Dental Microwear Texture Analysis of Early Pleistocene Hominin Prey:
A Test of Foraging Seasonality

By

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Abstract

The contribution of meat to the diet of Early Pleistocene hominins, and *Homo* in particular, is implicated in the emigration of *Homo* out of Africa, in the elongation of the legs and expansion of the brain, in the development of slow growth and long senescence, and in a variety of social dynamics hypothesized to underlie modern human behavior. It is notable that these critical developments originate not only with the earliest evidence for persistent hominin carnivory, but in the context of an increasingly seasonal and variable climate.

In this study, hominin foraging seasonality is assessed using dental microwear texture analysis (DMTA) and examined in light of carnivore competition in a highly seasonal environment. First, ecological constraints on hominins entering a predatory niche in eastern African savanna of FLK Zinj (1.848 Ma) at Olduvai Gorge, Tanzania are discussed. At a maximum of 52-63 kg, the FLK Zinj hominins would have been subordinate members of the carnivore guild. Nevertheless, archaeological sites clearly demonstrate that hominins and carnivores overlapped in habitat and prey preferences, and time and space. As omnivores, hominins had a broader array of foraging strategies available to them, including seasonal niche partitioning, prompting the question: did hominins forage for meat seasonally, and if so, was the strategy nutritional or non-confrontational?

Several previous studies have attempted to ascertain the seasonality of Early Pleistocene sites using taphonomic analyses, but their results have been inconclusive. To investigate hominin meat foraging seasonality at FLK Zinj and the penecontemporaneous carnivore site of FLK North, this dissertation tests the ability of DMTA, a new, non-destructive method, to determine the season of death (SOD) of prey animals. The method is tested on modern impala with known dates of death. The results suggest that DMTA is indeed capable of tracking SOD. The effect is subtle but statistically significant in the heterogeneity of microwear features across the occlusal molar surface at several scales of analysis, with wet season samples more heterogeneous than dry season samples. This pattern is unexpected, given the greater variability of food textures in the dry season impala diet, and is interpreted to reflect an increase in atmospheric grit in the dry season, as grit particles are known to homogenize microwear. These results bode well for the ability of DMTA to identify SOD in arid environments.

DMTA is then applied to anthropogenic FLK Zinj and the slightly younger carnivore site FLK North. Both sites accumulated during climatic phases of maximum aridity in wooded habitats within 200 m of freshwater springs. Both sites contain similar faunal assemblages dominated by extinct bovids *Parmularius altidens* and *Antidorcas recki*. Using DMTA analysis, the SOD of these species is compared between sites using mean heterogeneity at multiple scales of analysis. The research design accounts for the possibility that microwear heterogeneity reflects seasonality differently from the pattern observed in modern impala, and investigates whether hominins were operating during the same time(s) of year as peneconemporaneous carnivores.

The results reveal no statistically significant differences in heterogeneity between sites, suggesting that hominins were not employing seasonal strategies to avoid carnivores when foraging for meat. Despite being physically subordinate members of the carnivore guild, hominins had apparently developed behavioral and possibly technological strategies that enabled them to compete for animal resources during the same seasons and in the same places that leopards, lions, and extinct sabertoothed cats were operating. In conjunction with the evidence for increasing body size and brain size, and the development of the Acheulean, the present analysis of prey SOD at FLK Zinj appears to reflect a hominin rapidly-adapting to membership in the carnivore guild during a time of increasing climatic instability and seasonality. The results further suggest that meat and other animal resources had become an integral part of the foraging strategy of a carnivore-guild member, as it is for modern hunter-gatherers in similar environments.

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Chapter 1. Hominins as Predators in the Seasonal Savannas of the Early Pleistocene

Introduction

During the Pleistocene, eastern Africa became more arid and seasonal, creating a new suite of challenges in the evolution of early humans. Seasonal resource availability has been shown to have a profound effect on adaptive strategies. Developing a new morphological or behavioral suite to access available but challenging resources enables organisms to mitigate against the seasonal scarcity of other resources (e.g., Norconk, 1996) and may play a significant role in driving species radiations (Rosenberger and Strier, 1989). In the eastern African hominin record of 2.0 – 1.7 Ma, as many as four different species coexisted. Both environment and diet appear to have played major roles in hominin species radiation and niche partitioning (Reed, 1997; Leakey et al., 2001; Foley, 1993; Ungar et al., 2012).

Meat eating is integral to the evolution of the genus *Homo*. The earliest evidence for stone tools coincides with the earliest claims for carcass butchery (Harmand et al., 2015; McPherron et al., 2010; Dominguez Rodrigo et al., 2005; Semaw et al., 2003). While these australopithecines had an archaeologically visible taste for meat, it was not until *Homo* appeared that consistent carnivory became a hallmark of the hominin diet (Bunn and Kroll, 1986; Ferraro et al., 2013; Egeland and Dominguez-Rodrigo, 2008). By making this carnivorous leap, hominins went from prey to competitors in the carnivore guild. According to Root (1967: 335), a guild is “a group of species that exploit the same class of environmental resources in a similar way,” thereby overlapping “significantly in their niche requirements.” If we take the modern African carnivore guild as a model for predator dynamics in the Early Pleistocene, we may predict that meat eating hominins modified their behavioral niche to reduce competition and predation from guild allospecifics.

This study is the first to use dental microwear texture analysis (DMTA) to evaluate the role of seasonality in hominin foraging at Olduvai Gorge, Tanzania. Olduvai is among the best-studied localities dating to 1.9 –1.2 million years ago (Ma.; Leakey, 1971; Hay, 1976), and is at the center of debates about hominin meat foraging and landscape use (Binford, 1981; Bunn and Kroll, 1986; Blumenschine and Peters, 1998). The most prolific sites, including FLK Zinj, BK, FLK N, and FLK NN, are located within 200 meters of contemporaneous freshwater (Ashley et al., 2008, 2010a, 2010b), suggesting a functional relationship between foraging activities and freshwater in an otherwise arid habitat. Olduvai is therefore ideal to answer questions about early hominin foraging strategies in a highly seasonal environment. Did Early Pleistocene hominin meat-acquisition vary seasonally? If so, what role did freshwater play in organizing prey and predators on the landscape? Did hominins forage for meat competitively with carnivores or did they avoid confrontation? Identifying the effect of seasonal and perennial resources on foraging will advance research into the behavioral adaptations of Early Pleistocene hominins.

Objectives

1. Determine season-of-death (SOD) profiles in eastern African fossil prey assemblages using dental microwear analysis.
2. Evaluate the hominin foraging niche in the eastern African paleoenvironment through comparison with large felid, chimpanzee, and Hadza hunter-gatherer seasonal hunting patterns in analogous environments.

3. Contribute to our understanding of hominin foraging by providing additional ways to characterize hominin meat acquisition—as seasonal or annual, as competitive or risk-aversive.

Why Meat-Foraging Matters

Large game hunting has lain at the heart of what it means to be human in conceptual frameworks spanning the entire evolution of *Homo*, and is central to hypotheses about the evolution of the modern human body plan (Aiello and Wheeler, 1995; Bramble and Lieberman, 2004), emigration out of Africa (Anton, 2003; Ehrlich 1989), behavioral flexibility (Foley et al., 1991), food sharing and division of labor (Isaac, 1978), and modern life history (Hawkes et al., 1997; Kaplan et al., 2000). Each of these hypotheses presumes the substantial inclusion of meat in the diet of early *Homo*, but how this meat was acquired continues to be debated because it requires a degree of behavioral sophistication many researchers see as far too human.

Effective large mammal exploitation in the later Middle and Upper Pleistocene is considered evidence of modern human cognition by many researchers (e.g., Marean, 1998; McBrearty and Brooks, 2000; Henshilwood and Marean 2003; Binford, 1984, 1985; Klein, 2001; Milo, 1998; Thackeray, 1992; Gamble, 1994). What constitutes “effective” exploitation is heavily debated (Henshilwood and Marean, 2003). Binford (1989) cites planning depth, tactical mobility, and curation as the hallmarks of modern human cognition. He defines planning depth as "the potentially variable length of time between anticipatory actions and the actions they facilitate, amount of investment in anticipatory actions and proportion of activities so facilitated" (Binford, 1989:19). Tactical depth he defines as "the variable capacity, based on stored knowledge of mechanical principles, environmental characteristics, and hence opportunities" (Binford, 1989:19) to shift activities in response to situational demands. In other words, planning depth is the ability to work toward a future goal, and tactical depth is the ability to react to changing circumstances. Curation refers specifically to the manufacture, transport, and maintenance of tools in advance of their anticipated use.

Seasonal hunting of large game, in particular, is frequently treated as a marker of emerging cognitive abilities and the "human revolution" that was initially attributed to the Late Stone Age and Upper Paleolithic, and later extended to the Middle Stone Age and Middle Paleolithic (e.g., Kaufman, 2002; McBrearty and Brooks, 2000; Klein, 1994, 1995; Klein et al., 1999; Milo, 1998; Soffer, 1989). In higher latitudes, edible plant biomass is lower than in the tropics, and seasonally unavailable (Roebroeks et al., 1992). Hunting necessarily contributed to a large portion of the diet of modern and archaic humans across a variety of newly colonized habitats. Using prepared weaponry to ambush a seasonally-migrating herd as it passes through a narrow valley, rapidly dismembering the kill, and transporting it elsewhere to avoid encountering carnivores that have been alerted to the presence of a fresh carcass, constitutes a series of activities involving curation, planning, and tactical mobility. Together with the archaeological record for abstract thinking, innovativeness, and symbolic expression (McBrearty and Brooks, 2000), the seasonal use of the landscape is seen as an important source of evidence for cognitive evolution and modern behavior. Seasonal hunting strategies are well established at Late Pleistocene sites, for example in the Levant (Lieberman, 1993) and Spain (Pike Tay et al., 1999) using dental cementum analysis, and in South Africa (Klein, 2001) using the age of seasonally-breeding prey in archaeological assemblages.

Neandertals were once regarded by prominent paleoanthropologists as too primitive to engage in behaviors that required planning depth, tactical mobility, and curation (Binford, 1985, 1989). Over time, the archaeological record has accumulated to reveal Neandertal sites as rich as the Upper Paleolithic in evidence for seasonal hunting. From isotope and microwear studies, it is evident that Neandertals ate large quantities of meat comparable to the top contemporaneous carnivores (Richards et al., 2000; Richards and Trinkaus, 2009), that they acquired primarily by hunting big game (*e.g.,* Gaudzinski, 1996; Gaudzinski and Roebroeks, 2000; Stiner, 1994; Steele, 2004; Dusseldorp, 2009). Seasonal patterns of hunting have been documented at many Neandertal sites (Speth and Tchernov, 2001; Pike-Tay et al., 1999; Britton et al., 2011) using taphonomic, cementum, and isotopic analyses.

Earlier in the archaeological record, the discussion of foraging seasonality becomes more theoretical. Indeed, the method by which meat was procured remains hotly debated. Most researchers find sufficient evidence that hominins were established hunters by 1.0 Ma (Foley, 1987). Before this, there is significant disagreement about where hominin subsistence fell on the continuum of hunting – scavenging strategies, with some proposing an ambushing hunting strategy (e.g., Bunn and Pickering, 2010a; Bunn and Gurtov, 2014), others a power scavenging approach (e.g., Bunn and Ezzo, 1993), and yet others a passive scavenging niche (Binford, 1981; Blumenschine, 1986, 1987, 1995; for a review, see Dominguez-Rodrigo et al, 2007b). By suggesting that the earliest members of our genus were capable of hunting (e.g., Bunn and Kroll, 1986; Bunn, 2001; Bunn and Pickering, 2010a; Bramble and Lieberman, 2004; Ferraro et al., 2013), sharing meat surpluses (Isaac, 1978), or defending carcasses against other predators (Rose and Marshall, 1996), a greater degree of "humanness," or behavioral sophistication, is inferred than many researchers feel is unwarranted (e.g., Binford, 1981, 1985; Blumenschine and Cavallo, 1993; Blumenschine et al, 2012; Potts, 1984; Klein, 2001).

The earliest archaeological indication of meat eating derives from two fossil bones dated to ~3.39 Ma from Dikika, Ethiopia (McPherron et al., 2010). These are a right rib from a size 4 bovid, and a femur shaft from a juvenile size 2 bovid. Both retain surface modifications that McPherron and colleagues (2010) have identified as cut marks and percussion marks inflicted by stone tools with the aim of removing adhering tissues and marrow. This interpretation has been challenged on the basis of insufficient evidence and equifinality (Dominguez-Rodrigo et al., 2010, 2011, 2012), as well as supported by landscape taphonomy at Dikika (Thompson et al., 2015). Less contentious are the penecontemoraneous stone tools dated to ~2.6 Ma and cut marked bones dated to ~2.5, all found at Gona, Ethiopia (Semaw et al., 2003). These include Oldowan choppers, cores, flakes, and debitage made from a variety of raw materials, as well as a cut marked equid calcaneum and a bone flake. At nearby Bouri, Ethiopia, several cut marked and percussed bones, including a bovid mandible and tibia, and a *Hipparion* femur, are also dated to ~2. 5 Ma (de Heinzelin et al., 1999). Though no stone tools were found *in situ*, de Heinzelin and colleagues (1999) report finding Oldowan stone artifacts as isolated surface finds in the same stratigraphic horizon. At these very early dates, the maker of these assemblages may well be an australopithecine, though the earliest known fossil *Homo* is now ~2.8 Ma (Villmoare et al., 2015).

Evidence for persistent hominin meat eating begins to accumulate around 2.0 Ma. Ferraro and colleagues (2013) describe the assemblage at Kanjera South, Kenya, as the result of hominin acquisition and processing of numerous small, relatively complete, carcasses. These are dominated by bovids (mostly < 180 lbs), but also include equids, suids, and hippos. The relative abundance of tooth marks and epiphyses:shafts resembles frequencies for assemblages in which humans have first removed all available flesh and marrow from the bones before ravaging (Ferraro et al., 2013). They retain cut and percussion marks at low frequencies, but the survivorship of many elements rapidly consumed by carnivores supports an interpretation of first access to smaller bovids by hominins (Ferraro et al., 2013).

The earliest evidence for large game hunting is found at FLK Zinj, a locality in Olduvai Gorge, Tanzania, dated to 1.848 Ma. Whereas Kanjera South is dominated by size 2 bovids (50 – 250 lbs), FLK Zinj has a large assemblage of size 3 bovids (251 – 750 lbs) that retains substantial numbers of cut marked and percussed bones. Skeletal part representation, and cut and gnaw mark frequencies, described below, support the interpretation that hominins independently acquired the majority of carcasses that they transported to site. Because FLK Zinj is so early in the archaeological record, some researchers are hesitant to ascribe the cognitive and physical abilities necessary for organized hunting to the most primitive members of the genus *Homo* (e.g., Binford, 1983). It is generally accepted, however, that by 2.0 Ma, hominins were consistently butchering carcasses in remove some meat and marrow.

In the highly seasonal Early Pleistocene savanna of eastern Africa, it is likely that hominins experienced resource seasonality in both their plant and meat foraging. Variability in hominin dental microwear, which reflects the fracture properties of the diet, suggests that both australopithecines and early *Homo* relied on fallback foods frequently, which is often a response to seasonal dietary stress (Ungar, 2004). Prior to the present research, only one study examined seasonality at FLK Zinj. Speth and Davis (1976) compared faunal lists from the Olduvai fossil assemblages with prey SOD frequencies created by the !Kung and G/wi foragers. These foragers have a strongly seasonal pattern of bovid hunting in the dry season and tortoise collection in the wet season. When these data are plotted on a triangle graph, the Olduvai samples cluster tightly at the *Chelonia* and *Bovidae* axes, which represent the wet and dry SOD prey of the modern hunters, respectively. The authors interpreted this correlation as tentative support for equivalent patterns of seasonal hunting by hominins. However, the faunal lists used by Speth and Davis (1976) were preliminary. Moreover, there is no evidence that tortoises were exploited at any of the sites used in their study, and the mere fact of their presence at Olduvai Gorge does not mean *a priori* that bovids or tortoises were taken in the same season as they are hunted by modern foragers in the Kalahari. While highlighting an important aspect of hominin foraging dynamics, their methodological approach allowed only for speculation. Seasonality at FLK Zinj, and in the fossil record of early *Homo* more generally, remains to be explored.

Olduvai Gorge: A Case Study

Olduvai Gorge is an ideal site to study hominin foraging seasonality because it has produced some of the earliest evidence for consistent meat eating. The site has been investigated by researchers for over a century, beginning with Hans Reck in 1913. His report of fossils later attracted Louis Leakey to the gorge. Following several visits, Louis and Mary Leakey began regularly excavating in 1935, eventually discovering the famous *Zinjanthropus boisei* OH5 cranium, later assigned to *Australopithecus boisei*, in 1959. Mary Leakey's excavations subsequently produced dozens of hominin fossils belonging to *A. boisei* and *Homo habilis*, including the type specimen OH7, and multiple high density lithic and faunal accumulations. Among the latter are FLK Zinj, named for the onsite discovery of OH5, and FLK North, both found in the junction of the modern Main and Side Gorges.

Geology and Paleoenvironment

Olduvai Gorge is located in Tanzania on the western edge of the East African Rift, 3° south of the equator. It is situated in the rift basin between the Plio-Pleistocene Ngorongoro Highland to the east and Precambrian basement rock to the west. The Gorge itself is 50 km in length and splits into a Main Gorge and a Side Gorge roughly 8km west of the first fault, which marks the eastern margin of the Gorge. Fault lines can be found throughout the Gorge (Hay 1976; Ashley et al., 2010a, 2010b).

Over the last 5 – 7 million years, the eastern African climate has experienced a long-term drying and cooling trend, leading to a highly seasonal regime that promoted the spread of open woodlands and savanna grasslands, and the loss of forest habitats in Africa (Cerling and Hay, 1986). These trends became more pronounced around 2.8 million years, and again at 1.7 million years (deMenocal, 2004). Changes in insolation triggered by changes in the Earth's precession cycle also generated climate oscillations, causing the climate at Olduvai to cycle through wet and dry periods approximately every 21 ky. Mean precipitation varied from 700 mm/yr in the wet periods to 250 mm/yr in the dry periods (Magill et al., 2012a), which spans the modern mean annual precipitation of 550 mm/yr at Olduvai Gorge today (Hay, 1976; Ashley, 2007).

The earliest reconstructions of ancient Olduvai centered on the presence of a variably-sized saline-alkaline lake (Hay, 1976). Bed I was deposited by Paleolake Olduvai, which intermittently exposed and covered a wide mudflat zone. The lake fluctuated in size between 7 and 25 km in diameter, shifting to the west during the deposition of Tuff IA, placing the FLK Zinj and FLK North sites within the lake margin zone (Hay 1976). The lake was at its smallest dimensions during the Tuff IC and Tuff IF ashfalls (Magill et al., 2012a). Salinity was initially reconstructed to vary throughout the lake, with freshwater available where streams met the shoreline (Hay, 1976; Hay and Kyser, 2001). More recent analyses now indicate that the lake was never potable (Magill et al., 2012b).

Paleohabitat reconstructions of Olduvai Gorge indicate an arid to semi-arid environment that was predominantly open wooded grassland with intermittent patches of riparian woodland

(Sikes and Ashley, 2007; Bamford et al., 2008). Oxygen isotopes from carbonates (Bonnefille, 1984; Sikes, 1994), pollen analysis (Bonnefille, 1984), microfauna (Jaeger, 1976) and bovid frequencies (Plummer and Bishop, 1994) collectively indicate the presence of wooded and wet environments within the broader grassland context. These reconstructions led Olduvai researchers to characterize the paleo-basin as a largely inhospitable, open grassland environment with isolated resource patches surrounding a shrinking, unpotable lake (Blumenschine and Masao, 1991; Blumenschine and Peters, 1998; Blumenschine et al., 2008).

Recent survey work by Ashley (2010a, 2010b; Ashley et al., 2009) and Barboni and colleagues (2010) modifies some elements of the reconstruction by Hay (1976). Extensive geological surveys uncovered carbonate tufas, which form as a result of surfacing fresh groundwater. Fault lines in the underlying basalt diverted fresh groundwater to the surface, which supported the growth of a dense woodland mosaic in the immediate vicinity of the junction area (Barboni et al., 2010). Most notably, the densest sites in Bed I, including FLK Zinj and FLK N, accumulated within wood and densely wooded oases no more than 200 m from contemporaneous springs.

Olduvai Hominins

The hominins *Australopithecus boisei* and *Homo habilis* are both present and common enough to be preserved in the junction sites of Bed I, Olduvai. A possible but unlikely candidate for site accumulator at FLK Zinj is *Australopithecus boisei*, which endured at Olduvai Gorge throughout Beds I and II. The famous *Zinjanthropus boisei*, the namesake of the FLK Zinj level, is Olduvai Hominin (OH) 5, discovered at FLK in 1959. In combination with the small incisors, the enormous, flat, and thickly enameled molars, and the cranio-facial buttressing, dental microwear and stable isotope signatures of *A. boisei* reflect a diet high in fibrous grasses and sedges (Ungar et al., 2012; van der Merwe et al., 2008; Cerling et al., 2011).

The type specimen of *H. habilis,* OH7, consists of a partial hand, mandible, and parietal bones, and comes from the nearby site of FLK North North level 3, which is stratigraphically just below, and 200 m away, from the FLK Zinj level (Leakey, 1971). Its discovery in 1959 and 1960 was quickly followed by the unearthing of the OH8 foot at the same location, and the femur OH35 in the same year. Because of its more generalized, human-like features when compared with *P. boisei*, researchers have typically followed Leakey and colleagues' (1964) lead in attributing the stone tool and butchered fauna assemblages of Bed I to *H. habilis.* However, at an estimated 42 kg (McHenry, 1992), many prominent researchers have had a difficult time accepting it as anything but a scavenger (e.g., Binford, 1981; Shipman, 1986; Blumenschine et al., 1987; Blumenschine, 1995).

The recent discovery of a small, derived molar (unpublished) and a human-like fifth proximal phalanx OH86 (Dominguez-Rodrigo et al., 2015) at the site of PTK hints at the presence of larger-bodied *Homo* species at Olduvai Gorge. *Homo erectus* is known from eastern Africa as early as 1.9 Ma (Wood, 1991), and it is plausible that OH86 represents the first example from Olduvai Gorge. Should this be the case, *Homo erectus* is a third candidate for the maker of FLK Zinj and artifacts at FLK North, one which has a long-discussed body of evidence indicating carnivory (e.g., Walker et al., 1982; Shipman and Walker, 1989; Aiello and Wheeler, 1995; Navarette et al., 2011). Given that OH86 was announced less than a year ago, the potential impact of a large-bodied *Homo* in Bed I Olduvai has yet to percolate into reconstructions of hominin behavior at FLK Zinj and FLK N.

Olduvai Archaeology

FLK – Zinj

Level 22 at FLK (henceforth, FLK Zinj) is overlain by Tuff IC, dated to 1.848 (Deino et al., 2012). The excavation of the Zinj level, totaling 315 m^2, proved to be the most prolific of all the layers excavated at FLK (Leakey, 1971). The FLK Zinj assemblage is remarkably constrained vertically within a silty-clay lacustrine deposit 0.22 m thick overlain by the Tuff 1C ashfall, and laterally within a dense cluster of 10.6 – 26.3 bones/m2 spanning 98 m2, immediately surrounded by a low bone density of 1.5 bones/m2, and few lithic artifacts (Ashley et al., 2010a; Uribelarrea et al., 2014).

The site accumulated along the southern margin of Paleolake Olduvai. Excavations 200 m north of FLK Zinj at the site of FLK North North (FLK NN) uncovered a thick tufa underlying Tuff IC, contemporaneous with the Zinj level (Ashley et al., 2010a). The stable oxygen and carbon isotopes of the tufa record a strongly "freshwater" signal indicating a groundwater source. Ashley and colleagues (2010a, 2010b) have proposed that the water derives from rainfall occurring to the east of the rain shadow created by the Ngorongoro volcanic highlands. This water arrived through ground percolation at the FLK fault, where it then seeped to the surface. The chemical composition of the FLK NN tufa also reveals an increasingly arid climate in which Paleolake Olduvai evaporated and shrank (Ashley et al., 2010a, 2010b). The abundance of palm and woody plant phytoliths at FLK Zinj and FLK NN indicates a wooded to densely wooded habitat in the immediate vicinity of these sites, including Acacia woodlands and gallery forests. This interpretation is supported by microfauna (Fernandez-Jalvo et al., 1998) and bovid dietary and habitat reconstructions (Plummer et al., 2009; Kappelman 1984). Recent paleolandscape reconstructions show that the site accumulated along an elevated platform that is traceable for hundreds of meters, providing a well-drained ridge overlooking the lake and the spring (Ashley et al., 2010a; Uribelarrea et al., 2014).

Nearly 2,400 Oldowan lithic artifacts were recovered by Leakey (1971). These included numerous sharp-edged flakes as well as 60 tools and 135 items identified as utilized material (Leakey 1971). Approximately 1,000 light-duty lithics and bones show spatial patterning as part of an apparent circle 21 x 15 ft. A gap of very low artifact density of ~3 m separates the circular concentration from an arc of larger lithic and faunal remains. Leakey reports that J. D. Clark suggested that this arrangement could reflect the presence of a constructed or natural windbreak over which (or into which) hominins tossed the inconveniently large products of their activities (Leakey 1971).

The faunal remains at FLK Zinj are even more numerous. Mary Leakey initially reported 3,510 specimens, of which 1,090 were identified to taxon or element (1971). These included several bovid species as well as suids, equids, primates and reptiles. Reanalysis by Henry Bunn found that approximately 60,000 bone specimens were collected (Bunn and Kroll, 1986). Skeletal and taxonomic identification of all of the identifiable fragmentary specimens by Bunn yielded a comprehensive MNI of 48 large mammals, including 29 bovids, two giraffids, several small carnivores, a hippopotamus and an elephant, the latter represented by several tooth fragments. Each of the species excluding the hippopotamus and elephant were represented by at least one cut marked bone, totaling over 200 cut marked bones in the complete large mammal assemblage (Bunn, 2001). The high degree of bone breakage made identification difficult but careful analysis of the fragments produced 3,500 larger mammal bones identifiable at least to skeletal element (Bunn and Kroll, 1986), and more than 100 refitting sets (Bunn, 1982), which attests to the rapid burial and undisturbed context of the site.

FLK North levels 1 – 3

FLK N levels 1 – 3 is one of the densest assemblages at Olduvai, situated just under 100 m north of FLK Zinj. The site was located on the southern margin of Paleolake Olduvai, where the periodic flooding deposited a waxy clay over the accumulating assemblage (Ashley et al., 2010a). Unlike the temporally constrained FLK Zinj, FLK North 1 – 2 spans ~20,000 years and ~1 m of sediment that accumulated under Tuff IF (1.803 ± 0.002; Deino, 2012) in Bed I (Ashley et al., 2010a). As of 2009, a total of 94 m² have been excavated (Bunn et al., 2010). The Leakey collection has an MNI of 63 large animals (Dominguez-Rodrigo and Barba (2007a) and 2019 lithic specimens (Leakey, 1971). An additional 168 lithics (Diez-Martin et al., 2010) and 21 large animals were excavated between 2007 and 2009, and have yet to be fully integrated with the Leakey collection (Table 1.1; Bunn et al., 2010)

While the Leakey collection of FLK North 1 – 2 is well-published (e.g., Leakey, 1971; Bunn, 1982, 1986; Bunn et al., 2010; Dominguez-Rodrigo and Barba, 2007b), level 3 is included here because the distribution of specimens in lowermost level 2 and level 3 is not distinct once plotted post-excavation (Dominguez-Rodrigo and Barba, 2007b). The most recent taphonomic analyses present FLK North 1 – 3 as an undifferentiated geological unit (Dominguez-Rodrigo et al., 2010). Hereafter, FLK North 1 – 3 is referred to as FLK N.

Though the site accumulated during a period of increasing aridity in eastern Africa, FLK N was well-vegetated. The site was located in a dense but patchily distributed woodland with > ~40 – 90% canopy or bush cover in the immediate vicinity, and more open grassy woodlands with ~20 – 70% woody cover in the surrounding 2 km^2 to the southeast (Barboni et al., 2010). Ashley and colleagues (2010a) have identified multiple tufa formations indicating a contemporaneous freshwater springs, the largest of which is situated along the Zinj Fault 100 m to the southeast and the closest of which is ~30 m to the west. FLK N appears to have accumulated on a slight rise of about 1 m that kept the area well-drained relative to the lower-lying lake margin (Ashley et al., 2010a). Barboni and colleagues (2010; Ashley et al., 2010a) describe the FLK N site as a "groundwater palm forest/woodland or bushland" (pp. 344) comparable to that found at the modern Lake Manyara national park, Tanzania. There, a large, unpotable, saline-alkaline playa lake is fed seasonally by small rivers, but freshwater springs flow year round.

The Foraging Debate at Olduvai Gorge

One of the greatest debates about the behavior of early *Homo* concerns the species' ability to acquire meat—the hunting vs. scavenging debate. Hominins are variably characterized as near-modern hunter-gatherers with a division of labor, pair bonding and regular use of base camps (Leakey, 1971; Isaac, 1978), as assertive opportunists capable of hunting large game (Bunn and Kroll, 1986; Bunn, 2001, 2007a, 2007b; Bunn and Pickering, 2010a; Bunn and Gurtov, 2014), and as bipedal apes timidly awaiting their turn at the back of the line for carnivore kills (Binford, 1981; Blumenschine and Masao, 1991; Blumenschine and Cavallo, 1992; O'Connell et al., 1990, 2002; Faith et al., 2007).

FLK Zinj and FLK N were first presented as "living floors" or occupation levels by Mary Leakey, defined as a site where "the occupation debris is found on a paleosol or old land surface with a vertical distribution of only a few inches…" (p. 258, 1971). The living floor hypothesis closely resembles the "home base" model put forward Glynn Isaac. Based on his work on the KBS site at Koobi Fora, Isaac developed a highly influential model of hominin landscape organization (1978). His comparative study of subsistence strategies among *Pan troglodytes* and human hunter-gatherers underscored several key differences between the genera, some of which leave patterns in the material record. These include a range of variably complex behaviors present among humans, including abstract verbal communication, sexual division of labor, long-term mating bonds, food transport and sharing, and a diet focused to a greater extent upon animal proteins.

Large Animal MNI at FLK North and FLK Zinj

	FLK North	FLK Zinj	
Bovidae Taxa	**Bunn and Gurtov 2013[1]**	**Bunn and Kroll, (1986)[2]**	**Bunn and Gurtov 2013[1]**
Kobus sigmoidalis	0	9	12
Parmularius altidens	30	6	6
Antidorcas recki	21	6	5
Antilopini size 2	10	1	2
Alcelaphini size 2	3	0	1
Tragelaphus strepsiceros	3	1	1
Synceros acoelotus	1	1	1
Connochaetes sp.	0	3	3

	FLK North		FLK Zinj
Other Taxa	**Leakey Collection[3]**	**TOPPP[4]**	**Bunn and Kroll, (1986)[2]**
Suid	2	1	5
Equid	1	2	5
Giraffid	1	1	2
Hippopotamid	1	1	1
Elephas	0	0	1
Rhino	1	0	0
Carnivoa	8	1	3
Theropithecus	1	0	0

Table 1.1. Minimum number of individuals (MNI) in various taxonomic groups at FLK North and FLK Zinj. [1]Unpublished MNI from analyses undertaken by Bunn and Gurtov in 2013 on the Leakey collections house in the National Museum in Dar es Salaam, Tanzania. [2]MNI published in Bunn and Kroll (1986). [3]MNI of Leakey collections published by Dominguez-Rodrigo and Barba (2007b). [4]MNI from excavations conducted by The Olduvai Paleoanthropology and Paleoecology Project between 2007 and 2009.

When these behaviors are in effect, they are often oriented around a central place where group members reunite to share transported resources after hunting and foraging. The remains of these activities leave recognizable patterns in the form of dense concentrations of transported and butchered bones, stone tools, and scatters of lithic material resulting from the knapping activities that produced the butchering implements. Isaac categorized this particular pattern of abundant fossil remains, which he observed at KBS, as a Type C site or “home base”. The same pattern of remains was identified by Mary Leakey at FLK Zinj and FLK N, Olduvai Gorge. These behavioral models of carcass transport to preferred locations and meat consumption rest on two features of the archaeological sites: the association of bones and tools, and the density of bone remains relative to the surrounding paleolandscape. Both researchers attributed the anomalous concentrations to anthropogenesis.

Taphonomic studies have since demonstrated that felids, too, accumulate carcasses (Tappen, 1995; Cavallo and Blumenschine, 1998). However, there are key distinctions between the accumulations made by leopards or other carnivores and those seen in the archaeological record (Behrensmeyer, 1983; Tappen, 1992, 1995; Potts, 1988; Dominguez-Rodrigo et al., 2007a). Observations made in several eastern African national parks generated the following data:

1. Felid carcass accumulations rarely contain more than 3 individuals (Behrensmeyer, 1983; Tappen, 1992; Potts, 1988).
2. At felid kill sites, the bones are more dispersed than they appear at key sites in the discussion of hominin predatory behavior (Behrensmeyer, 1983; Potts, 1988; Tappen, 1995; Dominguez-Rodrigo et al., 2007a).
3. Repeated felid kill sites have carcasses that are ecologically homogenous (Bunn, 1982; Potts, 1988; Dominguez-Rodrigo et al., 2007a).

These observations contrasted strongly with the dozens of bovid carcasses exhibiting a range of habitat preferences found in dense concentrations at FLK Zinj.

The living floor and home base models for eastern African sites became the foundation for highly nuanced debate about the nature of hominin meat-foraging. The high density anomalies at FLK Zinj and FLK N in particular have generated several hypotheses about who was responsible for the accumulation of bones. The debate can be stated simply as an aggressive vs. passive meat acquisition argument, though the details of both positions have developed over time. Passive strategies include scavenging from carcasses that died of natural causes, and scavenging from abandoned carnivore kills. Aggressive, or active, strategies are those in which hominins drove predators from their kills early, allowing them to access carcasses before they are fully consumed, or hunted prey animals themselves.

To distinguish between these various meat-foraging strategies at a site, three additional lines of evidence are critical. The first is the relative abundance of axial vs. appendicular skeletal elements. Bovid limbs are the meatiest parts of the carcass and are among the first parts consumed by carnivores, particularly the hind legs (Schaller, 1972; Blumenschine, 1986). Bone surface modification is the second, and includes the analysis of bone breakage and stone-tool cut marks, their placement, and their relative abundance compared to carnivore tooth marks. Most recently, the mortality profiles of fossil bovids from FLK Zinj and FLK N have been compared to modern prey profiles of lions, leopards, and natural phenomena to see if the bone assemblages were generated by leopard and lion predation. Each of these evidentiary sources, described below, have been rallied in the interpretation of FLK Zinj and FLK N.

FLK Zinj: The site of FLK Zinj has featured prominently in the debate about early hominin meat-foraging capabilities and the humanness of early Homo. In the course of 30 years of taphonomic studies, the evidence has mounted in support of a highly evolved meat-foraging strategy that relied, at least in part, on active hunting (Bunn and Pickering, 2010a; Bunn and Gurtov, 2014).

The very human-like subsistence strategy proposed for FLK Zinj was initially rejected by researchers who view both the evidence and the hominins as too scanty to support active hunting (e.g., Binford, 1981, 1986; Shipman, 1986; Blumenschine, 1995). To explain the high-density anomaly at FLK Zinj, Binford (1981) proposed that the site was a lion kill site that accumulated over thousands of years, though unweathered bones, sharp flakes and limited vertical distribution suggest otherwise (Leakey, 1971). Using the preliminary limb counts presented by Leakey (1971), Binford (1981) reported that FLK Zinj was dominated by “heads and feet”, the skeletal elements that remain after a carcass has been killed and consumed by lions and hyenas.

