collapsed rockshelter, and portions of the front have eroded into the sea (Simmons 1999; Figure 3.1). *Aetokremnos* was first excavated between 1987 and 1990 by Alan Simmons (1999). Due to imminent erosion, a small team returned to excavate the last remaining square meter in June 2009. These investigations excavated the entire remaining portion of the site, covering some 50 sq. m.



**Figure 3.1 Image showing location of rock shelter Akrotiri *Aetokremnos* in relation to current sea level (Simmons 1999)**

*Akrotiri Aetokremnos* is a small collapsed rockshelter with well-preserved stratigraphy. The deposits consist of four distinct strata, two of which are seen as major occupation layers (Strata 2 and 4) and have thus been the focus of analysis. Stratum 1 consists of crushed/burnt shell and a small portion of bone. Stratum 2 contains 61.5% of the total chipped stone at the site, eight of the eleven identified archaeological features, and only 12% of the pygmy hippopotamus assemblage (Simmons 1999, 2014). Stratum 3 is an intermittent sterile layer that separates Stratum 2 from ‘bone midden’ that makes up Stratum 4. In contrast to Stratum 2, Stratum 4

contains 88% of the pygmy hippopotamus remains and three archaeological features, all of which are concentrations of burnt hippopotamus bones.

The faunal assemblage at *Aetokremnos* consists of over 300,000 bones, approximately 98% belonging to the pygmy hippo (Simmons 1999, 2014). Reese and Roler (1999) provided a brief descriptive summary of the assemblage, and Olsen (1999) conducted a taphonomic analysis on a sample size of 15,000 specimens.

The mean radiocarbon dates for layers 2 and 4 are a few hundred years apart in proper chronological sequence, though they are statistically indistinguishable (Simmons 1999, 2014). Due to this short time lapse between layers 2 and 4, many have interpreted *Aetokremnos* as evidence of human procurement and processing of this species, and hypothesize that the extinction of the pygmy hippo was at least in part the result of human hunting (Simmons 1999, 2004). However, the imbalance of bone and artifacts between these layers has led to explanations arguing for an early natural accumulation of bone followed by a later human occupation (Ammerman & Noller 2005; Ammerman 2007; Binford 2000; Bunimowitz & Barkai 1996).

It remains unclear why stratigraphic integrity has been continually debated, when work done by Mandel (1999) shows multiple lines of evidence to support Stratum 2 and Stratum 4 as intact separate layers. Regardless, this point has been continually rehashed by critics of Stratum 4 representing a cultural layer. Binford (2000) notes that “three other depositional zones occur on top of [Stratum] 4, yet no documented features originate within the bone bed.” This comment is somewhat misleading, however, as three of the eleven identified ‘features’ occur in Stratum 4.

Furthermore, the analyses of Stratum 3, the intermittent sterile layer, support the conclusion that strata are intact at the site. This unit is 15-30 cm thick across most of the site, but much thinner and absent in some areas, particularly near front and back of shelter (Mandel and

Simmons 1997). The stratum is separated in two sub-layers on the basis of texture- 3A and 3B. Geoarchaeological analyses suggest the majority of Stratum 3A is from windblown sediments with contribution by attritional sediments and rock fall. Stratum 3B directly underlies Stratum 3A or Stratum 2 where 3A is not present. All analyses conducted regarding the geoarchaeology of the site indicate that this sterile layer is unmixed, attritional sediment, and serves as a cap to the portions of Stratum 4 that it overlies (Mandel and Simmons 1997; Mandel 1999).

Perhaps the most compelling critique of the stratigraphic interpretation was from Grayson (2000) who noted there is no reported evidence of chipped stone or other artifacts in Stratum 4 where the sterile Stratum 3 directly overlies them. This would suggest that areas where artifacts were present in Stratum 4 could still have been the result of cultural material moving down. Analysis by Durand (1999) evaluated the distribution of chipped stone artifacts in relation to faunal remains for both Stratum 2 and 4. Noting that the distribution of chipped stone corresponds well with the distribution of faunal remains for each individual strata—and have no obvious correlation between strata, he concludes that the distribution of both faunal material and chipped stone at *Aetokremnos* demonstrates a “consistent pattern for two distinct behavioral strata” (Durand 1999). He further notes that these distributions support the conclusions of Simmons and Mandel (1999) that no mixing between Stratum 2 and 4 has occurred at the site, with the exception of the obvious but limited sections labeled as Stratum 2/4. In other words, as Mandel has argued (1999) the stratigraphy is clear and intact.

To further address this question, I conducted a brief review of the original excavation notes, published stratigraphic profiles and discussions on the distribution of artifacts (Held 1992; Durand 1999; Mandel and Simmons 1999; Simmons 1999) and compared the presence of cultural material in Stratum 4 with the distribution of Stratum 3 and or substantial rock fall from

roof collapse. This comparison shows that there are locations where cultural material within Stratum 4 does directly underlie the sterile Stratum 3. At minimum, it appears cultural material is present in excavation units 97N 88E, 98N 88E, 97N 89E (chipped stone associated with Feature 3) and in 96N 88E (chipped stone and one retouched stone tool) that directly underlay Stratum 3 (Durand 1999; Simmons 1999).

Based on the compilation of previous geoarchaeological analyses and the distribution of chipped stone related to the distribution of faunal material, it is apparent that the stratigraphy at *Aetokremnos* has not undergone significant mixing between Stratum 2 and Stratum 4. As a result, in this study each stratum is evaluated as separate occupational layers, and the relative impacts of humans on the faunal material in each layer is analyzed with consideration for all material present in each strata.

### **Assemblage and Analytical Units:**

To further explore the anthropogenic nature of Stratum 4, we must identify the nature of the taphonomic processes and skeletal representation throughout the site. Doing so requires attention to sampling and definition of relevant analytical units that will facilitate the evaluations of anthropogenic hypotheses within the site and between different strata or occupation events. To do this, I conducted a detailed taphonomic study of the pygmy hippo remains at the site, and evaluated the most appropriate units for analysis based on statistically significant similarities of skeletal representation.

Due to the size of the assemblage, in this analysis I followed the methodology presented by Faith and Gordon (2007) and looked only at the high survival elements that incorporate both high and low utility parts at *Aetokremnos*. High survival skeletal elements (cranium, mandible,

femur, tibia, metatarsal, humerus, radius and metacarpal) have been shown to be representative of the entire faunal assemblage for purposes of determining relative skeletal abundance and accurately assessing the evenness of assemblages (Faith & Gordon 2007). Sampling the assemblage by selecting these high survival elements made it possible to address the large amount of faunal material throughout the site.

All specimens were identified to element, region and side when possible. Larger fragments and fragments with diagnostic landmarks were drawn on pre-made element diagrams to ensure no overlapping of specimens while calculating the minimum number of elements (MNE) and minimum number of individuals (MNI) from each field unit. MNE represents the minimum number of a given element that can account for all identifiable fragments. The MNI then represents the minimum number of individuals that could account for all elements at the site, taking into account element side, and age. Field units are typically one by one meter excavation units, with the exception of small features that were assigned their own field unit numbers.

To calculate the MNE, all identifiable fragments were drawn for each excavated field unit to ensure no overlap of fragments. The MNE for these individual field units were then combined for strata and/or features for analysis and overall calculation of the total MNE and MNI calculations at *Aetokremnos*. Other values used in this analysis are the number of identified specimens (NISP), which accounts for all identifiable fragments at the site; the number of specimens (NSP), which accounts for all fragments even if unidentifiable; and the minimum animal units (MAU), which converts the MNE to being representative of the frequency in which those elements appear. For example, while a single individual may have an MNE of 4 left metatarsals and an MNE of 1 left femur, this represents only one limb—and an MAU of 1. All

direct observation of the faunal material was completed at the Episkopi museum in Episkopi, Cyprus.

A total number of specimens (NSP) of 92,420 were analyzed for evidence of direct human modification and evidence of natural taphonomic factors. Of the total number of specimens analyzed, 22,197 were identifiable to element (Table 3.1). As shown in Table 3.1, the majority of the analyzed elements were at least partially burnt. Burning was classified by visual evidence of heat exposure, and did not differentiate between intensive burning and minor heat alterations—although clear variation in burning intensity is present at the site. Any fragments or complete bones that showed evidence of burning even on a small portion was identified as being burnt. For this reason, percentage of burnt specimens reported here is significantly larger than that previously reported by Reese (1999) who distinguished between intensity of burning.

**Table 3.1 Number of Identified Specimens (NISP) and % burnt by element in each analytical unit. Burning was classified by visual evidence of heat exposure, and did not differentiate between intensive burning and minor heat alterations. Any fragments or complete bones that showed evidence of burning even on a small portion was noted as being burnt.**

Element	Number of Identified Specimens (NISP)					
	Stratum 2		Stratum 4		Feature 3	
		<i>% Burnt</i>		<i>% Burnt</i>		<i>% Burnt</i>
Cranium	158	<i>91.14</i>	5928	<i>58.10</i>	2834	<i>71.88</i>
Mandible	115	<i>84.35</i>	1890	<i>72.22</i>	270	<i>68.52</i>
Humerus	31	<i>93.55</i>	937	<i>74.28</i>	378	<i>89.95</i>
Radius/Ulna	45	<i>84.44</i>	1350	<i>69.85</i>	676	<i>83.28</i>
Femur	81	<i>98.77</i>	2046	<i>73.70</i>	669	<i>55.61</i>
Tibia	22	<i>95.45</i>	733	<i>74.76</i>	321	<i>77.26</i>
Metacarpal	15	<i>20.00</i>	226	<i>66.81</i>	60	<i>76.67</i>
Metatarsal	13	<i>69.23</i>	188	<i>62.77</i>	121	<i>88.43</i>
Long Bone Frags	16	<i>100</i>	227	<i>32.60</i>	-	-

Data were collected for nine features (labeled 1-9) and seven “sub-strata” (identified as 1/2, 2, 2/4, 4, 4a, 4b and 4c). These sub-strata were categorized based on sediment composition (color, texture and grain size). Before running analyses on the assemblage at *Aetokremnos*, a  $\chi^2$  test was done comparing the MNE values between Features and their associated Stratum (Table 3.2). By comparing the MNE values in the features and strata, I can identify if the samples from each feature and between strata are significantly different in composition, and therefore if they should be treated as their own analytical units. Statistically similar composition between features and their surrounding strata, or between strata, would suggest these units reflect similar taphonomic history (butchering, transport, and preservation), and will be aggregated with their surrounding strata.

While there were nine features recorded across the site, only Features 2, 3, 5, and 9 were evaluated. Features 1, 4, 6, 7 and 8 contained a minimum number of individuals (MNI) of 2 or less, and therefore were not included in this comparison and are combined with their associated Stratum 2 for analyses.

**Table 3.2 Comparison of element abundance (MNE) between Features and their associated stratum and between strata. All calculations based on MNE values. Features 1, 4, 6, 7 and 8 were not included as they all contained an MNI of 2 or less. All tests run with degrees of freedom equal to 7 and alpha= .05; critical value= 14.07**

Stratigraphic Unit	Comparative Unit	X <sup>2</sup>	P value	Result
Stratum 2	Feature 5	1.52	0.98	Combine with Stratum 2
	Stratum 1/2	7.41	0.39	Combine with Stratum 2
Stratum 4	Feature 2	9.01	0.25	Combine with Stratum 4
	Feature 3	40.77	0.0001	<b>Treat as own analytic unit</b>
	Feature 9	7.41	0.39	Combine with Stratum 4
Stratum 4b	Stratum 4a	1.91	0.96	Combine with Stratum 4b
	Stratum 4c	11.09	0.13	Combine with Stratum 4b
Stratum 2	Stratum 4 (no Ftr 3)	28.77	0.0002	<b>Treat as own analytic unit</b>
(combined)	Stratum 4 (w/Ftr 3)	30.87	0.0001	<b>Treat as own analytic unit</b>

Based on the  $\chi^2$  test, I identified three analytical units that will be used throughout the study: Stratum 2, Stratum 4 and Feature 3. All other features showed no statistically difference in composition from their surrounding stratum, and all sub-strata showed no statistical difference from their associated stratum.

Feature 3 was shown to have a significantly different element composition from its' surrounding Stratum 4. Feature 3 is a concentration of intensively burnt bone located in Strata 4a and 4b that covers a minimum of 6 square meters. This Feature is directly below Feature 1, but is clearly separated by the sterile Stratum 3 and a large piece of roof fall. Portions of the feature are capped by burned stones, which appear on top of stratum 4B. Stratum 3 shows no evidence of heat alteration, suggesting the burning in Stratum 2 could not have accounted for the coloring/burning in Stratum 4 noted as a possibility by Olsen (1999). Bones in Feature 3 are intensively burned, and have assumed a very friable state. Hippo remains in this feature account for 28.6% of all remains recovered from the site. Feature 3 has 22 chipped stone artifacts associated with it, although all are on the periphery, and none are formal tools.

Furthermore, Stratum 2 and Stratum 4 were shown to have significantly different element compositions (for runs with and without Feature 3 included in Stratum 4). Stratum 1/2 is noted as loose material originating from Stratum 2, and showed no significant difference from Stratum 2 faunal composition, and as a result is combined with Stratum 2 for analysis. When comparing Strata 4A, 4B and 4C, there is no significant difference between element distribution, and these substrata are also combined into a single analytical unit of Stratum 4.

As a result, the units used for analyses throughout this paper are Stratum 2, Stratum 4 and Feature 3. When appropriate, Stratum 2/4 is used as an analytical unit (e.g. density mediated attrition) however, it is not included in analysis regarding element frequencies and distribution,

nor in interpretations regarding potential behavior at the site due to its unknown association with either Stratum 2 or 4.

As noted above, the MNE and MNI were calculated for each individual excavation unit. These data were aggregated into three analytical units Stratum 2, Stratum 4 and Feature 3. MNI and MNE values for adults and juveniles are reported in Table 3.3. Based on this analysis, Stratum 4, which contains Feature 3, has an MNI of 235 adults and 78 juveniles. Stratum 2 contains a MNI of 21 adults and 7 juveniles. Combined, the site at Akrotiri *Aetokremnos* contains a MNI of 256 adults and 85 juveniles, for a total of 341 individuals. Age and size were taken into consideration when calculating these values.

It should be noted that this total MNI is significantly different from the previously reported MNI values by Reese (1999) who estimated a minimum of 505 individuals at the site. While limited data has been published to date noting the derivation of this MNI of 505, tables published by Reese (1999) showing MNI and MNE values by feature, stratum and element are in agreement with those values calculated in this study. However, Reese (1999) appears to have left all identified features as their own analytical units, and as a result calculates an MNI number for each feature. In this study, features that were not identified as statistically significant in element distribution from the surrounding matrix, faunal remains were treated as part of the stratum in which they were present, rather than a stand-alone feature and specimens. Treating each feature as a significant unit of analyses, and calculating the MNI for each of these features individually, would significantly inflate the overall MNI at the site.