The frequency of various skeletal elements at a site, relative to their frequency in a complete skeleton, is an important indication of whether prey are located where they died at the kill site, or were transported to their present location. It can also potentially reveal the decision-making on the part of the carcass butchers—whether they were selective in which parts of the animal they took, and if they prioritized these parts in a particular way. Because bone tissue structure varies in density, from very porous cancellous bone to compact laminar bone, the rate of taphonomic preservation differs among and within the various elements of the skeleton. Long bones, particularly limbs, have shafts (diaphysis) made of lamellar bone and epiphyses made of cancellous bone. In adult mammals, the pores within cancellous bone are typically filled with marrow, as are the cavities within the compact lamellar limb shafts. This makes cancellous bone particularly susceptible to damage and deletion from post-depositional processes, including bone-crunching predators and weathering (Lyman, 1994).

Perkins and Daly (1968) coined the term "schlepp effect" to describe the preponderance of goat and cow foot bones at an early hunter-gatherer site in Turkey. They proposed that after animals were butchered by hunters at the site of the kill, the bones were discarded and the meat was placed in the hide with the lower legs still attached for ease of schlepping. This publication inspired other researchers to consider the frequency of meaty limb bones relative to less-meaty axial parts at archaeological sites (e.g., Binford, 1981, Bunn and Kroll, 1986; Bunn, 1986, 1993; Blumenschine and Madrigal, 1993; Lupo, 1998). An updated optimal foraging version of the schlepp effect predicts that as carcass size and distance to preferred location increase, the number of transported elements will decrease. A high proportion of appendicular bones, such as limbs and mandibles (to which the tongue adheres), indicate selective transport of meat-rich parts to preferred locations by hominins, while the presence of axial parts, like crania and vertebrae reflect a kill site. But Bunn (1986, 1993) notes that the model is too simplistic to consistently accurately reflect the multitude of factors influencing carcass transport. Weather, time of day, proximity of predators, and personal taste can all affect how carcasses are transported, in addition to the distance between kill site and camp (Yellen, 1977; Binford, 1978; Bunn, 1986).

Even acknowledging these complexities, the presence of crania, particularly those that belong to medium and large prey animals, is highly suggestive of a kill site. Hyenas, for example, are major bone assemblage modifiers in African savannas, altering skeletal part representation after other agents (hominin or felid) have abandoned carcasses (Bunn et al., 1980; Bunn, 1982, 1986, 1991; Bunn and Kroll, 1986, 1988; Marean and Spencer, 1991; Marean et al., 1992). Hyenas preferentially delete cancellous limb bone ends, with the result that limb shafts are two – five times as likely to survive carnivore ravaging as limb bone ends (Bunn, 1980, 1982, 1986, 1991; Marean and Spencer, 1991). From an experimental assemblage of butchered carcasses subsequently ravaged by hyenas, Marean and colleagues (1992) found that vertebrae and pelves were consumed first, with vertebrae completely deleted and pelves destroyed 50% of the time. Limb shaft epiphyses were frequently destroyed while limb shafts survived almost 100% of the time. Thus, regardless of which elements were initially present, an assemblage can come to resemble the schlepp effect due to bone-crunching hyenas.

The essential distinction between a kill site and a central place to which hominins transport carcass parts is the presence of large, dense crania that remain at kill sites unconsumed by hyenas. Finding crania in an assemblage indicates the initial presence of an entire carcass. By referring to Leakey's (1971) skeletal part table, which reports on skull numbers without differentiating between cranial and mandibular elements, Binford's (1981) analysis of FLK Zinj artificially inflated the number of crania, causing the assemblage to resemble a kill site rather than a central place to which carcass parts were transported.

Prior analyses by Bunn (Bunn and Kroll, 1986; Bunn, 1993) demonstrated that FLK Zinj is instead dominated by appendicular elements. The relatively high number of limbs is a pattern known from actualistic studies with Hadza hunter-gatherers who, when constrained by very high large carcass transport costs, selectively transport limbs to their base camp after they processes the prey at the kill site (Bunn, 1993, 2001). These are the elements that are most optimally transported, particularly when carcasses are too large to be carried in their entirety.

For researchers interested in how hominins acquired carcasses, skeletal part representation is insufficient to distinguish between hunted and scavenged prey. To understand the role of hominins in the carnivore guild, and the relative contribution of meat to the hominin diet, taphonomists have turned to bone surface modification. Bunn and Kroll (1986) report that FLK Zinj produced at least 172 cut marked specimens (which omits specimens that had not been examined microscopically), the vast majority of which occur on upper limb bones (88%), particularly on the shafts at muscle attachment sites. Each of the ungulate species, excluding the hippopotamus and elephant, are represented by at least one cut marked bone (Bunn, 2001). The clustering of these cut marks is argued to reflect skinning, disarticulation, and defleshing of complete limbs (Bunn and Kroll, 1986). Though the site also contains about 400 specimens with carnivore gnaw marks, the sample is significantly smaller than is seen at sites accumulated by carnivores (Brain, 1981; Bunn and Kroll, 1986; Bunn and Kroll, 1986; Blumenschine, 1988, 1995; Capaldo, 1995).

Despite the well-acknowledged presence of cut marks on FLK Zinj specimens, their significance remained in debate. Noting the damage that contacting bone does to a sharp flake, Binford (1986) suggested that the cut marks instead reflected mistakes caused by the "extreme difficulty in processing already partially desiccated limb parts that had been previously ravaged by carnivores, leaving little usable meat available to the hominids" (pg 446). This apparent impasse led to a series of actualistic studies concerned with the amount of flesh and marrow available to hominins scavenging in the savanna.

Large felids consume carcasses in a predictable sequence, beginning with the flesh and viscera of the hindquarter, followed by forequarter flesh, ribs, and ribcage contents, and finally the accessible flesh of the head, before turning to the marrow contents of the limbs (Blumenschine, 1986). Notwithstanding Binford's (1986) argument that cut marks reflect the absence of flesh, a hominin scavenging from the abandoned kills would find very little flesh remaining after felids finished feeding, and very little carcass after hyenas were through. The practice of leopards caching carcasses in trees was suggested as one reliable, though minor, source of meat and marrow for hominins (Cavallo and Blumenschine, 1989). From these observations of carnivore behavior in the Serengeti (Cavallo and Blumenschine, 1989), and actualistic studies of gnaw mark frequencies (Blumenschine, 1988, 1995; Selvaggio, 1994; Capaldo, 1995, 1997), Blumenschine (1995; Blumenschine et al., 1996, 2005, 2012) developed an iteration of the hominin scavenging hypotheses referred to as the "carnivore-hominin-carnivore" model. In this model, the gnaw and cut mark frequencies at FLK Zinj reflect hominin butchery of transported carcass parts acquired from felid kills, which were subsequently ravaged by hyenas after hominins abandoned them on site.

The carnivore-hominin-carnivore model failed to account for the anomalous concentration of prey at FLK Zinj (Dominguez-Rodrigo et al., 2007b). If hominins were in fact scavenging for adhering remnants of flesh and limb marrow from cached leopard carcasses, their forging yields would be insufficient to promote transport to a preferred location. Instead, Dominguez-Rodrigo and colleagues (2007b) have suggested that hominins would have had to engage in power scavenging, or possibly hunting, to acquire enough meat to warrant central place foraging behavior. Moreover, the actualistic studies used to develop the model relied on three assumptions (Dominguez Rodrigo et al., 2007b): hominins and other primates are not potential agents in tooth marking, hominins are expected to thoroughly deflesh and demarrow each carcass, and all carcasses followed the same sequence of carnivore-hominin-carnivore exploitation. The gnaw mark frequencies at FLK Zinj are much more similar to actualistic studies in which whole bones, rather than demarrowed bones, are ravaged by carnivores (Dominguez Rodrigo et al., 2007b). When considered with the cut mark evidence, this suggests that hominins were not relegated to a marrow scavenging niche.

Moreover, ethnoarchaeological research with the Hadza demonstrates that cut mark frequency does not directly reflect butchery intensity (Bunn, 2001). In an analysis of cut mark location on whole carcasses butchered by Hadza, Bunn (2001) found that forelimbs, and humeri in particular, were more often cut marked than hindlimbs and femora, despite the fact that hindlimbs yield more flesh. This same pattern of relative cut mark frequency is also seen at FLK Zinj, suggesting that cut marks reflect anatomical attributes, like the relative strength of muscle attachments, rather than processing intensity.

An important breakthrough in the debate has come through the recent use of triangle graphs to analyze the faunal mortality patterns at FLK Zinj. By analyzing the chronological ages of lower bovid teeth, Bunn (2007) was able to create a mortality profile for the FLK Zinj prey. The results were compared to prey data collected for lions and leopards, the best carnivore analogs implicated by the FLK Zinj assemblage. Bunn (2007) found that within the appropriate size classes, neither of the faunal mortality patterns matched what leopards and lions are known to kill with 95% confidence. As ambush predators of small bovids, leopards create mortality profiles that are representative of the demographic distribution of their prey. At FLK Zinj, size 1 and 2 bovids were almost exclusively old males, which constitute a small portion of the living demographic distribution that is more proportionately sampled by leopards. Lions, too, are ambush predators, but prefer size 3 bovids. Once again, the size 3 bovids at FLK Zinj were not representative of a living structure, but were instead dominated prime-aged adults. To these data, Bunn and Pickering (2010a) added evidence from South African cave assemblages accumulated primarily by carnivores, and Bunn and Gurtov (2014) expanded the sample to include prey profiles created by living hunter-gatherers and mass wildebeest drowning.

The implication of these results is that scavenging, whether aggressive or passive, does not account for the FLK Zinj assemblage. This conclusion is further supported by follow up analyses of additional archaeological and felid-generated mortality profiles, all of which show that assemblages with >70% prime adults, as seen in the size 3 bovids at FLK Zinj, are a characteristic of human hunting (Bunn and Gurtov, 2014). When these data are considered with evidence for numerous cut marks at muscle-attachment sites on meat-bearing bones, and the abundance of these relative to axial elements, there is little doubt that the FLK hominins had access to significant quantities of meat unavailable to passive scavengers. Hominin hunting and differential carcass transport is the most plausible explanation for the FLK Zinj assemblage.

FLK N: The same analyses have been applied to FLK N to reveal a carnivore palimpsest quite taphonomically distinct from FLK Zinj. Initially, Leakey (1971) described FLK N as a "living floor" in acknowledgment of the high density concentration of Oldowan stone tools and large mammal bones, both of which were assumed to have been accumulated by hominins. The discovery of several bovid bones with stone tool butchery marks supported a causal relationship between stone tools and some fauna, but demonstrated a far smaller hominin behavioral contribution to the faunal assemblage than was found at FLK Zinj (Bunn, 1982, 1986). Indeed, while FLK Zinj contains numerous limb elements with hammerstone breakage and defleshing cut marks at muscle attachment sites, FLK N has very few, totaling just 21 cut marked bones and 12 bones possibly bearing percussion marks in the original Leakey collection (Dominguez-Rodrigo and Barba, 2007b). Of the individuals analyzed by Bunn (1986), a maximum of only 4 appear to have been transported and modified by hominins.

In contrast, carnivore gnaw marks and bone breakage abound at FLK N. A reanalysis of the site by Dominguez-Rodrigo and Barba (2007b) presents several important lines of evidence that FLK N was accumulated primarily by carnivores: fragmentation of skeletal elements is extensive, with specimens < 4 cm composing 20% of size group 3 – 4 bovids and 40% of size group 1 – 2 bovids, but limb bones are much more complete than those in experimentally hammerstone-broken assemblages aimed at extracting marrow (Blumenschine, 1988, 1995). The morphology, measurements, and frequency of notches, tooth pits and scratches all resemble carnivore bone breakage patterns, particularly those of hyenas which tend to leave more conspicuous bone damage than felids. The relatively greater preservation of dense limb shafts over cancellous epiphyses and axial elements also reflect extensive carnivore influence, although *A. recki* and *P. altidens* have different patterns of ravaging. Whereas 27% of *A. recki* limb bones are complete, only 7% of *P. altidens* limb bones survived without carnivore modification. Heavily broken specimens bear the marks of hyenid scavenging, while complete limb bones show furrowing at the epiphyses typical of modern felid gnawing. Dominguez-Rodrigo and Barba (2007b) interpret the greater survival rate of all *A. recki* elements relative to *P. altidens* to mean that felids, probably leopards, were the accumulators and consumers of these individuals because modern bovid skeletons of this size do not survive hyena ravaging. They further argue that *Dinofelis*, an extinct felid larger than a leopard but smaller than a lion (described below), is the best candidate for the accumulator of larger, size group 3A *P. altidens*, and that hyenas scavenged intermittently throughout the thousands of years of accumulation (Dominguez-Rodrigo and Barba, 2007b). Finally, the authors note that many of the stone tools at FLK N are better suited to hammering or battering than to slicing or butchering (Dominguez-Rodrigo and Barba, 2007a; Diez-Martin et al., 2010).

These findings strongly contradict Blumenschine's (2007; Blumenschine and Pobiner, 2007) assertion that hominins at FLK N had earlier access to the flesh and marrow of carcasses than hominins at FLK Zinj. The reason for this disagreement appears to stem from the early misidentification of many bone surface modifications as hammerstone percussion marks rather than straie caused by sediment abrasion or trampling at FLK N (Bunn et al., 2010), and the misidentification of biochemical erosion as carnivore gnawing at FLK Zinj (Dominguez-Rodrigo and Barba, 2007a). The result of these inflated surface modification counts is to artificially increase the apparent influence of hominins on the FLK N assemblage, particularly relative to FLK Zinj.

The taphonomic trends identified by Dominguez-Rodrigo and Barba (2007b) are maintained in specimens uncovered in the 2007 – 2009 TOPPP excavation seasons. Analyses of the Leakey and TOPPP collections by Bunn and colleagues (2010) continue to support the interpretation that FLK N was produced primarily by carnivore activities rather than hominin foraging. The 2007 – 2009 excavations unearthed faunal material with abundant carnivore and rodent gnaw marks, among which cut marked specimens are present but remain rare (Bunn et al., 2010). It is now well-established that the site is a palimpsest generated by carnivores, with independent visits by tool-making hominins drawn, perhaps, by the presence of the freshwater spring (Bunn et al., 2010; Dominguez-Rodrigo et al., 2010b; Ashley et al., 2010a).

Comparing and Contrasting FLK Zinj and FLK North

FLK Zinj and FLK North present a nearly ideal comparison between hominin and carnivore meat foraging activities on the landscape. At FLK Zinj, cut marks on bovid bones attest that hominins ate meat from fresh carcasses. At FLK North, heavily gnawed bovid bones point to carnivores as the primary accumulators. But in all other attributes of these sites, they are very similar.

Paleoenvironmental reconstructions for FLK Zinj and FLK N are nearly indistinguishable. Both sites occurred on slightly elevated natural platforms in wooded to densely-wooded habitats within 200 m of fresh water springs (Urribelariea et al., 2014; Ashley et al., 2010a, 2010b; Barboni et al., 2010). Despite being separated by ~0.045 Ma, the paleoclimatic reconstructs are also quite similar. Within the drying trend evident throughout the development of Bed I (deMenocal, 2004), cyclical fluctuations in aridity resulted in similar paleoenvironments during FLK Zinj and FLK N times. The δ13C leaf lipid and total organic carbon values from the paleolake sediments reveal a basin-wide trend toward dry-climate wooded – open grasslands during the accumulation of these sites (Magill et al., 2012a).

The sites are dominated by the same faunal species, with *Antidorcas recki* and *Parmularius altidens* especially well-represented. The absence of *Kobus sigmoidalis* at FLK N is striking, given its prevalence in the FLK Zinj assemblage, and this is likely related to the climatic trend toward increasingly arid conditions over the course of Bed I (deMenocal, 2004). This coincides with an apparent local extinction of *K. sigmoidalis*. Indeed, though the genus persists through upper Bed II, *K. sigmoidalis* is not found in Olduvai strata younger than Tuff IC (Leakey, 1971). Nevertheless, the paleofauanas seen at these sites reflect a comparable mammalian community in a comparable wooded grassland savanna.

The large assemblages of stone tools, cores, and debitage at both sites are made primarily on quartzite and basalt. Quartzite artifacts are more numerous than lava-derived lithics at both sites, though lava comprises a larger portion of the assemblages by weight (Leakey, 1971). Leakey (1971) and Brantingham (1998) have suggested that the higher proportion of shatter deriving from quartzite indicates that this raw material was knapped on location more intensively than the lavas, though it is a raw material more prone to shatter than basalt**.** The primary distinction between FLK

Zinj and FLK N is the frequency of sharp-edged flakes and tools at the former, and battering implements at the latter (Diez-Martin et al., 2010).

Lithic Assemblages of FLK North and FLK Zinj

	FLK Zinj		FLK North	
Lithic Type	**Number**	**% of Total**	**Number**	**% of Total**
Tools:				
Choppers	17	1	91	8
Proto-bifaces	0	0	5	0
Polyhedrons	9	0	5	0
Discoids	3	0	8	1
Spheroid and sub-spheroids	0	0	12	1
Heavy-duty scrapers	9	0	13	1
Light-duty scrapers	18	1	12	1
Burins	4	0	0	0
Others	0	0	3	0
Utilized material:				
Anvils	5	0	12	1
Hammerstones	13	1	62	5
Cobblestones	4	0	23	2
Nodules and blocks	40	2	49	4
Light-duty flakes and fragments	73	3	68	6
Debitage:				
Whole flakes	258	10	178	15
Resharpening flakes	0	0	3	0
Broken flakes	1862	75	575	48
Core fragments	155	6	86	7
Total	2470	100	1205	100

Table 1.2. Number and frequency of Oldowan artifacts at FLK Zinj and FLK North. From Leakey (1971).

This technological difference has been used to argue in support of intensive hominin butchering activities at FLK Zinj and plant-oriented foraging, largely independent of carnivore activities, at FLK N (Dominguez-Rodrigo et al., 2010). As Bunn and colleagues (2010) have suggested, “It is certainly plausible that hominin and felid activities [at FLK North 1 – 2] may have been largely offset seasonally, with hominins foraging there for plant foods in the wet season and felids ambushing prey in the dry season…" (pp. 360).

Regardless of these behavioral distinctions, both sites are characterized by Leakey (1971) as classic "Oldowan," with hammerstones, utilized cobbles, and flakes, as well as somewhat standardized products including various forms of choppers, polyhedrons, discoids, scrapers, and the rare subspheroid and burin (Table 1.2). The overlap in artifact typologies, despite differences in frequency, is strong support for the hypothesis that the hominins who produced FLK N were the cultural and biological descendants of those who created FLK Zinj.

Hominin-Carnivore Interactions in the Past

Hominins as Prey

The transition from nearly-exclusive herbivore to part-time carnivore almost certainly required both physical and behavioral changes in hominins. Contrary to some popular early hypotheses (e.g., Dart, 1949, 1957; Leakey, 1959), the earliest hominins did not consistently consume large quantities of meat, but instead provided it. With the introduction of taphonomic analysis to African paleoanthropology by CK Brain (e.g., 1969, 1970, 1981), it became apparent that the processes that aggregated the other fauna in assemblages were also responsible for the presence of hominins. In many cases, the processes included predation by large carnivores (Brain, 1969, 1970, 1981; Pickering et al., 2004; Su and Harrison, 2008). The skull cap of SK 54, an *Australopithecus robustus* from Swartkrans, provides a famous example in which two punctures in the parietal bones of this hominin juvenile matched perfectly the size and spacing of leopard lower canines (Brain, 1970). At Sterkfontein, South Africa, a reassessment of the original 45 *Australopithecus* fossils from Member 4 (Brain, 1981) in conjunction with an additional 42 *Australopithecus* bones found since the initial description, confirmed that the assemblage was indeed modified by carnivores as Brain initially proposed. The number of identifiable specimens (NISP) relative to the minimum number of elements (MNE) is comparable to that of large modern African felid and canid, but not hyenid, prey assemblages, and the Member 4 collection is dominated by cranial elements with a few heavily chewed postcranial elements that do rarely occur in felid bone accumulations (Pickering et al., 2004). Though the evidence is insufficient to identify carnivores as the primary accumulators, they were plainly part of the taphonomic process. The Swartkrans hominin sample is similarly rich in australopithecine craniodental remains relative to hominin postcranial, predominantly digital, elements. None of the craniodental fossils retain tooth marks, while most of the postcranial elements appear to have been digested and excreted, indicating separate predation scenarios account for the presence of these elements (Pickering, 2001). Pickering (2001) notes that these distinct elemental trajectories allow for an interpretation in which australopithecines were preyed upon on site, while the occasional hand and foot bones derived from *Homo* offsite.

Australopithecines in eastern Africa also bear evidence of carnivore predation. At Laetoli, Tanzania, australopithecine postcrania are similarly rare relative to craniodental remains, though the percentage of hominins among all fossils collected at Laetoli is far lower than at Sterkfontein and Swartkrans because the taphonomic context of open air sites differs significantly from the accumulative nature of cave sites (Su and Harrison, 2008). The rarity of hominin postcrania is attributed to several factors, including the need for timely ash fall, the scarcity of appropriate paleohabitats, and consumption by an active carnivore guild whose presence is attested by coprolites and frequent tooth marks on other fauna (Su, 2005; Su and Harrison, 2008).

Several hominin specimens from Olduvai Gorge bear the marks of carnivore consumption. OH80, a partial skeleton of *A. boisei* from the BK site (1.353 ± 0.035 Ma) of Bed II, shows multiple green breaks on the limbs consistent with static loading of fresh bone, much like the results of carnivore chewing, and tooth marks are visible on the femur (Dominguez-Rodrigo et al., 2013). Two specimens of *H. habilis*, the left foot of OH8 from FLK North North level 3 (> 1.848 Ma) and the left tibia and fibula of OH35 from FLK Zinj, are argued to have been ravaged by crocodiles (Njau and Blumenschine, 2012). Though both belong to the left lower limb, these bones are not stratigraphically related and were probably lost ~6,000 years apart (Njau and Blumenschine, 2012). Noting the bisected punctures and pits characteristic of crocodile gnawing were accompanied by other tooth marks on OH35, Njau and Blumenschine (2012) concluded that OH8 was disarticulated by crocodiles, while the proximal end of OH35 was gnawed by a leopard-sized felid and the distal end by a crocodile. Baquedano and colleagues (2012) counter that the tooth pits on the distal end of OH35 are indistinguishable from those of small mammalian carnivores like jackals. The parietal bone of OH7, the type specimen of *H. habilis* from FLK North North level 3, has several scores in it that have been attributed to an unidentified predator (Reader, 1981; Tobias, 1991), though the marks are too broad to belong to crocodiles (Njau and Blumenschine, 2006). Carnivore interference with the remains of these diminutive hominins is used by multiple researchers to discuss the safety and status of hominins in the Early Pleistocene (e.g., Njau and Blumenschine, 2012; Baquedano et al., 2012; Uribelarrea et al., 2014), echoing Binford's (1983: 57) expressive dismissal: "I have always been a little uneasy about the supposed *machismo* of little 90-pound Australopithecines confronting 350-pound African lionesses!"

Becoming a Predator

The transition from carnivore prey to carnivore competitor is a time of great significance in human evolution because it signals a behavioral grade shift**.** Based on comparative anatomy, archaeology, and modern behavioral referents, researchers have developed a number of predictions for the morphology and behavior of the first hominin meat eaters (e.g., Aiello and Wheeler, 1995; Shipman and Walker, 1989; Brantingham, 1998). Most analyses point to *Homo erectus* as the first hominin to display the characteristics of a habitual meat eater (Aiello and Wheeler, 1995; Wood and Collard, 1999; Leonard et al., 2003).

The ecological niche of herbivores and carnivores is distinguished by food acquisition strategies, food processing methods, and food web position (Odum, 1971; Shipman and Walker, 1989). When prey is mobile, predators must be capable of capturing it through speed or coordinated attack, or both. Shipman and Walker (1989) observed that African predator success rates are most influenced by their maximum pursuit speed—predators are not always faster than their prey, but the faster they are, the more successful they become—and degree of sociality, with group hunters experiencing better than expected hunting success. The pursuit speed of hominins transitioning to greater carnivory were constrained by bipedalism. Though it has been argued that hominin bipedalism evolved under selection to run down ungulate prey (e.g., Bramble and Lieberman, 2004; but see Pickering and Bunn, 2007; Steudel-Numbers and Wall-Scheffler, 2009), endurance running speeds are not hypothesized to be comparable to the pursuit and escape speeds of dedicated carnivores and their ungulate prey, respectively. Meat-foraging hominins would therefore have favored coordinated foraging strategies facilitated by the high degree of sociality that is typical of primates (Shipman and Walker, 1989; Brantingham, 1998). Brantingham (1998) has proposed that this dietary shift, and the concomitant increase in conspecific and interspecific competition, drove hominins to develop high levels of tactical mobility.

Predators have physical features adapted to processing meat. In the African carnivore guild, this includes enlarged canines with grasping and shearing blades, reduced incisors and grinding areas on molars, and a diminished digestive tract with a relatively longer small intestine and shorter large intestine and cecum (Ewer, 1973; Martin et al., 1985). These features reflect the need to disable, dismember, and digest meat. Though the hominin lineage is characterized by small, sexually monomorphic canines that would have been ineffectual for grasping prey, our ancestors compensated behaviorally by developing stone tool technology. Indeed, the earliest stone tool assemblages are associated spatiotemporally with cut marked bones (Bunn and Kroll, 1986; Harmand et al., 2015; Semaw et al., 2003; McPherron et al., 2010; Thompson et al., 2015; but see Dominguez-Rodrigo et al., 2010). In combination with a reduced digestive tract (Aiello and Wheeler, 1995), stone tools would have enabled hominins to acquire and digest meat.

To sustain themselves, predators must be at relatively low densities and their prey need to be able to reproduce sufficiently quickly in response to predation mortality. This is a principle of the trophic pyramid described by Odum (1971), in which each step up in the trophic web decreases the available energy to consumers by 80% - 90%. The effect of the trophic pyramid can be seen in population dynamics, where density is inversely correlated with body size for herbivores and carnivores, but the absolute population size is even lower for carnivores when body size is held constant because herbivorous prey take time to mature (East, 1984; Shipman and Walker, 1989). Hominins transitioning to habitual carnivory could have reached predator-prey population equilibrium in several ways: by already occurring at low densities before transitioning, by dying off to an appropriate population size, by decreasing body size, or by increasing geographical range.

The general trajectory of human evolution has been one of increasing body size and geographical range (Shipman and Walker, 1989; Anton et al., 2002), while the frequency of hominin bones in fossil assemblages seems to suggest that they already occurred at relatively low densities. In fact, the increase in *Homo erectus* body size may have functioned as a form of predator defense, as both body size and grouping behavior influence status in the guild hierarchy (Van Valkenburgh, 2001). During competitive interactions, large-bodied carnivores outrank and deter smaller-bodied allospecifics, but small-bodied carnivores can outcompete larger species by grouping together, much as hominins are believed to have done (Eaton, 1979; Van Valkenburgh, 2001).

Each of these predictions for a predator is met in the hominin *Homo erectus. Homo erectus* evolved in Africa by as early as 1.9 million years ago (Wood, 1991). The evolution of *H. erectus* is accompanied in the archaeological record by new lithic technologies (Diez-Martin et al., 2015) as well as a significant increase in the evidence for butchery and transport of carcasses to central places (Bunn and Kroll, 1986; Ferraro et al., 2013). Shortly after its appearance in Africa, *H. erectus* experienced a substantial range expansion, spreading throughout the old world and reaching the Caucasus and Java within one hundred thousand years (Gabunia et al., 2000; Swisher et al., 1994; Anton et al., 2002).

Yet *H. erectus* did not emerge as a fully-fledged member of the carnivore guild. The archaeological record is one of slowly mounting evidence for carnivorous behavior initially exhibited by earlier hominins (De Heinzelin et al., 1999; Dominguez-Rodrigo et al., 2005), with an inflexion around 2.0 Ma after which butchery evidence increases markedly (Ferraro et al., 2013; Bunn and Kroll, 1986). Within mammalian carnivore guilds, carnivore carcasses produced by intraspecific killing is common, and the carcasses are frequently left uneaten, suggesting that competition, rather than predation, drives these interactions (Van Valkenburgh, 2001). By extension, greater carnivory by hominins may have increased the incentive of carnivores to target hominins as competitors as well as prey. Potts (1988) writes:

> "Since all animal foragers must avoid predation to survive and since handling animal tissues would tend to increase such risks, how did Olduvai hominids manage to avoid predation? The facts of site formation and the inferences that follow from them regarding ecological overlap between hominids and carnivores imply that hominid strategies of predator avoidance were at a premium. Although we can infer nothing about social strategies of defense against predators, hominids apparently lacked other means that would have reduced the chances of carnivore interference at these sites. . . . This would leave the avoidance of predators itself as an important strategy, if not the primary means, by which Olduvai hominids coped with the attraction of carnivores to the sites of bone and artifact accumulation" (pp. 261).

The researchers evaluating hominin-carnivore competition strategies in the Early Pleistocene predict the following strategies for hominins entering the carnivore guild:

- Forage cooperatively (Rose and Marshall, 1996; Brantingham, 1998)
- Defend carcasses cooperatively (Rose and Marshall, 1996; Brantingham, 1998)
- Use tools in place of biological weapons to consume and defend carcasses (Treves and Treves, 1999)
- Operate diurnally (Van Valkenburgh, 2001)
- Avoid open environments (Van Valkenburgh, 2001)
- Forage for plant foods primarily at patches in open environments (Sept, 2001)

- Ambush hunt with weapons for killing and defending prey (Bunn and Pickering, 2010a)

When making predictions for the earliest hominin meat-eaters, most researchers have stopped short of considering the opportunities that omnivory affords for carnivore avoidance strategies in a highly seasonal environment. For example, by switching between meat and plant resources, hominins could have avoided direct competition with carnivores in peak hunting times around seasonal resources such as the freshwater springs at FLK Zinj. With the exception of the study by Speth and Davis (1976), the focus of seasonal foraging has been on scavenging opportunities (e.g., Blumenschine and Cavallo, 1992; Dominguez-Rodrigo, 2001), despite the strong evidence for hunting at FLK Zinj (e.g., Bunn and Kroll, 1986; Bunn and Pickering, 2010a; Bunn and Gurtov, 2014). The present study investigates the nature of hominin-carnivore competition along a spectrum of competitive and risk-aversive strategies by evaluating the seasonality of hominin meat-foraging. This is a line of inquiry that can be productively approached through careful comparison of the archaeological record with the dynamics of seasonal foraging and competition in extant faunal communities.

Ecological models for the Early Pleistocene: the Modern Savanna Ecosystem

Theoretical Basis for Using Modern Referents

The fossil record is a static consequence of the behaviors we wish to understand, and it is only through the observation of living taxa that we can make the connection between behaviors and results (Pickering and Dominguez Rodrigo, 2010). This must be done through conceptual modeling (Tooby and Devore, 1987), but such models cannot be built without actualistic research (Pickering and Domiguez Rodrigo, 2010). To understand the specific challenges meat-foraging hominins faced in eastern Africa, it is informative to examine predator-prey dynamics in modern savannas.

The following review outlines the particular ecological constraints inherent to savanna ecosystems with an emphasis on the effects of seasonal resource variability on large mammal dynamics. No modern savanna landscape is a perfect analog for the Early Pleistocene environment at Olduvai Gorge. However, if soil chemistry and moisture content, and drainage basin structure, influenced vegetation distribution in the past as they do today, then many inferences can be made about community dynamics based on analogy with modern ecosystems. The wildlife communities in eastern African parks have been extensively studied for many decades, allowing important insights into the impact of seasonal cycles on predator-prey dynamics. Unlike the well-studied but stocked and water-provisioned reserves in South Africa, the parks and reserves in eastern Africa are often larger and unfenced, allowing for the migration of large populations within and between habitats, which is essential given the importance of mobility in response to seasonality.

In this review of seasonal responses of bovid prey and their predators in a savanna setting, prey are presented as modern analogs for modeling phenology in Early Pleistocene eastern African savannas. Carnivores in this analysis function both as potential models for hominin meat foraging and as ecological analogs for carnivore community dynamics in the Early Pleistocene. Their descriptions are intended to lay out a figurative landscape of foraging opportunities and dangers in a Pleistocene savanna.

In contrast, Hadza, chimpanzees, and baboons are presented as potential models for hominin meat-foraging in a context of seasonally available foods and competing predators. As omnivores in woodland savannas, each referent is under similar constraints, though they vary greatly in their coping strategies. For this reason, the descriptions below are intended only to elucidate how each referent responds to seasonal patterns of food availability. In subsequent chapters, the suitability of each model will be evaluated for how well its seasonal foraging patterns match those of the Olduvai hominins at FLK Zinj.

The Savanna across Time

Savannas are ecosystems with a continuous layer of grasses and sedges, which may or may not include patches of trees and shrubs whose canopies are not interlaced (Solbrig et al., 1996; Reed and Rector, 2007). They are the most frequently found ecosystems in tropical and subtropical latitudes in Africa, and are all characterized by rainfall seasonality, with dry seasons lasting between three and nine months, and most commonly five to seven months. In the modern region of Olduvai Gorge, less than 20 mm of rain falls in each of the dry season months (June – October; Magill et al., 2012b), but these patterns vary across Tanzania and in the broader region of eastern Africa. Compared to temperate grasslands, topical savannas have high species diversity.

Geomorphology, fire, herbivory, and moisture are the primary influences on savanna characteristics and distribution (Solbrig et al., 1996; Reed and Rector, 2007). Because savannas are so heterogenous broadly and locally, there exists little consensus in how to define them. Some researchers use the density of tree cover to distinguish among savanna types (e.g., Sarmiento, 1984). Others have found utility in grouping savannas based on high and low rainfall, with dry savannas getting less than 700 mm of rainfall annually (Solbrig et al., 1996). Those with higher rainfall have higher productivity and species diversity, including greater numbers of herbivores

(Reed and Rector, 2007). The following review of seasonal dynamics is generalized across a variety of savanna types, regardless of which typological system is used.

Reed and Rector (2007) present an overview of Plio-Pleistocene hominin evolution in the context of increased seasonality and glacial cycling. Glacial periods created cooler, drier conditions with more open habitats, compared with the forests and deciduous woodlands of the early-middle Miocene. At the beginning of the Pliocene, between 5.4 – 4 Ma, the global climate was relatively warm and wet. Hominins living 4.2 – 3.0 Ma occupied mosaic savanna habitats with closed – open woodland, bushland, riverine forests, and seasonal floodplains, with dry seasons likely lasting less than 4 months. This climate regime was followed by a cooling and drying trend beginning 3.2 – 2.2 Ma that intensified 2.1 – 1.9 Ma and increased the distribution of open and dry grasslands to the detriment of forests and wet savannas. The distribution of savanna types has continued to change, particularly recently as a result of anthropogenic activity (Solbrig et al., 1996). Much of the current grassland in Africa is secondary due to continuous grazing and burning (Reed and Rector, 2007). The greatest challenge for most animals is finding enough food and water in dry savannas during the dry season.

Photographs 1.1., 1.2., Waterholes. Taken by the author in the Ngorongoro Crater, Tanzania, July 2015.