**Table 3.3 MNE and MNI by element and per analytical unit. Reported MNE's are for adults and juveniles in italics. Units defined discussed below. Note the mandible MNE accounts for a right and left mandible, and therefore is divided by two to calculate the minimum number of individuals (MNI) in each unit. Feature 3 is within Stratum 4 but is reported separately (see text).**

Element	Minimum Number of Elements (MNE)					
	Stratum 2		Stratum 4(exc. Fea 3)		Feature 3	
	ADULT	<i>JUV</i>	ADULT	<i>JUV</i>	ADULT	<i>JUV</i>
Cranium	13	<i>7</i>	171	<i>55</i>	64	<i>6</i>
Mandible	41	<i>6</i>	169	<i>76</i>	38	<i>11</i>
Humerus	17	<i>7</i>	234	<i>68</i>	68	<i>23</i>
Radius/Ulna	17	<i>2</i>	304	<i>71</i>	103	<i>25</i>
Femur	17	<i>8</i>	236	<i>75</i>	77	<i>30</i>
Tibia	9	<i>3</i>	230	<i>85</i>	80	<i>23</i>
Metacarpal	11	<i>4</i>	172	<i>16</i>	24	<i>7</i>
Metatarsal	14	<i>1</i>	166	<i>6</i>	66	<i>15</i>
<b>Minimum Number of Individuals (MNI)</b>	21	<i>7</i>	171	<i>55</i>	64	<i>23</i>

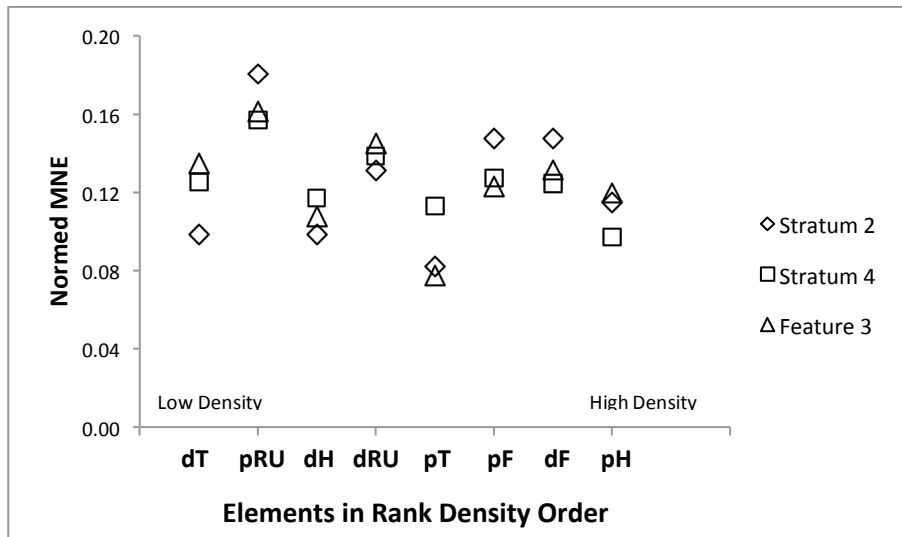
### Density Mediated Attrition

Evidence for density mediated attrition was calculated in several ways for *Aetokremnos*: through relative element densities, intra-element density, and frequencies of a single element (ulna). To evaluate the relative element density, within each analytical unit, the correlation between ranked density and abundance was tested using relative densities from Lyman (1994; Table 3.4, Figure 3.2). While relative densities for elements of *Phanourios minutus* are not available, Lyman (1994) finds that the relative densities of elements in artiodactyls is comparable between species. For this reason, the *Aetokremnos* assemblage was addressed using Lyman's ranked order. Abundance is reported in normed MNE—the MNE divided by the number of times that element appears in the complete skeleton. For each analytical unit there is no

significant relationship between relative density of elements and their frequencies. Correlation between relative density and element frequency is extremely low (Figure 3.2, Table 3.4). This would suggest density mediated attrition is not a factor at Akrotiri *Aetokremnos*.

**Table 3.4 Spearman’s rho and R<sup>2</sup> values for relative/rank densities compared to their MNE values; critical value for Spearman’s rho with N=8 is .738**

Analytical Unit	Spearman’s Rho	R <sup>2</sup>	P value
Stratum 2	0.133	0.002	0.754
Stratum 4	-0.524	0.336	0.183
Feature 3	-0.429	0.104	0.289



**Figure 3.2 Normed relative element abundance (measured by MNE) compared to relative density values, with dT:Distal Tibia, pRU: Proximal radius/ulna, dH:Distal Humerus, dRU: Distal radius/ulna, pT: Proximal tibia, pF: Proximal Femur, dF: Distal Femur and pH: Proximal humerus.**

While rank order inter-elemental data provides a big picture of the assemblage, it is important to note that the sampling strategy used on the assemblage was focused on selecting elements with high survivability, i.e. high density (Faith and Gordon 2007). Because of this, any evidence of density mediated attrition may be muted. By looking at variation in intra-element

density, however, we can provide more detailed insight to the dynamics of density mediated attrition at the site (Ioannidou 2003). As a second line of evidence to address density mediated attrition, intra-element density was correlated with diagnostic zone frequencies at Akrotiri *Aetokremnos* using the zoning system presented by Dobney & Reilly (1988) and extrapolated by Ioannidou (2003). Intra-element density calculations were done for different zones throughout each element for the mandible, humerus, radius/ulna, metacarpal, femur, tibia and metatarsal recognizing that in any given element different structural densities occur (Ioannidou 2003; Lyman 1994; Orton 2008; Lam and Pearson 2005). No bone density information is available for *Phanourios minutus*, nor any other pygmy/dwarfed hippopotamus or the modern hippopotamus, *Hippopotamus amphibius*. As a result, the density values used are derived from the species *Sus scrofa* based on its comparable size and bone structure (Ioannidou 2003; see also Lyman 1994; Orton 2008; Lam and Pearson 2005; Figures 3.3-5, Table 3.5). All values used are documented in minimum number of elements (MNE), calculated for each analytical unit and recalculated for each density zone discussed (Table 3.6).

**Table 3.5 Scan sites, densities and standard deviations (when available) of *Sus scrofa* as published in Ioannidou (2003); DN: Mandible, HU: Humerus, UL: Ulna, RA: Radius, MC: Metacarpal, FE: Femur, TI: Tibia and MR: Metatarsal**

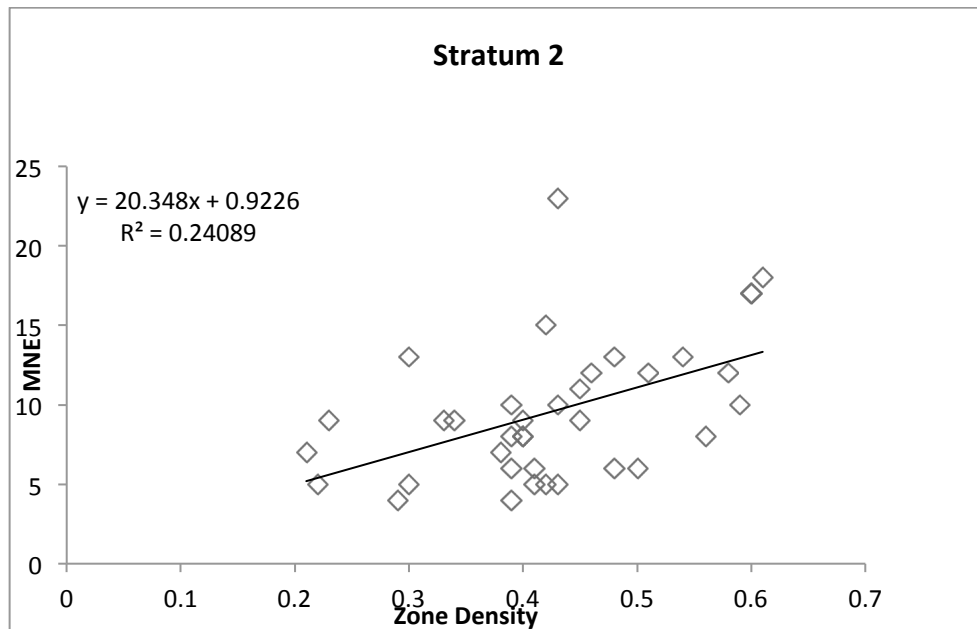
Scan Site	Density	SD	Scan Site	Density	SD
DN1	0.38		MC1	0.4	
DN2	0.58		MC2	0.45	
DN3	0.42		MC3	0.39	
DN4	0.43		FE1	0.34	0.08
DN5	0.6		FE2	0.4	0.02
DN6	0.61		FE3	0.39	0.02
DN7	0.59		FE4	0.51	0.01
DN8	0.6		FE5	0.41	0.02
HU1	0.21	0.04	FE6	0.23	0.1
HU2	0.22	0.11	TI1	0.3	0.01
HU3	0.43	0.3	TI2	0.29	0.02
HU4	0.41	0.16	TI3	0.5	0.09
HU5	0.39	0.01	TI4	0.39	0.05
UL1	0.33	0.1	TI5	0.48	0.02
UL2	0.43	0.1	MR1	0.3	0.03
RA1	0.45	0.05	MR2	0.48	0.16
RA2	0.54	0.02	MR3	0.46	-
RA3	0.56	0.04			
RA4	0.42	0.08			
RA5	0.4	0.07			

**Table 3.6 MNE values for each density zone/scan site at Akrotiri Aetokremnos; DN: Mandible, HU: Humerus, UL: Ulna, RA: Radius, MC: Metacarpal, FE: Femur, TI: Tibia and MR: Metatarsal**

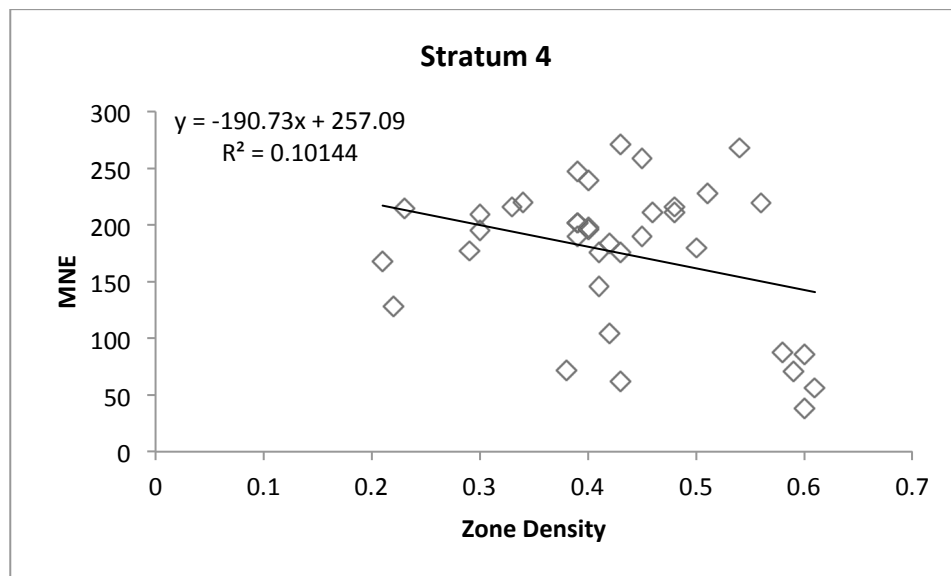
**Minimum Number of Elements (MNE) per Scan Site**

<b>Scan Site</b>	<b>Stratum 2</b>	<b>Stratum 4</b>	<b>Feature 3</b>
DN1	7	72	13
DN2	12	88	12
DN3	15	104	14
DN4	23	62	27
DN5	17	86	27
DN6	18	56	23
DN7	10	71	62
DN8	17	38	18
FE1	9	220	73
FE2	8	198	48
FE3	8	247	62
FE4	12	228	89
FE5	6	146	44
FE6	9	215	78
HU1	7	168	71
HU2	5	128	32
HU3	5	176	47
HU4	5	176	52
HU5	6	202	64
MC1	9	196	44
MC2	9	190	42
MC3	10	202	41
MR1	13	209	58
MR2	13	211	54
MR3	12	211	62
RA1	11	259	96
RA2	13	268	91
RA3	8	219	76
RA4	5	184	54
RA5	8	239	86
TI1	5	195	46
TI2	4	177	54
TI3	6	180	47
TI4	4	190	69
TI5	6	216	80
UL1	9	216	78
UL2	10	271	100

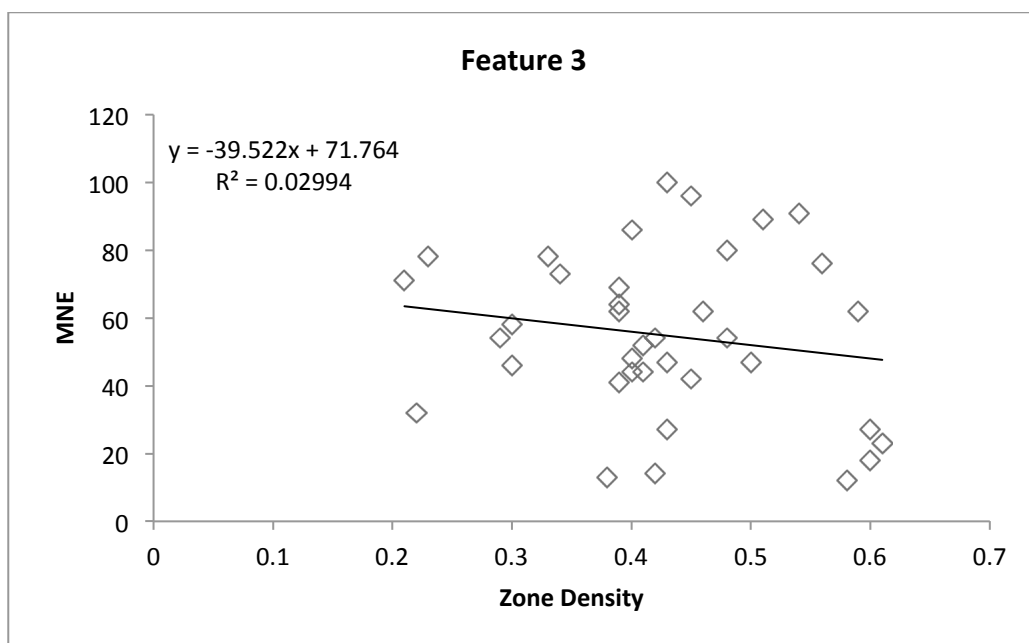
Stratum 4 and Feature 3 (Figures 3.4-5) show a weak and negative correlation between zone density and frequency, again suggesting that in these units density mediated attrition is not a factor in creating the elemental distribution seen at the site. Stratum 2 shows a non-significant, weak and positive correlation between zone density and frequency of elements (Figure 3.3).



**Figure 3.3** Comparing the MNE from Stratum 2 per zone identified in Table 3, using *Sus scrofa* bone densities;  $p = 0.002$



**Figure 3.4** Comparing the MNE from Stratum 4 per zone identified in Table 3, using *Sus scrofa* bone densities;  $p = 0.038$



**Figure 3.5 Comparing the MNE from Feature 3 per zone identified in Table 3, using *Sus scrofa* bone densities;  $p=0.402$**

To test whether the positive correlation between zone density and frequency seen in Stratum 2 is a function of natural processes, or an artifact of cultural processes such as butchery (where some portions of elements may be over/underrepresented due to human behavior), the frequencies of the olecranon process and the articular surface of the ulna were compared (Outram et al. 2005). These two portions of the ulna have appreciably different densities, but are unlikely to be separated by butchery due to their close proximity and associated utilities (Outram et al. 2005). A significant difference in frequencies between these two features would suggest the pattern seen in Stratum 2 (Figure 3.3) is due to density mediated attrition. The relative frequencies of the ulnar articular surface and the olecranon process were compared for each analytical unit at *Aetokremnos* (Table 3.7). The density of the olecranon process of *Sus scrofa* is 0.75 of the density of the articular surface (0.33 versus 0.43). Comparison of these two landmarks in the *Aetokremnos* assemblage shows a greater survivability of the olecranon process

than one would expect if density mediated attrition was a key factor in element representation. Overall, these three analyses suggest that density mediated attrition does not account for the MNE or the frequency of different portions of elements represented at *Aetokremnos*.

**Table 3.7 Comparison between the frequencies of the olacrenon process and articular surface for ulna.**

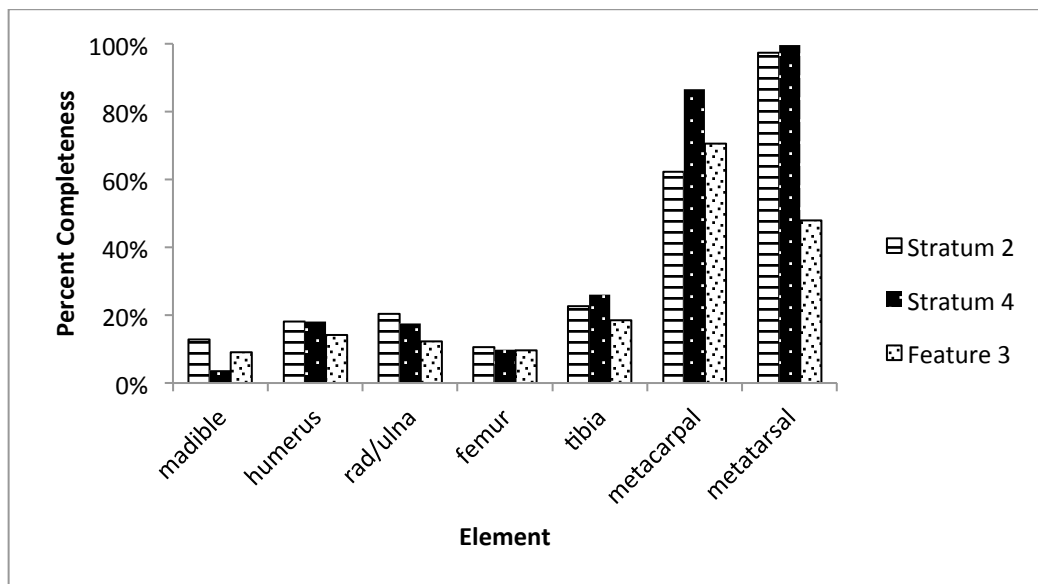
<b>Unit</b>	<b>Stratum 2</b>	<b>Stratum 4</b>	<b>Feature 3</b>
<b>Olacrenon Process</b>	9	216	78
<b>Articular Surface</b>	10	271	100
<b>Survivability of O. Process</b>	0.90	0.80	0.78

### **Breakage and Fragmentation**

The faunal assemblage at *Aetokremnos* is highly fragmented; however, the cause of this fragmentation is debatable. In a previous analysis, Olsen (1999) noted no evidence for fractures related to marrow extraction and argued the majority of fragmentation could be explained by a combination of trampling (by other hippos and elephants when accessing the cave) and exposure to heat from fires that overlie the faunal deposits (not in direct contact with). Other possible explanations for high fragmentation are processing, exposure to direct heat and/or the result of roof fall (Costamagno et al. 2002; Karr and Outram 2012a, 2012b; Lyman 1994; Outram et al. 2005; Olsen 1999). As noted above, carnivore damage is not a concern at this site due to the lack of predators or scavengers on the island of Cyprus at this time. In this section, I test the hypothesis that fragmentation patterning in the lower *Aetokremnos* deposits (Stratum 4 and Feature 3) is a result of non-anthropogenic roof fall and burning—both of which are widespread at the site and likely post-depositional taphonomic factors. However, potential selective fragmentation (presumably by humans) is evaluated quantitatively by calculating the percent completeness of different elements. To test the potential causes of fragmentation, I look at a

single element, the humerus, at Akrotiri *Aetokremnos* to experimental results from Costamagno et al. (2002) and Karr and Outram (2012b). Through this comparison I evaluate the likelihood of fragmentation being the result of intensive burning or roof fall.

Percent completeness is calculated using the formula described by Morlan (1994),  $(PP/NISP)/PD$  where PP represents “portions preserved” and PD is “portions defined” (Figure 3.6). The “portions” used are the same diagnostic zones defined by Ioannidou (2003) and used in the density mediated attrition analysis above. Using these diagnostic zones provides only an approximate percentage; however, the approach allows for rapid recording which proved necessary for an assemblage of this size (Outram et al. 2005).



**Figure 3.6 Percentage completeness by element and analytical unit.**

The most apparent trend when evaluating the percent completeness by stratum and element is the decrease in percent completeness of metatarsals in Feature 3 when compared to both Stratum 2 and 4. The percent completeness for all other elements remains fairly constant

across analytical units, and not surprisingly the metatarsals and metacarpals remain largely intact. However, the disparity between over 97% complete metatarsals in Strata 2 and over 99% complete metatarsals in Strata 4 down to fewer than 48% completeness in Feature 3 is a difference worth investigating. Furthermore, the data presented suggests that metatarsals in Feature 3 are not simply broken once, but fragmented more than once per element (e.g. 3+ pieces per MNE versus simply in half). The percent completeness analysis shows that all long bones are extensively fragmented in each analytical unit at the site.

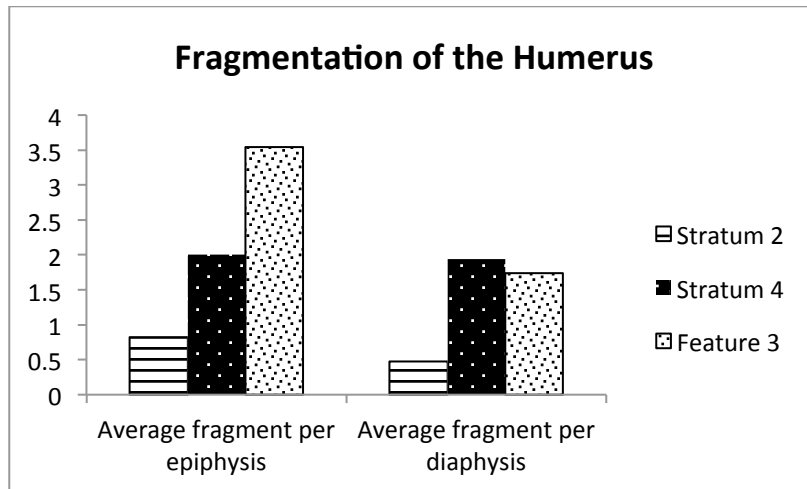
Of all fragments analyzed at *Aetokremnos*, over 68% are at least partially burned (Table 3.1), many intensively. In addition, there is evidence of significant rock fall throughout the site (Simmons 1999). Costamagno et al. (2002) show, through experimentation with the humerus, that there is a definable difference in fragmentation between diaphyses and epiphyses during burning. Variations of relative fragmentation were shown to be impacted by completeness of bone pre-burning and humidity of bone (old versus new). Diaphyses are subject to extreme fragmentation when burned intensely, while relatively the epiphyses' fragment considerably more than diaphyses when burned while attached and "fresh". Conversely, low fragmentation suggests burning when already detached from the shaft or 'old' bone that is lacking humidity. Additionally, Karr and Outram (2012b) explored the impacts of dynamic taphonomic processes such as rock fall. They found that when long bones were subject to dynamic impact, the diaphyses fragmented at a significantly greater rate than their epiphyseal ends. This pattern was observed regardless of conditions of the bone (eg. fresh, dried, frozen). In most cases the epiphyseal ends remained completely unbroken and in all cases none were analytically deleted (Karr and Outram 2012b).

Following these two studies: (1) high fragmentation of epiphyses and diaphysis should indicate either an intense burn of whole/attached bones or dynamic impact; (2) high fragmentation of epiphyses and low fragmentation of diaphysis suggest burning of whole or attached bones; and (3) low fragmentation of epiphyses and high fragmentation of diaphysis suggests either dynamic impact, or the burning of “old” or detached bone (Table 3.8).

**Table 3.8 Interpretations of causes for the relative degree of fragmentation of the epiphyses and diaphysis of the humerus.**

		Diaphysis Fragmentation	
		HIGH	LOW
Epiphysis Fragmentation	HIGH	Intense burning. Burning of whole/attached or humid/fresh bones.	Burning of whole/attached or humid/fresh bones.
	LOW	Burning of “old” or detached bones. Dynamic impact.	

To remain consistent with Costamagno et al.’s (2002) analysis, I evaluated all pygmy hippopotamus humeri fragments identified in the *Aetokremnos* assemblage- calculating the NISP for diaphyses and epiphyses. These NISP values were then compared to the MNE values and an average fragmentation per humerus was calculated. Comparing the average fragments per diaphyses and epiphyses in each analytical unit, we see that Stratum 2 has relatively low levels of fragmentation, suggesting that humeri are largely complete (Figure 3.7). Stratum 4 suggests relatively complete bones as well. Feature 3 shows a similar level of fragmentation in the diaphyses and an elevated level of fragmentation in the epiphyses.



**Figure 3.7 Comparison of average fragments per humerus; Calculated by dividing the NISP of each humeri portion by analytical unit MNE**

This analysis does vary from Costamagno et al.'s (2002) experimental study, however, in that Costamagno et al. were able to count fragments that effectively became unidentifiable. They started their study with only humeri, and therefore knew all fragments created were resulting from this element. In the archaeological record, the fragments that are too small for identification are not included, as they could result from a wide variety of elements. Despite this discrepancy, we still see a clear pattern at Akrotiri Aetokremnos when comparing diaphysis and epiphyseal fragmentation. This comparison suggests that intensive burning may have influenced the fragmentation pattern seen at Feature 3, where the burning of originally whole/attached or humid/fresh bones would account for the noted increase in epiphyseal fragmentation.

Rock fall appears to have little influence on fragmentation when humeri fragments are compared to the experimental procedures of Karr and Outram (2012b). Karr and Outram (2012b) found that when humeri are dynamically impacted— similar to what would happen under rock fall conditions— 100% of proximal humeri and 94% of distal humeri remained completely intact and retained 100% analytical survivorship when compared to the highly fractured humeri shaft

only retaining 81% analytical survivorship. This would show the reverse pattern for fragmentation seen in Figure 3.7—as we would expect to see elevated fragment counts for shafts and lower fragmentation of epiphyses.

From these two analyses, it appears that rock fall has little impact on fragmentation when looking fragmentation patterns at the entire site, as we don't see the high numbers of diaphysis fragments even with shaft fragments included. It also appears that one possible explanation for the fragmentation pattern seen in Feature 3 could be the result of intensive burning of whole/attached or fresh/humid bones. Fragmentation from burning was evaluated above as a potentially natural taphonomic process, however burning at the site, and particularly in Feature 3, is most likely attributed to humans. With intact stratigraphy in Feature 3, the lack of heat modification in its overlying layer, the presence of chipped stone in this feature's intact strata, and the indication that if burning impacted fragmentation the bones burned were likely fresh or whole/attached, all suggest that this Feature is anthropogenic in nature.

## **Discussion and Conclusion**

Review of the geoarchaeology and the original field notes for *Aetokremnos* shows that the cultural material in Stratum 4 is in situ and chipped stone directly underlies the sterile Stratum 3. These findings resolve concerns about mixing from Stratum 2. After compiling these data it seems clear that Stratum 4 and Stratum 2 at *Aetokremnos* both were formed, at least partly, by human agency. In addition, there is no evidence for density mediated attrition and patterns in element representation are not a function of differential preservation. Through three different analyses, taking into account relative element densities and intra elemental densities, the preservation at Akrotiri *Aetokremnos* appears to have no significant impact related to density.

Fragmentation at the site is widespread and appears to be a function of intense burning and not density related or the result of rock fall. Fragmentation is also more significant in the lower Stratum 4; however, this was measured using only the humeri which has a very low NISP value for the upper Stratum 2 when compared to Stratum 4 (17 specimens versus 274 respectively). Furthermore, the extensive burning in Feature 3 of whole/attached bones likely accounts for increased fragmentation in this feature, and may hint at human utilization of the species. In addition, fragmentation in Stratum 2 and Stratum 4, while not clearly attributed to burning or rock fall, could also hint at human modification. The significant fracturing of long bones compared to metapodials seen in Stratum 2 and Stratum 4 may suggest differential marrow extraction by humans.

Overall, these analyses show multiple lines of evidence that suggest post-depositional factors do not significantly alter the composition of pygmy hippopotamus remains at Akrotiri *Aetokremnos*. Therefore, the skeletal elements appear to accurately represent the faunal material at time of deposition. Having ruled out post-depositional taphonomic factors, we can begin to address the assemblage at Akrotiri *Aetokremnos* as an accurate representation of the faunal material that was deposited. As such, we can begin to answer questions related to the nature of accumulation (cultural versus natural) and if anthropogenic, how humans used these animals. As always, the relative impact of humans on this species' extinction event should be addressed within the larger context of the climate, species history on the island and early Mediterranean seafaring. Studies regarding the demographic profiles at the site, the relative skeletal abundance, and the population dynamics of this species leading up to the occupation of *Aetokremnos* could provide significant insight into possible anthropogenic impacts. Such studies would help to

explore the dynamics of human and hippopotamus interactions on Cyprus in the Late Pleistocene and add to the larger conversation regarding Late Pleistocene extinction events.

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## Chapter 4: Demographic evidence of human hunting and procurement of the extinct Cypriot Pygmy Hippopotamus

**Abstract:** Mortality profiles are useful tools for studying the nature of faunal assemblages in archaeological sites. Age distribution can provide valuable insight to the procurement of species, site formation and taphonomic processes. Here, I evaluate the assemblage of pygmy hippopotami, *Phanourios minutus*, at the archaeological site Akrotiri *Aetokremnos*. As one of the oldest archaeological sites on the Mediterranean island of Cyprus, and the only well-documented overlap between humans and this species, this accumulation at *Aetokremnos* has been hotly debated. To determine the depositional nature of the assemblage, I evaluate the age profile of the pygmy hippopotamus at this site and compare it to four ecological studies of the modern hippopotamus, *Hippopotamus amphibius*. This analysis suggests the assemblage at *Aetokremnos* is statistically different from an attritional or natural assemblage, and is statistically similar to age profiles created from culling events in the 1970s-1990s. These culling profiles and the profile represented at *Aetokremnos* appear to be prime-dominated. In the absence of direct evidence for humans procuring *Phanourios minutus*, this indirect measure suggests that humans may have hunted this species.

Use of demographics and mortality profiles of faunal components in archaeological sites traditional in the interpretation of archaeological site formation (Adler et al., 2006, Bunn & Pickering, 2010, Klein, 1982, Steele, 2005). Mortality profiles provide valuable information about the procurement of fauna by humans and clarify relevant taphonomic processes. Here I evaluate the demographics of the faunal assemblage from Akrotiri *Aetokremnos*, one of the earliest archaeological sites in Cyprus as well as one of the largest deposits of the pygmy hippopotamus *Phanourios minutus* (Simmons, 1999). Initial publications reporting on the 1980s excavations at the site led to its interpretation as an example of direct association between humans and pygmy hippos. However, discussion over this large faunal assemblage has sustained the debate over both the nature of this accumulation as natural or anthropogenic as well as the

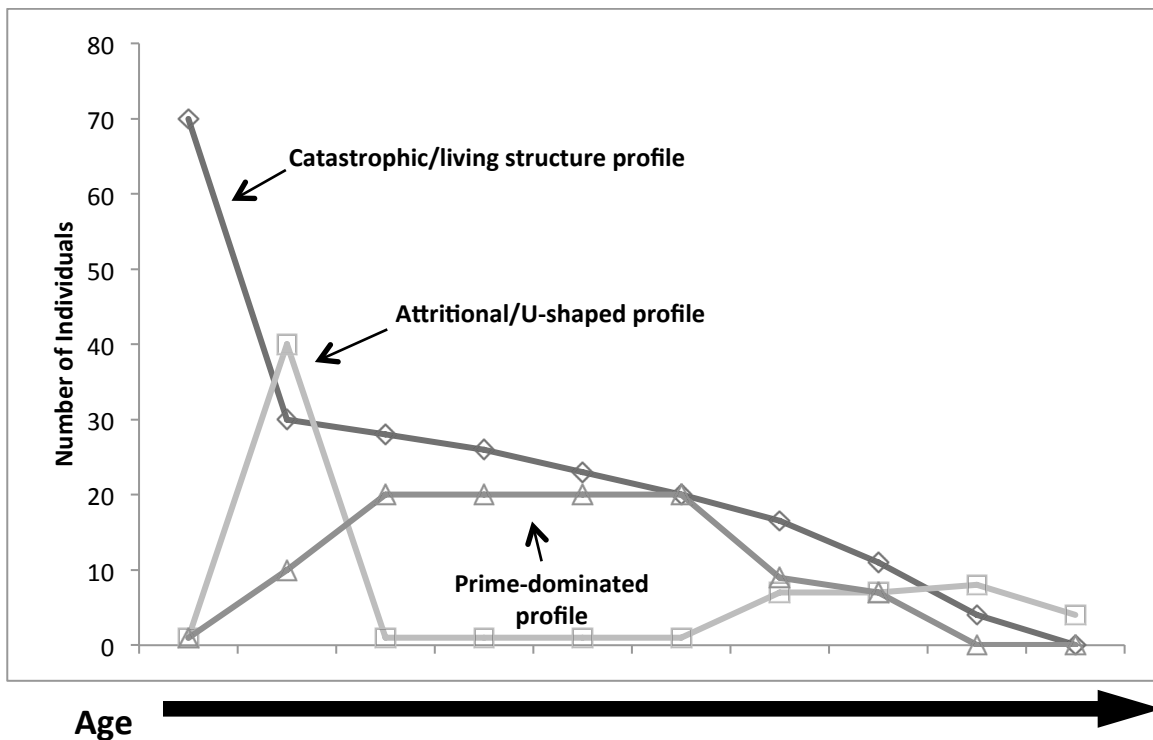
relative anthropogenic impact in the extinction of this species (Ammerman & Noller, 2005, Ammerman et al., 2007, Binford, 2000, Grayson, 2000, Reese, 1996, Simmons, 1996, Simmons, 1999, Simmons, 2004, Simmons & Mandel, 2007). While previous studies have shown the site to contain stratigraphic integrity, and no obvious biases from post-depositional taphonomic factors (Chapter 3), there remains no direct evidence of human hunting and/or processing of these animals (Held, 1992, Durand, 1999, Mandel, 1997, Olsen, 1999, Simmons, 1999). Comparing the mortality profile at Akrotiri *Aetokremnos* to theoretical profiles utilized by zooarchaeologists and actual profiles from ecological studies on modern hippos, *Hippopotamus amphibius*, we can identify an indirect measure of the likelihood of human procurement for this species.