Ungulate Responses to Seasonality

Eastern African ungulates employ various strategies to cope with resource seasonality. When the rains cease locally, some grazing species migrate to areas where higher annual rainfall supports green grass. Others use a mixed feeding strategy, incorporating foliage, forbs, seedpods, and bark when local grass is dry. Some have evolved to rely solely on the dew that collects on leaves overnight, or from the moisture within leaves, so long as these are available. And a few species exhibit ruts and narrow birthing seasons to time the greatest energetic stresses of reproduction with the greatest available nutrition (Ogutu et al., 2014). Despite the variety of adaptations, however, the dry season remains a physiologically stressful time of year for ungulates in savanna environments. As a result, mortality from food and water scarcity, and the susceptibility to disease and predation that results, is highest in the dry season (Mduma et al., 1999; Ogutu and Owen-Smith, 2003; Owen-Smith et al., 2005).

Rainfall, largely due to its influence on plant phenology, impacts the ungulate reproductive cycle through the effects of female nutritional health on her ability conceive, gestate a fetus to full term, and to produce milk postpartum (Ogutu et al., 2014). Rainfall conditions throughout development also affect age at first reproduction (Ogutu et al., 2014). Constrained seasonal reproduction makes females more susceptible to predation during the season of pregnancy, and males more vulnerable when male-male competition for access to females increases rates of injury and isolation from the herd (Owen-Smith, 2008; Molinari-Jobin et al 2004; Fitz-Gibbon, 1990).

Across equatorial eastern Africa, Ogutu and colleagues (2014) note wide variation in reproductive synchrony within species living in different habitats and rainfall regimes, but nevertheless conclude that rainfall seasonality strongly affects reproductive seasonality. In the Maasai Mara and adjacent Serengeti, the wet season is November-June and the dry season is July-

October. They found that topi (*Damaliscus lunatus*) and warthog (*Phacochoerus aethiopicus*) have the most restricted birthing peaks, zebra show intermediate reproductive seasonality, impala (*Aepyceros melampus*) and hartebeest have only mild birthing peaks in a year-round reproductive strategy, and giraffe are aseasonal (Ogutu et al., 2014). The Mara impala reproduction cycle differs significantly from that of southern African impala, which have a narrow 2 week period in which 80% of lambs are born from late November to early December. This variation relates the greater rainfall seasonality of southern Africa, where conception peaks after heavy rainfall and birth peaks at the beginning of the wet season (Murray, 1982). Thus, though many ungulates exhibit annual patterns of variation in birth rates, births are not restricted to a specific season (Estes, 1991).

Despite the variation in intraspecific birth peaks, Ogutu and colleagues (2014) still found substantial evidence that rainfall influenced fecundity in all of the eastern African species studied, and particularly by increasing the fat reserves of pre-conception females of topi, impala, and warthog. That reproduction is not more synchronized in these and other species likely results from the high interannual variability of rainfall in savannas (Rutberg 1987; Ogutu et al., 2014).

Rainfall seasonality also plays a significant role in the spatial distribution of large fauna in arid and semi-arid African savannas, again through its influence on plant phenology as well as the availability of drinking water (Western, 1975; Epaphras et al., 2007; Valeix et al., 2010; Valeix et al., 2009). The degree to which ungulates employ grazing or browsing, and their level of water dependency influences their daily and seasonal spatial distribution (Western, 1975; Lamprey, 1963, 1964). Species that incorporate browse in their diet are typically residential, traveling within smaller home ranges, and less water dependent than grazers, which are often migratory (Western, 1975). Notably, closely related species can vary in the degree to which they require water on a regular basis. While the browsing bushbuck, *Tragelaphus scriputs*, must drink daily, browsers kudu (*Tragelaphus strepsiceros* and *T. imberbis*) and eland (*Taurotragus oryx*) can extract sufficient amounts of moisture from the vegetation most of the year (Kingdon, 1997). Nevertheless, when water is available, eland and kudu will drink every few days (Lamprey, 1963; Valeix et al., 2007), as will other water independent species (Ritter and Bednekoff, 1995).

Most of the prey biomass of large carnivores disperse during the wet season in order to take advantage of more nutritional green grass (McNaughton 1985), alleviate feeding competition, and reduce predation risk (Fryxell et al., 1988). This increases predation pressure on residential species as carnivores are forced to take less preferred species in greater quantities (Ogutu and Dublin, 2004). Generally, while migratory species are regulated by food availability, residential ungulate population sizes are regulated by predation, which tends to maintain low densities in the dry season and evel lower densities in the wet season (Fryxell et al., 1988). Thus the overall risk of predation and non-predation mortality is greatest in the dry season when drought, starvation, and disease increase ungulate vulnerability and mortality rates and the need for water concentrates most ungulates to within a day's walk from the remaining waterholes.

Grazing ungulates in eastern Africa, particularly zebra, wildebeest, Thomson's gazelle and some Grant's gazelle, migrate in response to the changing spatial distribution of food and water resources over the course of the year (e.g., Hanby et al 1995; McNaughton, 1985; van der Werf, 2008; Lamprey, 1963, 1964; Schaller, 1972, Western, 1975). To the greatest extent possible, these species select for habitats in which the nutritional quality of the available forage is highest. A study by McNaughton (1985) in the Serengeti found that the contribution of different grass species changed significantly between wet and dry seasons for migratory wildebeests, zebras, and Thomson's gazelles. Large herds Thomson's gazelle and wildebeest migrate to the Serengeti Plains within 3 days of the first heavy rainfalls and stay until the end of the wet season plant productivity (McNaughton, 1985). Both taxa are able to include higher relative proportions of green forage in their diet than occur in the environment, and the relegation of Thomson's gazelle to less productive areas suggests resource partitioning based on species body size (McNaughton, 1985). Toward the end of the dry season, buffalo, zebra, Thomson's gazelle, and wildebeest are all drawn to the last remaining green plant species, when the total proportion of dry dietary forage is highest for all species (McNaughton 1985). Grant's and Thomson's gazelle make up the largest number of dry-season plains taxa, but topi, warthog, ostrich, kongoni, small groups of wildebeest, eland, oryx and giraffe also remain on the plains (Hanby et al.,1995).

While water dependent grazers must have access to drinking water throughout the year, water independent and dependent ungulates alike are drawn to waterholes by the end of the dry season when vegetation is dehydrated and cannot supply a sufficient amount of water (Davidson et al., 2013). In the Serengeti ecosystem, Thomson's gazelle, wildebeest, impala, reedbuck, waterbuck, bushbuck, and zebra can all be found within a daily commute of permanent water, which aggregates them around permanent waterholes during the dry season (Schaller, 1972; Ogutu et al., 2008). Tarangire National Park, Tanzania, and the Maasai Mara National Reserve, Kenya, likewise exhibit a dry season concentration of biomass around permanent water, excluding water independent taxa such as Grant's gazelle, gerenuk, oryx, and approximately half of the impala population, which tend to disperse within very small home ranges in the dry season (Lamprey, 1964). Most ungulates disperse into short grass plains and pastoral lands surrounding the Maasai Mara and Tarangire park during the wet season when grass height in the reserve increases predation risk and the ground becomes waterlogged, but return to the reserve in the dry season when surface water is scarce elsewhere (Ogutu et al., 2008; Lamprey, 1964). In the Amboseli ecosystem, the home range of water dependent ungulates contracts around available water sources, with 99% of the biomass concentrated within fifteen km of available water (Western, 1975).

African ungulates have the distinction of being among the leanest living large mammals (Speth, 2012). Sinclair (1974, 1975, 1977) showed that Serengeti ungulates subsist on diets that do not meet their physical maintenance requirements during parts of the year. African ungulates evaluated by Ledger (1968) and Eaton and Konner (1985: 285) had an average of 3.9% body fat, which dropped to less than 2 - 3% by the end of the dry season, including bone marrow fat content. Cordain (reported in Speth, 2012) has critiqued this estimate, noting that these data were derived from dissections rather than chemical analyses, but given that the present study is concerned with tool assisted hominins lacking boiling technology, these are likely appropriate estimates (Speth, 1987). As a result of water dependence and poorer body condition, the dry season is a time of particular vulnerability for most bovids.

Carnivore Responses to Seasonality

In the eastern African reserves, (e.g., Maasai Steppe, Serengeti, and Amboseli) lions change the size of their daily home range in response to the distribution of prey. Though lions select for prey vulnerability over prey abundance (Hopcraft et al., 2005), potable water sources that aggregate ungulates are often accompanied by thicker vegetation and function to expose prey within a microhabitat of obscured visibility. Throughout the African lion's range, researchers have observed a preference for hunting in this type of habitat year round (Hopcraft et al., 2005; de Boer et al., 2010; Davidson et al., 2013; Schaller, 1972; Elliott et al., 1977; van Orsdol, 1984). Davidson and colleagues (2013) found that lions living in the Hwange National Park of Zimbabwe preferentially hunted within 2km of waterholes year round. In Karongwe Game Reserve, South

Africa, lions make significantly more kills in the dry season, when they have greater success hunting riverine species than in the wet season (Lehmann et al., 2008).

Within this range of preferences, the seasonal distribution of prey affects the location of lions' hunting activities. In the dry season, their daily ranges further contract around woodland areas where prey biomass and vulnerability is highest (Schaller, 1972; van der Werf, 2008). In most cases, this means hunting more even frequently in the immediate vicinity of the waterhole (Lamprey, 1964). In response to the wet season dispersal of preferred prey such as wildebeest and zebra, lions improve prey encounter rates by increasing the size of their territory (Western, 1975; van der Werf, 2008; Hopcraft et al., 2005). Though their prey are more dispersed, Serengeti lions and leopards have access to a broader range of both residential and migratory species, including topi, impala, hartebeest, waterbuck, and warthog during this season. From June to December, roughly coinciding with the dry season, migration of zebra, wildebeest, and Thomson's gazelle into woodland areas leaves the plains nearly empty of large herbivores and their predators, focusing lion activities to within woodland zones (Schaller, 1972). Approximately 62% of Serengeti lion prey is variably absent over the course of a year (Schaller, 1972). Thus, in the Serengeti plains, the wet season densities of lions and their prey are 1: 0.45 km^2 and 272 : 1 km^2 respectively, and fall in the dry season to 1 : 1.16 km^2 and 24 : 1 km^2 (Frame, 1986).The frequency of species kills therefore reflects, in part, their seasonal presence within the lion's range.

Habitat use by subordinate members of the large carnivore guild is heavily influenced by the location of lions (see below). The exception is the leopard, which resides in the same well-vegetated locality for several years (Schaller, 1972). As residents, leopards make use of a wide range of resident species throughout the year, including smaller bovids up to 130 kg as well as small carnivores and rodents (Schaller, 1972). Because they inhabit heavily vegetated areas at low densities, leopard hunting behavior is poorly recorded, particularly in the wet season. Their status as residents nevertheless hints at an opportunistic diet that, like that of lions, reflects prey availability.

The spotted hyena strategically benefits from overlapping with lions and their prey (Pereira et al., 2014). Hyenas in the Maasai Mara prefer wildebeest over other prey, but opportunistically kill most species in accordance with their availability, relying on resident species 9 months of the year (Cooper et al., 1999). As their preferred prey migrate from the plains to woodlands in the dry season, Serengeti hyena groups fission and some become nomadic, following the herds. Females with cups tend to remain in their territories and venture only as far as the edge of the woodlands on daily commutes up to 30km (Schaller, 1972). In the dry season, Serengeti cheetah rely mainly on Thomson's gazelle, sometimes following them to woodland-adjacent areas within the daily ranges of lions and hyenas (Schaller, 1972; Frame, 1986). In Tarangire as well, part of the cheetah population follows dry season migrations of gazelle into the more heavily wooded park from the wet season surrounding plains (Gros, 2000). Wild dogs in the Serengeti have large ranges. Those that reside primarily in the plains still follow their prey to woodlands in the dry season (Schaller, 1972). Thus, even while enacting the predation avoidance strategies discussed below, carnivores are drawn into greater densities on the landscape in response to the distribution of their prey.

Hadza Responses to Seasonality

The Hadza are among the best-studied hunter-gatherers living in a seasonal savanna woodland setting. Though they are equipped with modern technologies such as poisoned arrows, metal knives, synthetic clothes, shoes, and containers, their foraging opportunities are nevertheless impacted by the seasonal availability of resources. The modern Hadza home range is a mixed savanna woodland with a large variety of plants and animals that become available at different times throughout the year. Annual rainfall on the eastern side of Lake Eyasi, where most studies are conducted, averages 300 – 600mm between December and May, with almost no rain the rest of the year (Bunn et al., 1988). During the wet season, Hadza move to higher ground, breaking up into smaller groups that average about 14 adults. In the dry season, Hadza form larger camps averaging 27 adults within close proximity to the few remaining waterholes (Woodburn, 1964).

Recent studies show that Hadza consume the same types of foods over the course of a year, but that their relative quantity varies seasonally (Hawkes et al., 1991; Marlowe and Berbesque, 2009). This is in contrast to the ethnographic research by Woodburn (1964) in the late 1950s, when he observed distinctly different foraging strategies for wet and dry seasons, particularly with regard to tubers, which were taken exclusively during wet months. The seasonal variation in hunting success appears to have remained the same over the last sixty years, however. Daytime opportunistic hunting is practiced year round when individuals or small groups of men leave camp. Always armed with a bow and arrows, any foray out of the camp is a hunting opportunity (Bunn, 2001). This method is more successful in the dry season because wounded animals are easier to track when the brush has been burnt off and footprints are more visible (Woodburn, 1964).

Hadza have their greatest hunting and scavenging success in the late dry season when they, their prey, and other predators are drawn to a few freshwater sources on the landscape (Woodburn, 1964; Marlowe, 2010; Hawkes et al. 1991, 2001; Bunn, 2001; Bunn et al., 1988). Men acquire the most animal meat in this season. The predictability of ungulate prey at waterholes allows Hadza to set up hunting blinds along game trails where they intercept animals on their way to drink (Woodburn, 1964; Bunn et al., 1988). The blinds are typically constructed just before sunset, after which the ambushers build up a fire and let the coals burn to keep themselves warm at night. This strategy is utilized when the moon is close to full, providing some light by which to see. Daytime ambush hunting is also practiced in the dry season. A single man will rise early, set up a blind hear the watering hole, and await prey as they come to drink early in the morning. Missing an animal in the crucial dawn timeframe means that success is far less likely. The next best opportunity is when the sun is setting (Marlowe, 2010).

The wet season is primarily a time for vegetable foraging (Woodburn, 1964). Less hunting is done in the wet season than in the dry, though there are more animal species available in better condition than in the dry season. The Hadza themselves make a strong distinction between wet and dry seasons, and their foraging activities reflect this. The Hadza say that roots and tubers, which are collected in the wet season, become shriveled and bitter in the dry season. This is true for some species, but not others. Nevertheless, they are rarely if ever collected once the season turns (Woodburn 1964).

Marlowe and Berbesque (2009) have found that the high intake of meat during the late dry season correlates with a small but significant increase in Hadza women’s body fat percentage. This observation contrasts with the prediction made by Speth (1987, 1989) that hominins living in the same environment would have avoided high intakes of meat during the dry season, seeking a caloric boost from foods high in fat rather than lean protein. According to Speth (1987, 1989), African bovids become so lean in the dry season that human hunters consuming large quantities of bovid meat are at risk for protein poisoning. Nevertheless, Hadza have greater hunting success and higher meat consumption in the dry season, a nutritional strategy that is paired with other plant foods to good effect (Marlowe and Berbesque, 2009). In the wet season, both men and women forage more broadly, sometimes traveling twice the distance as they would in the dry season to gather plant foods (O’Connell et al., 1988). Generally, Hadza body condition is stable throughout the year, thanks to the sequential availability of various plant foods and the year round availability of tubers as fallback foods (Marlowe and Berbesque, 2009). When interviewed, Hadza did not report finding one season more difficult than another (Marlowe, 2010).

Non-human Primate Responses to Seasonality

Chimpanzees (*Pan troglodytes*) are traditional referential models for early hominin behavioral ecology. Chimpanzees are our closest living taxonomic relatives, and, as such, are inferred to be equipped with the same cognitive abilities as early hominins by dint of shared ancestry (Pickering and Dominguez Rodrigo, 2010) as well as by reference to the plesiomorphic cognitive complexity of hominoids generally. Though recent analyses have indicated that chimpanzees are less relevant as morphological models for early hominins (e.g., White et al., 2015), they are omnivorous primates of comparable body size whose modern distribution includes a range of habitats in which hominins were thought to have evolved. As such, they have been under many of the same ecological pressures.

The chimpanzees of Ugalla, western Tanzania, of Fongoli, southwestern Senegal, and of Mt. Assirik in Niokolo-Koba National Park, Senegal, demonstrate the great breadth of chimpanzee habitat tolerance, living in an open woodland and grassland savanna with patches of gallery forest (Pruetz and Bertolani, 2009). Each of these sites average 900mm of rainfall, of which almost none falls in the dry season (Pruetz and Bertolani, 2009; Baldwin et al., 1982; Hernandez-Aguilar, 2009), putting considerable ecological stress on chimpanzees during the dry season. The Fongoli chimpanzee home range is a minimum of 65 km^2, which is 2 – 6 times the size of those living in forested habitats. The home range of Mt Assirik chimpanzees is similarly extensive (Baldwin et al., 1982), though establishing precisely what constitutes a home range is challenging (Hernandez-

Aguilar, 2009). When the entire range used by a community over the course of a year is considered, Mt Assirik chimpanzees travel over approximately 278 – 333 km^2 and Ugalla chimpanzees use 470 – 560 km^2. By every standard, the home range of savanna-dwelling chimpanzees far exceeds those of chimpanzees living in forested habitats.

Habitat preference in response seasonality differs between Tanzania and Senegal. At Ugalla, deciduous woodlands do not drop their leaves all at once in the dry season. Chimpanzees were able to nest in leafy trees year round and showed an invariable preference for woodlands (Hernandez-Aguilar, 2009). In contrast, Pruetz and Bertolani (2009) found that between March 2005 and June 2006, Fongoli chimpanzees spent twice as much time in forests during the dry season as they did in the wet season. Forests comprise only 2% of the available habitat within their home range, but are the only source of water during the dry season. Woodlands were used less in the dry season and more in the wet season than would be expected based on their availability. Mt. Assirik chimpanzees, like those at Fongoli, seasonally change their habitat use rates. In a study of nesting behavior, Baldwin and colleagues (1982) saw a shift from nearly 70% of nests built in woodlands in the wet season to approximately the same proportion built in gallery forest by the end of the dry season. Most of the diurnal observations of chimpanzees occurred in the season and habitat that reflected nesting behavior. Chimpanzees were also seen in the grasslands during the wet and early dry seasons, but never in the mid and late dry season. When the authors compared the habitat in which chimpanzees were observed with the most abundant source of food as determined by fecal analysis, they discovered that there was no overlap. Rather than food availability driving chimpanzee habitat choice, they conclude that water and shade availability may be more significant influences, especially in the late dry season when only two sources of flowing water and shade coincide, in the gallery forests (Baldwin et al., 1982). Hernandez-Aguilar

(2009) has suggested that the difference in habitat preference between Mt Assirik and Ugalla chimpanzees lies in the location of edible foods. At Ugalla, foraging opportunities were associated with the woodlands, so chimpanzees increased their ranges in order to drink and feed daily in the dry season (Hernandez-Aguilar, 2009).

Fongoli chimpanzees changed their daily traveling times, moving more at dawn in the dry season to avoid activity in the heat of midday (Pruetz and Bertolani, 2009). As noted below, carnivore activity shows crepuscular peaks, but large carnivores have been largely eradicated from the Fongoli area. In contrast, lion, leopard, spotted hyena, and possibly wild dog have been recorded at Mt. Assirik, but there is nothing published on the daily travel times of Mt Assirik chimpanzees. However, Tutin and colleagues (1983) found that when traveling longer distances between habitat types, Mt. Assirik chimpanzees formed large groups that averaged 19 individuals. This is significantly larger than groups engaging in other activities. They occurred most often in the dry season, and likely functioned as an anti-predator strategy, particularly given the silence observed by members of the “mass migration” (Tutin et al., 1983). Groups of various compositions, such as mixed, males-only, mother-offspring, or multi-mother-and-offspring groups, show no seasonal variation in group size (Tutin et al., 1983).

Compared to chimpanzee sites in forested habitats, vertebrates constitute a smaller portion of the Fongoli chimpanzee diet at approximately 0.5%, while at Assirik they compose closer to 2% of the diet (Pruetz, 2006). This is in contrast to Gombe, Tanzania, which is a strip of mixed vegetation of tropical forest where vertebrates make up 6% of the chimpanzee diet (Pruetz, 2006; Stanford, 1996). The vertebrate prey population is comparatively small at Fongoli, and hunting has been characterized as opportunistic (Pruetz, 2006). Recent observations of Fongoli chimpanzees using sharpened sticks to hunt galagos appears to exhibit a seasonal pattern, with sixteen of the twenty-two observations, occurring over 1.5 years among 10 individuals, taking place during the wet season (Pruetz and Bertolani, 2007). Though limited, these data suggest a contrasting pattern to the dry season peak in hunting success seen among the Hadza in a comparable habitat. However, the wet season, rather than the dry season, is the leanest fruiting season. If hunting were understood as a nutritional strategy, as some have suggested (e.g., Pickering and Dominguez Rodrigo, 2010), then the wet season can be understood as the lean season at Fongoli (Pruetz, 2006), but not in eastern African savannas where the dry season is the time of greatest nutritional stress.

From the savanna chimpanzee data, one would predict a hominin preference for remaining at shaded watering holes in the dry season when food is locally sufficient; group size stability throughout the year, with increased group sizes only when predation risk increases; large annual home ranges that utilize various habitat patches; and opportunistic hunting in the lean season.

As large-bodied, savanna-dwelling primates, papionins are also considered a useful modern analog for early hominin paleoecology and niche differentiation, not through homology but through analogy (for a theoretical discussion, see Jolly, 2001). Like the ungulates discussed above, most primates experience reproductive seasonality to some degree. In savanna dwelling primates, only baboons and humans eschew this trend (Alberts et al., 2001). This suggests that baboons and humans may have converged on some foraging strategies that allowed them to maintain nutritional stability in savanna habitats. In a study female baboon feeding and social behavior in Amboseli National Park between 1984 and 1999, Alberts and colleagues (2001) found that the largest food components in the baboon diet were “damped” seasonally. These foods are offset in their temporal availability, which varied across years somewhat independently of rainfall and season. During the long dry season, female baboons spent less time resting and more time foraging than in the wetter months. But by exploiting a wide range of foods across the year, the baboons achieved stability in their diet. They accomplished this through a “handoff” foraging strategy, in which different food items were taken successively as they became available. Baboons carefully tracked numerous plant species within their range in order to exploit them as their various edible parts come into season, much as the Hadza do. The authors concluded that the handoff strategy results in relatively steady nutrient quality throughout the year.

Notably, Female baboons did not turn to high return foods in the dry season, and little variation in animal proteins was observed throughout the year (Alberts et al., 2001). Rather, theirs is a strategy that relies on fallback foods. To some extent, this, too, is comparable to Hadza foraging, which incorporates larger quantities of tubers when other resources are unavailable, despite their low nutritional yield and high acquisition and processing costs (Marlowe and Berbesque, 2009). As modern referents on the opposite ends of the hominin cognitive spectrum, it is informative that both are able to maintain nutritional continuity throughout the highly seasonal year.

Critical elements of the baboon handoff strategy included a large home range that shifted in response to environmental changes, a diversity of food types, and the ability to eat grass (Alberts et al., 2001). Across their range, papionins are extreme ecological generalists. In a comparison of carbon stable isotope analysis of South African chacma baboons (*Papio ursinus*) and early hominins *Australopithecus africanus* and *Australopithecus robustus*, the high contribution of C_4 foods, annual, and spatial dietary variability in the baboon diet was still less than that of the early hominins (Codron et al., 2008). Codron and colleagues (2008) interpret this to mean that early hominins were even more extremely ecologically generalized than extant baboons in the same environments. Presumably, the early *Homo* clade evolved from ancestors with a similarly broad dietary adaptation.

The baboon model suggests that hominins would have moved throughout their home range in ways that are essentially unpredictable without detailed phenological data from the paleoenvironment. It makes no predictions about when meat-foraging might have been most strategic or accessible, but does indicate that nutritional stress inherent in savanna ecology need not have driven hominin carnivory. Rather, nutritional stress may have been imposed by competition with other hominin foragers (Sept, 2001).

Predictions for Hominin Foraging Seasonality

Sept (2001) has proposed that competition among hominins and other primates for seasonal and patchy, high-value resources may have contributed to dietary divergence. From an analysis of edible plant seasonality and spatial distribution in eastern African arid and semi-arid riverine settings, Sept (2001) created a model of optimal plant foraging for several early hominins. This model was developed using the "menu" of plant and animal foods consumed by modern humans, baboons, and chimpanzees in these habitats; seasonal transects of plant foods in Kenyan landscapes that are comparable in sedimentary and climatic features to Early Pleistocene archaeological sites; and the time:energy and cost/benefit of these plant resources for each species consuming them in each season. Together with evidence about the availability of tools and dietary adaptations of early hominins, Sept (2001) created plant food foraging models for a gracile australopithecine, a digging tool-endowed australopithecine, and an Oldowan-equipped early *Homo*.

For early *Homo*, the model predicts significant differences in foraging opportunities between the seasons. In a riverine environment receiving an average of 550 mm annually, which is the approximate average rainfall predicted for Bed I at Olduvai Gorge (Magill et al., 2012b), the long wet season is productive in both the floodplain and adjacent wooded grassland zones, or hinterlands. In the long dry season and subsequent short wet season, the unflooded hinterlands provide the best foraging opportunities based on modern plant phenology and time:energy of plant exploitation, while the floodplain and immediate riparian corridor remain the only source of water and shade. Only in the short dry season is plant food availability and foraging productivity marginal in the Kenyan habitat analogs, particularly in the hinterlands. The model indicates that with sufficient annual rainfall, hominins would have had their highest foraging returns in riparian floodplains only during the short dry season just preceding the long wet season. If this were the case, archaeological sites in wooded riparian habitats would reflect a broader regional foraging signature, with carcass transport back to locales offering other resources such as fresh water and shade (Sept, 2001).

Several zooarchaeologists have instead suggested that the long dry season is the time of greatest stress for hominins, much as it is for ungulates (but see Sept 1992; Bunn and Ezzo, 1993). This is also a season when Sept (2001) predicts that early *Homo* would have searched for plant foods farther afield than the riparian floodplain, especially in drier environments, where meat foraging opportunities would have differed from those predicted by Blumenschine (1986, 1987) in riparian woodlands. But the most marginal plant food returns in modern riparian woodlands and their surrounding habitat occurs during the (highly variable) short rains and short dry season preceding the main wet season. Sept (2001) proposed that insects, honey, and animal foods would have provided a good supplement during this time of low plant productivity. From phenological studies on the east side of Lake Eyasi, Marlowe and Berbesque (2009) report that honey becomes increasingly rare over the course of the dry season, but that the proportion of berries and meat in the Hadza diet grows. When measured by weight, berries provide 18% of the diet in the late wet season and increase to 31% in the early wet and late dry seasons, while meat increases from 10% of the dietary kg in the late wet season to 35% in the late dry season (Marlowe and Berbesque, 2009). This pattern of resource availability supports the hypothesis that meat, rather than honey or other plant foods, would have made up for caloric deficits from plant foraging during the long dry season.

Based on actualistic research, Blumenschine (1987) concluded instead that the dry season offers the best opportunity to scavenge carcasses in the Serengeti, and by extension, in the paleosavannas of eastern Africa. O’Connell and colleagues (1988) likewise observed a late dry season peak in carcass scavenging success among the Hadza, though their sample was small and largely limited to the dry season observations. The variance in scavengeable carcasses correlates with the seasonal movement of biomass through Hadzaland and the Serengeti, peaking in the late dry season as prey and predators amass around the remaining waterholes (O’Connell et al., 1988). Noting the greater scarcity of plant foods and coinciding concentration of prey biomass in the savanna dry season, Foley (1993) proposed that the ancestors of the more encephalized early *Homo* may have switched between carnivory in the dry season and herbivory in the wet season. For various reasons, then, including plant phenology in analogous landscapes, and the availability of abandoned carcasses in Hadzaland and the Serengeti, researchers have honed in on savanna dry seasons as the primary period of early hominin meat eating.

One principle detractor is Speth (1987, 1989, 2012; Speth et al., 1991), who has suggested that meat was too lean in the dry season to constitute an attractive energy source. Yet ethnographic studies from hunter-gatherers equipped with boiling technology, including the Tyua in Botswana (Hitchcock, 1988), the San in South Africa, and the Hadza in Tanzania (Bunn et al., 1988), show that the long dry season is when the largest quantities of meat are eaten. In the case of the San and Tyua, several studies suggest that this coincides with a significant loss of body fat (Wilmsen, 1978, 1982; see also Truswell and Hansen 1976; Truswell, 1977; Hitchcock, 1988). In the savanna woodland habitat of eastern Lake Eyasi, O'Connell and colleagues (2002) observed that in the late dry season of 1985, Hadza gorged on the meat of 30 large bodied ungulates over 47 days, but lost weight. When meat consumption was lower in the dry season of other years, the Hadza did not lose weight (O'Connell et al., 2002). Based on these data, and observations of seasonal resource stress in northern latitude and temperate hunter gatherers, Speth (1987, 1989, 2012; Speth et al., 1991) argues that lean season meat in the archaeological record would have been potentially detrimental to the physical health of foraging hominins because its consumption must be facilitated by eating other dry season resources that are high enough in fat to offset the energetic costs of digesting lean meat (Speth, 1987; 2012). Speth (1987) predicts that archaeological sites accumulated in lean seasons would be located near fresh water, and contain fewer prey animal bones, deriving largely from the fattier ungulate demographic. He further suggests that large game hunting served a political, social, and/or reproductive purpose, with calories and nutrients as a secondary benefit, or cost (Speth, 2012).

Contrarily, research by Lee (1979) with the San in earlier decades has shown that resource stress in the dry season was mild and did not equate to a hungry season season. Notably, the Tyua and San peoples live in the Kalahari Desert, where human population increases, environmental deterioration, and politico-economic changes are reducing the viability of hunter-gatherer subsistence (Hitchcock, 1988). The phenomenon of frequent droughts in this region is recent and traditionally effective strategies for minimizing cost and distributing risk are much less effective than they once were (Hitchcock, 1988). The relationship between meat-eating and body fat reduction among hunter-gatherers in the Kalahari Desert must be interpreted within this greater socio-environmental framework, which Speth (1987, 1989, 2012; Speth et al., 1991) fails to do.

The Hadza metrics also do not align well with Marlowe's (2010; Marlowe and Berbesque, 2009; also Bunn, *pers comm*) findings from discussing the subject with Hadza foragers, who reported no particular season as especially difficult. In fact, Marlowe and Berbesque (2009) found that Hadza physical condition remained statistically constant throughout the year, with the exception of a small but significant body fat increase in adult women in the dry season when meat eating was greatest. In addition to whole carcasses, Hadza have a variety of plant foods and honey that become available at different times during the year, though some of these are very low in nutritional value. Even the savanna baboons, which must forage longer in the dry season, are able to maintain their physical condition throughout the year relying on plants and insects (Alberts et al., 2001). Bunn and Ezzo (1993) further note that ungulate physiological condition is at least as dependent on the reproductive cycle as it is on nutrition, and differs significantly in peak times between males and females of the same species. From a review of African ungulate carcass content, they argue that a hominin actively procuring ungulates would have had access to relatively fattened individuals in every season, and that the viscera would provide a fatty counterbalance to lean muscle tissue year round. Most importantly, the social value of meat must derive from an intrinsic value, at least initially, if its acquisition were ever to have impressed anyone.

Thus, though reasons vary, most researchers agree that a seasonal hominin foraging strategy would emphasize meat in the dry season when it was more available for scavenging

(Blumenschine 1986, 1987), when plant resources were in decline (Sept, 2001; Bunn and Ezzo, 1993), or when hominin-hominin competition is at its peak (Sept, 2001).

Competition in the Modern African Carnivore Guild

Habitat, food type, and time are considered the critical dimensions of the ecological niche (Schoener, 1974). In a review of the literature on intraspecific resource partitioning within groups of closely related species from across the kingdom *Animalia*, Schoener (1974) reports that over half of groups segregated primarily by habitat, and most of the remaining groups by food type. Time segregation was both predicted and found to be the least common strategy for reducing competition among species. Because time is limited to a 24hr cycle, it rapidly loses its effectiveness as the number of competing species increases and the available circadian time slots are taken. Nevertheless, Schoener (1974) found that among the 5% of surveyed groups that relied on temporal niche partitioning, predators accounted for 82%. Among these was the African large carnivore guild. The results of an activity pattern analysis by Hayward and Slotow (2009) suggest that a top down perspective, in which the activity times of subordinate carnivores are reactive to the activity patterns of dominant carnivores, can help explain temporal partitioning. The following is a discussion of the habitat and prey preferences of the large African carnivores, and the competitive strategies they employ.

For the purposes of this analysis, the African large carnivore guild is comprised of lion (*Panthera leo*), leopard (*Panthera pardus*), spotted hyena (*Crocuta crocuta*), cheetah (*Acinonyx jubatus*), and African wild dog (*Lycaon pictus*). With regard to habitat, these taxa are broadly sympatric and spatially organized by the distribution of their prey, referred to as a bottom-up effect

(Hayward and Kerley, 2008; Sinclair et al. 2003). Due to their similar body size, members of the guild are reliant on large bodied prey greater than 45% of their body weight (Carbone et al., 1999), which have high handling costs and often require defense against kleptoparasites after capture (Hayward and Kerley, 2008). Predator density is positively correlated with prey biomass in the lean season (Van Orsdol et al., 1985; Fuller et al., 1992; Hayward et al., 2007). Together, the guild's reliance on large bodied prey for their dietary needs and spatial organization results in a high degree of dietary and habitat overlap. Lions, leopards, and hyenas have the greatest dietary breadth, while cheetahs and wild dogs exhibit narrow prey preferences that are encompassed within the diet of the rest of the guild (Hayward and Kerley, 2008).

Preferred Prey and Hunting Strategies

Lions are the largest of the African carnivores at 280 kg to 420 kg, and take a wide range of prey species and size classes. As such, they can be considered a keystone species in the top-down influence exerted by the hierarchy of guild members on their subordinates (Hayward and Slotow, 2009). Lions have greater success hunting at night than in the day, particularly during moonless phases (Van Orsdol, 1984). Like all felids, lions utilize features of the landscape to approach as closely as possible to their prey, with increased hunting success correlated with increased grass height and vegetation cover (Schaller, 1972; Elliott et al., 1977; van Orsdol, 1984; Hopcraft et al., 2005). Lions take prey at higher rates than those predicted by their availability—that is, they *prefer* prey—that weigh between 190 kg and 550 kg. This range meets expectations for an optimal foraging strategy that targets calorically-profitable taxa with handling expenditures below a certain threshold, and avoids taxa that fall outside the preferred size range regardless of their availability (Hayward and Kerley, 2005). Despite these preferences, lions are still known to take smaller prey as part of an opportunistic hunting strategy (Schaller, 1972), and to target larger prey when hunting in groups (Hayward and Kerley, 2005). For example, in the semi-arid, short-grass habitat of Etosha National Park, Namibia prey weighing less than 50 kg contributed 50% of the consumed biomass in a study period of 920 capture attempts and 156 kills (Stander, 1992). When compared with the other guild members, lions have the broadest range of actual prey species, and the second broadest range of preferred species (Hayward and Kerley, 2008). This relatively broad dietary niche subsumes many of the preferred prey taxa of the other guild members.