### **Demography and Age Profiles**

Archaeologists routinely define three kinds of demographic profiles: catastrophic, prime dominated and attritional (Figure 4.1) (Bunn & Pickering, 2010, Klein, 1982). A catastrophic profile has a strong resemblance to a living population and suggests that the death was not selective in terms of age or physical condition, i.e. a mass death (Bunn & Pickering, 2010). A prime-dominated profile is one that has an abnormally high number of middle-aged 'prime' individuals, who would have been the most healthy and resilient individuals in a population (Bunn & Pickering, 2010, Stiner, 1990). An attritional profile has an overabundance of very young and very old individuals who are inherently weaker than prime-aged individuals (Bunn & Pickering, 2010).

Catastrophic profiles are expected in the event of a mass death. These profiles can be the result of natural and anthropogenic causes. Natural events such as landslides, floods and disease

can cause an assemblage to represent an expected living population. Alternatively, catastrophic events could indicate a mass kill site or hunting using ambush tactics (Bunn & Gurtov, 2014, Eltringham, 1999, Lyman, 1994). Typically, the combination of this type of profile with other lines of evidence (presence of cutmarks, surrounding sediments, etc.) can determine the anthropogenic from natural circumstances of death. A prime—dominated profile is often characteristic of human hunting (Stiner, 1990) as it maximizes the caloric return from the prey and is significantly different from a natural death profile. A prime—dominated profile at *Aetokremnos* could implicate humans as procurers of the pygmy hippo even in the absence of direct evidence such as cutmarks. Finally, an attritional profile is most commonly associated with a natural accumulation (Steele & Weaver, 2002, Steele, 2005), but could also be the result of a scavenging strategy by humans (Bunn & Pickering, 2010).



**Figure 4.1 Idealized catastrophic, attritional, and prime-dominated age/mortality profiles. Adapted from Bunn and Pickering 2010.**

## Materials and Methods

All mandible first and second molars (M1 and M2) at Akrotiri *Aetokremnos* were evaluated for wear and age—providing a minimum number of elements (MNE) of 322. Each specimen was qualitatively assigned to one of three age groups (juvenile, prime, old), and placed within one of 20 age groups defined by Laws (1968; Table 4.1). When *in situ*, the mandible was separately evaluated for the three general groups of juvenile, prime and old to ensure agreement between tooth wear and bone growth. Laws' (1968) classification is based on examination of tooth wear in the mandible of over 3,000 individual *Hippopotamus amphibius*. Each of the 20 categories ties relative tooth wear to specific age groups spanning from as little as 6 months to three years. While *Phanourios minutus* likely had drastically different ages to maturity and lifespan from the much larger modern hippopotamus, the comparison of relative wear should adequately express the demographics for both species. Furthermore, the rate of tooth wear among all ungulates has been shown to be relatively consistent when compared to tooth size despite geographic and dietary variations (Steele & Weaver, 2002).

**Table 4.1 Relative age groups as defined by tooth wear of *Hippopotamus amphibius* (Laws 1968) and their associated ages for this species.**

<b>Group</b>	<b>Age (years)</b>	<b>Group</b>	<b>Age (years)</b>
<b>I</b>	0	<b>XI</b>	20
<b>II</b>	.5	<b>XII</b>	22
<b>III</b>	1	<b>XIII</b>	24
<b>IV</b>	3	<b>XIV</b>	27
<b>V</b>	4	<b>XV</b>	30
<b>VI</b>	7	<b>XVI</b>	33
<b>VII</b>	8	<b>XVII</b>	35
<b>VIII</b>	11	<b>XVIII</b>	38
<b>IX</b>	15	<b>XIX</b>	40
<b>X</b>	17	<b>XX</b>	43

The comparison of the age structures between strata and features at *Aetokremnos* using the  $\chi^2$  test at  $\alpha=.05$  shows no statistical difference in age distribution of *Phanourios minutus*. This result justifies treating all strata and features as one unit for the purposes of demographic analyses. Once constructed, the age profile from *Aetokremnos* was compared to four demographic studies conducted on *Hippopotamus amphibius* between the 1960s and 1990s as part of observation of attritional death and several culling operations (Laws, 1968, Marshall & Sayer, 1976, Suzuki & Imae, 1996). Laws (1968) presents data from 207 mandibles collected within the Queen Elizabeth Park (Uganda) from animals that were found dead (thus, collection often occurred “some time” after death). Cause of death for these animals is unknown but not attributed to hunting or predation, leading Laws to classify this as a natural death assemblage (1968). Results from two separate cropping (or culling) events in Eastern Zambia during 1970 and 1971 are used as comparative samples (Marshall and Sayer, 1976). In 1970, 374 hippos were

killed and analyzed, and in 1971, a total of 215 individuals were analyzed. The final group for comparison consists of 457 individuals culled during the “Hippo Project 1995” along the Luangwa River, Zambia (Suzuki & Imae, 1996). All five assemblages are presented in Table 4.2.

**Table 4.2 Assemblages used in comparisons; *Aetokremnos* represented as MNE, all other assemblages and number of individuals. *Aetokremnos* is abbreviated as “AK”; Laws (1986) assemblage represents a ‘natural’ accumulation from found carcasses; Marshall and Sayer (1976) assemblages (noted as M&S 1970 and M&S 1971) as well as Suzuki and Imae’s assemblage (noted as I&S 1995) all resulted from culling events.**

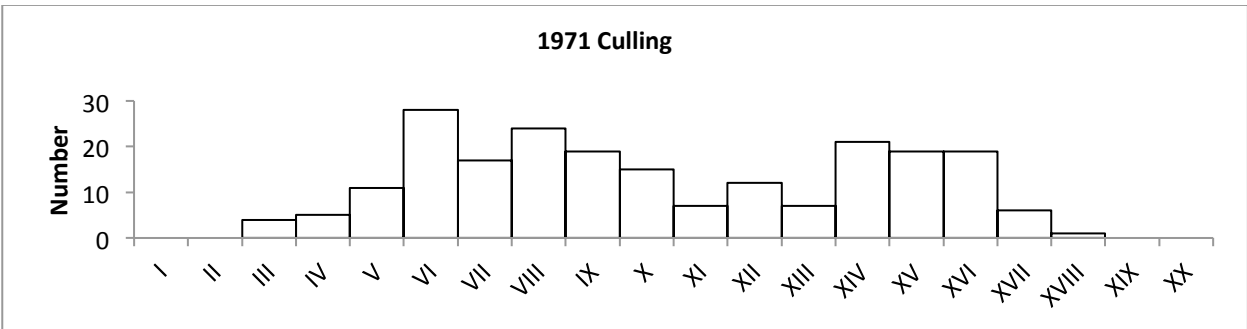
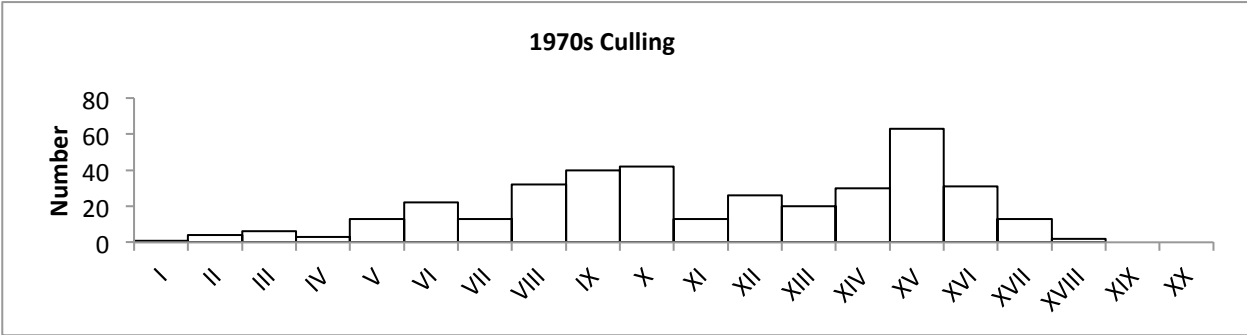
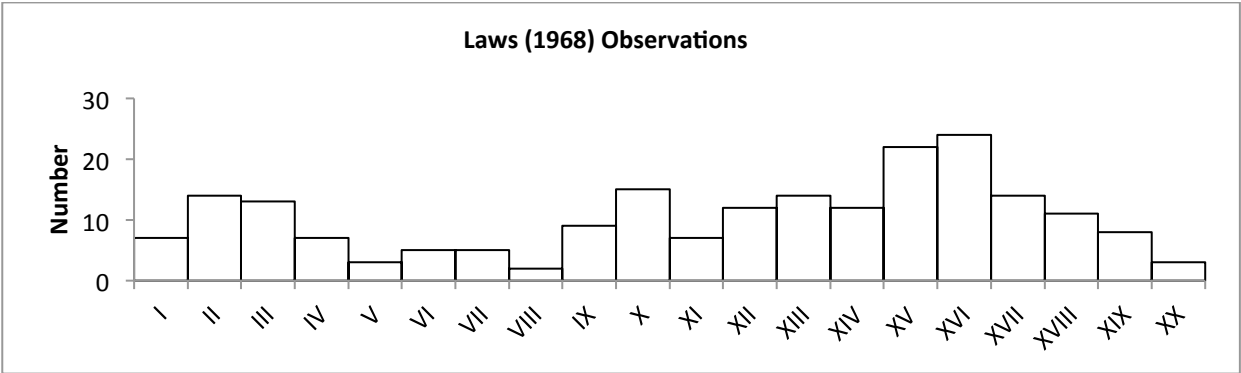
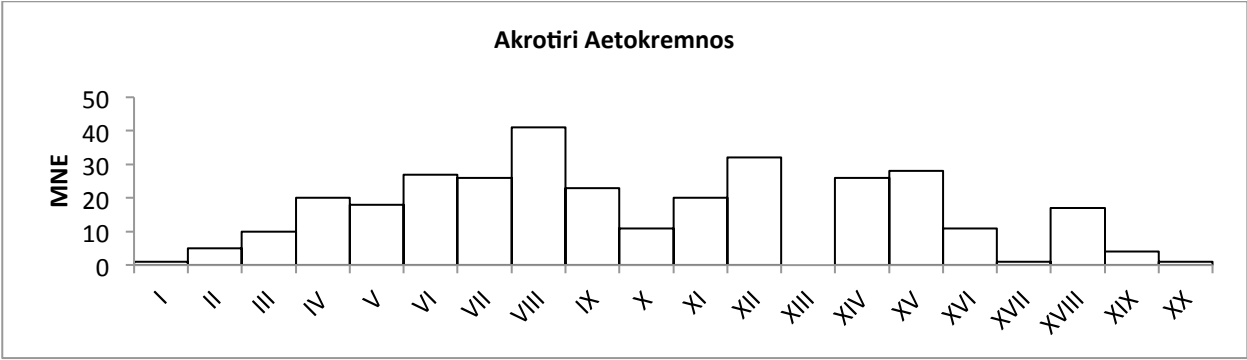
Group	AK	Laws (1986)	M&S 1970	M&S 1971	S&I 1995
I	1	7	1	0	1
II	5	14	4	0	1
III	10	13	6	4	13
IV	20	7	3	5	15
V	18	3	13	11	14
VI	27	5	22	28	15
VII	26	5	13	17	31
VIII	41	2	32	24	36
IX	23	9	40	19	39
X	11	15	42	15	52
XI	20	7	13	7	21
XII	32	12	26	12	28
XIII	0	14	20	7	22
XIV	26	12	30	21	47
XV	28	22	63	19	50
XVI	11	24	31	19	42
XVII	1	14	13	6	15
XVIII	17	11	2	1	10
XIX	4	8	0	0	4
XX	1	3	0	0	1

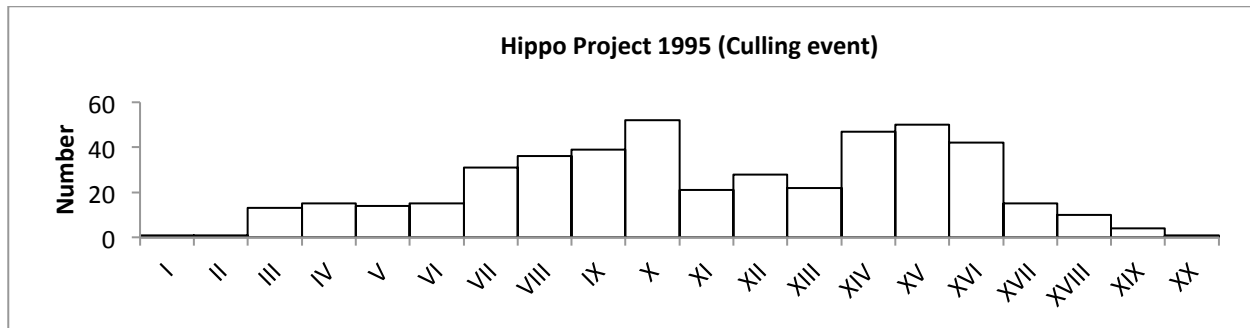
These five assemblages are visually compared using Laws’ (1968) age profiles and statistically compared by applying the modified triangular graph presented by Weaver et al. (2011). The cross-platform software for making statistical comparisons on a triangular graph, using the likelihood-based method, provided and described by Weaver et al. (2011) is used to evaluate the differences in these assemblages in terms of the three categories of juvenile, prime and old.

The classification of juvenile, prime and old can be somewhat arbitrary. For this study, the classification from juvenile to prime was set between the Laws' age groups V and VI. In *Hippopotamus amphibius* this transition correlates to the age of three years and is noted as the earliest this species reaches sexual maturity. Classifying the distinction between prime and old proves more difficult as tooth wear later in life can be drastically altered by diet composition and abrasive materials consumption. An initial transition from prime to old was chosen based on the observation of tooth wear and associated mandibles for *in situ* molars at *Aetokremnos*. This information suggests that the original transition occurred between age groups XV and XVI (which corresponds to the transition between 30 and 33 years in modern hippos). However, there is a marked decline in fecundity of modern hippos after 25 years of age (Sayer and Rakha, 1974, Wheaton et al., 2006). This age transition would correlate with the XIII to the XIV age groups. Two iterations of the triangular graph comparison were run using these two transitions as prime to old indicators—testing for any marked difference in results when this cut off is moved.

## **Results**

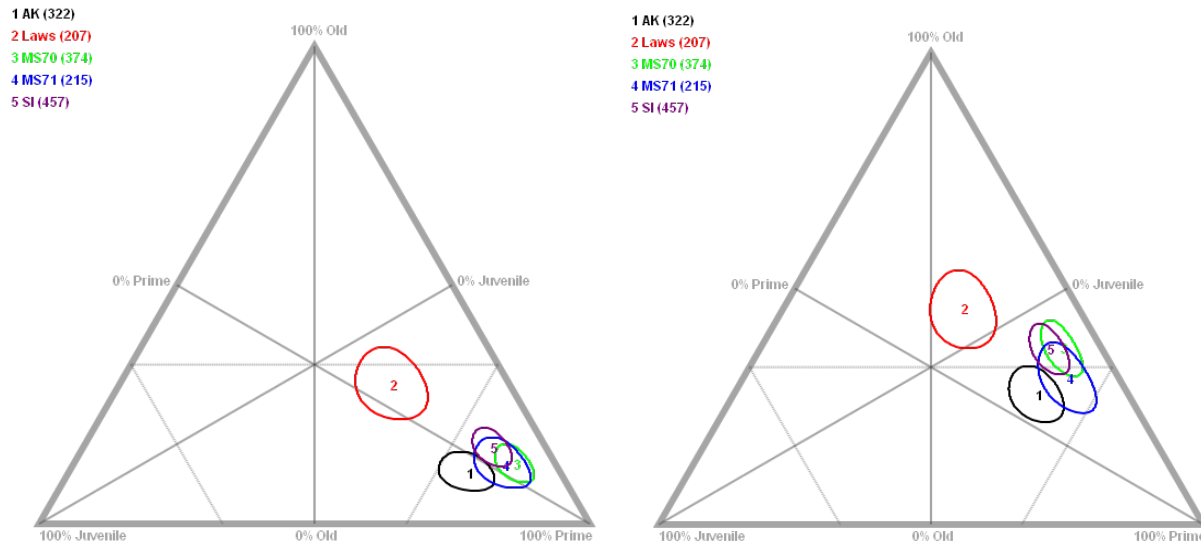
Comparison of age profiles between these five assemblages shows that all but the “natural assemblage” reported in Laws (1968) have increased numbers in the middle age categories (Figure 4.2). In addition, despite the Laws' (1968) assemblage being reportedly a natural accumulation, the profile does not follow that of an idealized attritional death assemblage (with high rates of juveniles). The assemblage at *Aetokremnos* appears most similar to the culling event from 1971, with the bulk of individuals within the age range from V to XII.





**Figure 4.2** Age profiles of five assemblages where group I is youngest age group and group XX is the oldest (Laws 1968). Akrotiri *Aetokremnos* represents the extinct species of pygmy hippopotamus of Cyprus, *Phanorius minutus*; all other assemblages represent the modern hippo, *Hippopotamus amphibius*.

The statistical comparison of these five species on a triangular graph, using the likelihood-based method (Weaver et al., 2011; available at [www.anthropology.ucdavis.edu](http://www.anthropology.ucdavis.edu)) shows that the assemblage at *Aetokremnos* is statistically different from the Laws' (1968) natural assemblage, and not statistically different from the other three culled assemblages at a 95% confidence interval (Figure 4.3). In addition, with the category cutoff for prime to old set at XV to XVI, the *Aetokremnos* assemblage falls entirely within the “prime—dominated” profile. Altering the transition from prime to old to XIII to XIV moves the *Aetokremnos* assemblage out of the exclusively “prime—dominated” category; however, it still remains statistically distinct from the natural assemblage identified by Laws (1968).



**Figure 4.3** Triangular graphs comparing juvenile, prime and adult categories using the likelihood- based method (Weaver et al. 2011) run at 95% confidence interval; *Left* Cutoff between “prime” and “old” categories occurring between age groups XV and XVI consistent with observations of tooth wear and associated mandibles in the *Aetokremnos* assemblage; *Right* Cutoff between “prime” and “old” categories occurring between age groups XIII and XIV which correlates with a drop in fecundity in modern hippos.

## Discussion

The analysis presented above reveals that: 1) the “natural” assemblage described by Laws (1968) does not follow the idealized attritional profile, and 2) the age profile for the *Aetokremnos* assemblage is statistically similar to documented culling events which are all statistically different from the “natural” accumulation.

The “natural” assemblage from Laws (1968) includes found mandibles, and while it is noted to not be tied to hunting or predation, other natural events, such as resource availability, disease, etc., are not discounted. It is possible that this assemblage reflects a catastrophic “event” which would create the expected/idealized living age profile found in Figure 2 (left). It is also possible that this data reflects the seasonality in which the individuals were collected, potentially decreasing the number of observed juveniles. Regardless of the nature of Laws’ (1968) data, it

remains clear that the *Aetokremnos* assemblage is significantly similar to the culling events of the 1970s- 1990s.

The process for culling hippopotami typically consisted of shooting hippos in the water from the bank, at which point the hippo would sink and several hours later rise due to gasses accumulating in the gut. The animal would then be towed to the bank for meat harvesting and, in the case of these three culling studies, specimen analysis (Eltringham, 1999). It was noted by Marshall and Sayer that “there was a tendency to crop hippopotamus where they could most easily be shot and recovered; isolated individuals or animals which were exceptionally timid were sometimes left while the hunters concentrated on larger groups” (Marshall and Sayer 1976: p395). This strategy resulted in the age profiles shown above which are statistically similar to *Aetokremnos*. In the absence of any direct evidence of hunting *Phanourios minutus*, this age profile may be the strongest line of evidence suggesting human procurement of the species.

*Catastrophic vs. Prime—Dominated Profiles:* The triangular graphs above show two distinct possible scenarios for the assemblage at *Aetokremnos*. I argue that the scenario with the age cutoff selected at XV to XVI (left image) represents the most logical evaluation. This initial cutoff was based on direct observation of the *Aetokremnos* assemblage, including mandibles where teeth were still *in situ*. The second scenario (right image) assumes the transition from prime to old occurs when fecundity drastically decreases in modern hippos. However, fecundity does not cease at this juncture, and a hippopotamus continues to grow in size into their third decade (Eltringham, 1999). Bunn and Pickering (2010) emphasize assigning “old age” to a prey animal should “convey the sense of a physically impaired, easy-to-kill individual, in contrast to a younger, physically robust, hard-to-kill or even dangerous individual” (p393). In either scenario,

the clear distinction from the Laws' (1968) assemblage and correlation with the culling events is evident; however if the earlier transition between prime and old categories is considered, then it is possible the *Aetokremnos* assemblage is more similar to a living profile or a profile created by a catastrophic event. This catastrophic event, in theory, could be the result of natural or anthropogenic impacts. When the stratigraphic integrity of the site and the direct association of cultural material with the faunal assemblage are taken into consideration, humans appear to be the logical factor.

The demographic data, combined with direct association of cultural material, suggest that *Aetokremnos* is an anthropogenic accumulation, resulting from humans' active procurement of the animals. How can this information inform the larger questions surround the extinction event? *Aetokremnos* remains the only well-studied site with humans and *Phanourios minutus* overlapping, and with limited information regarding the paleoecology of Cyprus in the Late Pleistocene, arguing human overkill for this species may still be a tenuous leap. Modern hippos are an extremely plastic species that alters their fecundity fairly readily in states of stress (such as drought) even over short time periods, so climatic conditions and resource availability could play a large role in the age profile of *Phanourios minutus* (Eltringham, 1999). Further work on the faunal assemblage at Akrotiri *Aetokremnos*, as well as discovery of new early sites on Cyprus, will undoubtedly shed more light on the dynamics of this extinction event.

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## Chapter 5: Direct human modification and relative skeletal abundance of the Cypriot pygmy hippopotamus at Akrotiri *Aetokremnos*

### Abstract

Akrotiri *Aetokremnos* is one of the earliest archaeological sites in Cyprus (ca. 12,000 cal. B.P.), as well as one of the largest deposits of the endemic and extinct pygmy hippopotamus, *Phanourios minutus*. Previous analyses have shown support for an anthropogenic accumulation at this site, and indirect evidence through demographic studies, that humans may have hunted the species. The association between humans and the pygmy hippo has been extrapolated to suggest a possible influence of human hunting on the extinction event of this species in several studies. However, to date no detailed zooarchaeological study has been completed on the extensive faunal collection. Here, I evaluate the pygmy hippo remains from Akrotiri *Aetokremnos* for any direct evidence of human impact—such as cutmarks or impact fractures, and discuss potential factors that may be obscuring this direct evidence. I then assess the relative skeletal abundance of the faunal remains and evaluate the distribution of burning across elements. While no one subsistence strategy is identified when looking at body part utility, several interesting patterns do emerge such as high frequencies of cranial elements. Through these analyses we can begin to start exploring questions about the way in which humans procured and used this species—ultimately leading to a discussion on relative impact for their extinction event.

Despite the abundance of *Phanourios* remains throughout the paleontological record throughout the Pleistocene, the species disappeared from Cyprus abruptly at or soon after the period represented at the archaeological site Akrotiri *Aetokremnos* (Reese 1996; Simmons 1996; Simmons 1999; Strasser 1996). This correlation between the earliest archaeological site and the latest pygmy hippopotamus remains has led to the hypothesis that human hunting contributed to the species' extinction (Simmons 1999, 2014). The hypothesis that human hunting played a role in the extinction of the pygmy hippo is based largely on the overlap of artifacts and features with pygmy hippo bones at *Aetokremnos* (Reese 1996; Simmons 1996, 1999, 2004, 2013a; Simmons & Mandel 2007), and to date has proven controversial. This controversy has been largely focused on the difference in composition between a lower Stratum 4 and upper Stratum 2 at the site. Fundamental to understanding the potential impact of humans on this extinction event, is to first

identify if and how humans interacted with this species, and how these interactions may have changed through time (or between these two strata).

In Chapters 3 and 4, I presented multiple lines of evidence that suggest the lower Stratum 4 is indeed represents a cultural accumulation. While past critiques focused on the possibility of the lower strata being a natural accumulation later accessed by humans—the demography of pygmy hippopotamus most similarly matches that of a culling, or hunting demographic profile. Further analyses evaluating potential taphonomic factors at the site have ruled out the possibility of the skeletal composition/representation being the result of density mediated attrition, and suggests that although there is extensive fragmentation throughout the site, this is likely not the result of dynamic impact such as roof fall and is more likely explained by the extensive burning at the site or other anthropogenic factors (such as processing etc). Furthermore, comparison of fragmentation between long bones and metapodials may suggest differential marrow extraction within Stratum 2 and 4. However, the research to date has not provided insight to the way humans may have procured and/or utilized this species. To address the latter, and infer human behavior, we must take a closer look at the faunal assemblage.

While using faunal elements to determine the nature of accumulation and equating this to human behavioral decisions is prominent throughout the history of zooarchaeology (Brain 1969; Brink 1997; Grayson 1988, 1989; Ioannidou 2003; Lyman 1985, 1988, 1991, 1992, 1994; Marean and Frey 1997; Savelle et al. 1996), using the archaeological record as a direct correlate of behavioral choices made prior to deposition can be misleading (Lam and Pearson 2005; Lyman 1994). Therefore, before extrapolating the RSA to potential human behavior, it is critical to address any post-depositional processes that may have affected the distribution and abundance

of elements within each analytical unit. These issues have been addressed within Chapter 3, and as a result, we can evaluate the evidence for direct human impact and interpret the faunal distribution at Akrotiri *Aetokremnos* as a proxy for human behavior—providing insight into the subsistence and behavior of the earliest Cypriots.

To gain better insight into the way in which this species was procured and or utilized by humans, and to start a discussion about site function, I **first** look for evidence of direct human modification (cutmarks or impact fractures) and **second** evaluate the relative skeletal abundance in an attempt to identify any distinct subsistence strategies. Through these three analyses we can start the dialogue about early Cypriot subsistence, and how the strategies represented at Akrotiri *Aetokremnos* can inform us about early Mediterranean seafarers.

### **Akrotiri *Aetokremnos* Assemblage and Analytical Units**

The faunal assemblage at *Aetokremnos* consists of over 300,000 bones, approximately 98% belonging to the pygmy hippo (Table 5.1; Simmons 1999, 2014). Reese and Roler (1999) provided a brief descriptive summary of the assemblage, and Olsen (1999) conducted a taphonomic analysis on a sample size of 15,000 specimens. The site is largely represented by two occupation layers, Stratum 2 and Stratum 4. Previous publications argued over the contentious nature of Stratum 4, that it may be a natural accumulation later accessed by the humans responsible for the accumulation of Stratum 2. Review of the sites geoarchaeology and stratigraphic integrity (Chapter 3) and evidence for the cultural accumulation of Stratum 4 (Chapter 3 and 4) strongly implies this is not the case and that Stratum 4 represents an intact earlier human occupation. While it appears clear that Stratum 2 and 4 are both human

occupations, there are striking differences between the two in both species composition and artifact frequencies (Simmons 1999). Most pertinent to this discussion is the observation that the older Stratum 4 contains over 88% of the pygmy hippo remains, but under 40% of chipped stone at the site, whereas the more recent Stratum 2 contains less than 20% of hippo remains and over 60% of all chipped stone. In order to begin to decipher the human behavior that may be responsible for some of these striking differences, we must take a closer look at the faunal composition—focusing both specifically on the pygmy hippo and the frequencies of other taxa present.

**Table 5.1 Number of Identified Specimens (NISP) of all fauna at Akrotiri *Aetokremnos* as reported by Reese (1999)**

	Stratum 2	Stratum 4	Total
<i>Vertebrates</i>			
Pygmy hippopotmai	26,124	192,335	218,459
Pygmy elephant	5	224	229
Deer*	4	-	4
Pig	10	4	14
Genets	2	-	2
Mice	5	-	5
Birds	2,660	547	3,207
Snakes	227	18	245
Tortoises	17	8	25
Toads			1
Fish	-	1	1
<i>Invertebrates</i>			
Marine Inverts	71,291	2074	73,365
Land snails	62	28	90

Inferring human behavior from faunal remains requires attention to sampling and definition of relevant analytical units. To do this, I conducted a detailed taphonomic study of the

pygmy hippo remains at the site, and evaluated the most appropriate units for analysis based on statistically significant similarities of skeletal representation. Due to the size of the assemblage, in this analysis I followed the methodology presented by Faith and Gordon (2007) which is discussed in detail in Chapter 3. I looked only at the high survival elements that incorporate both high and low utility parts at *Aetokremnos*. The minimum number of elements (MNE) and minimum number of individuals (MNI) were calculated for each analytical unit defined in Chapter 3: Stratum 2, Stratum 4 and Feature 3 (Table 5.2). A total number of specimens (NSP) of 92,420 were analyzed for evidence of direct human modification and evidence of natural taphonomic factors. Of the total number of specimens analyzed, 22,197 were identifiable to element (Table 5.2).

**Table 5.2 Number of Identified Specimens (NISP) and minimum number of elements (MNE) in each analytical unit.**

Element	Stratum 2		Stratum 4		Feature 3	
	NISP	MNE	NISP	MNE	NISP	MNE
Cranium	158	91.14	5928	58.10	2834	71.88
Mandible	115	84.35	1890	72.22	270	68.52
Humerus	31	93.55	937	74.28	378	89.95
Radius/Ulna	45	84.44	1350	69.85	676	83.28
Femur	81	98.77	2046	73.70	669	55.61
Tibia	22	95.45	733	74.76	321	77.26
Metacarpal	15	20.00	226	66.81	60	76.67
Metatarsal	13	69.23	188	62.77	121	88.43
Long Bone Frags	16	100	227	32.60	-	-

As noted above, the MNE and MNI were calculated for each individual excavation unit and then the data were aggregated into three analytical units: Stratum 2, Stratum 4 and Feature 3. MNI and MNE values for adults and juveniles are reported in Table 5.3 (also see Chapter 3.3). Based on this analysis, Stratum 4, which contains Feature 3, has an MNI of 235 adults and 78 juveniles. Stratum 2 contains a MNI of 21 adults and 7 juveniles. Combined, the site at Akrotiri *Aetokremnos* contains a MNI of 256 adults and 85 juveniles, for a total of 341 individuals. Age and size were taken into consideration when calculating these values.

It should be noted that this total MNI is significantly different from the previously reported MNI values by Reese (1999) who estimated a minimum of 505 individuals at the site. While limited data has been published to date noting the derivation of this MNI of 505, tables published by Reese (1999) showing MNI and MNE values by feature, stratum and element are in agreement with those values calculated in this study. However, Reese (1999) appears to have left all identified features as their own analytical units, and as a result calculates an MNI number for each feature. In this study, features that were not identified as statistically significant in element distribution from the surrounding matrix, faunal remains were treated as part of the stratum in which they were present, rather than a stand-alone feature and specimens. Treating each feature as a significant unit of analyses, and calculating the MNI for each of these features individually, would significantly inflate the overall MNI at the site.

**Table 5.3 (Reprint of Table 3.3) MNE and MNI by element and per analytical unit. Reported MNE's are for adults and juveniles in italics. Units defined discussed below. Note the mandible MNE accounts for a right and left mandible, and therefore is divided by two to calculate the minimum number of individuals (MNI) in each unit. Feature 3 is within Stratum 4 but is reported separately.**

Element	Minimum Number of Elements (MNE)					
	Stratum 2		Stratum 4(exc. Fea 3)		Feature 3	
	ADULT	<i>JUV</i>	ADULT	<i>JUV</i>	ADULT	<i>JUV</i>
Cranium	13	<i>7</i>	171	<i>55</i>	64	<i>6</i>
Mandible	41	<i>6</i>	169	<i>76</i>	38	<i>11</i>
Humerus	17	<i>7</i>	234	<i>68</i>	68	<i>23</i>
Radius/Ulna	17	<i>2</i>	304	<i>71</i>	103	<i>25</i>
Femur	17	<i>8</i>	236	<i>75</i>	77	<i>30</i>
Tibia	9	<i>3</i>	230	<i>85</i>	80	<i>23</i>
Metacarpal	11	<i>4</i>	172	<i>16</i>	24	<i>7</i>
Metatarsal	14	<i>1</i>	166	<i>6</i>	66	<i>15</i>
<b>Minimum Number of Individuals (MNI)</b>	21	<i>7</i>	171	<i>55</i>	64	<i>23</i>

### Visible Human Modification

As noted in Chapter 3, evaluation of stratigraphy, density mediated attrition and fragmentation all support the assumption that natural taphonomic factors have not significantly altered the pygmy hippo faunal assemblage at Akrotiri *Aetokremnos*. Before interpreting the relative skeletal abundance and inferring potential human behavior, evidence for direct human modification needs to be addressed as potential taphonomic factors. Below I discuss the evidence for visible human modification including cut marks/impact fractures, and burning. While processing could certainly be a major factor for fragmentation at a cultural site, and may account for the variation between long bone and metapodial fragmentation seen in Stratum 2 and 4

(Chapter 3), within the scope of this paper it is not discussed in great length. Processing and fragmentation will be covered in a future publication.