A review of leopard hunting-behavior studies from across Sub-Saharan Africa reveals the highly opportunistic dietary strategy of this solitary carnivore (Hayward et al., 2006a). Leopards range in body mass from 20 to 90 kg. At the low end of this range, they are able to temporarily subsist on small vertebrates and invertebrates, and have been observed to take birds, rodents, catfish, and hares (Kingdon, 1997; Ott, 2004; Mitchell et al., 1965). However, because they are on average larger than the 21.5 kg at which a predator becomes an obligate carnivore, they exceed the body mass threshold at which vertebrate carnivory becomes obligate for terrestrial carnivores (Carbone et al., 1990). Though leopards have three significantly preferred species (bushbuck, common duiker, and impala) and a preferred prey weight range of 10 to 40 kg, they take over 100 prey species in approximate proportion to their availability, including carnivores such as cheetah, black backed jackal, and African civet (Hayward et al., 2006a). They are second to lions in the range of actual prey species taken, and first in the guild for the range of preferred species (Hayward and Kerley, 2008). Like lions, leopards rely on vegetative cover to ambush their prey, which limits their intake of open grassland grazers relative to their abundance on the landscape

Unlike both lions and leopards, spotted hyenas share with cheetahs and wild dogs a cursorial hunting strategy that targets weaker individuals. Weighing between 45 and 80 kg, spotted hyenas are flexible hunters of medium and large bodied prey. Hyenas hunt alone and in groups, with greater success in open grasslands, and frequently engage in kleptoparasitism from lions and leopards in less favorable hunting habitats (Pereira et al., 2014). When in sympatry with lions, spotted hyenas target similar prey species and form the fiercest competitor dyad with lions (Hayward and Kerley, 2008; Mills and Harvey, 2001). In an analysis of prey preferences across southern and eastern Africa, Hayward and colleagues (2006b) determined that spotted hyenas do not have preferred species and avoid very few. Preferred prey mass is between 56 kg and 182 kg, with the most commonly taken prey weighing 102 kg, but range from less than 10kg up to 750kg. Within this range, most species are taken in proportion to their abundance, putting hyenas in direct competition with lions and the other large predators for many prey species. Notably, hyenas are capable of breaking and consuming bone in order to obtain the marrow inside. This results in the rapid and complete consumption of smaller ungulates within minutes, and larger ungulates within hours, depending on the size of the group (Kruuk, 1972; Estes 1991).

Cheetahs are highly specialized cursorial predators weighing between 30 kg and 72 kg. Though they are recorded taking prey between 2 kg and 270 kg, they prefer prey species that are abundant within their habitat and weigh 23 kg to 56 kg (Hayward et al., 2006c). Prey in open grassland habitats are at the highest risk of predation by cheetahs, reflecting their hunting niche as the fastest land mammal (Mills and Harvey, 2001). Among the large carnivores, cheetahs have the greatest hunting success, with nearly half of all pursuits resulting in kills (Frame, 1999) and a greater success rate when hunting in groups (Eaton, 1979). Despite this, they are extremely susceptible to kleptoparasitism from lions and spotted hyenas, losing as much as 12% of their kills in this manner (Kruuk, 1972; Schaller, 1972). Hayward and colleagues (2006) describe cheetahs as “competitively inferior to virtually all other large predators, even vultures” (pg 616), noting the infrequency with which cheetahs attempt to scavenge from other predators (see also Frame, 1999; Schaller, 1972). Cheetahs are second to wild dogs in the narrowness of both preferred and actual prey (Hayward and Kerley, 2008), a liability that they link to their status as “vulnerable” on the International Union for Conservation of Nature (IUCN) and the continued decline of their population (but see Durant, 1998). In addition to human encroachment, competition with larger predators, lions and hyenas, contributes directly to the low density of cheetahs in sympatry (Durant, 1998).

Wild dogs are a naturally rare species with declining numbers (Creel et al., 2004; Woodroffe et al., 2004). Currently, they are the most vulnerable of the large African carnivores, listed as “endangered” by the IUCN. Wild dogs hunt cooperatively and opportunistically in a wide variety of Sub-Saharan habitats, excluding forests and extreme deserts (Hayward et al., 2006d; Creel and Creel, 2002), where they are concentrated around the highest biomass of small and medium sized prey (Ginsberg and Macdonald, 1990). Despite a body mass of 17 kg to 36 kg that ranges below the 21.5 threshold for obligate large vertebrate carnivory (Carbone et al., 1999), all wild dogs are obligate vertebrate carnivores that acquire larger prey through pack hunting. Within a range of hunted prey species from >1 kg to 432 kg, wild dogs have a bimodal prey size preference of 16 – 32kg and 120 – 140 kg (Hayward et al 2006d). Wild dogs generally overlap with other carnivores in prey species, sharing a preference for bushbuck with leopards, for Thomson’s gazelle with cheetahs, and for impala with both carnivores. Despite the competitive pressure exerted by these larger carnivores, the preferred and actual prey breadth of the wild dog is the lowest in the guild (Hayward and Kerley, 2008). Across various habitats, wild dog hunting success rates vary from 13% - 100%, with a mean of 44%, putting them near the top of the guild for hunting success (Hayward et al., 2006d). However, they suffer the highest rates of kleptoparasitism, losing as much as 50% of their kills in open habitats to spotted hyenas (Kruuk, 1972). Wild dogs are often targeted by lions, which is the most common cause of death in some populations (Ginsberg et al., 1995; Mills and Gorman, 1997).

The five members of the African large carnivore guild overlap considerably in their prey preferences, which derive primarily from the family Bovidae. Because the density of predators is positively correlated with preferred prey biomass, food appears to be an organizing and strongly limiting factor resulting in exploitative competition (Hayward and Kerley, 2008). Within the guild, the smallest of the large carnivores, cheetah and wild dog, experience the highest rates of kleptoparasitism and predation by the larger members (Haywayrd and Kerley, 2008; Laurenson 1995; Creel and Creel 1996; Carbone et al. 1997; Mills and Gorman 1997; Gorman et al. 1998; Vucetich and Creel 1999; Durant 2000).

Competition avoidance strategies

The large carnivores have evolved many strategies to cope with the competition that results from sympatry and dietary overlap. The dominant species, lions, hyenas, and leopards, have the greatest amount of temporal overlap at 80% of their active hours, and often engage directly. They spend the most time active throughout the circadian cycle, and are more nocturnal than cheetahs and wild dogs (Hayward and Slotow, 2009). Lions are the most active throughout the 24 hour cycle, likely at times that maximize their hunting success, while the hyena is the most nocturnal (Hayward and Slotow, 2009).

As the keystone predator with the largest mass, the group-living lions are often able to forgo the energetic costs of hunting in exchange for scavenging (Kruuk, 1972), but must also defend their own kills. Lions and hyenas are the most directly competitive dyad in the guild. Group hunting increases both species' hunting success and carcasses defense against massing hyenas or lions (Cooper, 1991; Honer et al., 2002; Pereira et al., 2014). The amount of hunting vs. scavenging employed by lions and hyenas is dependent on their relative density, which is in turn related to habitat type. In open grasslands, hyenas obtain prey primarily through hunting, and may outnumber lions by 4:1 or more. In these habitats, where cover for ambush hunting is lacking, lions scavenge from hyena kills frequently (Pereira et al., 2014). In vegetated areas, up to one third of the hyena's diet may come from scavenging from lion kills where they may only outnumber lions 1.5 – 2:1 (Pereira et al., 2014). A further portion of the lion and hyena diet is supplemented by scavenging carcasses from leopards.

In contrast with the other guild members, leopards are solitary hunters, and must employ other means to compete with lions and hyenas. On average, leopards lose between 5% - 10% of their kills to kleptoparasitism from their competitors, and compensate by scavenging from other predators at approximately the same rate (Bertram, 1979; Hayward et al., 2006a). To reduce the threat of kleptoparasitism, leopards often cache the remainder of their kills in trees (Pienaar, 1969; Kruuk, 1972; Bailey, 1993; Pereira et al., 2014). The success of this strategy varies in different habitats, with 57% of cached carcasses scavenged in Kruger National Park (Bailey, 1993) but only 9% in Kaudom (Stander et al., 1997).

Cheetahs and wild dogs rely most heavily on temporal and spatial niche partitioning to avoid direct encounters with dominant species. In their review of activity patterns among the five large carnivores, Hayward and Slotow (2009) found that, while all guild members experience intraguild predation and kleptoparasitism, the subordinate taxa, cheetah and wild dog, are at greatest risk. In combination with habitat partitioning that avoids areas in which lions are most common whenever possible (Palomares and Caro, 1999; Durant, 1998), predation risk has resulted in naturally low population densities in large territorial ranges (Pereira et al.,2014). Wild dogs are a strictly crepuscular species, with over half of their activity time occurring at dawn and dusk, and the remainder during daylight hours. They have the least overlap with the activity times of their preferred prey and dominant predators (Hayward and Slotow, 2009). Cheetahs overlap 67% with wild dogs in hours of activity, but are more active at dusk than dawn. Both wild dogs and cheetahs have significantly reduced active time throughout the day relative to the other members of the guild, with which they overlap 50% and 56%, respectively (Hayward and Slotow, 2009). Together, their status as small, subordinate carnivores with limited activity periods and large ranges designed to reduce carnivore competition, results in low population density and a precarious survival strategy.

Hadza Interactions with the Modern Carnivore Guild

Within their foraging lands, Hadza encounter numerous carnivores, including lions, hyenas, leopards, wild dogs, foxes and jackals, each of which constitute a scavenging target (Marlowe, 2010). Like hunting, opportunistic scavenging provides significantly more meat in the dry season than the wet season (Bunn et al., 1988). Scavenging by men and women accounts for approximately 20% of the carcasses, or 14% of the annual meat intake by weight (O'Connell et al., 1988; Bunn 2007c). Interference competition, often referred to as power scavenging in the hominin foraging literature, provides much more meat than passive scavenging, in which the carcass is taken only when it is fully abandoned by substantially-sized carnivores.

In the day, circling vultures lead predictably to carcasses, though these may have little flesh remaining by the time the Hadza arrive. At night, Hadza will listen for the sounds of a kill but refrain from tracking it down until dawn the next morning (Marlowe, 2010). Nighttime is a more dangerous activity period for Hadza, such that men hunting from bush blinds in the dry season frequently operate in pairs to protect themselves from lions and leopards that employ the same crepuscular and nocturnal strategies (Marlowe, 2010).

Scavenging Hadza get carcasses with considerable meat remaining if the predator is large and the kill site is discovered early. Carcasses cached in trees by leopards are found and scavenged occasionally. When the leopard is present, men with bows and arrows and women armed only with digging sticks can successfully drive it from its kill (Bunn et al., 1988; O'Connell et al., 1988; Marlowe, 2010). However, when lions are present, the scavenging party may wait nearby until the lions have finished feeding, or, if the lions are sated, chase them away by shooting an arrow into their midst (Marlowe, 2010). In the dry season of 1986, Bunn and colleagues (1988) did observe that three out of four encounters with feeding lions were resolved by actively driving the lions from their kills. Thus, when lions are involved, Hadza prefer to scavenge passively but will actively interfere if warranted. On the rare occasion that a lion or leopard is killed, it too is eaten (Marlowe, 2010).

In sum, the meat foraging methods employed by the Hadza have elevated them to top predator status, capable of sympatry and interference competition with large carnivores. Nor do they appear to suffer from contact with dangerous game animals. Woodburn (1964) noted that although Hadza hunt some of the most dangerous animals in the world, including lions, leopards, rhinoceros and buffalos, none of the people he interviewed could recall an incident in which Hadza were killed while hunting. Even so, Hadza often operate in groups at night when lions, hyenas, and leopards are hunting. This, in addition to a wet season camp dispersal strategy (Gould and Yellen, 1987), eases interference competition with the carnivore guild.

Competition in the Pleistocene Carnivore Guild

Understanding niche dynamics in the carnivore paleocommunity is important for reconstructing early hominin meat foraging because of its impact on hominin predation and resource competition (Lewis, 1997). Of particular interest here is to determine if hominins were under the same pressure to develop carnivore avoidance strategies in the Pleistocene as they would be by the extant eastern African carnivore guild (see Treves and Treves, 1999). There are several ways to approach the question of hominin-carnivore competition and kleptoparasitism. Given the nature of the archaeological record, most researchers have focused on the availability of carcasses in the Pleistocene based on modern African carnivore communities (Blumenschine 1986, 1987; Cavallo and Blumenschine, 1989; Dominguez-Rodrigo, 2001), the ecomorphology of extinct carnivoran fossils (Marean, 1989; Lewis, 1997), and the taphonomic condition of fossil prey assemblages (Egeland, 2007, 2014; Blumenschine et al., 2005; Dominguez-Rodrigo and Barba 2006, 2007a; Bunn and Kroll, 1986; Bunn and Ezzo, 1993; Bunn, 2001; Bunn, 1991; Ferraro et al., 2013; Bunn and Pickering, 2010a, 2010b; Bunn and Gurtov, 2014). The site of FLK Zinj, described above, was an anthropogenic site to which hominins transported carcasses that they acquired independently of other carnivores. Nevertheless, hominin scavenging opportunities, or the amount of flesh left on carcasses when they're abandoned by their predators, have been used extensively to analyze the degree of carnivore competition in a given habitat (Potts, 1984). The following review of carcass availability is intended to elucidate this aspect of carnivore dynamics and the degree of competition Early Pleistocene hominins may have experienced, and not their scavenging opportunities per se.

Carnivore density strongly impacts the rate of encounter (Van Valkenburgh, 2001). Between 4.2 and 0.9 Ma, the number of carnivoran taxa rose and fell twice. Between 2.1 and 1.5

Ma, there were an average of ~24 carnivorous taxa in eastern Africa, after which carnivoran taxa declined in number until it reached ~10 carnivorans at 0.9 Ma (Lewis and Werdelin, 2007). This means that the equivalence of fossil and modern competitive dynamics, something which must be evaluated rather than assumed (Turner, 1990; Lewis, 1997; Van Valkenburg, 2001). Notably absent today are the saber-toothed cats. In eastern Africa, *Dinofelis barlowi*, *Megantereon cultridens,* and *Homotherium latidens* were present until 1.5 Ma (Turner and Anton, 1998). Together, the Pleistocene carnivore guild likely created different scavenging opportunities and competitive pressures than do modern carnivores, but extant species remain the best reference for interpreting how dense prey assemblages were generated in the past (Marean, 1989; Lewis, 1997; Blumenschine, 1986; Dominguez-Rodrigo, 1999; Van Valkenburgh, 2001).

Olduvai Gorge Bed I fossils include paleomorphs of *Panthera leo*, *Panthera pardus*, *Acinonyx jubatus, Crocutta* sp., and wild dogs that were anatomically comparable to the extant species, and at least two sabertoothed cats (Table 1.3). *Homotherium* is absent from Bed I, but the presence of the other taxa suggests that the Early Pleistocene carnivore guild of Olduvai Gorge was not only more numerous, but also more densely packed, with narrower ecological niches carved out of the same habitat that is currently occupied by the less numerous and more generalized extant carnivores (Lewis, 1997).

Carnivores Present in Bed I, Olduvai Gorge

Taxon	**Common Name**
Canis africanus	African dog
Canis mesomelas	African wild dog
Acinonyx jubatus	Cheetah
Dinofelis sp.	False sabertooth cat
Panthera leo	Lion
Panthera pardus	Leopard
Megantereon sp.	Sabertooth cat
Crocuta sp.	Hyena

Table 1.3. From Lewis (1997).

Neither *Homotherium, Megantereon*, nor *Dinofelis* share postcranial pursuit or capture adaptations with living felids or with each other (Lewis, 1997). As saber-toothed felids, their masticatory adaptations are also more specialized for shearing than any modern carnivoran, which precludes even the meager bone crushing abilities of modern felids due to the potential for canine breakage (Marean, 1989). *Megantereon* belongs to the subfamily Machairodontinae, and is most closely related to extant jaguars, with radii that were functionally very similar. *Megantereon* was likely intermediate between jaguars and leopards in body size (Lewis and Werdelin, 2007) and probably targeted prey similar to that of extant lions (Lewis, 1997). *Dinofelis* is commonly called a "false sabertooth" due to its sturdier canines and more primitive carnassial when compared to the masticatory apparatus of true sabertooths (Marean, 1989). This taxon is considered by many paleontologists to be most closely related to extant species of the *Panthera* genus, though its placement in either Machairodontinae or Felinae is debated (Marean, 1989). Like living leopards and lions, *Dinofelis* had great forelimb strength and flexibility, but shared with the extinct saber-toothed felids relatively greater hindlimb musculature. In body size it fell between living leopards and lions (Lewis, 1997).

Though no *Homotherium* fossils have been found at Olduvai Gorge, the taxon is known from comparable paleoenvironments of Early Pleistocene eastern Africa, and may have been present in the broader Olduvai savanna region. Indeed, the ecomorphology of *Homotherium* suggests that it preferred open habitats. Relative to the other saber-toothed cats, *Homotherium* was larger and better adapted to cursorial activities, with relatively longer limbs but more gracile musculature than living lions and tigers (Turner and Anton, 1997; Lewis, 1997). The forelimb had great flexibility, indicating prey grappling capabilities approaching those seen in extant lions and tigers, while the hindlimb was relatively shorter than the forelimb as seen in extant hyenids. This latter feature is thought to reflect a compromise between locomotion and prey transport ability (Spoor, 1985). The combination of long limbs and gracile physique suggests a unique prey capture strategy unseen among the living and extinct carnivores (Lewis, 1997).

The brachial index of living carnivorans reflects their preferred habitats. When the length of the radius is divided by the length of the humerus and multiplied by 100, living carnivorans that prefer open habitats, such as cheetahs and wild dogs, have brachial indices above 100, and those in closed habitats, like pumas and tigers, fall below 100 (Marean, 1989). *Dinofelis* and *Megantereon* had brachial indices well below 100, placing them in the mixed-closed habitat range (Lewis, 1997). *Homotherium*, by contrast, had a higher brachial index, indicating a preference for open habitats. Notably, no extant African large carnivore is as adapted to dense forests as *Dinofelis* and *Megantereon*, though they need not have occupied them exclusively (Van Valkenburgh, 2001).

There is significant disagreement about the availability of abandoned, partially fleshed carcasses in the Early Pleistocene. Most researchers concerned with this subject are interested in the plausibility of a dedicated passive scavenging niche for the earliest hominin meat-eaters (e.g., Schaller and Lowther, 1969; Blumenschine, 1987; Cavallo and Blumenschine, 1989; Marean, 1989; Lewis, 1997; Van Valkenburgh, 2001; Bunn and Ezzo, 1993; Bunn and Kroll, 1986; Bunn, 1988, 2001, 2007a, 2007b, 2007c; Bunn and Pickering, 2010a; Bunn and Gurtov, 2014). This discussion is also revealing about the degree of competition within the paleoguild, as higher competition will result in fewer carcasses abandoned before they are fully consumed, and greater investment by carnivores in the defense of their kills (Van Valkenburgh, 2001; Dominguez-Rodrigo, 2001). Some researchers have concluded that a greater array of species specialized for shearing flesh, but not dismembering and cracking bone, would have created more passive scavenging opportunities for early *Homo*, with its ability to access brains and marrow using stone tools (Blumenschine, 1987; Cavallo and Blumenschine, 1989; Marean, 1989).

Riparian forests feature prominently in early actualistic studies of carnivore competition because they were inferred to have been important habitats for hominins at Olduvai Gorge (Hay, 1976). Blumenschine (1987) investigated the availability of carcasses in the Serengeti and Ngorongoro Crater and their taphonomic similarity to Pleistocene archaeological assemblages, particularly FLK Zinj, concluding that hominins would have had ample passive scavenging opportunities for marrow in the relatively low competition riparian habitats. The morphology of eastern African bone-crunching species of the Early Pleistocene is comparable to modern hyenids, indicating that they contributed similarly to carcass deletion (Lewis, 1997). In contrast, the delicate structure of *Megantereon* dentition would have made dismembering and fully defleshing carcasses a dangerous risk (Marean, 1989). The sturdier shape of *Dinofelis* canines could have withstood this type of activity better, but would still have risked damage (Lewis, 1997). Blumenschine (1987) observed that hyenas avoided the closed, riparian environments to which felids retreat with their kills, and carcasses there lasted up to several days before they were completely consumed. Under these conditions in a riparian habitat, Blumenschine (1987) predicted that abandoned size 2 and 3 carcasses would contain brain and possibly marrow, while size 4 carcasses would also retain some flesh, creating an open niche for tool-carrying hominins to exploit these resources, particularly in the dry season when prey is abundant near water.

Similarly, in a study spanning three consecutive dry seasons in the Maasai Mara National Park, and Kulalu and Galana ranches, Kenya, Dominguez-Rodrigo (2001) also observed that carcasses in riparian woodlands lasted far longer than those in open environments. No scavenging species overlapped, such that a single species fed on a carcass at a time. Carcasses lasted an average of 1 – 2 days in some locations and up to 7 days in others. The behavior of lions consuming carcasses in woodlands underscores the low degree of competition at these sites. Rather than abandoning carcasses within 2 – 3 hours as they did in open areas of the parks (but see Bunn and Ezzo, 1993, for longer lion feeding duration), lions remained hear their kill and consume it in several phases over a longer period of time.

A subsequent study by Cavallo and Blumenschine (1989; Blumenschine and Cavallo, 1992) explored the passive scavenging opportunities from tree-cached leopard prey in the Serengeti. The authors concluded that there would have been adequately low competition for these carcasses from allospecifics, and that hominins would have found them a sufficiently attractive and regular source of calories. Lewis (1997) describes the forelimbs of *Dinofelis* and *Megantereon* as flexible and capable of facilitating climbing, much as they are in leopards, potentially enabling these taxa to cache partially defleshed carcasses in trees (Lewis, 1997). However, the fragile *Megantereon* canines would have made carcass transport difficult, if not impossible, without damage to the masticatory apparatus. The canines of *Dinofelis* may have withstood carcass transport, but its robust body is thought to have precluded tree-caching because of the energetic costs of hoisting a medium-sized ungulate along with its own frame (Lewis, 1997; Lewis and Werdelin, 2007). Pleistocene leopards are known to have cached carcasses in trees (Brain, 1981) and were present in Olduvai Gorge Bed I, but this does not guarantee that they practiced tree caching there. Among extant leopards, this behavior is absent where other large-bodied climbing carnivores are present, such as Sri Lanka, suggesting that leopards are responsive to arboreal kleptoparasitism by other carnivores (Van Valkenburgh, 2001). Lewis (1997) concludes that if hominins were frequently successful, leopards would have ceased expending the energy to drag carcasses into trees, or would have been more diligent in defending them. The apparent climbing ability of *Dinofelis*, *Megantereon*, lions and hominins suggests that kleptoparasitism from trees by allospecifics was either rare, so common as to discourage leopards from continuing the practice, or a highly competitive strategy in which hominins would have faced extreme danger from other carnivores (Lewis, 1997; Van Valkenburgh, 2001).

Tappen (2001) has critiqued the use of the Serengeti as a model for the environment of evolutionary adaptiveness (EEA) for australopithecines and early *Homo*. The Serengeti and Kenyan parks studied by Dominguez-Rodrigo (2001) fall toward the dry end of savanna habitats in the degree of rainfall seasonality and migration patterns, resulting in seasonal gluts and dearths of biomass in various regions. This has informed Blumenschine's (1986, 1887, 1989; Blumenschine and Peters, 1998) models of hominin seasonal scavenging and resource competition. In a comparable study of Virunga National Park in the Democratic Republic of the Congo, Tappen (2001) reports that scavengeable carcasses were encountered at an average rate of 1 every 9 days from the height of the dry season through the height of the wet season (July – November, respectively) in 1995. The average remaining long bone marrow, brain, and flesh amounted to ~2,000 kcal per carcass, or about 215 kcal per day. If hominins scavenged in groups, the energy intake rates drop to a few tens of kcal per individual. Tappen (2001; see also Dominguez-Rodrigo, 2001) also found that hyenas in Virunga were more common in wooded areas, while lions were to be found more often in the plains, and that the plains provided the greatest number of scavenging opportunities. Where, or when, precipitation exceeds 550 mm/year, habitats like Virunga may provide better models of resource competition. FLK Zinj and FLK North, however, accumulated during drier phases in the climatic fluctuations at Olduvai, but within wooded patches near permanent sources of freshwater (Ashley et al, 2010a, 2010b; Magill et al., 2012a; Ashley et al., 2013). As such, neither the Serengeti and associated ecosystems, nor Virunga, can provide exact estimates of carcass availability or carnivore competition.

The value of these studies for interpreting resource competition and predation pressure at FLK Zinj is debatable for additional reasons. Size 4 carcasses, which are reported to retain some flesh after abandonment, are uncommon at both FLK Zinj and FLK N, and so their significance to the hominin foraging strategy, and associated predation risk from scavenging from carnivore kills, cannot be determined. More importantly, these studies explore the plausibility of a scavenging niche based on access to marrow, brains, and the occasional scrap of meat. At neither site is there evidence of cranial exploitation. In fact, crania are rare at FLK Zinj, where limbs and mandibles dominate. And though both studies suggest that scraps of meat remained for hours or days on size 4 bovids, they do not accurately model an assemblage like FLK Zinj, where the presence of cut marks reflects greater abundances of flesh than is available on abandoned carcasses (see Bunn and Ezzo, 193; Bunn, 2001, 2007a). Therefore, to the extent that these carcass frequency studies are intended to illuminate carnivore competition in the Early Pleistocene, they are inappropriate for the particular case of FLK Zinj.

Due to the presence of several woodland adapted carnivores at Bed I Olduvai, wooded habitats were very likely higher pressure environments than they are today (Van Valkenburgh, 2001). The apparent adaptation to closed habitats of *Dinofelis* and *Megantereon* indicates that riparian woodlands in Early Pleistocene eastern Africa would have been more competitive than was predicted based on modern carcass availability surveys. Lewis (1997) predicts that the greater behavioral and dietary breadth of the paleoguild would have created more occasions for competitive encounters with large-bodied carnivores in all habitats. Unless hominins were top carnivores, power scavenging would have been an extremely dangerous endeavor, and passive scavenging would have been more limited. Moreover, the wildlife reserves used in these actualistic studies, particularly the Serengeti ecosystem in Tanzania, are not pristine environments. Carnivores there have been hunted for a variety of reasons over the centuries and through the present day, which artificially lowers modern carnivore populations and, by extension, estimates of carnivore density in the past (Van Valkenburgh, 2001). Nevertheless, most researchers agree that riparian woodlands and similarly vegetated areas would have provided lower-competition environments than open grasslands and woodlands (Blumenschine, 1986, 1987; Dominguez-Rodrigo, 2001; Egeland, 2007, 2014; Cavallo, 1997; Capaldo, 1995). The general consensus of these researchers is that saber-toothed cats preyed on large ungulates in closed environments (Blumenschine, 1987; Cavallo and Blumenschine, 1989; Lewis, 1997; but see Van Valkenburgh, 2001) but that wooded areas would still have been the safest habitat for hominins seeking refuge from the predator guild (Dominguez Rodrigo, 2001; Egeland, 2007; 2014). Wooded habitats are precisely where eastern African Early Pleistocene hominin activities are most common.

Hominin-Carnivore Interactions at Olduvai Gorge

When hominins entered the carnivore guild, they were not top predators. Predation and kleptoparasitism by a denser and more diverse paleoguild could have selected for hominins to reduce competitive encounter rates through a variety of means, including diurnal activity, carnivore habitat avoidance, and low competition prey selection (Van Valkenburgh, 2001); defensive technologies and strategies (Treves and Treves, 1999; Lewis and Werdelin, 2007); and grouping behavior (Rose and Marshall, 1996; Brantingham, 1998). Because the costs of joining the predator guild are great, so too must have been the caloric rewards (Van Valkenburgh, 2001). Once hominins evolved these strategies, in combination with active hunting success, they would have become dominant within the guild, and may have precipitated carnivoran extinctions that began 1.8 Ma and increased significantly after 1.5 Ma (Lewis and Werdelin, 2007).

Predator-prey and carnivore intra-guild dynamics in modern savannas yield the following predictions for meat-eating hominins at FLK Zinj:

- Guild membership: In the modern African carnivore guild, smaller species are subordinate to larger species. Given the weight distribution of Pleistocene predators, hominins just entering a meat-eating niche are expected to have been subordinate members of the guild. The largest known hominin of the time, *Homo erectus*, was at the low end of the carnivore weight range at 52-63 kg (McHenry, 1992), smaller than most wild dogs and comparable to cheetahs. Even group-foraging hominins are predicted to have been reacting to the top-down influence of dominant carnivore behavior.

- Habitat: Because of the many resources that woodlands offer, including shade, camouflage, plant foods, and potentially lingering pools of water, hominins are predicted to have operated primarily in wooded areas like those reconstructed for FLK Zinj and FLK North. The threat of dominant predators compels cheetahs and wild dogs to avoid spatial overlap with lions by avoiding areas with extensive cover. This is something that hominins did not do, as attested by the presence of large tooth pits on bones at hominin sites, and the heavy reliance of lions on waterholes like those near both FLK Zinj and FLK N. This means that the habitat preferences of hominins and large carnivores overlapped.

- Diet: the cut marked carcasses at FLK Zinj belong to the same species eaten by carnivores at FLK North. Both sites are dominated by medium sized bovids (size group 3), which are the prey preference of lion sized predators, indicating a dietary overlap between hominins and top Pleistocene predators.

- Time: The threat of dominant predators is sufficient to drive cheetahs and wild dogs into diurnal niches. Hominins were diurnal as well. The presence of gnaw marks on cut marked bones at FLK Zinj demonstrates that carnivores were present to locate carcasses while they retained nutritional value, though there is debate about the intensity of carnivore competition for these resources. As omnivores, hominins had the ability to seasonally, as well as diurnally, offset the timing of meat-eating in order to preferentially forage when carnivore competition in open woodlands was lowest, that is, in the wet season when prey and predators are dispersed.

Was FLK Zinj a site of high competition, as indicated by its proximity to fresh water and the abundance of popular prey items? Or was it a low competition site, accumulating during the "off season" of carnivore activity in wooded areas? The nature of hominin-carnivore interactions at Olduvai Gorge has been a point of debate since the 1970s (e.g., Isaac 1978), particularly in regards to hominin meat foraging. Hominins are variably characterized as assertive opportunists capable of hunting large game (Bunn and Kroll, 1986; Bunn, 2001, Bunn, 2007a, 2007b, 2007c; Dominguez-Rodrigo et al., 2007b; Bunn & Pickering, 2010a), and as bipedal apes timidly awaiting their turn at the back of the line (e.g., Binford, 1983; Blumenschine and Cavallo, 1992; Blumenschine et al., 2012; O'Connell et al 1990). For instance, while proposing a central-place foraging strategy based on food-sharing, Isaac (1978) suggests that hominins occupied a very weak position in the carnivore guild: "…we cannot judge how much of the meat taken by the protohumans of East Africa came from opportunistic scavenging and how much was obtained by hunting… For the present it seems less reasonable to assume that protohumans, armed primitively if at all, would be particularly effective hunters" (pp. 102). The statement reflects the understanding of the time that *Homo habilis*, or even an australopithecine, was responsible for the FLK Zinj accumulation, and that scavenging from large carnivores was a less dangerous method of meat acquisition than hunting. As described above, the pattern of butchery marks at FLK Zinj reflects the presence of flesh on bones, which requires early and direct confrontation in order to intercept carcasses before they are fully consumed. Now that the remains of a large bodied *Homo* species have been found at Olduvai Gorge (Dominguez-Rodrigo et al., 2015), and the origins of the genus are pushed back to 2.8 Ma (Villmoare et al., 2015), there seems little reason to posit a small-bodied hominin as the creator of FLK Zinj.

Researchers have come down on both sides of the debate about competition intensity at FLK Zinj. The presence of carnivore remains at FLK Zinj, in addition to prey carcasses, indicates significant intra guild predation on site (Potts, 1984). Handling carcasses in this context made hominins especially vulnerable to kleptoparasitization and predation. For this reason, Potts (1988) argues that hominins would have made efforts to minimize the amount of time spent at FLK Zinj. Blumenschine and colleagues (2012) suggest that the presence of carnivore gnaw marks on the faunal assemblage reflects high predation pressure as well. Key sites, like FLK Zinj and FLKNN 3 that retain evidence for multiple carnivore agents acting on hominin specimens, demonstrate that hominins were under significant threat from both mammalian carnivores and crocodiles (Njau and Blumenschine, 2012). The resources that attracted hominins, such as potable water, refuge trees, and scavengeable carcasses, would always have attracted carnivores as well. Njau and Blumenschine (2012) conclude that these were areas of high predation risk that were visited briefly by small groups of non-breeding hominins to acquire and processed food that they consumed on the spot or transported elsewhere (see also Blumenschine and Peters, 1998; Njau and Blumenschine, 2006).

Using similar taphonomic analyses, other studies have reached an alternative view of FLK Zinj as a place of refuge. In a study of hominin carcass butchery and carnivore carcass ravaging, Egeland (2014) concluded that there is no discernable spatial relationship between carnivore and hominin activities in Bed I. The same held true for lithic discard patterns and carnivore competition (see also Brantingham, 1998). However, the lower-than-expected frequency of gnaw marks combined with the paucity of axial parts rapidly deleted by carnivores, suggests that hominins preferentially transported select carcass parts to FLK Zinj (Dominguez-Rodrigo et al., 2010). Egeland (2014) proposes that habitat preference and occupation intensity in Bed I were not directly responsive to carnivore competition, but that FLK Zinj may have provided a safe haven for hominins engaged in activities beyond butchery and feeding. Baquedano and colleagues (2012) also noted that, despite the presence of crocodilian modifications to OH8 and OH35, the overall evidence for crocodile gnawing at FLK Zinj, FLK N, and the surrounding landscape is well below expectations based on actualistic research with feeding crocodiles, indicating low predation pressure from these carnivores as well. In a particularly far-sighted statement, Bunn and Kroll (1986) wrote, "We do not know the frequency of activities at the FLK *Zinjanthropus* site, beyond the indication from the bone weathering data of a relatively short period of accumulation. It is certainly possible that many of the hominid feeding events at FLK *Zinjanthropus* could have occurred during a seasonally restricted period of less predator damage to carcasses" (pp. 441).

Hypotheses

The analysis of meat foraging seasonality presented in this dissertation provides a new but anticipated avenue for understanding the place of hominins in the carnivore guild. Based on the preceding discussion, three related hypotheses are proposed and tested in the following chapters:

> (H1) Dental microwear values demonstrate no statistical relationship between ungulate mortality and season. Under this null hypothesis, the DMTA signatures of each animal in an assemblage have an equal chance of appearing in the wet or dry season. A Satterthwaite's t-test on the wet and dry season samples will yield a non-significant p value. If a significant p value is obtained, it will reflect statistically identifiable

differences in the texture of the ungulate diet between wet and dry seasons. This is tested in Chapter 2.

H2. If bovids were sufficiently fat-depleted in Early Pleistocene dry seasons, then dry season archaeological sites should reflect hominin selectivity for bovid demographics and skeletal elements with better fat retention, as argued by Speth (1987, 1989, 2012; Speth et al., 1991). This is evaluated in Chapter 3 by identifying modern referents for extinct bovids at FLK Zinj, and analyzing these for patterns of fat retention that can systematically identify selection on this trait in a faunal assemblage. If selection for fat retention cannot be identified, either due to weak demographic and skeletal patterning in modern referents, or due to conflicting archaeological signals, then an alternative method for identifying dry season site use is needed.