**CUT MARKS:** The presence of cut marks on *Phanourios* bones would prove compelling evidence for direct hunting/butchering of the pygmy hippo by humans. In a previous analysis of over 15,000 bones, Olsen (1999) found no evidence of cut marks or direct burning, leading to the interpretation of the site as a natural accumulation. Simmons (2014) notes that while the analyses for evaluation cutmarks is unquestionably sound the interpretation of the lack of these features for inferring the nature of the site proves problematic when placed within the context of other evidence. As a second form of cutmark analyses, all 92,420 specimens analyzed were examined and evaluated for evidence of cutmarks. This analysis includes the long bones most likely to bear evidence of butchering (femur, tibia, metatarsal, humerus, radius and metacarpal) as well as the cranium and mandible (Lyman 2005). No ribs or vertebrae were analyzed in this sample, and butchery near these elements would not have been identified. All specimens identified during analysis were evaluated for inconspicuous markings. All markings and marking locations were noted on lab notes used for calculating MNE values. Markings were categorized as follows: 1- potential cut marks requiring closer analysis with hand lens and/or microscope; 2-marks from weathering, staining or clearly other non-anthropogenic taphonomic processes; and 3- marks resulting from excavation and/or post excavation handling and storage. Marks classified as category 1- potential cut marks, were classified very conservatively, and all bones with this classification were photographed and analyzed under 20x microscope.

Category 1 marks recorded—potential cut marks— were all located in spots that would be inconsistent with butchering assumptions. No marks identified and photographed under the

microscope were determined to be unequivocally pre-depositional, and instead all are attributed to various taphonomic factors and excavation/post excavation marks. Nevertheless, there are significant taphonomic factors that may impede identification of cut marks on bone at this site. In Stratum 4, 76.9% of the fragments identified were either burned, coated heavily in surrounding cementum matrix, or treated with acid post-excavation to remove that matrix. In Stratum 2, over 80% of the specimens analyzed were affected by one of these factors. For Feature 3, over 71.9% of the material is intensively burned. Those elements coated in cemented matrix do not have the surface of the bone exposed, and any potential cut marks that may have been present are covered/obscured. Acid treatment of some bones following excavation (designed to remove the cemented matrix) removed the outermost layer of the bone, often leaving a discolored and striated surface—any subtle cut marks would have been removed during this process. Finally, intensive burning alters the surface of bone in addition to increasing friability and fragmentation—again, obscuring any small cut marks that may have been present at one point. So, while no cutmarks have been identified to date these significant taphonomic factors should be taken into consideration when discussing this as negative evidence.

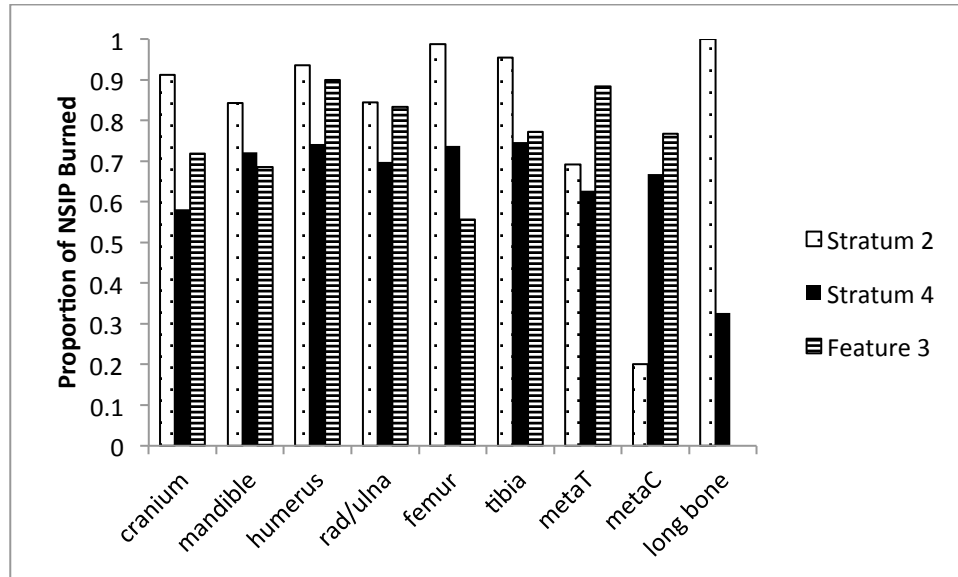
**BURNING:** As noted previously, burning is extensive at *Aetokremnos*. Burned bones are found in every stratum with varying frequencies. Stratum 4C had the lowest proportion of burned bone when considering all species (14.6%), with higher frequencies stratigraphically above (as published by Reese and Roller 1999). Previous analyses of burning as related to fragmentation (Chapter 3) suggest burning at *Aetokremnos* was most likely anthropogenic. For example, Feature 3, with over 73% of all identified fragments at least partially burned, has intact stratigraphy, lacks evidence of heat modification in its overlying layer, contains chipped stone in

the intact strata, and shows evidence that fragmentation of bones result from the burning of fresh or whole/attached bones. Identifying the purpose for anthropogenic burning is a more difficult issue. Burning may have derived from food preparation; however, the extensive burning at this site is more severe than recorded cases in the archaeological record that reflect ordinary cooking practices and might be more likely the result of burning bone for fuel (Costmagno et al. 2002; Kent 1993; Schiegl et al. 2003; Thery-Periset 2001, 2002; Villa et al. 2002).

The source of burned bone in archaeological sites has been extensively discussed in the literature (eg. Bennett 1999; Brain 1981; David 1990; Monton Subias 2002; Spenneman and Colley 1989; Stiner et al. 1995; Thery-Periset 2001, 2002; Villa et al. 2002). To address the nature of burning at *Aetokremnos*, the distribution of burning across elements is quantified and correlated with element type within and between all analytical units. In addition, ratio of burning between long bone ends and shafts were calculated to identify any evidence of food preparation practices. More frequent burning on articular surfaces might indicate roasting (Russell 1999) while concentration of burnt patches on shaft fragments may indicated use of fire to facilitate cracking for marrow which often leaves distinctive patterns of post-burning (Marchiniak 2005; Serjeantson 2006).

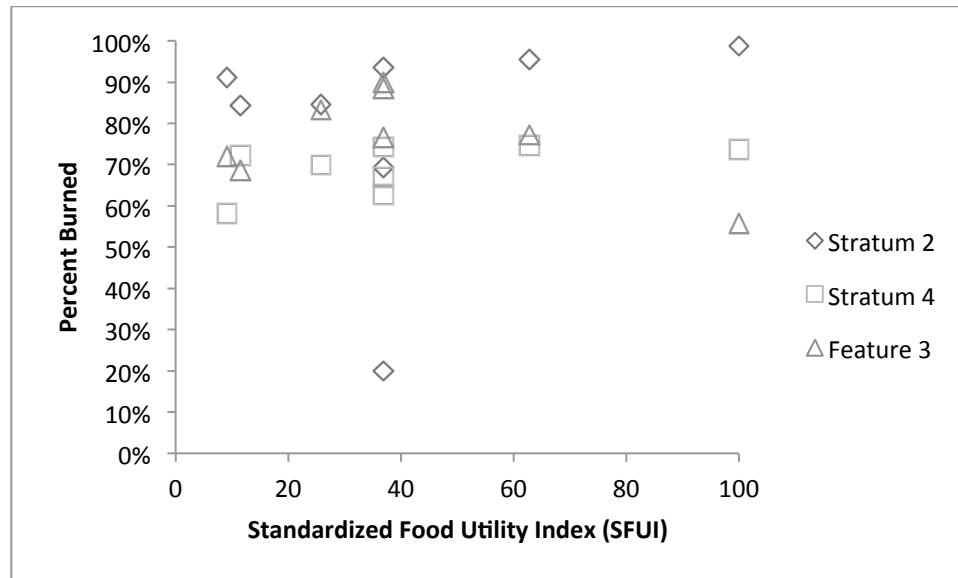
Fragments analyzed were classified as burnt if they visually showed any signs of burning. No distinction was made between those fragments that were intensely and/or completely burnt and those with mild burning or burning on small portions (e.g. one end of a complete bone). The proportion of the NISP burnt for each element within each analytical unit was calculated (Chapter 3, Table 3.1). Comparison of the proportion of burnt fragments for each element shows the extensive amount of burnt pygmy hippopotamus remains at the site (Figure 5.1). All elements have high frequency of burning with the exception of the metacarpals in Stratum 2. This rate of

only 20% burnt metacarpal fragments is the result of three burnt metacarpal fragment out of a total of 15 specimens in Stratum 2, and may be a function of sample size.



**Figure 5.1 Proportion of identified burnt specimens per element and analytical unit.**

If anthropogenic burning of bones were related to processing meat and/or extraction marrow or grease for consumption, there should be an increase in burning of those elements with a higher utility or caloric return. To test if burning correlates with utility of a given element, I compared the number of individual specimens (NISP) of burnt and unburned fragments with their associated Standardized Food Utility Index (SFUI). I use the modified measure of Standard Food Utility Index (SFUI) proposed by Faith and Gordon (2007), derived from the commonly used economic utility indices proposed by Metcalfe & Jones (1988). The SFUI shows similar patterns between the burned and unburned categories suggesting that there is no difference in the distribution of burning according to the elements present at the site (Figure 5.2).



**Figure 5.2 Percentage of burned fragments compared to the SFUI, showing no preferential burning of high utility elements at *Aetokremnos*.**

Overall, there appears to be no evidence that a given element was targeted for burning more extensively than any other—i.e. no elements were preferentially burned. The burning of pygmy hippopotamus bones at *Aetokremnos* appears to reflect the same patterns of the element distribution at the site. This does not, however, negate the possibility that this burning is anthropogenic. As noted above, burning bone for fuel is common in the archaeological record. Future work at the site should focus on identifying various degrees of burning intensity, and relate this to the rich literature surrounding burning for fuel in the archaeological record. Another possible explanation for an even distribution of burning across elements could be resource depression. During times of resource depression and resulting stress, one would expect a more even utilization and more intense use of bones with differing caloric returns. As resource depression and burning for fuel are not within the scope of this paper, these claims should be addressed elsewhere to more succinctly determine the nature of the extensive burning at this site.

## **Determining Site Function**

Having ruled out several potentially key taphonomic factors that may have influenced skeletal distribution at Akrotiri *Aetokremnos* in Chapter 3, inferring behavior from the faunal remains becomes less tenuous. It is apparent that skeletal abundance is not dependent on density mediated attrition or rock fall/dynamic impact. In addition, there are multiple lines of evidence that the lower strata 4 is anthropogenic, and demographic analysis suggest these animals were procured through hunting (Chapter 4). As noted above, because of these previous analyses we can ask more discrete questions about the way humans utilized this species. As a result, we can use an analysis of the Relative Skeletal Abundance (RSA) to infer possible anthropogenic behaviors at the site.

### ***Relative Skeletal Abundance***

Faunal analysts have a long tradition of using the relative abundance of skeletal elements to determine archaeological site function, carcass-acquisition strategies and butchery and transport decisions (Bartram & Marean 1999; Broughton 1994, 1999; Faith & Gordon 2007; Faith 2009; Grayson & Cannon 1999; Lyman 2005; Marean & Cleghorn 2003; Nagaoka 2005, 2006). Body parts of prey are associated with high or low utility, defined by their caloric return under differing procurement/transport strategies (Binford 1978). This caloric return takes into consideration meat, marrow and grease returns, as well as transport and processing costs. This allows the distribution of elements at a site to provide valuable information on the subsistence strategies employed by humans.

Hunting large mammal species, such as the pygmy hippopotamus, has a high caloric return. However, their size may come associated with considerable transportation cost if hunted

at any distance from the location of their processing and consumption (Binford 1978; Faith & Gordon 2007). If humans were hunting pygmy hippos far from the site they would have been presented with transport decisions. These decisions could be detected by body part utility, with high utility parts being transported to the site and low utility parts left behind (Faith & Gordon 2007). This, in turn, can be detected by analyzing relative skeletal abundance, and, in particular, by examining the evenness of those abundances (Faith and Gordon 2007). An uneven distribution of elements at *Aetokremnos* would suggest selective transport of body parts and evidence of a human influenced accumulation (Faith & Gordon 2007). An even distribution of large mammal skeletal remains would suggest either a natural accumulation (natural death assemblage) or a massive kill site where the remains are found at the location where they were killed or within very close proximity (Binford 1978; Faith & Gordon 2007; Faith 2009; Metcalfe & Jones 1988).

Here I apply the relative skeletal abundance of the assemblage to commonly used economic utility indices (Metcalfe & Jones 1988) using the modified measure of Standard Food Utility Index (SFUI) proposed by Faith and Gordon (2007). I measure the statistical evenness of the assemblage and evaluate utility index based predictions concerning butchery and transport decisions. The sample size proposed is more than adequate for this method to be appropriate (Faith & Gordon 2007), and while this methodology only evaluates high survival elements, earlier analyses support that assumption that density mediated attrition is not a factor at this site. This methodology makes the assumption that using this combination of high and low utility, across high survival elements, provides a representative sample of butchering practices at the site.

The relative skeletal abundance analysis was conducted for each analytical unit: Stratum 2, Stratum 4 and Feature 3. Each unit was evaluated independently in an attempt to parse out differing strategies at different time periods (Stratum 2 and Stratum 4), and within different behaviors (between the intensely burned Feature 3 and its surrounding Stratum 4). For all analytical units, the correlation between element abundance and Standardized Food Utility Index (SFUI) was calculated to assess whether only high utility, only low utility or a combination are present at the site. Comparisons of anatomical profiles using both number of individual specimens (NISP) and minimum animal units (MAU) were calculated and compared between the analytical units—as NISP is a common value used in utility curves, and MAU is a measure of elements present that accounts for a natural frequency of elements in the body (e.g. 4 metatarsals for every 1 femur).

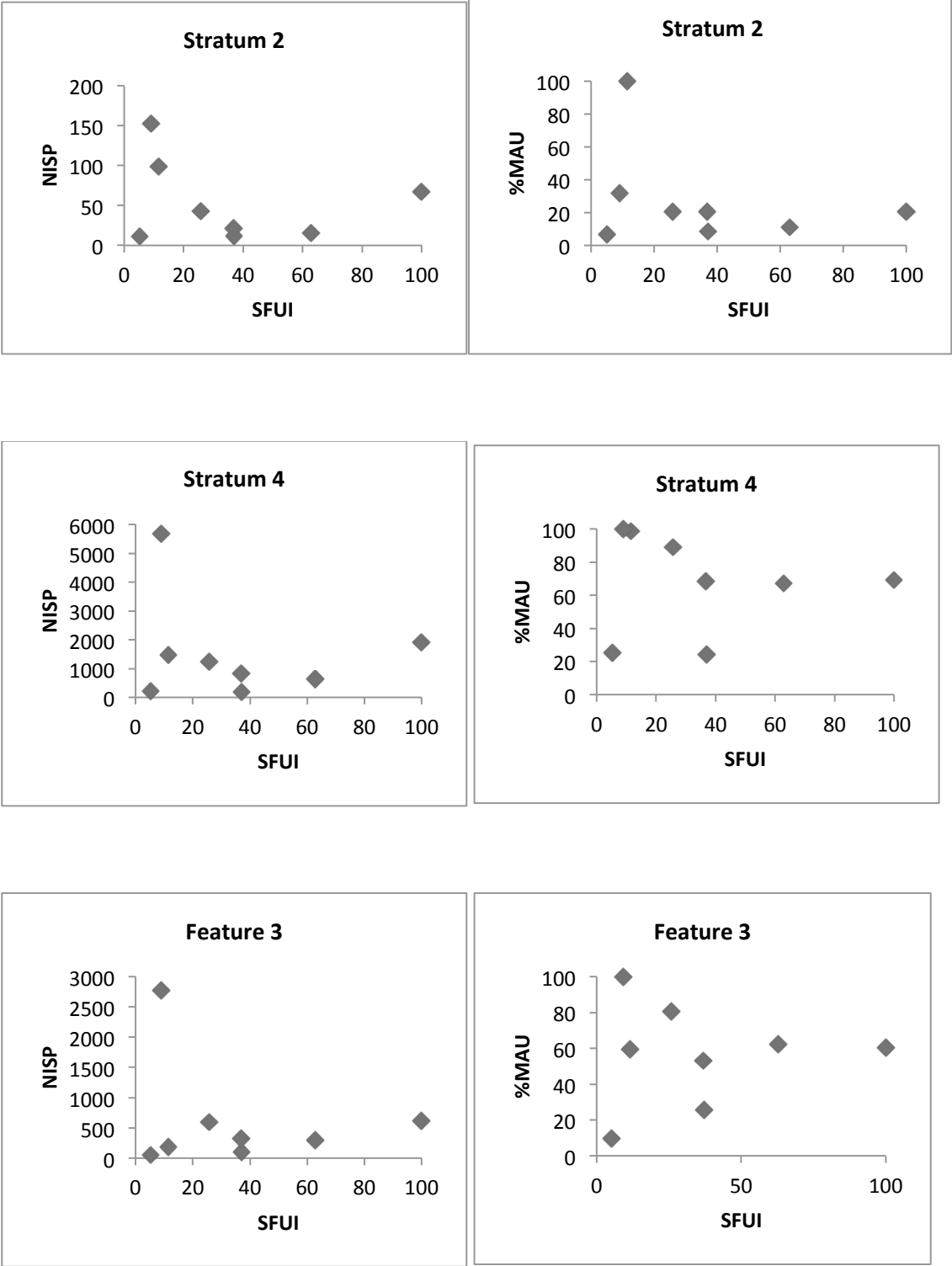
First, I evaluated the diversity of elements and evenness within each unit by calculating the Shannon Weaver Index of evenness. As the number of elements increases, and the evenness (more equal representation) of elements increases, the Shannon Index increases. For all analytical units the Shannon Weaver Index of evenness is very high, suggesting high element composition with a high diversity ( $H'$ ) of elements (Table 5.4).

**Table 5.4 Measurement of evenness and diversity of *Phanourios minutus* elements analyzed (cranium, mandible, humerus, femur, tibia, humerus, radius/ulna, metacarpal and metatarsal) in each unit at *Aetokremnos*.**

Analytical Unit	Shannon Index Evenness	$H'$	$R^2$
Stratum 2	0.890	0.804	0.093
Stratum 4	0.943	0.852	0.006
Feature 3	0.937	0.846	0.141

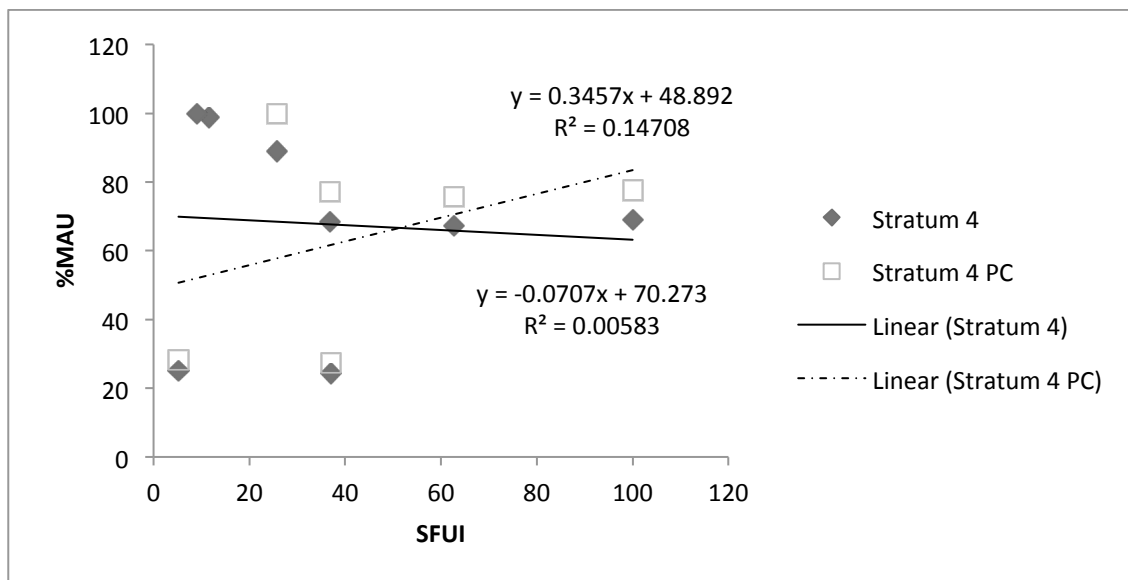
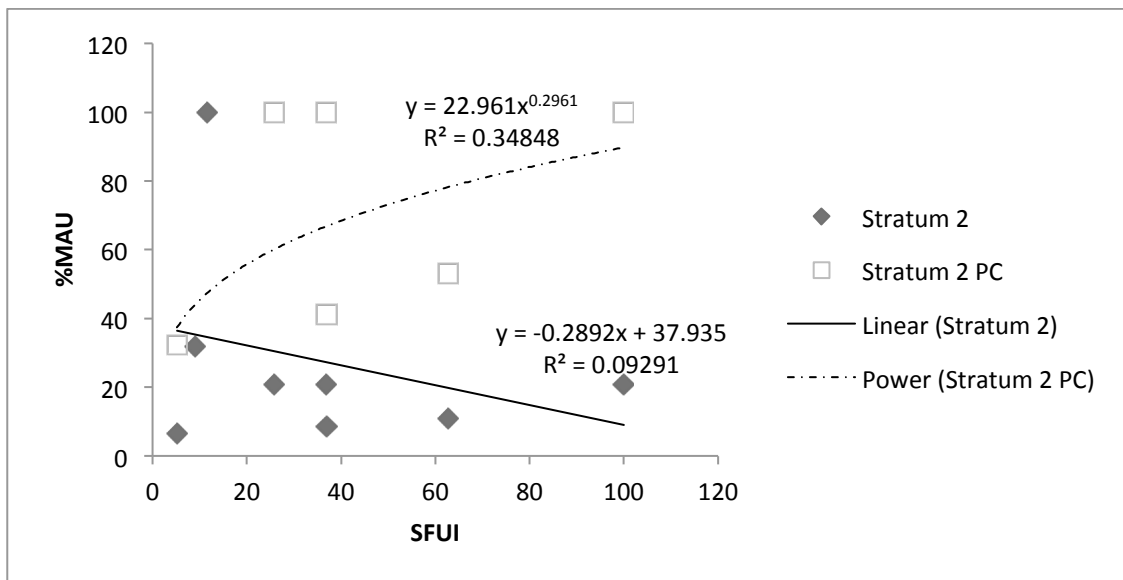
Before comparing NISP and MAU to the SFUI, MAU was converted to %MAU. %MAU is calculated by dividing the MAU corresponding with that element divided by the maximum

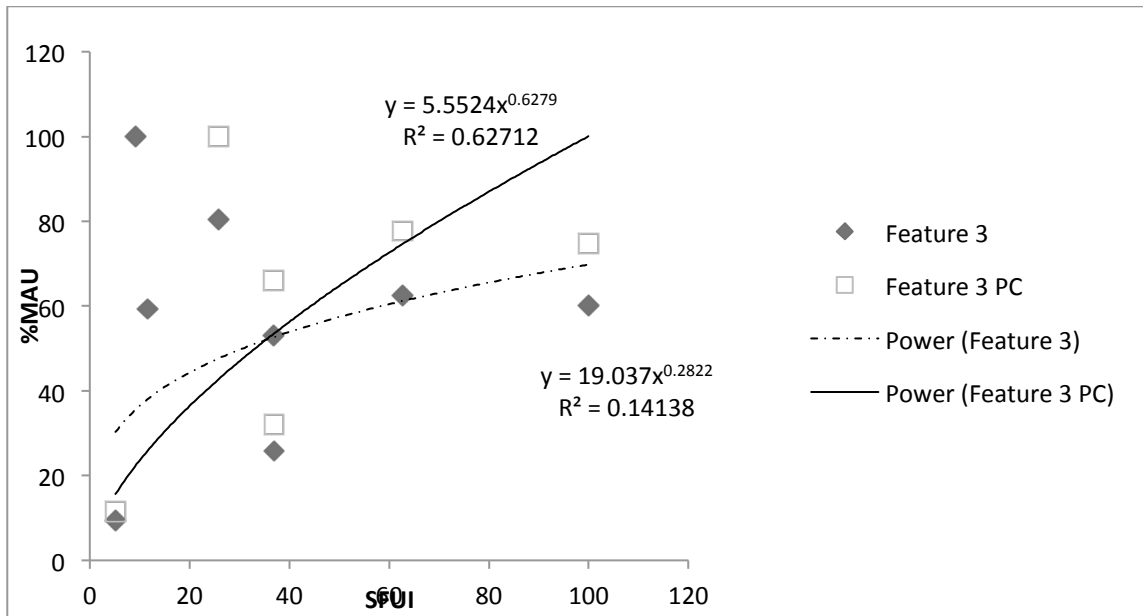
MAU in the unit. When comparing the element distribution with SFUI in Stratum 2, both comparisons with NISP and %MAU appear to be a reverse utility curve (Figure 5.3). Reverse utility curves in rock shelters can be controversial due to the potential impacts of density mediated attrition (e.g. Lyman 1994); however our results regarding density mediated attrition show no significant correlation between element distribution and density. Other reasons for false reverse utility curves can be calculation of MNE's and therefore the MAU (as MAU is derived from the MNE), based only on epiphyseal ends that are more easily identified to a given element (Lyman 1994). This implied preservational bias between long bone ends and shafts are based on relative densities within a given element—ends being less dense, and shafts being more dense—yet, again, we've accounted for this intra-element density above, and density mediated attrition shown to not be a factor. In addition, for this study long bone shafts were included in all MNE calculations. As a result, the reverse utility curve present in Stratum 2 appears to be a legitimate pattern, although still just a visual interpretation. When evaluating Stratum 4 and Feature 3, the NISP versus SFUI graphs show a similar reverse utility curve noted in Stratum 2 (Figure 5.3). However, once converted to %MAU, the pattern visually takes on a positive correlation between elements and utility with the exception of high values for cranium and mandible, although again this is a visual interpretation and not statistically significant.



**Figure 5.3** Figures on the left compares NISP in each analytical unit to the SFUI; Figures on right compare %MAU to the SFUI in each analytical unit.

To further explore the impact of the high frequency of cranium and mandibles (both low utility in the SFUI used), I ran the same %MAU comparison based only on post cranial elements. With the removal of the cranial element data, all analytical units show a positive correlation between %MAU and the SFUI (Figure 5.4). Feature 3 shows a positive correlation between %MAU and SFUI with and without the cranial elements, however the post cranial analysis suggests a stronger correlation.





**Figure 5.4** Figures comparing %MAU to SFUI for each analytical unit with and without cranium and mandible. PC= post cranial elements only.

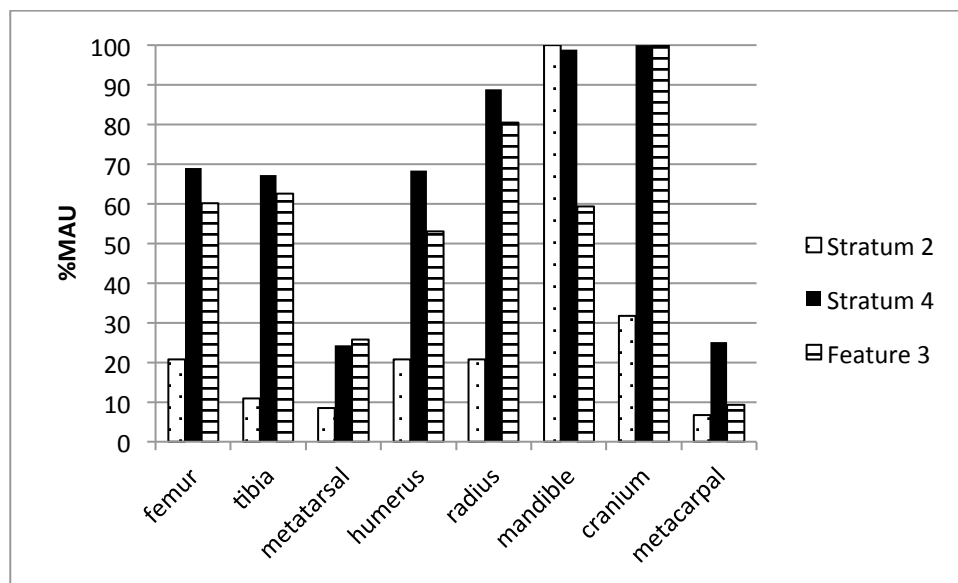
This pattern between post cranial and full skeletal analysis has been argued to reflect density mediated attrition and/or the lack of inclusion of long bone shafts in MNE estimates at other sites (Grayson 1989; Lyman 1985, 1992; Marean and Frey 1997), ultimately resulting reverse utility curves. However, since we have ruled out density mediated attrition at *Aetokremnos* in Chapter 3 and shaft fragments are included in the MNE values, other explanations for the unexpectedly large number of cranial and mandibular components should be considered.

### Discussion and Conclusion

Despite the lack of cutmarks evidence, the extensive burning at the site appears to be anthropogenic. Burning of Feature 3 is highly unlikely to be the result of heat from above because of capping of the feature by sterile Stratum 3 and absence of thermal alternation of

Stratum three by fire from above. Extensive burning in Feature 3 and around Stratum 4, in which it is situated, combined with the intact stratigraphy would suggest direct anthropogenic impact on this species. However, the burning appears to be non-selective regarding skeletal parts, and elements reflect the overall distribution at the site. However, this may be an artifact of the sampling strategy, as elements analyzed were done so based on their ability to answer food utility questions, not their potential as use for fuel. The difference in combustion potential between axial and non-axial elements is noted by many, and axial elements are not included in this study (Costamagno et al. 1998, 2002; Thery-Parisot 2001, 2002).

Relative skeletal abundance appears fairly even with robust diversity between elements, yet does not correlate significantly with any defined procurement/butchering/transport strategies. Comparison between element representation and SFUI generally shows a non-significant reverse utility curve. This is likely not the result of density mediated attrition (shown in Chapter 3). When only post cranial elements are evaluated, the utility curves appear to be more similar to an unbiased or bulk strategy; however none of the relationships are significant.



**Figure 5.5 %MAU of all elements in each analytical unit—noting the high frequency of mandibles and craniums.**

Disproportionate representation of cranium and mandible fragments and %MAU pose an interesting point for discussion, particularly when considering the hippopotamus (Figure 5.5). The SFUI used is based on a standardized artiodactyl value that takes into consideration return from meat, marrow and grease. It is possible that the food utility for the pygmy hippopotamus varies, allowing the cranial elements to overcome its low food utility due to a return of a different nature. One such feature present in the hippopotamus is the tusk. Hippopotamus tusks are known to be slightly softer than “true” ivory from elephant and mammoth, and easily carved and has been sought after more frequently in the Levant due to its ‘whiter color’ that does not yellow over time (Horwitz and Tchernov 1990; Reese 1985). In Europe, during the later Chalcolithic period, raw hippopotamus ivory (unworked) was imported to the Aegean mainland from Egypt or the Levant (Kryzyszkowska 1983, 1984; Reese 1982, 1985). A quick calculation based on the number of tusks identified in Feature 3 by Reese (1999) compared to the MNE values for cranium and mandibles shows significantly fewer tusks than one would expect to be present at the site if either a natural accumulation or if tusks were discarded with the crania. Reese (1999) identified an MNI of 15 upper incisors corresponding to the MNE of 64 craniums, and an MNI of 12 lower incisors compared to an MNE of 38 mandibles. This suggests that at least at Feature 3, only 23.4% of expected upper incisors are present and 31.6% of lower incisors. Unfortunately, incisor information was not collected for this study and the only published information by Reese (1999) relates to Feature 3. Calculating the frequency of tusks remaining at the rest of the site would provide valuable information about whether or not these items were removed from the site. Conversely, if incisor ivory was of significant value, one could question why any pieces at all remained in Feature 3. Comparison of incisor information

across analytical units may help clarify the potential role of hippopotamus ivory procurement may have had on the resulting utility curves.