H3. If dental microwear texture analysis can distinguish wet and dry season bovid deaths, then hominin meat foraging seasonality can be evaluated at FLK Zinj, presented in Chapter 4:

> H3a. If hominin meat eating was nutritionally driven, then it should occur in the dry season, which is the lean season in eastern African svannas, when plant foods require longer foraging times and are less nutritious.

H3b. If meat-eating occurred around a predator avoidance strategy, then it would take place in the wet season (contra Blumenschine, 1987; Blumenschine and Cavallo, 1992**;** Foley, 1987: 199 - 210; Marean, 1989)

H3c. If meat-eating was an integral part of the foraging strategy of a carnivore-guild member, as it is for the Hadza, it will occur year-round.

Assessing Seasonal Foraging at Olduvai Gorge

I will approach the question of foraging seasonality by evaluating the same assemblages that have featured prominently in early hominin foraging debates, but I will do so in a novel way: scale-sensitive fractal analysis on dental microwear, referred to as dental microwear texture analysis (DMTA). Foods consumed by animals leave microscopic abrasions and polishes on the enamel of their teeth. In seasonal environments, microwear co-varies with diet (Teaford and Robinson, 1989). Seasonal differences in microwear have been documented in modern capuchins (Teaford and Robinson, 1989), roe deer (Merceron et al. 2010), and in the European archaeological record (Rivals and Deniaux, 2005), but no one has applied this technique to the African Pleistocene.

Microwear analysis has many advantages over traditional methods for ascertaining seasonality, particularly in terms of data quality. Microwear is subject to the "last supper" phenomenon, which refers to the rapid turnover rate of enamel abrasions, providing a great degree of SOD precision by recording only the food texture properties of the last few days or weeks (Teaford and Oyen, 1989). Most importantly for archaeological samples, the method samples those skeletal elements most likely to survive—the teeth. Inter-element studies have shown that upper and lower first and second molars from the same individual retain equivalent microwear (Merceron et al., 2004, Schubert et al., 2006). As a non-destructive method, microwear analysis permits independent verification of results and protects cultural heritage from damage. Tooth molds can easily be made at museums or onsite and transported to a confocal microscope for analysis. Together, these advantages favor microwear analysis over stable isotope analysis, which can only document seasonal variation in developing teeth, and cementum analysis, which is a destructive technique requiring perfect preservational conditions (Lieberman et al., 1990).

Microwear analysis of tooth occlusal surfaces has been in use since the mid-1970s (Scott sources). Early studies relied on counting the number of pits and scratches visible with a light microscope. As the methods developed, researchers introduced the use of the scanning electron microscope, and later, combined conventional light microscopy with digital photography and image analysis software (Merceron et al., 2004a, 2004b). Studies using these methods have found evidence for seasonality in the food fracture properties of various organisms (e.g. Solounias et al., 1988; Solounias and Semprebon, 2002; Merceron et al, 2006). Among living and extinct ruminants, Solounias and colleagues (1988) found that the number of scratches on the molar occlusal surfaces of seasonal and regional mixed-feeders exhibited a bimodal frequency that placed them with either the strict browsers or strict grazers. In a broad survey of extant African bovid microwear using DMTA, Scott (2012) was unable to separate generalists and mixed feeders into their known dietary categories, which was attributed to the seasonal or regional variation of the sample (Scott, 2012). DMTA has also been used to identify differences in diet at the scale of individuals, sex, and intra-population seasonal differences among *Capreolus capreolus* from France (Merceron et al., 2010).

The present study approaches hominin foraging seasonality by analyzing the dental microwear signal for SOD in hominin and carnivore prey using dental microwear texture analysis (DMTA). DMTA is shown to better assess dietary differences in both herbivores and carnivores than traditional dental microwear methods that rely on counting pits and scratches (DeSantis et al., 2013). DMTA analyzes microscopic pits, scratches, and gouges on the occlusal surface in three dimensions and at multiple scales using a Sensofar PLμ white-light confocal profiler (Solarius Development Inc., Sunnyvale, CA) and scale-sensitive fractal analysis software packages Sfrax and Toothfrax (Surfract Corp.). Fractal analysis at various scales allows researchers to consider surfaces that may be smooth at one scale but course at another, and to evaluate those differences in light of food fracture properties. Five key variables have been developed toward this end: area scale fractal complexity (*complexity* or *Asfc*), scale of maximum complexity (*Smc*), length scale anisotropy (*anisotropy* or *epLsar*), texture fill volume (*Tfv*) and heterogeneity of area scale fractal complexity (*Heterogeneity* or *HAsfc*). The median values obtained for each variable are interpreted to reflect the food fracture properties in the diet of the organism under consideration based on extensive comparative analysis of modern species with known diets (e.g. Scott et al., 2005; Krueger et al., 2008; Ungar et al., 2007; Scott et al., 2009; Krueger and Ungar, 2010; Schubert et al., 2010; Donohue et al., 2013; DeSantis et al., 2012; Schulz et al., 2013). These variables will be discussed further in Chapter 2.

The success of microwear analysis in identifying season of death in temperate-dwelling bovids suggests that the season of death in seasonal mixed feeders living in a seasonal savanna may also be identifiable by DMTA. To date, no such study has examined the potential of this method in an African savanna. In the following chapters, I test DMTA's ability to determine SOD in a modern mixed feeder, I discuss the need for such a method in archaeological samples given the short-comings of current approaches, and I apply it to the bovid assemblages at FLK Zinj and FLK North discussed above. With new evidence for the timing of hominin foraging at the dawn of persistent hominin carnivory, new aspects of the ecological niche can be explored, including the nature of hominin-carnivore competition and the role of meat in the hominin diet, in the context of seasonal savanna ecology.

Chapter 2. Dental Microwear Texture Analysis of Impala Season-of-Death: A Test of Methods

Introduction

Members of the Family Bovidae are instrumental in interpreting the preferred habitats of hominin taxa. Bovids are considered an especially reliable proxy for reconstructing the African paleoenvironment because they are ubiquitous and their diets can be discretely categorized (e.g. Vrba 1974, 1975; Solounias and Semprebon, 2002; Gagnon and Chew, 2002; Scott, 2012). Toward this end, many aspects of bovid ecology have been examined, including ecomorphological adaptations (Reed, 1997; Owen-Smith, 2013), dietary continuity through time (Scott, 2012), niche partitioning (Rivals et al., 2014); environmental change (Merceron and Ungar, 2005; Scott, 2012); and seasonal dietary variation (Teaford and Robinson 1989; Rivals and Deniaux, 2005; Rivals et al., 2009).

Bovids have been used to explore hypotheses about the ecological and dietary flexibility of *Australopithecus, Paranthropus* and *Homo* in the face of increased aridity at the start of the Pleistocene in Africa (e.g. Wood and Strait, 2004). Shipman and Harris (1988) noted the presence and absence of particular bovid tribes at hominin sites in order to reconstruct the predominant habitat of *Paranthropus aethiopicus* as closed and wet. Reed (1997) used bovid ecomorphology and the ecological diversity in large mammal communities to interpret the preferred habitats of early hominins, finding that while *Australopithecus* and *Paranthropus* both preferred wet and closed habitats, *Homo* was the first hominin associated with arid grasslands. These and other findings are critical components of a holistic understanding of hominin evolution in its environmental context (Wood and Strait, 2004).

Bovids are also useful in interpreting localized hominin activity sites within regional paleoenvironmental reconstructions. While the general bovid composition of Olduvai Bed I (~2.0 – 1.75 Ma) places it among the driest and most open hominin sites between 3.6 – 1.6 Ma (Reed and Russak, 2009), an analysis of the Antilopine – Alcelaphine criterion developed by Vrba (1980) at archaeological localities within Bed I indicate a range of open to closed vegetative conditions (Kappelman, 1984). The distinction between basin-level environment and locality-specific habitats is informative when considering the types of resources that may have attracted hominins to particular places on the landscape (e.g. Peters and Blumenschine, 1995; Blumenschine and Peters, 1998; Ashley et al, 2010).

In this paper, I examine the potential for bovid dental microwear texture analysis (DMTA, referred to elsewhere as scale sensitive fractal analysis, or SSFA) to act as a proxy for seasonal patterns of human hunting in modern tropical savannas, and its applicability to archaeological sites in the past. Intrannual dietary variation is of particular interest because it tracks the profound effect that strong seasonality has on the spatial and temporal availability of food and water. This variation in the distribution of resources creates a suite of selective pressures that influence foraging behavior of both humans and their prey. By identifying the season of death (SOD) of prey, I can extrapolate seasonal patterns of human hunting in the present, and assess the utility of this approach for the past.

Background

Extending DMTA to the analysis of seasonal dietary variation in savanna-dwelling bovids is the first step in extending this methodology to understanding the seasonal foraging strategies of hominins at sites in Pleistocene Africa. Among extant bovids, migration and dietary shift are the primary modes of adapting to changing seasons. When analyzing an assemblage, migration can often be assessed by the presence or absence of taxa. In the case of residential bovids in temperate regions, seasonal diets are evident in the pattern of microscopic pits and scratches found on dental enamel surfaces (Mainland, 2003, 2006; Merceron et al., 2010).

Early quantitative analyses of dental microwear relied on counting the number of pits and scratches revealed by binocular light microscopy and, later, scanning electron microscopy (for a review, see Scott, 2012). These studies were able to document a predictable relationship between food fracture properties and molar microwear in extant species. But because of the rapid turnover of microscopic abrasions caused by chewing, a taxon's typical or total diet may be obscured, hindering reconstructions of the paleoenvironment (Walker et al, 1978; Grine, 1986; Teaford and Oyen, 1989). Known as the "last supper" phenomenon (Grine, 1986), this turnover is instead useful for studying a narrow time slice of an animal's diet just before death, a timeframe ranging from hours to weeks (Teaford and Oyen, 1989). In highly seasonal environments, where resource availability varies, dental microwear texture analysis (DMTA) may distinguish fine scale dietary differences that reflect the season of death (SOD).

Bovid diets are typically categorized along a browser-grazer spectrum (Solouniaset al., 1988). Grazers and mixed feeders feed on graminoids, including grasses, sedges, and rushes, and are characterized by high numbers of microscopic scratches when viewed using a scanning electron microscope (Solounias and Semprebon, 2002). Browsers that incorporate seeds and fruits differ in their microwear from browsers that exclusively eat leaves, and both have comparatively low numbers of scratches (Solounias and Semprebon, 2002). Solounias and Semprebon (2002) describe two categories of mixed feeder that differ in their temporal intake of browse and graze. “Seasonal/regional” mixed feeders have microwear patterns that resemble grazers or browsers, depending on the composition of their diet shortly before death. “Meal by meal” or “generalist” mixed feeders have high numbers of both pits and scratches. When examined using a white light confocal profiler and scale sensitive fractal analysis (DMTA, Figure 2.2), browsing taxa have higher fill volume, complexity, and heterogeneity values than grazing taxa. Obligate grazers have the highest anisotropy values, followed by browser-grazer intermediates, then generalists and variable grazers, and finally frugivores and browsers (Scott, 2012). By linking dental microwear patterns to these general dietary categories, it is possible to extrapolate the type of immediate environments in which extinct bovids and associated fauna lived.

Several studies have detected inconsistencies or bimodalities in the dental microwear of bovid mixed feeders that appear to track seasonal changes (e.g. Solounias et al, 1988; Solounias and Semprebon, 2002; Merceron et al, 2006). In a broad study of living and extinct ruminants, Solounias and colleagues (1988) found that seasonal and regional mixed feeders exhibited a bimodal frequency of scratches that placed them with either the strict browsers or strict grazers. A survey of extant African bovid microwear using DMTA was unable to predictably separate generalists and mixed feeders into their known dietary categories, which was thought to result from seasonal or regional variation (Scott, 2012). DMTA was also found to detect differences in diet at the scale of individuals, sex, and intra-population seasonal differences among *Capreolus capreolus* from France (Merceron et al., 2010).

The presence of non-dietary wear-causing particles adds nuance to the interpretation of diet from DMTA. Soil and airborne grit are also implicated in a number of dental microwear studies. Teaford and Glander (1996) found an elevation in dust content in the canopy habitat of mantled howler monkeys to be associated with an increase in dental microwear features even when diet remained constant or decreased in endogenous abrasive content. In an analysis of sheep dung by Mainland (2003), the phytolith concentrations in browsers were equivalent to grit concentrations in grazers, indicating that differences in microwear patterning are driven, in part, by exogenous abrasive particles. Two recent studies (Lucas et al, 2013, 2014) called into question the ability of phytoliths to cause any enamel wear, with dire implications for the study of diet using DMTA. Subsequent research (Xia et al, 2015) has demonstrated that particles softer than silica dust can indeed deform enamel, and that rather than the hardness of enamel hydroxyapatite setting the lower limit on abrasive hardness, contact with dietary items need only be forceful enough to break the bonds between proteins holding enamel together.

This study tests the hypothesis that variation in the dental microwear of extant impala (*Aepyceros melampus*) tracks seasonal changes in food fracture properties in an eastern African savanna when controlling for location. As a residential species, impala fall into the category of seasonal mixed feeder (Solounias and Semprebon, 2002) or browser-grazer intermediate (Gagnon and Chew, 2002), seasonally modifying their diet rather than their location. Generally, the impala diet consists of 10% fruits, 45% dicots and 45% monocots (Gagnon and Chew, 2002). This composition changes seasonally, such that impala maximize their grass intake in the height of the wet season (Rogers, 1976; Kutilek, 1979; Dunham, 1980). These dietary preferences are reflected in their preference for light cover, though they spend much of their time in open edge areas where they can escape cursorial predators at top speeds. This habitat preference is referred to as "ecotone" or "edge" by other researchers (Estes, 1991; Kingdon, 1997). In each of these respects, it resembles the fossil bovid *Antidorcas recki*, which is common at both fossil sites FLK Zinj and FLK North in Bed I at Olduvai Gorge Tanzania (Chapters 3 and 4). This makes the impala an idea subject for a test-of-method examining the ability of DMTA to distinguish wet and dry SOD.

The degree to which impala modify their diet seasonally varies by sex. In a study at Lake Mburo National Park in Uganda, females were observed to browse more than males, particularly during the dry season (Wronski, 2002). Likewise, at Kruger National Park in South Africa, analysis of stable carbon isotopes showed that females browse more annually than males (Sponheimer et al, 2003). Rumen samples determined that diet also varied by social organization, such that territorial males consumed more monocots than the females in their herd and non-territorial bachelor males (van Rooyen & Skinner, 1989). Impala dental microwear is therefore predicted to reflect seasonal dietary changes, though the degree of seasonal difference may vary by sex.

***Aepyceros melampus* Diet and Habitat Preference**

Study	Diet	Habitat
Gagnon and Chew (2000): literature summary	Browser-Grazer Intermediate: 45% monocot, 45% dicot, 10% fruit	
Estes (1991): literature summary	Intermediate feeder: prefers green grass, eats browse if unavailable	Woodland edges (ecotone), short and medium height grasslands
Kingdon (1997): literature summary	Exclusively grass in the wet season, 30% grass and 70% browse in the dry season	Edges between grassland and woodland
Plummer and Bishop (1984): metapodial ecomorphology		Intermediate cover
Kappelman et al (1997): femoral ecomorphology		Open country (edge or ecotone)
Spencer (1997):Chewing apparatus functional morphology	Mixed Grass Feeder	Woodland
Cerling et al (2003): C_3/C_4	Mixed Feeder, 52% C_4: dental enamel δ13C mean: -6.0, SD: 3.0	

Table 2.1. Terminology that has been used to refer to impala diet and habitat preferences.

Materials and Methods

Sample

The impala sample derives from an ethnoarchaeological collection of individuals shot with a bow and arrow by Hadza hunter gatherers on the east side of Lake Eyasi, Tanzania, during several wet and dry seasons between 1984 and 2009. The impala dentitions were collected by Henry T. Bunn from observed kills and abandoned seasonal camps with known times of occupation. From these collections, 29 impala individuals, represented by upper and lower M1s and M2s, were selected for analysis. Both upper and lower M1s and M2s have yielded comparable results in previous studies of bovid dental microwear (Merceron et al, 2004).

Unlike other collections currently housed in museums, the Lake Eyasi impala is a large sample from the same locality, allowing for control over the impact of regional habitat differences. Lake Eyasi runs southwest to northeast and abuts the southern foot of the Serengeti Plateau in the base of the Great Rift Valley of northern Tanzania. Paralleling the east side of the salt lake basin is a low ridge supporting a savanna woodland habitat with freshwater springs (Hughes and Hughes, 1992). This elevated strip of land is where most Hadza hunter-gatherers live today. Like the Serengeti to the west, the region is highly seasonal and receives an average of 600 mm annually in direct precipitation (Hughes and Hughes, 1992; http://www.worldweatheronline.com). The majority of rainfall occurs during the long wet season months of March – May, with a shorter, less dependable period of precipitation in November – December. These seasons dramatically change the availability of food and water resources, particularly for year-round resident species (Woodburn, 1964).

When a kill is brought back to camp, it is the practice of Hadza hunters to distribute it to all members of the group, and any visitors who happen to be present (Woodburn, 1964; Marlowe, 2002; personal observation). This has the effect of spreading the skeletal remains of a single individual across the campground. As a result, the Bunn collection of impala teeth was not initially organized by individual, but rather by dental specimen. In order to avoid over-representing the dental microwear of an individual, it was necessary to determine the minimum number of individuals (MNI) present in the collection.

The MNI analysis was accomplished in two steps. First, each tooth was directly compared with other tooth rows and isolated specimens in order to find morphological matches within each site. The teeth were separated into upper and lower dental arcades, and then into lefts and rights. Many of the teeth were still in partial mandibles and maxillae, making the direct association of most same-quadrant M1s and M2s a matter of noting their catalog number or refitting tooth roots into empty alveoli. Within the upper and lower groupings, size, wear, and morphology were compared between left- and right-sided teeth to identify specimens belonging to the same individual. Upper and lower tooth rows were not directly compared because it is notoriously difficult to match them using the occlusal surfaces.

Next, the MNI was calculated based on the number of individuals in each age class. Each tooth row or molar was aged using the system developed by Spinage (1971), which is here modified to reflect an average impala lifespan of 12 years as reported by Roettcher & Hofmann (1970). Dental individuals were then assigned to one of several broad age classes, namely Young Juvenile, Subadult, Early Prime Adult, Late Prime Adult, and Old Adult (see Bunn and Pickering, 2010b). At each site, the best represented dental arcade (either the upper or lower tooth row) in each age class was selected for analysis. For example, in 1998 the NSL site produced upper dentitions from 3 Early Prime Adults, and lower dentitions from 6 Early Prime Adults, resulting in an MNI of 6 for that age group. In this case, only one lower molar from each individual in the

Early Prime Adult class was included in the MNI Sample in order to give each individual equal weight in the analysis.

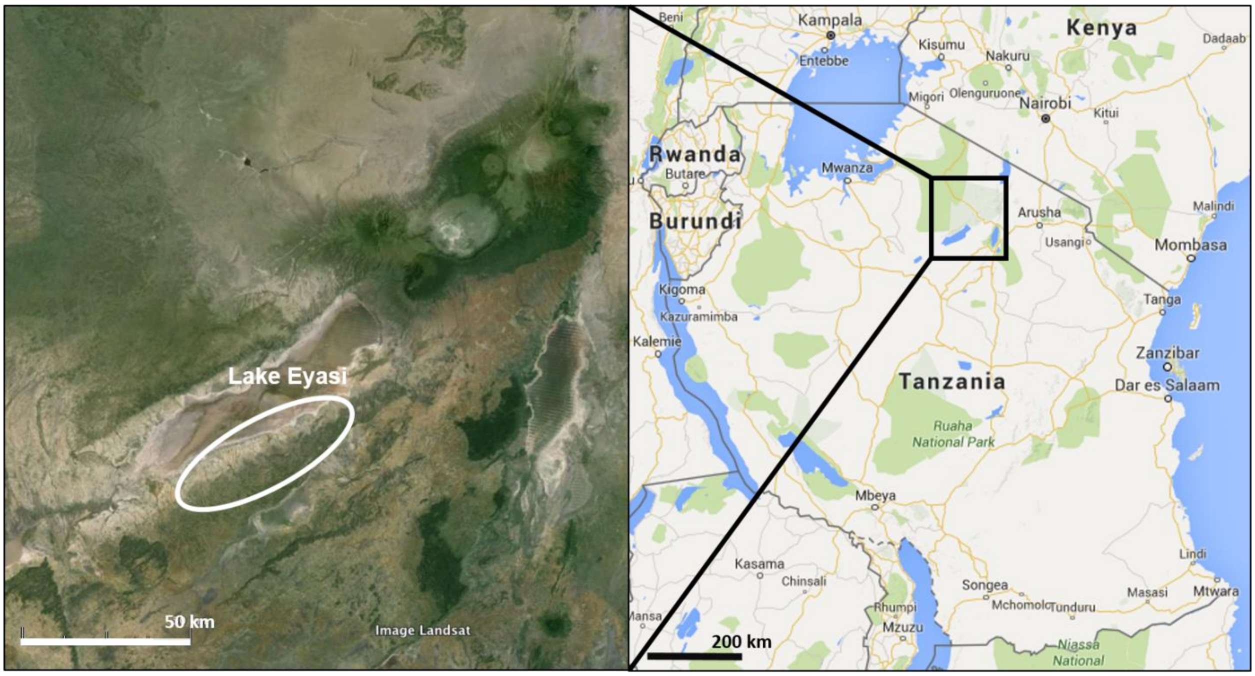


Figure 2.1. Left: Lake Eyasi, Tanzania, with area of sampling in Hadzaland circled. Right: Map of Tanzania, with Lake Eyasi and Hadzaland selected. Maps courtesy of Google Maps, Inc.

Impala age classes are derived from Bunn and Pickering (2010b) based on slight modifications to the aging system developed by Spinage (1971) for extant impala. Age class is determined by the degree of dental wear, which is dependent on the rate of wear, and is, by extension, related to the size of the animal. Impala belong to size group 2 (50 – 250 lbs; Bunn, 1986) and have a lifespan of ~12 years (Spinage, 1971). Only weaned impala were included.

- Sub-Adult (~1 year, ~8% of lifespan): the M_3 begins erupting and deciduous premolars are heavily worn or replaced by permanent premolars.

- Early Prime Adult (~4 years, ~33% of lifespan): the M_3 is fully occluded and the mesial infundibulum of the M_1 is lost.
- Late Prime Adult (~7 years, 58% of lifespan): the mesial infundibulum is lost on the M_2.
- The Old Adult (~9 years, 75% of lifespan): the remaining infundibulae of M_2 are largely or completely worn away.

Where possible, M2s were used to represent an individual, as this is the preferred molar in many studies (Merceron et al, 2005, 2006; Rivals et al 2009, Scott, 2012). The MNI analysis resulted in two datasets: the “Total Sample” in which *n* = 59 teeth with known associations (Appendix 1), and the “MNI Sample” in which *n* = 29 individuals each represented by a single tooth (Table 2.2.**)**. A DMTA study by Scott (2012) of impala housed at the Field Museum of Natural History in Chicago provides a third dataset and a baseline comparison. This sample includes upper and lower first and second molars from male and female impala shot in the dry season of Botswana and Zimbabwe in 1930, 1961, and 1987, referred to in this study as the “FMNH Sample” (n = 13; Table 2.3).

MNI Sample of Impala

Catalog Number	Element	Season	Age Class	Collection Year	Facet
NSL 537	Left M_2	Wet	Subadult	1998	7
NSL 95	Right M_1	Wet	Subadult	1998	1
NSL 7	Right M_2	Wet	Subadult	2007	1
NSL 977	Left M^2	Wet	Subadult*	1998	1
NSL 444	Right M_1	Wet	Early Prime Adult	1998	4
NSL 1187	Right M_2	Wet	Early Prime Adult	1998	4
NSL 7	Left M_1	Wet	Early Prime Adult	2007	1
NSL 547	Right M_2	Wet	Early Prime Adult	1998	2
NSL 538	Right M_2	Wet	Early Prime Adult	1998	4
NSL 524	Left M_2	Wet	Early Prime Adult	1998	2
NSL 498	Right M^2	Wet	Early Prime Adult	1998	1
NSL 934	Left M^1	Wet	Early Prime Adult	1998	1
NSL 531	Right M^1	Wet	Late Prime Adult	1998	1
UK 023 26	Right M_2	Wet	Early Prime Adult	2009	4
UK 023 35	Left M_2	Wet	Early Prime Adult	2009	5
UK 023 9	Left M_2	Wet	Early Prime Adult	2009	2
UK 023 20	Right M_2	Wet	Late Prime Adult	2009	1
OB-14	Left M^2	Wet	Early Prime Adult	2009	6
BA 029 21	Left M_2	Wet	Subadult	1986	5
BA 029 1	Right M^2	Wet	Early Prime Adult	1986	7
BA2 113	Left M^2	Dry	Early Prime Adult	1986	1
BA2 1210	Left M^2	Dry	Late Prime Adult	1986	1
SN 1553	Right M^1	Dry	Early Prime Adult	1984	3
SN 600	Left M^2	Dry	Early Prime Adult	1984	5
SN 4585	Right M^2	Dry	Early Prime Adult	1984	2
SN 6800	Right M_2	Dry	Late Prime Adult	1984	6
SN 714	Right M_2	Dry	Late Prime Adult	1984	1
SN 2356	Right M_2	Dry	Late Prime Adult	1984	4
SN 5474	Right M_2	Dry	Late Prime Adult	1984	5

Table 2.2. The MNI sample of impala (n=29). *This subadult individual was collected with a mandible and maxilla, and the left M^2 was in the best condition.

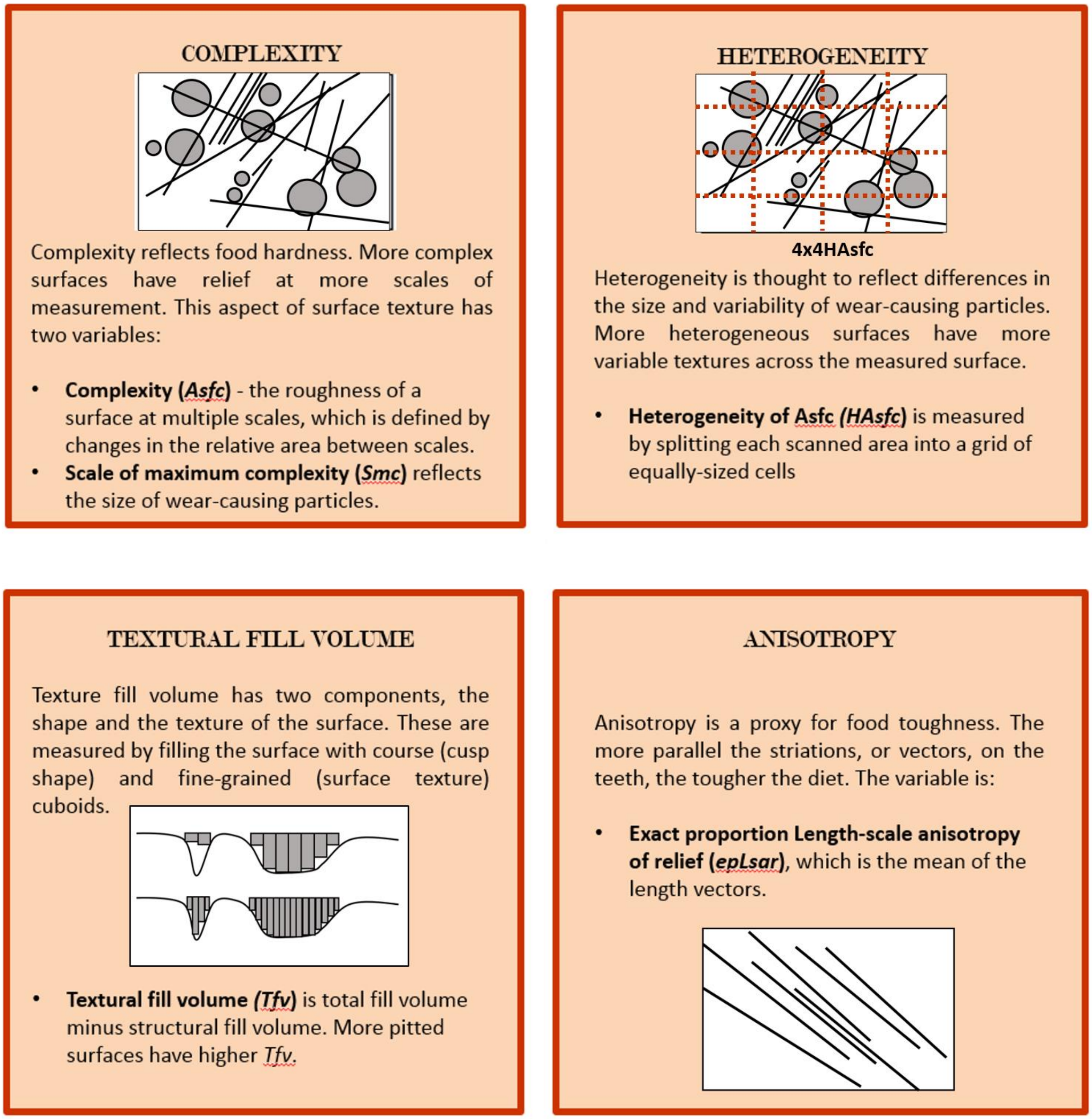
FMNH Sample of Impala

Catalog Number	Sex	Country	Collection Year
34470	Female	Botswana	1930
34472	Female	Botswana	1930
34473	Male	Botswana	1930
34474	Male	Botswana	1930
34475	Male	Botswana	1930
34476	Male	Botswana	1930
34477	Male	Botswana	1930
34478	Female	Botswana	1930
34479	Male	Botswana	1930
34480	Female	Botswana	1930
95838	Female	Zimbabwe	1961
95841	Female	Zimbabwe	1961
134359	Male	Botswana	1987

Table 2.3. The FMNH Sample of impala analyzed using DMTA by Scott (2012). This sample derives from the dry season exclusively and includes upper and lower first and second molars (*n* = 13).

Cast Preparation

Specimens were molded and casted in accordance with conventions developed previously (e.g. Grine, 1986; Ungar, 2003). First, each tooth was cleaned using clean cotton swabs dipped in acetone to remove fixatives from the occlusal surface. This treatment was followed by cotton swabs dipped in 95% isopropyl alcohol to remove oils and other adhering particles. Molds of the occlusal surface were made with President Jet Regular Body dental impression material extruded from an applicator gun (Coltene-Whaledent Corp.). When necessary, the depth of the mold basin was increased by wrapping a rim of dental putty (Exaflex) around the edge. The molds were then cast in high resolution epoxy (Epotek 301), which is capable of preserving surface features less than a micron in size (Beynon, 1987; Teaford and Oyen, 1989).



COMPLEXITY

Complexity reflects food hardness. More complex surfaces have relief at more scales of measurement. This aspect of surface texture has two variables:

- **Complexity (*Asfc*)** - the roughness of a surface at multiple scales, which is defined by changes in the relative area between scales.
- **Scale of maximum complexity (*Smc*)** reflects the size of wear-causing particles.

HETEROGENEITY

Heterogeneity is thought to reflect differences in the size and variability of wear-causing particles. More heterogeneous surfaces have more variable textures across the measured surface.

- **Heterogeneity of Asfc *(HAsfc)*** is measured by splitting each scanned area into a grid of equally-sized cells

TEXTURAL FILL VOLUME

Texture fill volume has two components, the shape and the texture of the surface. These are measured by filling the surface with course (cusp shape) and fine-grained (surface texture) cuboids.

- **Textural fill volume *(Tfv)*** is total fill volume minus structural fill volume. More pitted surfaces have higher *Tfv.*

ANISOTROPY

Anisotropy is a proxy for food toughness. The more parallel the striations, or vectors, on the teeth, the tougher the diet. The variable is:

- **Exact proportion Length-scale anisotropy of relief (*epLsar*)**, which is the mean of the length vectors.

Figure 2.2. DMTA microwear variables (Scott et al., 2006).

Data Collection

Casts were scanned using “Connie,” a Sensofar PLμ white-light scanning confocal profiler (Solarius Development Inc., Sunnyvale, CA) with a 100x objective lens. For each tooth, four adjacent scans were taken along a single enamel cusp to produce a total surface area of 204 x 276 μm^2. Each scan was leveled and edited to erase adhering dust particles using Solarmap Universal software (Solarius Development Inc., Sunnyvale, CA). The resulting enamel surface profiles were then fed into Toothfrax and Sfrax software packages (Surfract Corp.) that measured the complexity (*Asfc*), scale of maximum complexity (*Smc*), anisotropy (*epLsar*), texture fill volume (*Tfv*), and heterogeneity (*HAsfc*). Following established protocol (Scott et al., 2006), medians of the measurements for each of the four scans were used in the descriptive statistics.

Analysis

To test the hypothesis that seasonality can be interpreted from dental microwear, two statistical tests are used. First, the DMTA variables and SOD are compared using a Satterthwaite's *t*-test to determine if season has an influence on the fracture properties of impala diet. This test (also known as Welch's, Aspin-Welch, Welch-Satterthwaite, Aspin-Welch-Satterthwaite *t*-test) is appropriate for small samples sizes < 10, samples of unequal size, and samples of unequal variance (McDonald, 2014). Then a logistic regression is used to show the probability of a specimen with a specific measurement having a wet or dry SOD in order test the hypothesis that SOD can be predicted based on specific microwear values. The logistic regression analysis is performed using the statistics software package Stata on the Total Sample, with specimens belonging to the same individual calculated as dependent.

In order to assess the comparability of values derived from the Lake Eyasi impala with previous research, a Satterthwaite's *t*-test is performed to compare the MNI Sample and the FMNH impala sample on those values that prove significant. The test indicates if the MNI Sample and the FMNH Sample derive statistically from the same population (Table 2.5).

It was necessary to depart in one respect from the DMTA protocols followed in other bovid studies (e.g. Scott 2012; Merceron et al., 2004) due to the condition of the dental samples. In order to standardize microwear analysis, researchers have focused on the upper paracone lingual facet and the lower protoconid buccal facet of the first and second molars, which occlude during the chewing-shearing phase of mastication (check Teaford and Walker, 1984; Janis, 1990; Merceron et al, 2004). Despite immediate or seasonal collection, many of the impala teeth were damaged (i.e., broken during butchery) and retained a limited number of well-preserved facets. The enamel ridges that compose the facets are narrow (~2mm wide) and rounded, which makes confocal microscopy challenging, though by no means impossible. In the present study, the most promising facets were initially identified using an optical microscope at low magnification. In many cases, several facets were then examined using the confocal before a sufficiently pristine surface was selected. As a result, multiple facets were included in analysis. To evaluate the influence of the enamel facet on microwear, the data were rank transformed and analyzed using a one way MANOVA (Conover and Iman, 1985; Donohue et al., 2013).

Another concern is sex-based dietary variation (Wronski, 2002; Sponheimer et al, 2003). Though impala are sexually dimorphic, the Henry T. Bunn collection is impossible to sex; many of the teeth remain embedded in bone, obscuring the base of the tooth where a reliable maximum width could be measured. Because these teeth are not clearly sexually dimorphic and were collected long after the original carcass was butchered, distributed around the camp, eaten, and discarded, it is not possible to link them to the original kill records. To address the potential impact of sex on dental microwear, a Satterthwaite’s t-test of all variables by sex was performed on microwear values on the FMNH Sample.

The raw DMTA results are reported in Appendices 2. and 3.