An additional factor that may affect the SFUI value of the Hippopotamus mandible and encourage a reevaluation of utility curves, is the occasional mention of prehistoric and historic groups targeting a ‘nutritious root’ at the base of the canine- providing an excellent source of marrow (Hill 1983; Horwitz and Tchernov 1990). I was unable to find any detailed information on this possibility, but if it were truly a significant source of nutrition, root extraction could account for an abundance of mandibles at *Aetokremnos*.

In addition to evaluating the distribution of the pygmy hippo at this site, future work should include an expanded look at all of the fauna present. When looking at complete assemblage (Table 5.1) there is a clear and distinct change in subsistence between Stratum 2 and 4. The frequency of hippopotami decrease and the breadth of taxa found at the site increases considerably. So while there doesn’t appear to be a single subsistence strategy utilized within each analytical unit at Akrotiri *Aetokremnos* while looking at the hippopotamus remains, we cannot ignore the other potential subsistence available to early Cypriots. Using the Shannon Weaver Index of evenness to evaluate the diversity and evenness of species within and between each analytical unit, we see a distinct change between Stratum 2 and 4.

Looking at the diversity of elements and evenness within each unit by calculating the Shannon Weaver Index of evenness we see that for Stratum 4 the Shannon Weaver Index of evenness is very low, suggesting an uneven assemblage with a low diversity ( $H'$ ) of species (Table 5.5). This is markedly lower than in Stratum 2, where it becomes clear that there are more taxa being utilized at the site as the number of pygmy hippos declines. This shift in subsistence could be the result of several factors. It could mark the decline in hippopotamus availability and

subsequent shift towards a more broad diet. This decline in hippos, however, could be the result of either climatic/habitat change, or of increased predation by humans. A closer evaluation of the species involved in this transition should shed light on the ultimate cause for changing subsistence.

**Table 5.5 Measurement of evenness and diversity of all species present at Akrotiri *Aetokremnos* as reported by Reese (1999)**

Analytical Unit	Shannon Index Evenness	H'
Stratum 2	0.278	0.309
Stratum 4	0.035	0.039

Overall, the analyses to date show intact strata with artifacts in each analytical unit, no evidence of post-depositional taphonomic biases, support of anthropogenic burning, and a prime dominated assemblage. All of these lines of evidence suggest that Stratum 4 at Akrotiri *Aetokremnos* is likely a non-natural accumulation and is anthropogenic in nature. Furthermore, the demographics at the site suggest that the mortality profiles present are representative of human hunting. As a result, it appears that the pygmy hippopotamus assemblage at *Aetokremnos* is anthropogenic in nature in both strata. While there is no identified evidence of cut marks at the site, the heavy modification by burning serves as potential evidence for direct human impact.

Relating the faunal assemblage at *Aetokremnos* with human behavior is difficult, as no one utility based strategy clearly matches the assemblage—a common problem when addressing relative element abundance in rock shelters and caves. This may be the result of a behavioral shift of strategies through time, or the methodological need for a re-evaluation of the food utility as it relates to this species. There is ethnographic evidence that suggests people process modern hippopotamus mandibles for access to a nutritious root—making the argument for a new food utility relevant. Furthermore, the non-food based utility of the tusks corresponding with the

mandible and cranium of the hippopotamus should be considered when evaluating the overall strategy at *Aetokremnos*. In addition, future inclusion of low survival elements, such as ribs and vertebrae, may provide the added clarity needed to assess procurement and processing strategies at the site—and rejecting density mediated attrition as a biasing factor, it may be possible to get a high resolution for these remaining elements.

While there appears to be evidence for direct involvement in the formation of the lower strata (Stratum 4 and Feature 3), the origin of the faunal remains and the relative impact of humans on this species' extinction event remains unclear and should be addressed within the larger context of the climate, species history on the island and early Mediterranean seafaring. Studies regarding the population dynamics of this species leading up to the occupation of *Aetokremnos* could provide significant insight into possible anthropogenic impacts are the ultimate cause or simply a proximate cause for extinction. Such a study would help to explore the dynamics of human and hippopotamus interactions on Cyprus in the Late Pleistocene and add to the larger conversation regarding Late Pleistocene extinction events.

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## Chapter 6: Conclusion

Identifying the ultimate cause of extinction for the Cypriot pygmy hippo, as with all large mammal extinctions in the Late Pleistocene, is a complicated and multifaceted task. The four studies presented in this dissertation examine critical aspects of the environmental, archaeological and morphological context and characteristics of the *Phanourios minutus* assemblage at Akrotiri Aetokremnos that shed light on the role of humans in creating the assemblage and the larger conditions that may have influenced the species' extinction. While questions surrounding the relative impacts of humans and climate change on this extinction event remain incompletely resolved, the research presented here helps to clarify the picture of this species and its interactions with humans and its environment.

Through these studies, it becomes apparent that humans did interact with this species and this interaction is evident in the archaeological site Akrotiri *Aetokremnos*. In Chapter 3, “**Evaluating post-depositional taphonomic processes**”, concerns regarding potential biases at the site were addressed. This research shows that the two most likely post-depositional taphonomic processes at this site (density mediated attrition and fragmentation from burning or roof fall), do not impact the skeletal composition at the site. This step is critical in being able to move forward with analyses of the faunal assemblage. Eliminating these biases allows for a clear and confident statement about the skeletal representation at the site accurately reflecting the assemblage at time of deposition. With evidence that this assemblage reflects the original deposition, we can begin to look at the demographics, skeletal distribution and other taphonomic factors (such as evidence for processing through cutmarks and burning), and begin to infer human behavior on Cyprus during this time period.

In Chapter 4 and 5 I examined how humans may have procured and/or utilized this species. Chapter 4, “**Demographic evidence of human hunting and procurement**”, provides clear evidence that the Cypriot pygmy hippo remains at Akrotiri *Aetokremnos* most resembles a prime-dominated, or hunted, population when compared to theoretical and ecological profiles. In the absence of any identifiable cut marks, this demographic study is—to date—the most compelling evidence for human hunting and utilization of this species. While these studies both show that humans interacted with and procured this species they do not implicate humans for the actual extinction of these animals. Chapter 5, “**Direct human modification and relative skeletal abundance**”, while not providing evidence of cutmarks or impact fractures, reiterates the likelihood of anthropogenic burning. No clear subsistence or transport strategy is noted which could reflect changing strategies through time amongst other scenarios. Interesting patterns are documented that are worth pursuing in the future—such as the elevated numbers of crania and mandibles and the issue of valuable ivory, as well as the changing diet breadth between the lower Stratum 4 and upper Stratum 2.

Through these four chapters, we see several key issues resolved: 1) the faunal remains at the site appear to have little natural taphonomic bias to be considered when inferring associated human behavior at the site (e.g., no evidence for density mediated attrition or fragmentation from natural processes), 2) the lower strata appear to be cultural in nature and humans are likely agents of site formation; and 3) humans have procured the species likely through hunting. These three results, as related to the larger question of potential human impact on the species, are a critical first step in making the argument for human influence on this extinction event. However, evidence for human procurement and utilization is not evidence for impact on the extinction event. Rather it makes it a potential explanation.

Before definitively implicating humans, we must first fully understand the population dynamics and paleocological context of what is happening leading up to and during the extinction event. Chapter 2, “**Inferring behavior and subsistence**”, examines the dietary preference and habitat constraints of this species. This chapter shows that while humans may have been hunting the Cypriot pygmy hippopotamus, the dramatic climate change and inferred habitat change could have impacted the hippopotami’s viability to a significant level. Looking at skeletal and tooth morphology, it becomes clear that the Cypriot pygmy hippopotamus was adapted to rocky terrain, was terrestrialized, and preferred a browsing subsistence strategy. This browsing subsistence strategy is in agreement with the presumed ecology of Cyprus during the Pleistocene—consisting of a closed habitat with abundant trees. When looking at the stable isotope analyses, we see that at the time of Akrotiri *Aetokremnos*, the Cypriot pygmy hippopotamus shows signs of increasing aridity that mirrors those habitat and climatic shifts of the surrounding mainland. While modern hippos show the ability to adapt to changing vegetation, island species tend to be more insular and highly specialized—often making dramatic shifts in vegetation, climate, and/or habitat intolerable for the species. As a result, it seems very likely that this shift in climate change and habitat, which is registered on some level in the isotope values from the remains at Akrotiri *Aetokremnos*, would have a dramatic impact on the species.

Not addressed here are the indirect anthropogenic impacts that may have influenced the survivability of the species. The two most likely indirect anthropogenic impacts on Cyprus at this time would be: 1) the introduction of a novel competitor; and 2) habitat alteration. *Aetokremnos* contains the first remains of the wild boar, *Sus scrofa*, on Cyprus (Simmons 1999; Vigne 2009). The species appears to be a domesticated dwarfed version of its mainland counterpart (Vigne

2009). The presence of dwarfing and the inability of the wild boar to access the island by other means have led to the hypothesis that humans are the cause for this species' introduction (Vigne et al. 2009). Vigne et al. (2009) argue that this species was first introduced 11,400-11,700 cal. years ago. The fact that the species is the only recognized novel competitor on the island at this time, combined with the short overlap of the two species, suggests that this introduction may have contributed to the decline of the hippos. The potential interaction between these two species and the impact the wild boar may have had on this extinction event deserve attention.

To date, the idea of habitat alteration on the island during the Late Pleistocene has not been explored. While several other early and/or contemporaneous sites have been proposed in the past ten years, most sites appear to be expedient or seasonal use locations. Overall, little about the paleoecology of the island and of the earliest inhabitants during the Late Pleistocene is known. With continued work on the island, and potential identification of more inland sites, these impacts can be better addressed.

Overall, while the studies presented here provide more clarity surrounding this extinction event, they do not address the ultimate cause of extinction. As it stands, this extinction may be due to be a combination of factors with both human hunting and climatic change influencing the fate of the Cypriot pygmy hippopotamus. While the hypothesis that humans hunted this species is supported through demographic evidence, it is highly likely that the dramatic climate change occurring simultaneously may have made the species more susceptible to extinction. In addition to further work identifying potential indirect anthropogenic factors, insight and work on determining the population dynamics of this species would provide profound insight into the relative impacts of these factors. This work could be achieved by documenting the population

history of this species through time, then correlating population fluctuations with human and climatic influences.

### **Future Work: Population History and Ancient DNA**

Extinction dates are determined from the latest presence in the fossil record, or the last appearance dates (e.g. Bover & Alcover 2008; Faith & Surovell 2009; Jablonski & Chaloner 1994; MacPhee 1999). However, the presence of a species in the fossil record gives little indication of the stability of the species at that time. It is possible that the species had been slowly dwindling in numbers for thousands of years, gradually approaching extinction. It is also possible the species had previously undergone a severe bottleneck from which it never fully recovered, lowering its population size well before the last appearance in the fossil record (Drummond 2005; Shapiro 2004). Therefore, looking for causal relationships between stressors present around the last occurrence of the species and the extinction event may be misleading. Addressing these issues requires the development of a detailed population history of the extinct species that allows for the detection of any previous population decline, as well as evaluating the population size at the time of their last known appearance. For the pygmy hippopotamus, the last known appearance is represented at Akrotiri *Aetokremnos*.

Future work can be focused around using ancient DNA (aDNA) analysis to calculate the effective population size (number of breeding females) present at the last occurrence of the species and assess the feasibility of determining the effective population size prior to the last occurrence of *Phanourios minutus*. With this information, it's possible to detect any previous bottlenecks the species may have gone through and to what degree, if any, the species was able to recover from them. More importantly, we would be able to determine if pygmy hippopotami

were already declining in numbers before the presence of humans, and if this decline correlates with a change in hippopotamus diet and/or climate. If the population was thriving at the time of Akrotiri *Aetokremnos*, and no significant bottleneck was present in their population history, one can then assume that the species' extinction was more catastrophic in nature and occurred very rapidly around the time period represented at *Aetokremnos*. Population dynamics can be addressed through ancient DNA analysis of the species from paleontological and archaeological sites.

Ancient DNA analysis has become increasingly important for understanding the changes in size of prehistoric and historic populations (Chan 2005; Hadly 2003; Ramakrishnan & Hadly 2009). It is possible to estimate population parameters directly from gene sequence data by using coalescent theory, a stochastic process that describes how population genetic processes determine the shape of the genealogy of sampled gene sequences (Drummond 2002, 2005; Griffiths & Marjoram 1996; Kuhner 1998, 2000). It is also possible to create population histories for species to better understand the timing and frequency of bottleneck events that may explain present day population sizes and/or lack of genetic diversity (Chan 2006; Chan 2005; Hadly 2003; Ramakrishnan & Hadly 2009). These tools have been utilized to correlate population fluctuation with climate change and/or human impacts, such as with the Late Pleistocene cave bear extinction and the population decline of North American bison (Drummond 2005; Stiller 2010; Shapiro 2004). Applying this methodology to the island of Cyprus, correlating the population dynamics of the pygmy hippopotamus with human influence and/or climate change, could provide similar insight into the timing and relative impacts on the species' extinction.

The pygmy hippopotamus is thought to have arrived on the island of Cyprus at least hundreds of thousands of years ago (Knapp 2010; Sondaar 1986), some suggesting as early as

1.8 million years ago (Sondaar and van der Geer 2002). This provides ample time for the species to acquire enough genetic variation for the creation of a population dynamics history (Prost 2010). As part of this dissertation work, nine samples (five teeth and four bone) of the Cypriot pygmy hippo were processed and evaluated for the presence of ancient DNA. Unfortunately, no DNA was recovered from these samples. However, the time available for lab work was limited and as a result there was insufficient time to adequately troubleshoot lab protocol and designed primers. Because previous work has successfully extracted aDNA from other faunal remains at the Akrotiri *Aetokremnos* site (Poulakakis 2006), and I was successfully able to extract a 264 base pair segment of hippopotamus mitochondrial DNA from a single sample of pygmy hippopotamus bone from the Cypriot paleontological site Ayia Napa *Spelios tou Tapa*, a larger scale study involving aDNA and population dynamics of this species should be considered feasible.

### **Larger Implication for Cypriot Prehistory and Lingering Questions**

While this study focuses on the extinction of the Cypriot pygmy hippopotamus, the site Akrotiri *Aetokremnos* has remarkable implications for understanding not only the earliest Cypriots, but the larger questions of movement and seafaring in the Mediterranean. This is an active area of research, with a relatively recent emphasis on identifying the earliest archaeology on the island. Understanding people's subsistence strategies and potential movement within and throughout the islands of the Mediterranean are still not fully understood (Knapp 2010; Panteli 1984; Price 1977). Perhaps more poorly understood are their mainland interactions. Many remarkable changes were happening in the nearby Levant during the Late Pleistocene, which undoubtedly would have influenced those who were sea-faring throughout the Mediterranean.

Understanding human influence and utilization of the pygmy hippos of Cyprus is a critical piece to the overall picture during this time—as many other Mediterranean islands hosted their own unique insular fauna, including other species of pygmy hippopotami and/or dwarfed elephants. These large mammals and what they could provide by means of subsistence and materials (such as ivory) should not be overlooked when discussing the strategies employed by what are largely viewed as highly mobile fisher foragers accessing the islands at this time.

Focusing on the earliest Cypriots, this research raises a variety of questions relating not only to their subsistence strategies, but their overall use of the island and their material procurement. The location of this site, at the very southern tip of a peninsula which may have been a small sub-island at the time, is puzzling. Why accumulate over 300 individual hippopotami in such a remote location compared to the mainland? The increased number of crania and mandibles compared to the rest of the skeletal remains also raises another question related to the potential use of ivory. This latter question is easily tested by calculating the number of incisors at the site, and may provide some valuable insight into the behavior and decisions of these early inhabitants and their potential relationships with other island and mainland groups.

Overall, the archaeological site Akrotiri *Aetokremnos* is a unique and pivotal site for understanding not only the extinction event of a large mammal during the Late Pleistocene, but for gaining a deeper understanding of the earliest sea-farers in the region. This site will continue to be instrumental in understanding this earliest occupation of Cyprus. In addition, the holistic approach to studying this extinction event can be applied to other individual species—allowing for a deeper understanding of the dynamics involved in Late Pleistocene extinction events before extrapolating larger global and regional patterns.

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