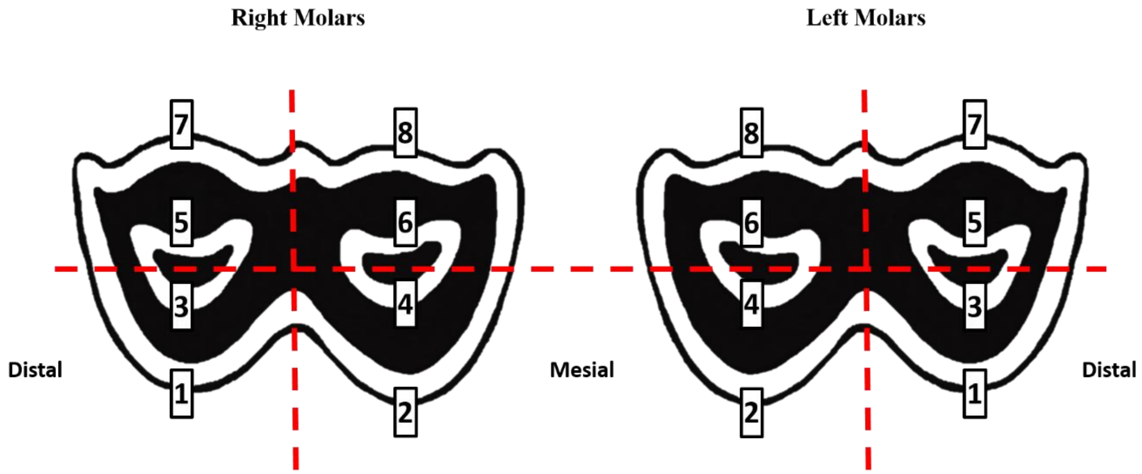


Figure 2.3. Schematic showing how enamel ridges are divided into facets for the purpose of this study.

Results

Neither the facet of the tooth nor the sex of the individual has a significant influence on the microwear values in this analysis. The rank-transformed one-way MANOVA on facet and DMTA variables revealed no significant influence of facet on microwear (Table 2.4.). Likewise, the Satterthwaite's t-test on the FMNH Sample, all of which derive from the dry season of their respective locations when sex-based differences are greatest (Wronski, 2002), did not show a significant effect for sex on microwear values (Table 2.5).

The results of the Satterthwaite's t-test on the MNI Sample indicate that, in this collection of impala, measures of area-scale fractal complexity (Asfc), scale of maximum complexity (Smc), length-scale anisotropy of relief (epLsar), and texture fill volume (Tfv) do not distinguish wet and dry season diets. The microwear variable that does approach significance at the 95% confidence level is the heterogeneity of area-scale fractal complexity (HAsfc; Table 2.6.) At each of the near-significant scales (4x4, 7x7, and 9x9), HAsfc has a higher wet season mean and a range that includes higher values than the dry season sample (Figure 2.5.). Given that the commonly-used confidence interval of <0.05 is arbitrary, and that the sample is small and biological in nature, these results were deemed significant enough to warrant continued investigation.

With mean HAsfc demonstrably indicative of SOD, a logistic analysis was run on the HAsfc values at each scale in order to determine the predictive power of individual tooth measures (Figure 2.6, Appendix 4.). As the HAsfc value approaches zero, the likelihood that it belongs to an individual that died in the dry season increases. Conversely, values at the high end of the range are more likely to belong to individuals that died in the wet season. The values in the middle of the range are the least predictive. The results suggest that HAsfc values may be used to predict the SOD of the individual with an acceptable degree of certainty for comparable seasonality studies.

One-way MANOVA of the Total Sample of Impala

Dependent Variable	F	Significance
Rank of Asfc	1.588	0.173
Rank of EpLsar	0.407	0.870
Rank of Smc	0.732	0.626
Rank of Tfv	1.408	0.232
Rank of Ftfv	1.045	0.409
Rank of 3x3HAsfc	1.007	0.433
Rank of 9x9HAsfc	1.119	0.366

Table 2.4. One-way Multivariate Analysis of Variance on the Total Sample of impala. Total Sample *n* = 59 specimens comprising 29 individuals. Degrees of freedom = 6.

Satterthwaite's t-test: sex and DMTA variables of FMNH Sample

	Levene’s test		t–test for equality of means				
Variable	**F**	**Sig.**	**t**	**df**	**Sig. (2-tailed)**	**Mean Difference**	**Std. Error Difference**
Asfc	0.490	0.499	-0.669	10.662	0.518	-0.178	0.266
Smc	4.756	0.052	-1.024	6.001	0.346	-6.563	6.411
EpLsar	0.465	0.509	-0.529	9.930	0.609	-0.001	0.001
Tfv	2.004	0.185	-1.938	8.700	0.086	-868.250	448.094
3x3HAsfc	0.175	0.683	-0.049	8.883	0.962	-0.005	0.103
9x9HAsfc	5.038	0.046	-0.815	7.334	0.440	-0.129	0.158

Table 2.5. Satterthwaite's t-test comparing impala sex and DMTA variables of FMNH Sample of impala.

Satterthwaite's t–test: SOD and DMTA variables of MNI Sample

	Levene's test		t–test for equality of means				
Variable	**F**	**Sig.**	**t**	**df**	**Sig. (2-tailed)**	**Mean Difference**	**Std. Error Difference**
Asfc	0.310	0.582	0.036	17.682	0.972	0.031	0.885
epLsar	1.115	0.300	-0.616	11.392	0.550	0.000	0.001
Smc	2.262	0.144	1.040	20.654	0.310	0.086	0.083
Tfv	0.004	0.948	-2.024	14.693	0.062	-2029.034	1002.624
2x2HAsfc	0.004	0.952	0.882	15.289	0.392	0.038	0.043
3x3HAsfc	0.139	0.713	0.911	18.707	0.374	0.038	0.042
4x4HAsfc	0.528	0.474	2.082	19.364	0.051	0.091	0.044
5x5HAsfc	0.084	0.774	0.981	14.693	0.342	0.063	0.064
6x6HAsfc	0.636	0.432	1.984	20.964	0.060	0.109	0.055
7x7HAsfc	0.324	0.574	2.067	19.857	0.052	0.134	0.065
8x8HAsfc	0.407	0.529	1.892	20.160	0.073	0.134	0.071
9x9HAsfc	0.549	0.465	2.040	23.380	0.053	0.192	0.094
10x10HAsfc	0.659	0.424	1.818	24.389	0.081	0.161	0.088
11x11HAsfc	0.898	0.352	1.958	26.579	0.061	0.209	0.107

Table 2.6. Satterthwaite's *t* –test on the season of death and DMTA variables of MNI Sample of impala. Gray highlights indicate samples that approach the standard 95% confidence interval.

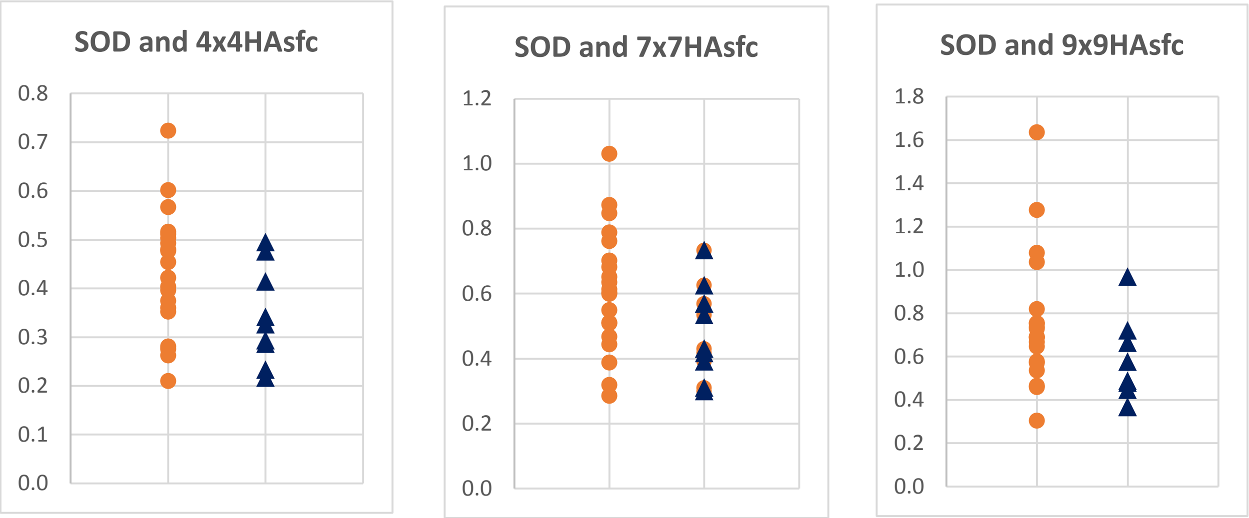


Figure 2.4. Scatterplots of the near-significant scales of Heterogeneity values for wet and dry SOD of the MNI Sample. Orange circles = wet SOD, dark blue triangles = dry SOD.

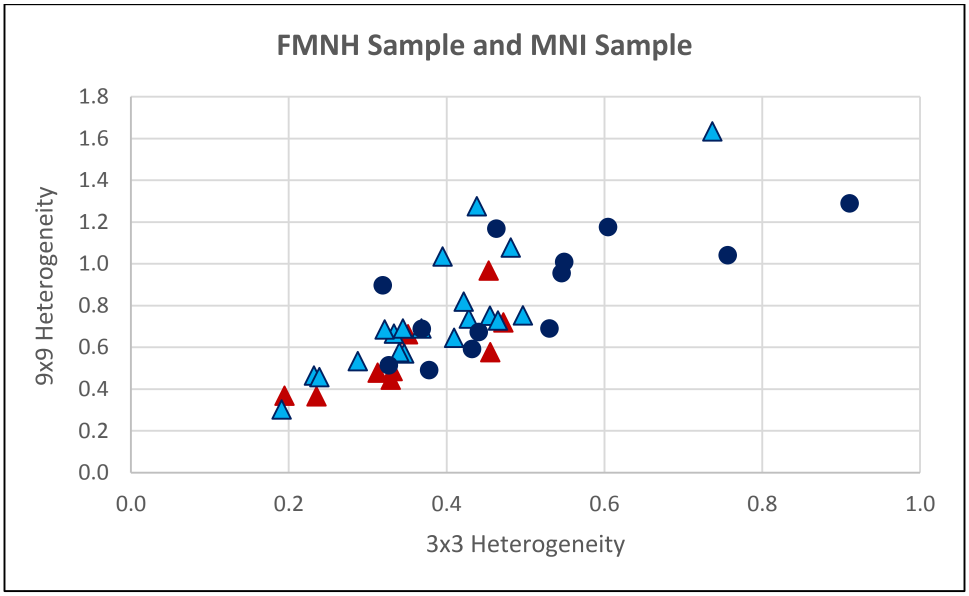
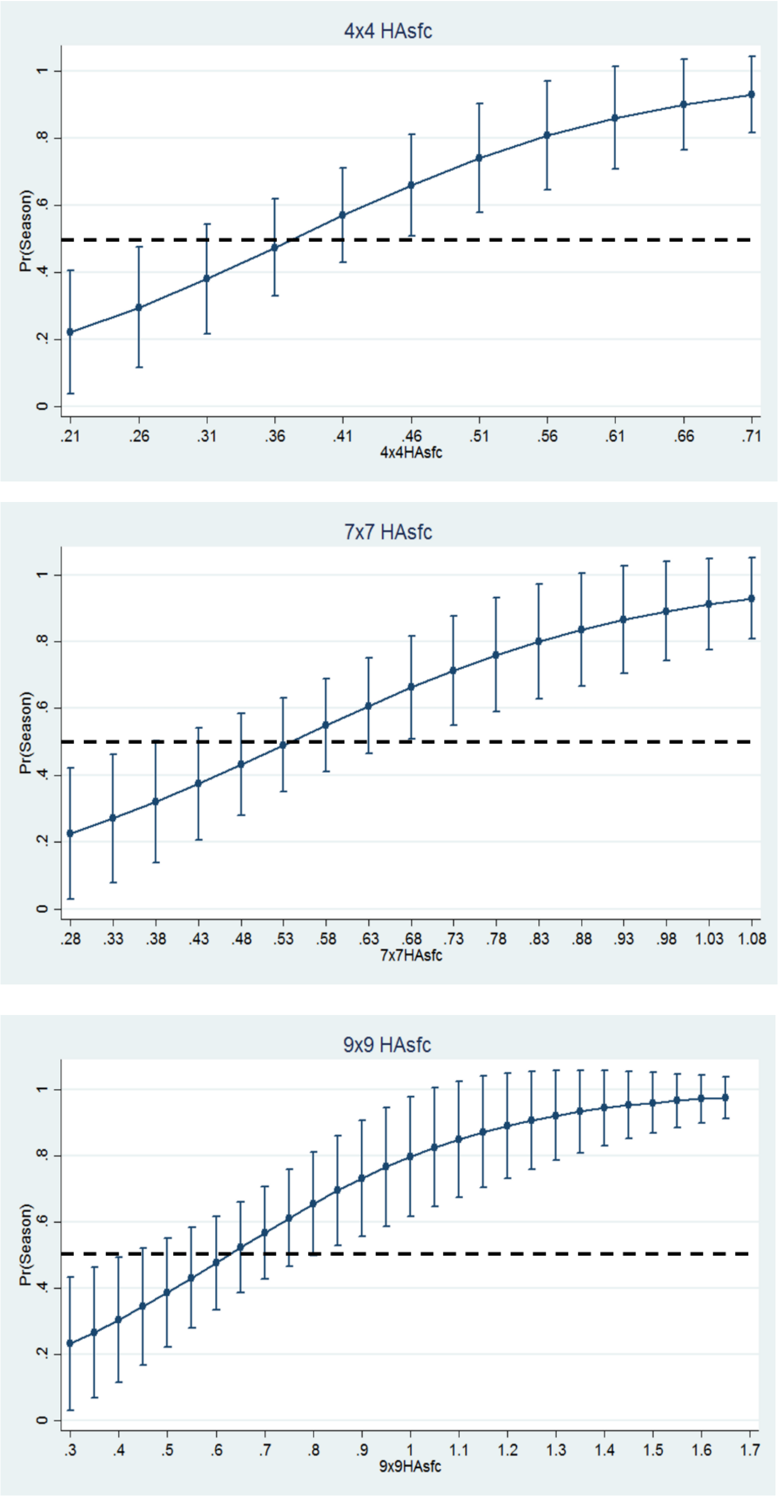


Figure 2.5 Scatterplot showing the distribution of the dry season FMNH Sample (= dark blue circles) and the MNI Sample (dry season = red triangles, wet season = light blue triangles).



Values	**N of Wet**	**N of Dry**
4x4 HAsfc		
0.21 - 0.25	1	2
0.26 - 0.30	3	2
0.31 - 0.35	0	2
0.36 - 0.40	4	0
0.41 - 0.45	2	1
0.46 - 0.50	4	2
0.51 - 0.55	3	0
0.56 - 0.60	1	0
0.61 - 0.65	1	0
0.66 - 0.70	0	0
0.71 - 0.75	1	0
Total	**20**	**9**
Above 50% Probability	**60%**	**33%**
7x7 HAsfc		
0.28 - 0.37	2	2
0.38 - 0.47	3	3
0.48 - 0.57	3	2
0.58 - 0.67	5	1
0.68 - 0.77	3	1
0.78 - 0.87	2	0
0.88 - 0.97	1	0
0.98 - 0.107	1	0
Total	**20**	**9**
Above 50% Probability	**60%**	**22%**
9x9 HAsfc		
0.30 - 0.49	3	5
0.50 - 0.69	6	2
0.70 - 0.89	7	1
0.90 - 1.09	2	1
1.10 - 1.29	1	0
1.30 - 1.49	0	0
1.50 - 1.69	1	0
Total	**20**	**9**
Above 50% Probability	**55%**	**22%**

Figure 2.6. Logistic regressions showing the three near-significant scales of HAsfc measurement for distinguishing SOD. The dotted line demarcates the 50% probability of a value belonging to the wet season. Above the dotted line, values have a >50% probability of belonging to an individual with a wet SOD. **Tables:** the thin horizontal line demarcates the approximate values above which there is a greater probability that they are wet SOD than dry SOD. Additional logistic graphs can be found in Appendix 4.

Discussion

The analysis of impala dental microwear is intended to evaluate the potential of DMTA to statistically distinguish between wet and dry SOD. However, before reliable results can be ascertained, it was first necessary to measure the influence of enamel facet and sex on the DMTA values. These are described below, followed by a discussion of seasonal patterns in impala dental microwear and the implications thereof.

Influence of Enamel Facet and Sex on Dental Microwear

Following established protocol, this study performed DMTA on enamel facets from upper and lower M1s and M2s. However, due to the partially damaged occlusal surfaces of many teeth, it was not possible to consistently sample the same enamel facets that are used in other microwear studies. Instead, the measured facets were recorded and their influence on the HAsfc values was analyzed with a MANOVA and found to be non-significant.

Masticatory adaptations influence the form that microwear takes on enamel facets. The power stroke, which brings teeth into occlusion (Crompton and Hiiemae, 1970) varies in directionality among taxa, resulting in differently oriented microwear striae (Butler and Mills, 1959). Using a primate model, Kay and Hiiemae (1974) define a bimodal power stroke in which the continuous stroke incorporates two sequential directions of movement referred to as Phase I and Phase II. Phase I facets are produced when opposing cheek teeth first come into contact through concentric occlusion, and Phase II facets are produced as teeth move out of occlusion (Kaiser and Fortelius, 2003). Much of the subsequent research on enamel facet as it relates to the chewing powerstroke has focused on primates, which exert less force during Phase II of the power stroke (Krueger et al, 2008).

It is still unclear, however, if this distinction is applicable or useful in ungulate DMTA. Protocol in most recent ungulate microwear studies is to use the mesio-buccal enamel band on the mesial cusp of the upper M1 and M2, and disto-buccal enamel band of the mesial cusp of the lower M1 and M2 (Teaford and Walker, 1984; Merceron et al, 2004; Scott, 2012). These facets are known to be in occlusion during the power stroke (Janis, 1990; Merceron et al, 2004). However, the evolutionary trajectories of ungulates and primates have led them toward opposite masticatory adaptations, with primates enlarging the Phase II facets, and ungulates developing a long Phase I facet for shearing fibrous foods, sometimes to the complete elimination of Phase II facets in grazers. In all ungulates, the lower molars glide past the upper molars in a single, unidirectional translatory stroke (Janis, 1979). Given the reduced role of Phase II facets in ungulates, and the non-significant results of the MANOVA, the choice of enamel facet for DMTA appears to be less critical for impala than it is for primates.

There appears to be no significant difference between males and females in the dry season FMNH Sample. Future research should extend this analysis to a wet season sample of known sex, but this is an informative initial result given that the dry season is a time of greater dietary divergence between sexes (Wronski, 2002).

Season of Death and Dental Microwear

Impala modify their diet throughout the year in response to the seasonal distribution of resources, a strategy referred to as seasonal mixed-feeding (Solounias and Semprebon, 2002). The results of the present study show that DMTA is sufficiently sensitive to distinguish between Lake Eyasi impala that died in the wet and dry seasons, with the heterogeneity (HAsfc) differing significantly between SOD groups. More heterogeneous surfaces have more variable textures across the measured surface, reflecting differences in the size and variability of wear-causing particles. These wear causing particles differ according to diet, which in turn varies with the season. The ability of HAsfc to distinguish wet and dry SOD in impala is supported by two findings.

First, despite the overlap in the range of heterogeneity values between the wet and dry season in the MNI Sample, Satterthwaite's t-test revealed a near-significant (at the 95% confidence level) difference in mean heterogeneity between SOD groups at several scales of measurement (4x4, 7x7, and 9x9). The same t-test did not distinguish males from females in the FMNH sample, in which season was held constant. Because mean HAsfc values at some scales differ at near-significance between wet and dry seasons, and track observed seasonal changes in impala diet (e.g. van Rooyen & Skinner, 1989; Dunham, 1980; Wronski, 2002; Kutilek, 1979), this method appears to be an appropriate test of seasonality when comparing two or more impala assemblages of unknown SOD.

Second, the logistic regression further clarifies the predictive capacity of the HAsfc measurement from each tooth in the Total Sample, suggesting that >55% of the wet season and >67% of the dry season HAsfc values can be assigned to SOD with a reasonable degree certainty. This type of analysis may be useful when studying seasonality in a single sample with individuals of unknown SOD, as well as among several samples. Few HAsfc values offer a sufficient degree of certainty to analyze seasonality on a specimen by specimen basis, but it is possible to compare multiple specimens to determine if an assemblage has a stronger signal for wet or dry SOD. Together, these analyses support future applications of DMTA to studying seasonality in other mixed-feeders, and to fossil assemblages from comparable habitats and climatic regimes.

Causes of Seasonal Microwear at Lake Eyasi

Though the ability of DMTA to detect seasonality among the Lake Eyasi impala is in line with previous research using conventional microwear methods, the pattern of heterogeneity values is not. Past research on ungulate diet using pit and scratch counts revealed a bimodal frequency of scratch counts among seasonal and regional mixed-feeders (Solounias and Moelleken, 1993a, 1993b; Solounias and Hayek, 1993; Solounias and Semprebon, 2002; Merceron et al, 2004, 2005, 2010; Schubert et al, 2006). These frequencies placed mixed–feeders either among browsers (low scratch counts) or grazers (high scratch counts), presumably because of seasonally-varying quantities of dicots and monocots in the diet. In an analysis of 25 extant African bovids using DMTA, bovid browsers were found to have the highest heterogeneity values, while variable and obligate grazers had the lowest (Scott, 2012). Among mixed feeders, browser–grazer intermediates that eat 30 – 70% monocots, as impala do, had higher heterogeneity values than variable grazers that eat 60 – 90% monocots (Scott, 2012). The studies concur that heavily grazing taxa had higher scratch counts or anisotropy values, which are related measurements (DeSantis et al, 2013), than those incorporating more browse.

In contrast, the Lake Eyasi impala have a greater range and higher HAsfc values in the *wet season* group, when grass is consumed almost exclusively, than in the dry season group, when impala subsist primarily on browse. This reversal of the expected pattern is apparent when compared with the FMNH impala, which has dry season HAsfc values at the higher end of the Lake Eyasi distribution (Figure 2.6.).

In addition to containing larger quantities of siliceous phytoliths than dicots, grasses are often coated in soil because of their proximity to the ground. Both particles are known to cause microwear (Schulz et al., 2013). Additionally, due to their high fiber content and tough cell walls, grasses require repeated chewing that may provide more opportunity to scratch the occlusal enamel (Lucas et al., 2014). Differences in dental microwear patterns between dietary categories have been variously attributed to the higher phytolith content (Baker et al 1959; Walker et al, 1978; Gugel et al, 2001) and the greater exogenous grit load (Kay and Covert, 1983; Mainland, 2006; Sanson et al, 2007; Lucas et al, 2013) of grasses. In a study of rabbit dental microwear, Schulz and colleagues (2013) found that a silica-rich diet resulted in less variable microwear. It remains a challenge to determine which of, or to what degree, the various possible agents influence dental microwear, but it is clear that quartz particles found in soils are both sufficiently hard and angular to abrade enamel surfaces (Lucas et al, 2013; Lucas and Van Casteren, 2014). Even a small amount of dust can cause significant wear and leave abundant scratches (Lucas et al., 2013).

The Serengeti and its adjacent regions, including Lake Eyasi, experience significant aridity during the months of June – September (Karatu rainfall, http://www.worldweatheronline.com). During the dry season the amount of airborne dust increases due, in part, to the minimal ground cover of the southeastern Serengeti, accumulating as a fine layer on foliage around Lake Eyasi (Bell, 1971; Ashley, 2007). This highly abrasive airborne dust typical of the dry season at Lake Eyasi may function to obliterate all other potential microwear features caused by the more variable fracture properties of the browse diet. The overall lack of significance between seasons of death for most microwear variables demonstrates that diet is primary driver of dental microwear in these impala, but that exogenous windblown grit is seasonally influencing the heterogeneity across the occlusal surface.

Conclusion

The dental microwear texture analysis of the Henry T. Bunn impala collection indicates that season of death can be ascertained in a savanna-dwelling seasonal browser-grazer bovid. It further suggests that among bovids that graze extensively, molar tooth facets may be interchangeable, allowing for the analysis of fragmented teeth. The hypothesis that bovids ingesting seasonally-variable quantities of grit will have a seasonal microwear signal is supported by the range and means of impala microwear heterogeneity in the wet and dry season groups. As others have noted (Mainland, 2003, 2006; Schulz et al., 2013), these non-dietary particles can complicate paleoenvironmental reconstructions based on dental microwear.

This study emphasizes the importance of performing a complementary paleoclimatic study of fossil sites of interest, in this case one which assesses the significance of airborne dust in dry periods, particularly as it may cause the environment to appear “grassier”. In addition, modern analogs that closely approximate the paleoenvironment as reconstructed from other proxies must be selected with attention to the habitat of origin. Nevertheless, in conjunction with a research design that controls for variability in local environments, DMTA is a promising method for investigating season of death, particularly where the amount of ingested grit is likely to vary seasonally. In future analyses I will continue to test the efficacy of DMTA and the impact of airborne grit by expanding the modern sample of Lake Eyasi ungulates to determine if microwear heterogeneity is similarly patterned across seasonal samples in other species.

Chapter 3. Traditional Taphonomic Studies Cannot Assess Seasonality at FLK Zinj

Introduction

Hominin foraging seasonality in the Early Pleistocene is a central aspect of niche creation at a time when the hominin lineage was highly speciose and savanna seasonality was on the rise. As one of the largest Early Pleistocene butchery sites, FLK Zinj at Olduvai Gorge, Tanzania, has the potential to provide important insights into the seasonality of meat-eating in the initial stages of the evolution of this behavior. Because a carcass would only be utilized when relatively fresh, the act of butchering directly ties hominins to the prey season of death (SOD), regardless of how it was killed. As yet, the seasonality of the butchered bone assemblage has yet to be analyzed. This study evaluates the feasibility of determining prey SOD at FLK Zinj using existing ecomorphological, behavioral ecological, and taphonomic methods.

To date, only one study has examined the archaeological evidence for foraging seasonality at Olduvai Gorge. Speth and Davis (1976) compared an composite species list from fossil assemblages in Beds I and II (1.9 – 1.2 Ma) with the prey capture patterns of the !Kung and G/wi foragers. The foragers exhibit a strongly seasonal pattern of bovid hunting in the dry season and tortoise collecting in the wet season. When these data are plotted on a triangle graph with Carnivora, Chelonia, and Bovidae apices, the Olduvai samples cluster tightly at the Chelonia and Bovidae apices, much like the wet and dry season prey distribution of the foragers, respectively. The authors interpreted this correlation as tentative support for equivalent patterns of seasonal hunting by Olduvai hominins. While innovative, this study assumed that hominins were responsible for accumulating each of the dense faunal accumulations at Olduvai Gorge. Since this publication, a vast taphonomic literature has developed a consensus that only the sites of FLK Zinj in Bed I, and BK in Bed II are primarily anthropogenic (e.g. Bunn and Kroll, 1986; Bunn and Pickering, 2010a; Dominguez-Rodrigo et al., 2007a; 2009).

Site seasonality remains a largely unexplored topic. Speth has since suggested that dry season animals, particularly members of the family Bovidae (bovids), would be avoided because they are especially lean (Speth, 1987, 1989). In a number of publications, Speth (1987, 1989, 2012; Speth et al., 1991) has detailed the evidence for lean meat avoidance in ethnographic accounts of protein poisoning, fat-oriented foraging, and the abandonment of fleshed carcasses by nutritionally deprived hunters. These observations led Speth to argue that large game hunting constituted a political, social, psychological, or reproductive strategy. He argues that large game hunting was not primarily motivated by nutritional interests because plants and insects provide sufficient nutrition throughout the year, while the value of lean protein has been severely overestimated in nutritional science until recently (Speth, 2010).

Following from the hypothesis that hominins avoided lean protein, Speth (1987) has suggested that the primary season of hominin meat-foraging activity could be revealed by determining the demographic distribution and physiological condition of bovids at archaeological sites. Omnivorous hominins, capable of targeting the most nutritious plant and animal foods, are predicted to selectively avoid the extremely lean meat of bovids at the height of the dry season so as to avoid protein poisoning (Speth, 1987, 1989). This leads to three predictions for dry season archaeological sites (Speth, 1987):

1. Dry season sites are likely to be located close to permanent water.
2. On sites that represent the peak period of stress, total faunal remains may be relatively scarce.
3. Dry season faunal remains are likely to display a high degree of selectivity in favour of:
    a. species that tend to maintain high fat levels during the dry season (small vertebrates may prove to be extremely important in this regard);
    b. individuals within a population who, because of their age, sex, reproductive status, or other factors, are less susceptible to fat-depletion at that time of year; and
    c. specific skeletal parts that are least prone to fat mobilization (e.g. marrow bones from distal limbs). If hominids are scavenging from carnivore kills, and the carnivores themselves are resource stressed, the faunal remains retrieved by the hominids may be restricted largely to the least accessible remaining fat deposits in a carcass (e.g. marrow in the metapodials, phalanges and mandibles). [Text from Speth (1987, pg. 22); numbering and lettering by author].

The discussion below is intended to provide a more detailed picture of paleoecological reconstructions for the most numerous bovids at FLK Zinj, including *Antidorcas recki*, *Parmularius altidens,* and *Kobus sigmoidalis,* in order to determine if the behavior of their modern analogs, alone, is sufficient to diagnose an anthropogenic site as wet, dry, or aseasonal following the predictions presented by Speth (1987). This study aims to answer three questions:

1. What do ecomorphological studies suggest as good modern analog species for the most common bovids at FLK Zinj?

2. What does the seasonal behavior and physiological condition of the modern analogs suggest about seasonal site usage at FLK Zinj?
3. Are Speth's dry season site predictions corroborated by modern forager behavior in a similar ecological context?

Background

Fossil bovid studies have a long history of use for inferring the ecological context of hominin evolution (e.g., Gentry, 1970; Scott, 1979, 1985; Vrba, 1980, 1995; Greenacre & Vrba, 1984; Kappelman, 1984, 1986, 1988, 1991; Kappelman et al, 1997; Shipman & Harris, 1988; Solounias & Dawson-Saunders, 1988; Plummer & Bishop, 1994; de Menocal, 2004; Scott, 2012). The taxonomic assignment of fossil bovids is determined largely on the basis of craniodental features, leading many researchers to focus on these characteristics when inferring ecological preferences. Initially, such studies inferred a direct relationship between the habitat preferences of extant relatives and their fossil ancestors. This is referred to as the "uniformitarian" approach by Kappelman and colleagues (1997) because it depends on ecological continuity through time. Many of the early uniformitarian studies focused on species turnover (Vrba, 1988, 1989, 1995; Behrensmeyer et al, 1997) and relative abundance (Kappelman, 1984; Shipman and Harris, 1988; Reed, 1997; Bobe et al, 2002; Bobe and Eck, 2001).

Research became more nuanced through ecomorphological studies that analyzed the correlation between functional morphology and dietary or locomotor behavior in extant taxa within the context of specific environmental parameters. Studies have examined the relationships between ecology and dental hypsodonty (e.g. Janis, 1988; Spencer, 1997; Cerling et al, 2003), craniomandibular morphology (Spencer, 1997; Mendoza et al, 2002), and astragalus, metapodial, and femoral functional anatomy (Plummer and Bishop, 1994; Kappelman et al, 1997). The resulting ecomorphological models are then applied to fossil bovids, enabling a finer distinction in habitat and dietary adaptations than was previously possible (e.g., Kappelman, 1988, 1991; Solounias & Dawson-Saunders, 1988; Plummer & Bishop, 1994; Spencer, 1995; 1997; Kappelman et al, 1997).

Other researchers have focused on the stable carbon isotope signature in bovid dental enamel apatite to infer diet and, by extension, habitat (Cerling et al, 2003; Lee-Thorp and van der Merwe, 1993; Lee-Thorp et al, 1994; Sponheimer and Lee-Thorp, 2003; Plummer et al, 2009). Between 2.7 - 2.5 Ma, bovids underwent an evolutionary radiation in which many arid-adapted species appeared (Vrba, 1995). This coincided with a pulse in the spread of savanna grasslands environments following 3.0 Ma. These grasses use the C4 metabolic pathway, and their relative contribution to the diet can be measured using the δ^{13}C component in bovid dental enamel. This is also expressed as the C_3/C_4 ratio of bovids, with grass grazers having higher C_4 ratios than browsers that forage on plants using the C_3 pathway, and mixed feeders falling between the two.

These studies have revealed some general trends in bovid ecology. Evidence supports the inference that fossil bovids in Tribe Alcelaphini share habitat and dietary preferences with their extant relatives (Sponheimer and Lee-Thorpe, 2003; Kappelman et al, 1997). In contrast, modern and fossil Antilopini appear to have diverged in a number of respects, so that the preferences of modern antilopine taxa are less informative when reconstructing fossil antilopine diets (Sponheimer and Lee-Thorpe, 2003). For example, a stable carbon isotope study of fossil antilopines at Laetoli, Tanzania, dated to 4.36 – 2.66 Ma revealed mostly mixed C_3/C_4 feeding patterns that are more variable than the specialized foraging patterns of their extant relatives, which are more exclusively grazers (Kingston, 2011). However, Bobe and colleagues (2007) suggest that while bovid diets may have changed over time, habitats appear to have remained stable, particularly in the case of alcelaphines and antilopines, which radiated into seasonal habitats early in the evolution of these tribes.

Bovid ecology studies have also found a correlation between body size and habitat preference that appears to reflect constraints imposed by diet and predator avoidance strategies (Estes, 1974; Jarman, 1974; Kappelman et al, 1997). Small bovids are typically solitary and found in more closed habitats where they can rely on stealthy behavior to avoid detection. These taxa are more often territorial and consume higher quality but more patchily distributed fruits and browse that use the C3 metabolic pathway (Estes, 1974; Jarman, 1974; Gagnon and Chew, 2000; Cerling et al, 2003). In contrast, large bovids tend to be open country species where their larger mass or herding behaviors enable them to rely on vigilance as a predator defense. They are often grazers that subsist on lower quality grasses for which they must migrate regularly (Kappelman et al, 1997; Gagnon and Chew, 2000). This diet is reflected in the height of the tooth crown, which is taller, or more hypsodont, in order to sustain grazers throughout life as they wear down their teeth by consuming grit-coated grasses (Cerling et al, 2003). Similar ecological constraints appear to have been in operation in the Pleistocene too (see below).

Paleoecological reconstructions using bovids at FLK Zinj indicate a mosaic environment ranging from dense woodlands in the immediate vicinity of the site to open grasslands in the broader Olduvai Basin. In an analysis of the relative abundance of open and arid adapted bovids using the Antilopine-Alcelaphine criterion developed in pioneering work by Vrba (1980), Shipman and Harris (1988) found that FLK Zinj was intermediate between dry/open sites and wet/closed sites elsewhere in Bed I. Plummer and Bishop (1994) concur based on their analysis of metapodial ecomorphology. In a study using femur morphology to infer narrower habitat categories, Kappelman and colleagues (1997) found that the FLK Zinj bovids reflected a range of habitat preferences that encompasses that of all modern bovids, suggesting a wide variety of habitats that were predominantely open but included heavy cover and potentially forest. Stable carbon isotopes likewise support the presence of both grasslands and woodlands based on the presence of mixed-feeders (Plummer et al, 2009). These interpretations are supported by other paleoecological reconstructions based on microfauna (Jaeger, 1976), geology (Hay, 1976), geochemistry (Hay, 1976; Cerling et al, 1986; Sikes, 1994; Ashley et al., 2010), and flora (Bonnefille, 1985; Bamford et al., 2008; Barboni, 2010a). Most significantly, it is now known that FLK Zinj accumulated within 200 meters of a freshwater spring, which likely supported the dense woodlands in the area (Ashley et al., 2010a; Barboni et al, 2010).

Omnivorous hominins may well have subsisted year round within this broad range of FLK Zinj habitats, but the increasingly seasonal environment (deMenocal, 2004; Magill et al., 2012a) would have offered different resources at different times. Speth (1987, 1989) has suggested that meat would have been avoided in the dry season, when bovids are in the poorest condition. By evaluating the seasonal behavior and condition of modern analogs for *A. recki, P. altidens,* and *K. sigmoidalis*, which together represent 76% of the bovids at FLK Zinj, this study aims to determine if seasonal meat-foraging at FLK Zinj can be inferred.

Materials and Methods

This review begins by summarizing paleoecological reconstructions for *A. recki, P. altidens*, and *K. sigmoidalis* in the Early Pleistocene with the aim of determining the best modern analog species based on dietary and habitat preferences. The seasonal behavior and physiological condition of each analog is then summarized so that it can be used to model the behavior of the fossil bovids at FLK Zinj.

The behavioral ecology of the modern analogs is then compared with the demography of bovids at FLK Zinj. Minimum number of individuals (MNI), age, and sex distribution of fossil bovids at FLK Zinj were analyzed by myself and Bunn at the National Museum in Dar es Salaam in 2013. MNI was analyzed using all dental specimens, and dental individuals were determined by comparing morphology, wear patterns, and crown height amongst upper and lower dental rows. Because upper and lower dentitions are difficult to assign to a single individual, the most abundant dental arch (upper or lower) in each age class was used (for a more detailed description of MNI analysis, see Chapter 2). Age classes were assigned using tooth eruption rates, sequence, and degree of wear, following Bunn and Pickering (2010b). When possible, sex was inferred from dental size dimorphism. Comparing these demographic distributions at FLK Zinj with the seasonal mobility, diet, reproduction, and physiological condition of their modern counterparts allows an evaluation of seasonality at FLK Zinj based on Speth’s (1987) model.

Finally, Speth’s (1987) dry season site predictions are compared with modern human foraging seasonality in similar habitats. If seasonal lean meat avoidance is a nutritional imperative in the present, then it was likely important in the past. If, however, bovids are taken in the dry season, Speth’s predictions are undermined, and alternative methods for evaluating seasonality in the past must be sought.

FLK Zinj Size Group and Bovid Species MNI

Size Group c.f. Bunn (1986)			FLK Zinj Bovids		
Category	**Lbs**	**~ Kg**	**Taxon**	**MNI**	**Size Group**
Size Group 1	< 50	< 23	*Kobus sigmoidalis*	12	3b
Size Group 2	50 – 250	23 – 113	*Parmularius altidens*	6	3a
Size Group 3	251 – 750	114 – 340	*Antidorcas recki*	6	1
(3a)	251 – 450	114 – 205	*Connochaetes* sp.	3	3b
(3b)	451 – 750	206 – 340	Antilopini size 2 and/or 3a	3	2 and 3a
Size Group 4	751 – 2000	341 – 907	*Syncerus aceolotus*	1	4
Size Group 5	> 2000	> 907	*Tragelaphus strepsiceros*	1	3b

Table 3.1. Size groups and MNI of bovids at FLK Zinj.

Fossil Bovids

Antidorcas recki (Tribe Antilopini) was a size 1 bovid found across eastern and southern Africa, including Olduvai Gorge Beds I – IV in Tanzania (Gentry and Gentry, 1978; Spencer, 1997). Its temporal range began 3.0 Ma and persisted through the Middle Pleistocene (Spencer, 1997). *A. recki* is believed to be the direct ancestor of the extant springbok, *Antidorcas marsupialis* (Vrba, 1973), which has a more limited geographical range in southwestern Africa (Cain et al, 2004).

Paleoecological reconstructions for *A. recki* have ranged across dietary categories, but studies have tended to agree on an intermediate to open habitat preference. Gentry and Gentry (1978) suggest that *A. recki* was a mixed feeder in arid and open bushlands or savanna plains, like extant springbok. Lee-Thorp and colleagues (1994) found a browser C_3/C_4 signature in the enamel of *A. recki* and its extinct relative *A. australis* at Swartkrans Members 1 and 2 (1.6 Ma; de Ruiter, 2003), South Africa, which may reflect differences in habitat tolerance as well (Sponheimer and LeeThorp, 2003). A browsing signature was also determined for *A. recki* at Sterkfontein Member 4 (2.5 to 2.0 Ma). In contrast, Blumenschine and colleagues (2003) report high $\delta^{13}C$ values for the enamel of *A. recki* from Olduvai Gorge Bed I, which they attribute to diets dominated by the C_4

photosynthetic pathway. This range of results is corroborated by the most recent enamel C_3/C_4 analysis by Plummer and colleagues (2009) comparing penecontemporaneous *A. recki* at Olduvai Gorge Bed I sites (1.87 to 1.78 Ma), Sterkfontein Member 4, and Kanjera South Bed 2 (2.3 to 1.95 Ma). This study found that, like extant antilopines, *A. recki* had a highly variable diet reflecting an ability to switch between browse and graze as needed (Plummer et al, 2009). Notably, these $\delta^{13}C$ values for *A. recki* at Olduvai placed the specimens in the browser-grazer intermediate range, suggesting that its diet was not dominated by C_4 foods, as Blumenschine and colleagues (2003) suggested.

In an analysis of habitat preference using metapodials from Olduvai Gorge Bed I, Plummer and Bishop (1994) found support for an "intermediate" woodland and bushland environment. Analysis of the femur produced similar results, with *A. recki* specimens from Olduvai Gorge Bed I and II, and Koobi Fora signifying a preference for open to light cover (Kappelman et al, 1997). The authors conclude that *A. recki* preferred the more open part of the "intermediate" habitat inferred by the Plummer and Bishop (1994) study. They suggest that these areas bordered open habitats. Because *A. recki* is small, surface obstacles in light cover habitats may have posed greater locomotor challenges than they would have for larger bovids. For this reason, Kappelman and colleagues (1997) propose that this bovid's relatively variable femora occasionally group with larger, closed cover bovids, which must also contend with complex substrates.

Spencer's (1997) craniodental study of specimens from Olduvai Gorge Beds II and IV, Koobi Fora (provenience unknown), and Kromdraai A (1.89 and 1.63 Ma; Herries et al, 2009) placed *A. recki* with mixed grass feeders in secondary grasslands. Though mandibular traits suggest an affinity with the dicot feeding klipspringer, *Oreotragus oreotragus*, rather than the springbok, cranial shape traits grouped *A. recki* in the zone of overlap between grass, dicot, mixed grass, and mixed dicot feeders. Noting that relative premolar row length is a highly diagnostic morphology, the strongest evidence places *A. recki* with grass and mixed feeders, in contrast with the browsing isotope signature from Lee-Thorp and colleagues (1994). A principal components analysis of the craniodental shape traits grouped *A. recki* with mixed grass feeders, with the short premolar row suggesting a preference for secondary grasslands (Spencer, 1997), in agreement with the intermediate habitat preference determined by Plummer and Bishop (1994) and Kappelman and colleagues (1997).

Together, these analyses portray *A. recki* as a highly flexible forager capable of adapting to local dietary and habitat opportunities. Differences between studies are likely related to this paleoecological flexibility, and not to sampling or methodological errors. In many regards, *A. recki* resembles its modern descendant, the springbok, which is a mixed feeder at the low end of size group 2 that inhabits secondary grasslands in southwestern Africa. Springbok graze while grasses are green, and otherwise rely on a broad diet of browse (Estes, 1991; Kingdon, 1997). Setting aside this phylogenetic relationship, *A. recki* also shares its dietary and habitat adaptations with modern impala. Both impala and springbok are adaptable mixed feeders that prefer firm footing, leading to a rather clumpy modern impala distribution throughout southeastern Africa (Estes, 1991; Kingdon, 1997). Notable differences include water dependency and mobility. In the dry season impala remains within a few kilometers of watering holes, but it is a residential bovid that moves relatively short distances from grassland to woodland within its range. Springbok, in contrast, are capable of deriving sufficient water from plants, though they will drink when water is available (Estes, 1991; Kingdon, 1997). Before they were severely depleted and relegated to wildlife reserves, springbok migrated seasonally (Estes, 1991). Comparison of *A. recki* with impala and springbok illustrates the behavioral breadth of bovids with these feeding and habitat preferences, the implications of which will be considered below.

***Antidorcas recki* Paleoecological Reconstructions**

Study	Diet	Habitat
Gentry and Gentry (1978): uniformitarianism[1]	Mixed Feeder	Open
Lee-Thorp et al (1994): C_3/C_4[2]	Browser	-
Blumenschine et al (2003): C_3/C_4[3]	C_4 dominated diet	-
Plummer et al (2009): C_3/C_4[4]	Browser Grazer Intermediate (Olduvai Bed I only)	Grassland / bushland
Plummer and Bishop (1984): metapodial[5]	-	Intermediate cover
Kappelman et al (1997): femoral[6]	-	Open to Light Cover
Spencer (1997): craniodental[7]	Mixed Grass Feeder	Secondary grasslands

Table 3.2. Terminology definitions from each source:
[1] Mixed feeders consume both grass and browse in unwooded or sparsely wooded grasslands.
[2] Browsers in this study have dental enamel $\delta^{13}C$ that is between -14.5‰ and -11.0‰.
[3] Not defined.
[4] Dental enamel $\delta^{13}C$ that is between -8.0 and -1.0 ‰ PDB belongs to browser-grazer intermediates. Authors refer to several sources with varying habitat definitions. Generally, grasslands are “open” habitats with >75% C4 plants, and bushlands are “intermediate” habitats that are often *Commiphora* dominated with a canopy <8 meters (c.f. Kingdon, 1997), containing shrubs and tree canopy cover > 20% (c.f Spencer, 1997).
[5] Intermediate habitats include bushland, woodland, swamp, and ecotone.
[6] Open habitat includes ecotone, open country, and arid country. Light cover habitat includes light bush, tall grass and hilly areas.
[7] Mixed grass feeders incorporate dicots, but prefer grass. Secondary grasslands are dry savanna grasslands typical of equatorial Africa.

Parmularius altidens (Tribe Alcelaphini) is a size group 3A bovid whose genus is extinct. Fossil *P. altidens* is found throughout Olduvai Gorge Bed I and lower Bed II, Tanzania; in the Turkana Basin, Kenya; and the Shungura Formation, Ethiopia (Gentry and Gentry, 1978; Egeland and Dominguez Rodrigo, 2008). Its first appearance is 2.4 - 2.2 Ma in the Shungura Formation and its last appearance is < 1.34 Ma in Olduvai Bed II (Bobe and Behrensmeyer, 2004; Egeland and Dominguez Rodrigo, 2008).

There are fewer paleoecological reconstructions of *P. altidens* than of *A. recki*. Gentry and Gentry (1978) describe the Olduvai alcelaphines together as grazers “on short grass in open country or in clearings with good visibility that could have tolerated greater aridity than reduncines or *Hoppotragus*” (pg 54). An earlier member of the genus, *P. pandatos* from the Upper Laetolil (3.76 to 3.46 Ma; Kingston and Harrison, 2007) was found to have a range of carbon isotope signatures placing it in the “mixed feeder” to “variable grazer” categories, though younger alcelaphines from the Upper Ndolanya Bed (2.58 to 2.66 Ma) grouped almost exclusively in the “variable grazer” range (Kingston and Harrison, 2007; Kingston, 2011). Dental microwear analysis by Scott (2012) of *Parmularius* sp. from the Upper Laetolil Beds clustered with extant grazing species, particularly the modern waterbuck *Kobus ellipsiprymnus*, a variable grazer in tribe Reduncini that resorts to browse when green grass is scarce (Kingdon, 1997). These data are potentially informative about phylogenetic constraints on dietary preferences, the reconstructions by Kingston (2011) and Scott (2012) do not bear directly upon the particular paleoecology of *P. altidens* from younger sites.

Plummer and colleagues (2009) performed stable carbon isotope analysis on 4 alcelaphines, thought to be *P. altidens*, from Kanjera South Bed 2 (2.3 to 1.95 Ma). Their signatures fall at the high end of $\delta^{13}C$ enamel values for “variable grazer” and in the “obligate grazer” range. The authors ascribe this species to an obligate grazer status, and suggest a grassland habitat preference. *P. altidens* shares this classification with extant alcelaphines, which are predominantely pure grazers based on their C_3/C_4 signatures and dental microwear (Scott, 2012), excluding the variable grazer, the hirola (*Beatragus hunteri*; Cerling et al, 2003).

The craniodental analysis by Spencer (1997) is one of the few studies to focus on *P. altidens* from Olduvai Gorge. It revealed a feeding apparatus comparable to other small extant grazing alcelaphines, which have shorter faces than the majority of living grass feeders in secondary grassland habitat. The relative diastema length of the mandible and relative predental length of the cranium are small, like extant dicot and mixed feeders and unlike most grass feeders, allying *P. altidens* with the hirola and blesbok, the two smallest alcelaphines, both of which are primarily grazers. The short premolar row suggests that *P. altidens* preferred secondary grasslands.

Despite the variety of terminology used to describe dietary and habitat preferences, these studies largely agree that *P. altidens* was a grazer that inhabited grassland settings. Its presence at FLK Zinj has been used to suggest that secondary grasslands, which were rare before 2 Ma, had become widespread by Bed I times at Olduvai Gorge, and in eastern Africa more generally (Spencer, 1997; Plummer et al, 2009). The trend in *Parmularius* is one of increasing grass consumption between 4.0 to 1.3 Ma, but its strongest affinities appear to be with the hirola, rather than with the obligate or hypergrazing alcelaphines.

The hirola is an arid adapted variable grazer that prefers green grasses (Andanje and Goeltenboth, 1995) in the upper end of size group 2. Its habitat ranges from open grassland to light cover (Bunderson, 1981). Though it is able to subsist without drinking water for much of the year, it is drawn to green grasses and browse near waterholes in the height of the dry season, which is when it has been observed to drink (Bunderson, 1981; Dahiye, 1999; Andanje, 2002). The hirola has enamel δ^{13}C enriched to 0.03 (SD 0.03) (Cerling et al, 2003). This is much lower than wildebeest and hartebeest, which are 2.2 (SD 1.3) and 1.9 (SD 1.3) respectively (Cerling et al, 2003). The carbon stable isotope study by Blumenschine and colleagues (2003) is the only one to present values for *Parmularius altidens* at Olduvai Gorge Bed I. However, these are included in a generalized discussion of bovid $\delta^{13}C$, which is reported to range from -3.6 - +1.2 per mil (Peedee Belemnite standard). By the standards presented in Cerling and colleagues (2003), this range encompasses dietary categories including "mixed feeders," "grazers," and the lower limit of $\delta^{13}C$ enrichment for "hypergrazers." Without greater specificity, this study is unclear as to the degree of C4 plants in the diet of *P. altidens* at Olduvai. *P. altidens* at Kanjera South is shown to have been an obligate grazer, but paleosol carbonates from this site indicate a "woody grassland" to "open grassland" setting with >75% C_4 vegetation. Olduvai Gorge Bed I, in contrast, has a mix of C3 and C4 plants that range from "open woodland" to "woody grassland," with FLK Zinj falling in the middle of the range in a "grassy woodland" (Plummer et al, 2009). It is possible, therefore, that *P. altidens* at Olduvai Gorge inherited a more variable dietary adaptation from *P. pandatos* that resembled the feeding habits of the modern hirola, with whom it shares many aspects of its feeding apparatus. If this were the case, *P. altidens* would be expected to gravitate toward well-watered grazing areas in the height of the dry season.

Parmularius altidens **Paleoecological Reconstructions**

Study	Diet	Habitat
Gentry &Gentry (1978): uniformitarianism[1]	Grazer	Open Country
Blumenschine et al (2003): C_3/C_4[2]	C_4 dominated diet	-
Plummer et al (2009): C_3/C_4[3]	Obligate Grazer	Grassland
Spencer (1997): craniodental[4]	Grass Feeder	Secondary Grasslands

Table 3.3. Terminology definitions from each source:
[1] A feeder relying primarily or exclusively on grass in unwooded or sparsely wooded grasslands.
[2] Not defined.
[3] Dental enamel $\delta^{13}C$ that is enriched ≥2.0 ‰ PDB belongs to obligate grazers, which consume >95% C_4 plant foods.
[4] Grass feeders eat primarily grass. Secondary grasslands are dry savanna grasslands typical of equatorial Africa.

Kobus sigmoidalis (Tribe Reduncini) was a size group 3B bovid found across Plio-Pleistocene eastern Africa at sites from Olduvai Gorge Bed I, Tanzania; the Shungura Formation, Ethiopia; Kanjera and the Turkana Basin, Kenya; the Lusso Formation in the Democratic Republic of Congo (Gentry and Gentry, 1978); and the Chiwondo Beds in Northern Malawi (Schrenk et al, 1993). This species is thought to be ancestral to the modern waterbuck *Kobus ellipsiprymnus*, and previous dietary reconstructions were inferred based on this relationship (Gentry, 1985). Extant waterbuck live in a variety of equatorial habitats where permanent water is available, preferring edge areas adjacent to grassland (Kingdon, 1997). Like *K. ellipsiprymnus, K. sigmoidalis* has been described as grazer preferring medium height floodplain grasses in close proximity to water (Gentry, 1985). Stable carbon isotope analyses are consistent with this interpretation, placing *K. sigmoidalis* in the C_4 diet category (Blumenschine et al, 2003) or variable to obligate grazer range, as in the case of *Kobus* sp. from Kanjera South Bed 2 (Plummer et al, 2009).

Ecomorphological studies also support the uniformitarian prediction for *K. sigmoidalis* diet and habitat. Kappelman and colleagues' (1997) femoral morphometric analysis of a single specimen from East Lake Turkana (date unreported) grouped *K. sigmoidalis* with species preferring open habitat or light cover. This differs only in part from *K. ellipsiprymnus*, which falls variably in the heavy cover, light cover, and open country categories, as do the kob (*Kobus kob*) and Nile lechwe (*Kobus megaceros*) (Kappelman et al, 1997). Based on craniodental ecomorphology of 9 specimens from Koobi Fora ranging in age from 2.0 – 1.39 Ma, Spencer (1997) found that the mandible of *K. sigmoidalis* was indistinguishable from extant waterbuck using pairwise tests of linear measurements. Cranial measurements also grouped *K. sigmoidalis* with extant grass feeders and reduncines inhabiting edaphic grasslands, like *K. ellipsiprymnus*. A principal components analysis of 9 shape variables confirmed the general result that *K. sigmoidalis* was a grass feeder, though it did not cluster most closely with *K. ellipsiprymnus* for the first two principal components (71% of the total variance). Spencer (1997) interprets this to mean that the feeding behaviors of the extinct species and extant waterbuck differed in some indeterminable characteristics. Nevertheless, Spencer (1997) concludes that *K. sigmoidalis* was a grass feeder, a category comparable to "grazer" and encompassing the δ^{13}C enriched end of "obligate grazer."

These studies are in agreement that *K. sigmoidalis* closely resembles the modern waterbuck, also a size 3B bovid. Waterbuck are found in grasslands near light cover throughout equatorial Africa, but are possibly the most water dependent of all antelopes, capable of subsisting only within a few kilometers of water (Estes, 1991). Waterbuck are a residential species that is most dispersed in the wet season, when females and calves spend more time in woodlands (Estes, 1991; Kingdon, 1997). Presumably, *K. sigmoidalis* would have followed suit, remaining near water sources throughout the year.

Kobus sigmoidalis **Paleoecological Reconstructions**

Study	Diet	Habitat
Gentry &Gentry (1978): uniformitarianism[1]	Grazer	Floodplain Grassland
Blumenschine et al (2003): C_3/C_4[2]	C4 dominated diet	-
Plummer et al (2009): C_3/C_4[3]	Variable Grazer	Edaphic Grassland or Riverine Woodland
Kappelman et al (1997): femoral[4]	-	Open to Light Cover
Spencer (1997): craniodental[5]	Grass Feeder	Edaphic Grassland

Table 3.4. Terminology definitions from each source:

[1] A feeder relying primarily or exclusively on grass.

[2] Not defined.

[3] Variable grazers have a δ^{13}C of -1.0 to 2.0 ‰ and consume 75% to 95% C_4 plant foods. Edaphic grassland refers to floodplain grasslands that result from waterlogged soils on a seasonal or constant basis.

[4] Open habitat includes ecotone, open country, and arid country. Light cover habitat includes light bush, tall grass and hilly areas.

[5] Grass feeders eat primarily grass. Edaphic grassland refers to floodplain grasslands that result from waterlogged soils on a seasonal or constant basis.

Results

Modern Analogs

Summary of Modern Analog Characteristics					
Modern Analog	**Diet**	**Water Dependence**	**Seasonal Mobility**	**Reproduction**	**Body Condition**
Springbok (for *A. recki*)	Browser-grazer[1,2,3]	Independent, but attracted to waterholes in dry season[1]	Residential (typically); aggregate in wet season grassland, disperse in dry season woodland[1,4,5,6,7]	Perennial with rutting peaks in the early dry season and birthing six months later[1,4]	Poorest at the end of the dry season, in older individuals, and lactating females[8]
Impala (for *A. recki*)	Browser-grazer[1,2]	Dependent on waterholes in the dry season[1]	Residential; small home ranges near water, grassland edges in wet season, open woodland in dry season[1,2,9,10]	Perennial in eastern Africa, with a minor birthing peak at the end of the dry season[11]	Poorest at the end of the dry season, in older individuals, and lactating females[12]
Hirola (for *P. altidens*)	Grazer[3]	Independent, but rely on green grasses nearby in dry season[13, 14, 15]	Residential; dispersed woodlands and bushy grasslands in wet season, aggregated near waterholes in dry season[2,3,13]	Seasonal, with a birthing peak in the short wet season following the long dry season[2,13]	Little or no seasonal variation observed, late-term pregnant and lactating females in poorest condition[13,16]
Waterbuck (for *K. sigmoidalis*)	Grazer[17,18]	Dependent, live near drinking water[19]	Residential; dispersed in woodlands during wet season, aggregated along waterways in dry season[17,18,20,21]	Perennial with a minor birthing peak in the wet season[1,18]	Poorest at the end of the dry season, poorer in males than females, and poorer in late-term pregnant and lactating females than other females[18,22]

Table 3.5. Summary of extant bovid ecological characteristics.

[1] Estes (1991)
[2] Kingdon (1997)
[3] Gagnon and Chew (2000)
[4] Jackson et al. (1993)
[5] Ritter and Bednekoff (1995)
[6] Child and Le Riche (1969)
[7] Crowe and Liversidge (1977)
[8] Turner et al. (2012)
[9] Jarman (1979)
[10] Murray (1981)
[11] Ogutu et al. (2014)
[12] Gallivan et al. (1995)
[13] Andanje (2002)
[14] Bunderson (1981)
[15] Dahiye (1999)
[16] Probert (2011)
[17] Tomlinson (1980)
[18] Spinage (2012)
[19] Taylor et al. (1969)
[20] Tomlinson (1981)
[21] Wirtz and Oldekop (1991)
[22] Child and Von Richter (1969)

The table above (Table 3.5) summarizes results of a behavioral and physiological review of modern bovid referents that can be found in Appendix 5. The modern referents that best fit the extinct fossil bovids reveal the following trends: though all four species are found near waterholes in the dry season, even those that can derive sufficient moisture from their diet in the wet season maintain territories that keep them within a few kilometers of waterholes, making their availability in the vicinity perennial. With the exception of the hirloa, reproduction in these species is aseasonal or shows only minor seasonal peaks, such that the presence of infants is not indicative of a particular season. Body condition does follow seasonal trends, with the lowest fat content at the end of the dry season, again with the exception of the hirloa, which shows little seasonal variation. In all four species, old individuals retain less fat than prime aged individuals, and late-term and lactating females are in worse condition than other females.

Museum Analyses

FLK Zinj Bovid Sex Distribution

Sex	***A. recki***	***P. altidens***	***K. sigmoidalis***
Female (n)	-	0	1
Male (n)	-	6	4
Sex Unknown (n)	6	-	6*
Total Dental MNI	6	6	12

Table 3.6. Sex determinations for three FLK Zinj bovids. *Four of these individuals are fetal/newborn.

FLK Zinj Bovid Age Distribution

Age Class	***A. recki***	***P. altidens***	***K. sigmoidalis***
Fetal/Newborn	0	0	4
Young Juvenile	0	0	1
Subadult Juvenile	1	3	0
Early Prime Adult	1	2	3
Late Prime Adult	0	0	4
Old Adult	4	1	0
Total Dental MNI	6	6	12

Table 3.7. Age determinations for 3 FLK Zinj bovids.

Sex and Age analyses of *A. recki, P. altidens,* and *K. sigmoidalis* from the Leakey Collections stored at the National Museum of Dar es Salaam are presented in Tables 3.6 and 3.7. In the smaller *A. recki*, it was not possible to determine sex. In the larger bovids, sex is skewed toward male. Age classes are more variable between species. Two thirds of *A. recki* are old adults, whereas *P. altidens* has a single old adult and *K. sigmoidalis* has none. Instead, *P. altidens* is dominated by weaned subadults and early prime adults, while *K. sigmoidalis* shows a bimodal distribution with five unweaned individuals (four newborns and one young juvenile), no subadults, and seven prime adults (three early prime and four late prime).

Discussion

Speth (1987) makes three predictions for a Pleistocene dry season site. The first is that hominins would situate dry season sites near perennial water sources. The second is that, as the dry season progresses, hominins would shift their foraging away from animal products and toward plant foods, particularly those with high fat content, resulting in a relatively small faunal assemblage.

Lastly, the faunal remains present at a dry season site are predicted to reflect hominin selectivity for species, demographics, and skeletal elements that maintain the highest fat levels throughout the year.

FLK Zinj meets Speth's first prediction for a dry season site, located only 200 m away from a freshwater spring that would have flowed continuously year round, but it does not meet the second prediction of being faunally depleted. FLK Zinj is one of the largest assemblages of hominin-butchered bones in the Early Pleistocene. Therefore, the location and size of the assemblage are insufficient sources of evidence for seasonal hominin behavior in this context. The last prediction, that hominins would demonstrate greater discrimination in favor of fat-rich animal parts, is assessed below.

Seasonal Availability of Prey

Hominins could only show selectivity in transporting bovid remains from the group of species and demographics that were present nearby. In temperate environments, the presence and age of particular fauna can be a seasonal indicator resulting from migration patterns and restricted birthing periods. However, the modern analogs reviewed above were likely present in the immediate vicinity of FLK Zinj year round. The site would have offered valuable resources to certain bovid demographic segments of throughout the year, and would have been highly attractive to all demographics in the dry season.

Extrapolating to FLK Zinj and the Olduvai paleo-lake basin, waterbuck, isolated territorial springbok males, and dispersed hirola would be found within the woodlands in the wet season. Impala would graze nearby, preferring the open edge regions within their small ranges. As none of these species are migratory, the larger female groups and male bachelor herds would be dispersed throughout the grasslands in the wider paleo Olduvai basin. In the dry season, large numbers springbok, impala, and hirola from all demographics would be found consistently in close proximity to the spring near FLK Zinj. Excluding females with newborn calves concealed in the woodlands, waterbuck would target any remaining green grasses, which were likely found at the woodland edges near the spring, rather than along the paleo-Lake Olduvai salt pan.

Despite these strongly seasonal patterns of demographic organization, the presence of particular ages and sexes at FLK Zinj reveals very little about the season of death (Tables 3.6. and 3.7.). As an aseasonal reproducer with minor sexual dimorphism, *A. recki* individuals cannot be assigned to sex based on any skeletal element (Reynolds, 2007), nor can the season of death be inferred based on their age distribution. *P. altidens* is represented entirely by male individuals at FLK Zinj, but its modern analog, the hirola, does not exhibit a behavioral pattern that allows a seasonal interpretation of this sex distribution. Lone males defend territories of up to two km through which females, calves, and bachelor groups move. Bachelor groups are often composed of the full range of ages, and aggregate between April and December, which is from the midst of the long rains to the end of the short rains, and encompasses the long dry season from June to October (Andanje, 2002). Thus, while it is clear that males were targeted, it is not possible to establish a season of death because territorial males are perennially present, and bachelors assemble for three quarters of the year.

The sex of some *K. sigmoidalis* individuals was difficult to determine, but the presence of 4 fetal or newborn calves suggests that females were also temporarily present. However, because waterbuck breed year-round, this highly vulnerable newborn sample indicates nothing about season of death. Like the highly water-dependent waterbuck, *K. sigmoidalis* is expected to have remained near the FLK Zinj spring year-round. Were this a carnivore kill site, the high proportion of a size 3B bovid typical of *Panthera leo* (lion) preferred prey (Hayward and Kerley, 2005) could signify a dry season pattern. Lions will drag size 3 carcasses into shady or protected areas, but these distances are typically 100 m or less (Schaller, 1972). To accumulate multiple adults within 100 m of FLK Zinj during the short duration of deposition would likely require a dry season aggregation of waterbuck. Yet multiple lines of evidence indicate that the FLK Zinj bovids were transported by hominins (e.g. Bunn and Kroll, 1986; Bunn and Pickering, 2010a; Bunn and Gurtov, 2014), which could have sampled bovids from a much broader radius.

In sum, the modern analogs are always present in habitats like FLK Zinj. Though their demographic distribution change seasonally, the presence or absence of certain ages and sexes cannot provide a clear indication of seasonality as it would in seasonally-breeding or sexually segregated species. Ultimately, the lack of a breeding season or mass migration means that these fossil bovids were always within a reasonable distance for hominins to transport their remains to FLK Zinj.

Selectivity for Prey in Good Condition

Given the availability of *A. recki*, *P. altidens,* and *K. sigmoidalis* throughout the year, hominins foraging in the dry season may have instead shown selectivity for demographics that remain fat-rich in peak times of stress. Yet the demographic distribution at the site does not support the prediction that marrow fat was the primary target. Based on the review above, a fat-seeking hominin should exclusively target non-breeding hirola, or their fossil analog *P. altidens*, in the height of the dry season. The fact that all six *P. altidens* are full-grown or almost full-grown males would support a dry season interpretation based on Speth's (1987) criteria if they were the only fauna present. These individuals represent the largest, prime condition individuals in the population. The other bovid species and demographics, however, do not suggest strong selectivity for fat-rich targets. Among *K. sigmoidalis* individuals whose sex could be determined, four were male and one was female, despite waterbuck females maintaining higher fat content than males year-round (Spinage, 2012). Four of the unsexed *K. sigmoidalis* individuals are calves whose body condition cannot be assessed through its modern analog, but which are frequently low-fat in living waterbuck (Gallivan et al., 1995), and which would have offered significantly less absolute fat by weight than an adult. The *A. recki* sample is dominated by old adults, which are in poor condition in both springbok and impala. Therefore, the age and sex of the assemblage could reflect annual site usage, with *P. altidens* as the primary target in the dry season, or it could reflect a lack of discrimination in favor of fat. These two possibilities cannot be distinguished by the available evidence.

Selectivity for Elements with High Fat Content

Speth's (1987) final prediction is that dry season sites would be composed of those skeletal elements that retain fat the longest. In bovids, fat is carried in the organs, the mesentery, the brain, and the marrow cavities. Analysis of African bovid fat mobilization has focused on marrow largely as a result of the distribution of elements at FLK Zinj, where crania are scarce but mandibles and limbs are common (Bunn and Kroll, 1986). Using skeletal part profiles derived from Bunn and Kroll (1986), Blumenschine and Madrigal (1993) argue that the element assemblage of small and medium ungulates at FLK Zinj correlates most strongly with a marrow-targeting strategy by scavenging hominins (Blumenschine et al, 1991; but see Bunn and Ezzo, 1993). They note that, following the consumption sequence of carcasses by primary carnivores, marrow, brain, and bone grease are all that remain to be scavenged.

Marrow cavities contain the last fat to be utilized by a calorically stressed ungulate (Sinclair and Duncan, 1972), with proximal limb fat mobilized before distal limb fat (Blumenschine and Madrigal, 1993). When the absolute quantity of fat is considered, smaller distal marrow cavities increase in value relative larger proximal marrow cavities undergoing fat mobilization. At FLK Zinj, Blumenschine and Madrigal (1993) found that the profile of limb bone elements in small bovids (size groups 1 – 2) resembled the fat distribution of extant bovids in moderately good health, while those of medium sized bovids (size groups 3 – 4) reflected the distribution of marrow fat in bovids with excellent health. These results were interpreted to mean that hominins were not under nutritional stress, which would have resulted in collecting all available fat, but were rather selectively targeting limb elements with the highest yields.

A second study by Lupo (1998) using fat extraction rates during butchery concluded that the FLK Zinj assemblage cannot be used to assess carcass condition or foraging efficiency. Size 3 and 4 bovid limb proportions and exploitation revealed no correlation between FLK Zinj element profiles and fat extraction rates. The FLK Zinj assemblage also exhibited no correlation with extant size 3 bovids in poor, moderate, or excellent condition, in contrast with the Blumenschine and Madrigal (1993) study using fat distribution alone (Lupo, 1998).

Both limb fat studies assume that hominins could only access carcasses by scavenging from other predators. Noting that ungulate physiological condition is at least as dependent on reproductive cycle as it is on nutrition, and differs significantly in peak times between males and females of the same species, Bunn and Ezzo (1993) argue that hunting hominins would have had access to relatively fattened individuals in every season. Assessing the relative value of limb elements in the context of whole carcass butchery is even more nebulous, and these contradictory results suggest that the limb element profiles at FLK Zinj can indicate little beyond the fact of marrow processing by hominins.

Modern African Hunter-Gatherers Eat More Meat in the Dry Season

The dry season site predictions proposed by Speth (1987) are biologically sound in that they reflect the hominin imperative of drinking water and the declining bovid condition in the height of the dry season. The first prediction states that dry season campsites should be located near perennial water sources. Among Hadza hunter-gatherers living on the east side of Lake Eyasi, Tanzania, the need for drinking water is one of the primary motivators for moving camp closer to waterholes (Woodburn, 1964). !Kung groups living in the Kalahari also tend to camp together around permanent waterholes in the winter dry season (Lee, 1972). The second and third predictions, which relate to the fat content of bovid prey, reflects the well-established decrease in bovid fat stores over the course of the dry season and concomitant increase disease susceptibility (Mduma et al., 1999; Ogutu and Owen-Smith, 2003; Owen-Smith et al., 2005).

Yet Speth's (1987) prediction that bovid meat was seasonally avoided at African Early Pleistocene sites is not supported by living forager behavior in comparable environments. Speth and Davis (1976) make this observation in their own seasonality study when they note that !Kung and G/wi foragers in the Kalahari have much higher bovid hunting success in the dry season than in the wet season. Hadza foragers living on the east side of Lake Eyasi, Tanzania, also procure significantly more bovids in the dry season. This success is largely due to the organizing effect that waterholes have on the distribution of prey species on the landscape (Woodburn, 1964; Marlowe, 2003, 2010; Hawkes et al. 1991, 2001; Bunn, 2001; Bunn et al., 1988). Because most bovids must drink regularly when their plant foods are desiccated, Hadza can predictably shoot bovids on their way to drink from hunting blinds strategically located along game trails (Woodburn, 1964; Bunn et al., 1988).

This reliable source of game in the dry season translates into meat intakes that are highest in the late dry season (Woodburn, 1964; Marlowe and Berbesque, 2009) when most bovids are leanest. Rather than suffering from a negative energetic budget from processing large quantities of protein, the Hadza maintain a fairly consistent physiological status across seasons, and women experience a small but significant increase in body fat in conjunction with this meat consumption increase (Marlowe and Berbesque, 2009). Marlowe and Berbesque (2009) attribute the minimal variation in Hadza body condition, despite dramatic habitat seasonality, to a foraging strategy that continuously replaces disappearing foods with newly available ones. In this way, the nutritional needs of all group members are met through a division of foraging labor and food sharing. The high protein diet of the late dry season is thereby enabled by nutritional plant foods, as well as access to the fat from whole carcasses.

While Speth (1987) makes no pronouncement about whether early Pleistocene hominins hunted for scavenged for meat, the mode of procurement has important implications for how lean the available meat would have been. Carnivores feed on carcasses in a predictable manner, beginning with the hindquarter flesh and viscera, followed by the forequarter flesh, ribs, and ribcage contents, and subsequently the accessible flesh of the head, hindlimb marrow and forelimb marrow (Blumenschine, 1986; Bunn and Ezzo, 1993). Thus the first two targets of a carnivore include the omentum and fatty organs that would have provided their consumers with significant quantities of fat (Bunn and Ezzo, 1993). If hominins scavenged from carnivores, these resources would be rarely available even in the case of early access. If hominins hunted bovids, then they would have had first access to high quality fat in addition to lean protein. Bunn and Ezzo (1993) note that most of the bovid elements at FLK Zinj belong to parts of the carcass that are consumed first by carnivores. The presence of butchery marks on many of these indicates that hominins had early or first access, else they would no longer retain meat worth removing (Bunn and Ezzo, 1993). Recent research exposing differences between modern and fossil carnivore prey mortality profiles and those of modern hunter-gatherers and anthropogenic sites appear to corroborate the hypotheses that hominins opportunistically hunted a significant portion of their prey (Bunn and Pickering, 2010a; Bunn and Gurtov, 2014).

This fundamental contradiction between Speth's (1987) rationality for predicting a deficit of faunal remains at dry season sites, and the pattern of meat consumption seen in living foragers, suggests seasonality cannot be modeled using existing taphonomic studies if the hominins in question did not occupy a strictly marginal scavenging niche. In combination with the highly variable pattern of fat depletion in different bovid demographics, the residential lifestyle, and the aseasonal birthing of most bovids, the analysis of seasonal site usage at FLK Zinj remains theoretical.

Conclusion

Using the best modern analogs for *A. recki*, *P. altidens,* and *K. sigmoidalis,* no reliable pattern of seasonal foraging could be discerned at FLK Zinj using the model presented in Speth (1987). This result does not indicate that FLK Zinj was used year round. Rather, the patterns in bovid mobility, demography, and physiology cannot be attributed strictly to the influence of seasonality. FLK Zinj taphonomy, too, reflects complex foraging behaviors that continue to be debated, but which indicate some frequency of whole carcass access. The seasonality of FLK Zinj cannot be ascertained through bovid paleoecological reconstructions or taphonomic analysis because the bovids are aseasonally breeding residents with variable energetic requirements. Without these constraints, the dry season site model is inappropriate.

To study hominin foraging seasonality, and its implications for hominin diversity in the Early Pleistocene, an alternative method is necessary. In the previous chapter, I tested the ability of dental microwear texture analysis (DMTA) to distinguish between wet and dry season deaths of a residential mixed feeder, the impala (*Aepyceros melampus*). The results indicate that microwear can distinguish between impala seasons of death when comparing two samples. It was proposed that a seasonal increase in atmospheric grit, rather than dietary changes, was the primary driver of seasonal microwear texture differences between wet and dry season samples. The application of DMTA to FLK Zinj and the penecontemporaneous carnivore site of FLK North is a new and promising approach to studying foraging seasonality in the Early Pleistocene, and is presented in Chapter 4.

Chapter 4. Assessing Hominin Foraging Seasonality at FLK Zinj

Introduction

The evolution of human carnivory is a subject that captivates scientists across a wide spectrum of research interests. Hominin meat-foraging strategies are central to hypotheses about the evolution of the modern human body plan (Aiello and Wheeler, 1995; Bramble and Lieberman, 2004; Pontzer et al., 2010), behavioral flexibility (Foley et al., 1991), and modern life history (Hawkes et al., 1997; Kaplan et al., 2000). Each of these studies presume the substantial inclusion of meat in the diet of early *Homo*, but how this meat was accessed remains a controversial issue. Hunting, particularly of large game, is associated in the archaeological literature with the development of modern cognitive capabilities like planning depth and tactical mobility (Binford, 1989). These are viewed as the hallmarks of archaic and modern humans (e.g., Klein, 2001; Kaufman, 2002; McBrearty and Brooks, 2000; Klein, 1994, 1995; Klein et al., 1999; Milo, 1998; Soffer, 1989). As such, the interpretation of butchered animal bones as evidence of hunting in the Early Pleistocene is a challenge to the common conception that early hominins were too behaviorally unsophisticated and diminutive to compete with an expanded Pleistocene carnivore guild.

The earliest evidence for persistent meat eating appears around 2.0 Ma in the increasingly arid eastern African savannas. Though stone tools dating as early as 3.3 Ma are contemporaneous with evidence for defleshing marks on faunal remains, (Harmond et al, 2015; McPherron et al., 2010; Thompson et al., 2015; Semaw et al., 2003; Dominguez-Rodrigo et al., 2005), these finds indicate only the occasional tool-assisted consumption of mammal remains. Kanjera South (2.0 Ma) and FwJj20, Koobi Fora (1.95 Ma), in Kenya, and FLK Zinj (1.848 Ma) at Olduvai Gorge in

Tanzania, represent some of the oldest assemblages with repeated and substantial hominin carcass butchery (Ferraro et al., 2013; Bunn and Kroll, 1986). These sites are temporally clustered around an inflexion in the climatic conditions that facilitated the spread of savanna ecosystems between 2.1 and 1.8 Ma, following general shifts at ~3.0 Ma and 2.5 Ma toward cooler and drier conditions than those prevailing in the Miocene and Pliocene (deMenocal, 2004; Reed and Rector, 2007). These changes led to increasingly seasonal and climatically instable habitats (Ashley, 2007; Potts and Faith, 2015), and it is in this context that hominins created the Kanjera South, FwJj20**,** and FLK Zinj assemblages.

Seasonal changes have the ability to dramatically change the distribution of food and water on the landscape, creating the potential for strong selection on advantageous morphological and behavioral responses. However, selection for adaptability in the face of such climatic and seasonal variability can have the effect of lowering fitness in any particular environmental context (Potts and Faith, 2015; Chiu et al., 2006; Woods et al., 2011). It is notable, therefore, that the time period between 2.0 and 1.8 Ma is associated with the evolution of a new hominin species, *Homo erectus* (Wood, 1991), as well as a rise in the behavioral evidence for tool-assisted meat eating. Many researchers have proposed that these sites reflect passive scavenging from abundant abandoned carcasses (Binford, 1981; Blumenschine, 1986, 1987, 1995; for a review, see Dominguez-Rodrigo et al., 2007b), while others have noted the incongruity between passive scavenging yields and taphonomic patterns at the earliest large butchery sites (Bunn and Kroll, 1986; Bunn and Ezzo, 1993; Bunn, 2001, 2007a, 2007b; Bunn and Pickering, 2010a; Bunn and Gurtov, 2014; Ferraro et al., 2013). In either case, it is reasonable to consider the evidence for a new foraging strategy in the context of seasonal resource variability.

In modern savannas, precipitation seasonality results in redistributions of large mammals and their food. Few modern savannas exhibit the kind of large scale of bovid migration seen in the Serengeti, but there is a consistent pattern of prey and predator aggregation around waterholes in the dry seasons, and dispersal in the wet season, across savanna ecosystems (e.g., Lamprey, 1963, 1964; Western, 1975; Epaphras et al., 2008; Valeix et al., 2010b; Valeix et al., 2009). Water dependency varies between and within bovid genera, such that some species must remain within daily walking distance of surface water (e.g., Bushbuck, *Tragelaphus scriputs*), others switch between grazing and browsing to acquire sufficient moisture from food in close proximity to dry season watering holes (e.g., Impala, *Aepyceros melampus*), and still others are capable of going without standing water indefinitely (e.g., Springbok *Antidorcas marsupialis*) (Estes, 1991). Regardless of these adaptations to rainfall seasonality, most bovids gravitate toward available water-either standing or in plant foods in the dry season (Schaller, 1972; Ogutu et al., 2008; Davidson et al., 2013). This may mean that, like modern hunter gatherers (e.g., Woodburn, 1964; Marlowe, 2010; Hawkes et al. 1991, 2001; Bunn, 2001; Bunn et al., 1988), hominins operating in such a habitat would have greater access to meat in the dry season.

The dry season is also a time of resource scarcity for primates in eastern African savannas. Baboons in Amboseli National Park, for example, depend on a “hand off” foraging strategy, in which they monitor and make use of various plant resources as they come into season (Alberts et al., 2001). In the lean dry season, these baboons turn to fallback foods, items which require longer to process and/or have lower nutritional yields, but which are widely available. This results in prolonged feeding times, but enabled the baboons to maintain stability in their nutritional intake (Alberts et al., 2001). These observations point toward the dry season, especially during periods of high climatic variability, as a time of increased selective pressure on foraging efficiency.

Whether scavenging or hunting, entering a carnivorous niche made meat eating hominins competitors in the carnivore guild as well as potential prey. The distribution of prey makes dry season waterholes an environment of increased carnivore predation pressure for subordinate allospecifics, including hominins. In the modern savanna, large carnivores exert a top down influence on subordinate members of the guild through predation and competition (Hayward and Slotow, 2009). Cheetahs and wild dogs, especially, use temporal and spatial avoidance strategies to reduce the opportunities for predation and competition with lions (Hayward and Slotow, 2009; Palomares and Caro, 1999; Durant, 1998). Aside from leopards, dominant lions and striped hyenas prefer habitats that provide cover but which are not densely vegetated (Schaller, 1972; Elliott et al., 1977; van Orsdol, 1984; Hopcraft et al., 2005). Cheetahs and wild dogs operate further afield, in open habitats that enable cursorial hunting. In the dry season, however, the aggregation of prey biomass forces all the large predators to risk overlapping in the more densely wooded habitats associated with perennial water (Schaller, 1972; Pereira et al., 2014; Frame, 1986; Gros, 2000).

Woodlands in the Early Pleistocene are hypothesized to have provided hominins with a range of resources, including water, shade, plant foods, and camouflage (Blumenschine and Peters, 1998). Ecomorophological studies of extinct sabertoothed cats reveal adaptations to more complex substrates, suggesting that the larger carnivore guild in the Early Pleistocene would have made woodland habitats a more competitive environment than they are today (Marean, 1989; Turner and Anton, 1997; Lewis, 1997; Van Valkenburgh, 2001). The wet season dispersal of bovids into grasslands, also inferred from ecomorphological and modern analog studies (e.g., Plummer and Bishop, 1994; Spencer, 1997; Kappelman et al., 1997; see Chapter 3) would have reduced competition in woodlands relative to the open and edge environments in which many dominant carnivores operate. However, as a water dependent taxon, hominins are likely to have remained within daily travel distances of water, and any associated woodlands, year round.

Given the dangers inherent to becoming carnivorous in this context, an important consideration is how hominins reduced carnivore competition. Predictions have included increasing body size (Shipman and Walker, 1989), increasing group size (Rose and Marshall, 1996; Brantingham, 1998), improving defensive technologies (Treves and Treves, 1999), and avoiding open habitats (Van Valkenburgh, 2001). Modern carnivores also employ temporal strategies to reduce direct competition, with the most subordinate species, wild dogs and cheetahs, active more in the daytime when dominant carnivores are at rest (Hayward and Slowtow, 2009). As diurnal primates, hominins would already be largely limited to daytime activities, perhaps with peaks at dawn and dusk when hunting opportunities are maximized (Hayward and Slowtow, 2009).

Researchers have rarely considered the role that hominin omnivory may have played in reducing intraguild competition. Unlike other carnivores, which remain dedicated meat eaters throughout the year, hominins are known to have had extremely variable diets. While *Australopithecus boisei* is reconstructed as a specialized, grass-feeding herbivore (Cerling et al., 2011; Ungar et al., 2012), dental microwear and stable carbon isotope analyses indicate that the earliest members of the genus *Homo* had a broad, unspecialized diet. The sample of *Homo habilis* from Olduvai Gorge appears to reflect a range of food types, but one with limited reliance on extremely fracture-resistant foods, which is in keeping with occlusal morphology that better enables shearing of tough but malleable items than that of the australopithecines (Ungar, 2004; Ungar and Scott, 2009; Ungar et al., 2012). Stable carbon isotope analysis of *Homo habilis* at Olduvai also indicates a mixed diet with a quarter to a half of all foods utilizing a C4 metabolic pathway (van der Merwe et al., 2008). This C_4 signature can be acquired through consuming the plant foods themselves as well as the fauna that consume them.

Homo erectus is not yet known from Bed I at Olduvai (but see Dominguez-Rodrigo et al., 2015), but is found elsewhere in eastern Africa beginning ~1.9 Ma (Wood, 1991). This taxon exhibits an even broader range of food fracture properties than is seen in *Homo habilis*, *A. afarensis, A. africanus,* or *A. boisei*. The dental microwear of African and Georgian *H. erectus* most closely approaches that of *A. robustus*, which is reconstructed as an occasional hard-object feeder, but the former is less extreme in this regard than the latter (Ungar et al., 2012; Pontzer et al., 2011). Precisely what type of food items these results are consistent with is still under investigation, but the microwear and occlusal morphology clearly reflect an increase in the breadth of food types, and incorporated tough and fracture resistant items like meat or tubers (Ungar et al., 2012; Pontzer et al., 2011). A study of stable carbon isotopes in *Homo* sp. 2.0-1.4 Ma from the Turkana Basin, Kenya, revealed an increasing contribution of C_4 plants, or perhaps more likely, their consumers, to the diet (Cerling et al., 2013; Klein, 2013).

This paper explores the evidence for seasonal meat foraging strategies by the FLK Zinj hominins in the context of carnivore competition. The danger of joining the carnivore guild, the increasingly seasonal environment, and the evidence for dietary breadth in early *Homo* yield the following hypotheses:

> H1. If meat-eating occurs around a predator avoidance strategy, then it should occur in the wet season (contra Blumenschine, 1987; Blumenschine and Cavallo, 1992**;** Foley, 1987: 199 to 210; Marean, 1989)

H2. If meat eating is nutritionally driven, then it should occur in the dry season, when plant foods require longer foraging times and are less nutritious.

H3. If meat-eating was an integral part of the foraging strategy of a carnivore-guild member, as it is for the Hadza, it will occur year-round.

To test these hypotheses, season-of-death (SOD) profiles for prey species at FLK Zinj were created using dental microwear texture analysis (DMTA) on bovid teeth, and compared with SOD profiles for the penecontemporaneous site of FLK North levels 1-3 (1.803 Ma; henceforth, FLK North) in Bed I, Olduvai Gorge. While the assemblage at FLK Zinj is anthropogenic (Bunn and Kroll, 1986; Bunn, 2007a; Bunn and Pickering, 2010a; Bunn and Gurtov, 2014), taphonomic studies point to carnivores as the accumulators of the faunal assemblage at FLK North, despite an abundance stone tools (Domingeuz-Rodrigo and Barba, 2007b; Bunn et al., 2010). In most other regards, however, including habitat, climate, lithics, and faunal composition, the sites are strikingly similar (Urribelariea et al., 2014; Ashley et al., 2010a, 2010b; Barboni et al., 2014; Magill et al., 2012a; Leakey, 1971; Bunn and Kroll, 1986; Dominguez-Rodrigo and Barba, 2007b; see Chapter 1). By analyzing the SOD profiles of hominin and carnivore prey, their primary season of activity at each site can be determined.

Background

Paleoreconstructions place FLK Zinj and FLK North in wooded to densely-wooded habitat supported by the seepage from freshwater springs ~200 m and ~30 m away, respectively (Ashley et al., 2010a; Barboni et al., 2010, 2014). Both sites were deposited on the eastern shore of a variably sized lake, in a broader wooded grassland setting (Hay, 1976; Ashley, 2007; Bamford, 2008). The lithological record encompassing these sites records a series of lake expansion and contraction cycles in which the Tuff IF that caps FLK North was deposited in a dry phase of maximum lake size reduction (Ashley, 2007). These cycles have an average duration of 21 Ka, reflecting the Earth's precession cycles (23 Ka to 19 Ka; Ashley, 2007). Though this sedimentological analysis was based on Tuff dates that are now obsolete, the new dates for FLK Zinj and FLK North place these sites 45 Ka apart in time, or roughly two lake/precession cycles apart (Deino, 2012). This strongly indicates that both sites accumulated in a cooler, drier phase when lake levels were relatively low and, by extension, precipitation was highly seasonal and variable. Total organic carbon and leaf lipid carbon isotopes from paleo Olduvai Lake sediments support this interpretation, placing these sites in approximately the same stage of the vegetation succession, in a wider wooded to open grassland (Magill et al., 2012a).

Available dust flux records for the time when FLK Zinj accumulated add yet another data point reflecting a xeric period in the oscillating climate. In the DMTA study of modern impala presented in Chapter 2, seasonal differences in microwear are interpreted to be driven by an increase in atmospheric and adhering grit in the dry season. This phenomenon is caused by the rain shadow cast by the eastern arm of the Great Rift, resulting in severe rainfall seasonality and windborn sedimentary particles that adhere to foliage in the dry season (City of Karatu, Tanzania; http://www.worldweatheronline.com). A similar phenomenon is very likely to have operated in

Bed I Olduvai Gorge. Environmental reconstructions of the broader basin show that both FLK Zinj and FLK North accumulated during contracted lake levels caused by reduced precipitation, perhaps as low as 250 mm/year (Magill et al., 2012a). Under these conditions, the playa lake margin would have served as a reservoir of dust in the Olduvai basin in the same manner as the short grass plains of the Serengeti do for Hadzaland.

The lithic assemblages at both sites are classic examples of the Oldowan, containing a very similar array of tool types made from the same raw materials (Leakey, 1971). Archaeologists have noted the prevalence of battering implements at FLK North when compared with cutting implements at FLK Zinj (Diez-Martin et al., 2010). This is not unexpected, given the near absence of carcass butchery at FLK North, but the extent of difference may be over stated. Stone flakes are common at both sites, accounting for 63% of the lithics at FLK North and 85% at FLK Zinj (Leakey, 1971).

The faunal assemblages, too, share many species in common, as evidenced by the minimum number of individuals (MNI) (Bunn and Kroll, 1986; Dominguez-Rodrigo et al., 2007a, 2010; Bunn and Gurtov, *personal observation*). Among the bovids, the most significant difference is the absence of waterbuck (*Kobus sigmoidalis*) and wildebeest (*Connochaetes* sp.) at FLK North. This will be discussed below. Otherwise, the array of species indicates a very similar faunal community (Table 4.1.).

This analysis is focused on the two largest bovid samples shared between FLK Zinj and FLK North, *Antidorcas recki* and *Parmularius altidens*. Based on analogous modern bovids like the springbok, impala, and hirola (see Chapter 3), both *A. recki* and *P. altidens* are likely to have made seasonal use of the wooded habitats and springs at FLK Zinj and FLK North. Because the dietary reconstructions and handling costs associated with *A. recki* and *P. altidens* differ, hominin foraging seasonality for these bovids may also differ. By evaluating the seasonality of butchery at FLK Zinj, and carnivore consumption at FLK North, hominin meat foraging at FLK Zinj can be evaluated as competitive or risk aversive, and as consistent or intermittent.

Ecomorphological, isotopic, and DMTA studies indicate that *A. recki* (Tribe Antilopini) was a mixed feeder that alternated seasonally between browsing and grazing in ecotone habitats that included secondary grassland, bushland, and woodland edges (Gentry and Gentry, 1978; Spencer, 1997; Lee-Thorp and van der Merwe, 1993; Plummer et al., 2009). If this reconstruction is accurate, *A. recki* would have moved seasonally between woodland edges with green grass in the wet season to wooded habitats with moister forage in the dry season, which provide different opportunities for foraging, vigilance, and predation avoidance for hominins.

As a small bovid estimated at ~30 – 50 lbs (size group 1; Bunn, 1986), *A. recki* is typical of leopard, cheetah, and wild dog prey (Hayward et al., 2006a, 2006b, 2006c). The primary predators of *A. recki* likely included paleomorphs of these modern predators as well as the sabertooths *Dinofelis* and *Megantereon*. While the particular hunting and ranging habits of the latter species are unknown, leopards remain in the same area for several years, hunting species in their range year round (Schaller, 1972). The inferred seasonal movement of *A. recki* would have resulted in spatial overlap with cursorial predators like cheetahs and wild dogs in the wet season, and with woodland-adapted species like leopards, *Megantereon* sp., and *Dinofelis* sp. year round (Lewis, 1997). The carnivore generated assemblage at FLK North is therefore hypothesized to represent an assemblage accumulated during all seasons of the year.

Large Faunal MNI at FLK North and FLK Zinj

	FLK North	FLK Zinj	
Bovidae Taxa	**Bunn and Gurtov 2013[1]**	**Bunn and Kroll, (1986)[2]**	**Bunn and Gurtov 2013[1]**
Kobus sigmoidalis	0	9	12
Parmularius altidens	30	6	6
Antidorcas recki	21	6	5
Antilopini size 2	10	1	2
Alcelaphini size 2	3	0	1
Tragelaphus strepsiceros	3	1	1
Synceros acoelotus	1	1	1
Connochaetes sp.	0	3	3

	FLK North		FLK Zinj
Other Taxa	**Leakey Collection[3]**	**TOPPP[4]**	**Bunn and Kroll, (1986)[2]**
Suid	2	1	5
Equid	1	2	5
Giraffid	1	1	2
Hippopotamid	1	1	1
Elephas	0	0	1
Rhino	1	0	0
Carnivora	8	1	3
Theropithecus	1	0	0

Table 4.1. Minimum number of individuals (MNI) in various taxonomic groups at FLK North and FLK Zinj based on dental remains.

[1] Unpublished MNI from analyses undertaken by Bunn and Gurtov in 2013 on the Leakey collections house in the National Museum in Dar es Salaam, Tanzania.

[2] MNI published in Bunn and Kroll (1986).

[3] MNI of Leakey collections published by Dominguez-Rodrigo and Barba (2007b)

[4] MNI from excavations conducted by The Olduvai Paleoanthropology and Paleoecology Project between 2007 and 2009, from Dominguez Rodrigo and colleagues (2010). These represent additional specimens, but the MNI for the combined excavations has yet to be determined.

P. altidens (Tribe Alcelaphini) is an extinct grazer between 251 – 450 lbs (size group 3A; Bunn, 1986). This bovid is expected to have preferred open, secondary grasslands like those in the wider Olduvai basin (Gentry and Gentry, 1978; Spencer, 1997; Blumenschine et al., 2003;

Plummer et al., 2009; Bamford, 2008; Magill et al., 2012a). As a size 3B bovid, *P. altidens* is the most preferred prey size of extant lions (Hayward and Slowtow, 2009). Lions maintain home ranges and occupy different areas depending on the season and the location of their prey (Schaller, 1972; Hopcraft et al., 2005). In the Serengeti, lions hunt most often where vegetation facilitates ambush hunting, which changes seasonally in the broader context of prey location, such that lions hunt in woodland and adjacent areas year round, but more often in the dry season than in the wet season (East 1984; Carbone & Gittleman 2002; Hopcraft et al., 2005). They are known to drag prey of this size up to 300 meters, but no further (Schaller, 1972).

In the wet season, a grazer like *P. altidens* would not be expected to remain within 300 meters of wooded areas so long as the grasses in secondary grasslands are sufficiently moist. With butchering technology, hominins could have transported portions of *P. altidens* over greater distances than lions. The *P. altidens* sample at FLK North is hypothesized to reflect this greater utilization of woodland areas in the dry season, but to retain a wet season signal from the less frequent but ongoing use of woodland edges in the wet season. Therefore, the seasonal distribution of *P. altidens* and the preference of modern lions for ambush cover suggest that *P. altidens* at FLK North would reflect a stronger dry SOD signal, against which FLK Zinj is compared.

Materials and Methods

Research Design

Dental microwear analysis is an established method for analyzing food fracture properties in an individual's recent diet (e.g., Scott, 2006; Ungar et al., 2003; Scott, 2012). Foods consumed by animals leave microscopic abrasions and polishes on the enamel of their teeth. In seasonal environments, dental microwear co-varies with diet (Teaford and Robinson, 1989) because it is subject to the “last supper” phenomenon (Teaford and Oyen, 1989). This refers to the rapid turnover rate of enamel abrasions, which has the potential to provide a great degree of SOD precision by recording only diet of the last few days or weeks. Most importantly for archaeological samples, the method samples those skeletal elements most likely to survive—the teeth. Inter-element studies have shown that upper and lower first and second molars from the same individual retain equivalent microwear (Merceron et al., 2004, Schubert et al., 2006). Seasonal differences in dental microwear have been documented in modern primates (Teaford and Robinson, 1989; Teaford and Glander, 1996; Gogarten and Grine, 2013) and ungulates (Merceron et al. 2006, 2010; Solounias and Semprebon, 2002), and in the European archaeological record (Rivals and Deniaux, 2005; Rivals et al., 2009), but its application to seasonality analysis in the African Early Pleistocene is novel.

This study uses DMTA to interpret the SOD of the extinct bovids *A. recki* and *P. altidens* at FLK Zinj and FLK North. Traditional microwear analysis methods have relied on counting the number of pit and scratch features on the occlusal surface of the tooth, ascertained by scanning electron microscope, but this method is prone to inter-analyst error (Grine et al., 2002). DMTA utilizes 3-dimensional occlusal surface scans acquired by Sensofar white light scanning confocal microscopy (Solarius Development Inc., Sunnyvale, CA). The 3-dimensional surfaces are then subjected to scale-sensitive fractal analysis (SSFA) by Toothfrax and Sfrax software package (Surfract Corp), allowing better assessment of dietary differences in both herbivores and carnivores than traditional dental microwear methods (DeSantis et al., 2013).

Of the five microwear variables measured by DMTA, a test-of-methods found that *heterogeneity* was significantly different between extant impala that were killed in the wet and dry seasons (Chapter 2). The heterogeneity variable is thought to reflect variability in the properties and types of wear-causing particles in the diet (Scott, 2012). Impala are mixed feeders that consume green grasses, associated with low heterogeneity, in the wet season and increase the forage intake, associated with higher heterogeneity, in the dry season (Gagnon and Chew, 2000; Scott, 2012). Unexpectedly, the wet season impala sample had more heterogeneous microwear than the dry season sample, and this is interpreted to reflect the greater quantities of atmospheric grit that settles on foliage during the dry season, which grind away more variable microwear features (Schulz et al., 2013; Chapter 2). Based on those results, and the evidence for comparably arid environmental conditions at during the site depositions, the present analysis compares the within-species heterogeneity of *A. recki* and *P. altidens* between samples from FLK Zinj and FLK North. It is standard practice to present heterogeneity at two scales, one that divides the surface into 9 equally-sized areas of comparison (3x3HAsfc) and one that divides the surface into 81 equally-sized areas of comparison (9x9HAsfc).

This study makes two untested assumptions about the seasonality of FLK North based on analogy with modern leopards, lions, and their preferred prey. In the case of the former, leopard sized prey *A. recki* is presumed to have been hunted throughout the year because leopards are residential carnivores that hunt in wooded and ecotone environments where *A. recki* is found. Lion sized prey *P. altidens* was more likely to be in ambush-enabling vegetation in the dry season, when they were drawn to the remaining green grasses supported by spring seepage. At FLK North, the *P. altidens* sample is hypothesized to reflect a stronger dry season signal, but to still include individuals that were hunted in the wet season as well.

Even if these assumptions are false, the present study remains viable. Regardless of which season or seasons the sites accumulated in, FLK North represents the timing of carnivore activity.

With the climate, habitat, and prey held constant, deviations in mean heterogeneity between FLK North and FLK Zinj can be interpreted as differences in foraging seasonality between carnivores and hominins.

Sample

All specimens from FLK Zinj derive from the original Leakey excavations and are housed in the National Museum in Dar es Salaam as of 2012. Specimens from FLK North include individuals from the Leakey excavations as well as from excavations conducted by The Olduvai Paleoanthropology and Paleoecology Project (TOPPP) between 2007 and 2013. The minimum number of individuals (MNI) for both taxa was carefully determined by comparing the recently excavated teeth with those from the Leakey collection to ensure that each bovid individual is represented by a single molar. The integrated TOPPP MNI is preliminary, but more closely reflects the number of individuals at FLK North.

The *A. recki* dental sample consists of 5 individuals from FLK Zinj, each represented by a left or right lower second molar (LLM2 and RLM2, respectively). These five individuals are ~83% of the total MNI for *A. recki* at FLK Zinj (n = 6). The *A. recki* sample from FLK North is composed of 14 individuals represented by upper and lower M1s and M2s, comprising ~67% of Leakey MNI (n = 21), and ~61% of integrated TOPPP MNI (n = 23). Because it is not possible to determine which upper and lower tooth rows belong to the same individual, *A. recki* from FLK North were divided first into age classes. From these, the larger sample of molars—either upper or lower—was selected. Thus, Late Prime and Old Adult *A. recki* are represented by upper molars because the MNI is larger for upper molars in these age classes. In contrast, there were more Early Prime

A. recki individuals represented by lower molars than upper molars, so lower molars were selected in that age class. For further discussion of age class and MNI determination, see Chapter 2.

The *P. altidens* dental sample represents a smaller fraction of the total number of individuals from FLK Zinj and FLK North, with 11 individuals from FLK North (~37% of Leakey MNI [*n* = 30], and ~27% of integrated TOPPP MNI [*n* = 41]) and 3 individuals from FLK Zinj (50% of Leakey MNI [*n* = 6]). This small sample size due to imperfections in the casts that arose during the casting process and will be discussed below. The methods for determining MNI for *P. altidens* were the same as for *A. recki*.

Cast Preparation

Each molar was cleaned using fresh cotton swabs dipped in acetone to remove any glue or preservatives applied to the occlusal surface, followed by cotton swabs dipped in 95% isopropyl alcohol to remove oils and other adhering particles. Once the molars had dried, the tooth crowns were molded with President Jet Regular Body dental impression material extruded from an applicator gun (Coltene-Whaledent Corp.). The molds were cast with high resolution epoxy (Epotek 301), which is capable of preserving surface features less than a micron in size (Beynon, 1987 in Scot dis; Teaford and Oyen, 1989). Molds that were too shallow to hold the epoxy were deepened by wrapping a rim of dental putty (BRAND) around the rim. Casts were allowed to cure for one week.

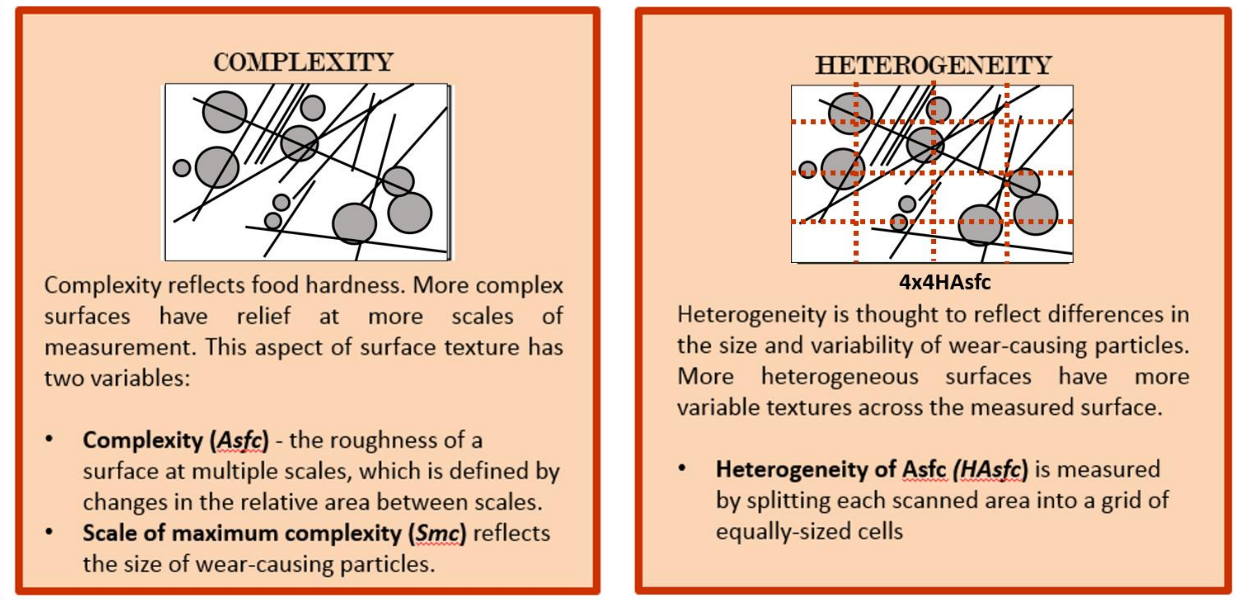
Bovid Samples from FLK Zinj and FLK North

***Antidorcas recki* Sample**				***Parmularius altidens* Sample**			
Site	**Specimen**	**Element**	**Age Class**	**Site**	**Specimen**	**Element**	**Age Class**
FLK North	1281	RUM1	Young Juvenile	FLK North	067/1096	LLM1	Subadult
FLK North	1511	LUM2	Young Juvenile	FLK North	841	RLM2	Early Prime Adult
FLK North	1045	RLM2	Early Prime Adult	FLK North	128	RLM1	Early Prime Adult
FLK North	503	LLM1	Early Prime Adult	FLK North	265	LLM2	Early Prime Adult
FLK North	067-339	LUM1	Late Prime Adult	FLK North	8045	RLM2	Early Prime Adult
FLK North	067-402C	RUM1	Late Prime Adult	FLK North	38	LLM1	Late Prime Adult
FLK North	067-402D	RUM1	Late Prime Adult	FLK North	7798	LLM2	Late Prime Adult
FLK North	067-459B	LUM2	Late Prime Adult	FLK North	7933	LLM2	Late Prime Adult
FLK North	627	RUM2	Late Prime Adult	FLK North	10144	RLM2	Late Prime Adult
FLK North	7266	RUM2	Late Prime Adult	FLK North	8728	RLM2	Late Prime Adult
FLK North	067-414	LUM2	Old Adult	FLK North	1099	LLM2	Old Adult
FLK North	067-463	LUM2	Old Adult	FLK Zinj	D42	RLM2	Early Prime Adult
FLK North	1152	LUM2	Old Adult	FLK Zinj	G361	RLM2	Early Prime Adult
FLK North	NoNum	RUM2	Old Adult	FLK Zinj	D111	RLM2	Early Prime Adult
FLK Zinj	B188	LLM1	Subadult				
FLK Zinj	B119	RLM2	Early Prime Adult				
FLK Zinj	B492	LLM2	Old Adult				
FLK Zinj	D154	RLM2	Old Adult				
FLK Zinj	D35	LLM2	Old Adult				

Table 4.2. Specimens of *A. recki* and *P. altidens* used in this analysis. Each specimen represents one individual, and no individual is represented by more than one specimen. Element: the first letter indicates right (R) or left (L); the second letter indicates upper (U) or lower (L) dental arcade; the third letter M is for molar, and the number indicates first (1) or second (2) molar. *Antidorcas recki*, left: the analyzed sample is 14 individuals from FLK North and 5 individuals from FLK Zinj. *Parmularius altidens*, right: the analyzed sample is 11 individuals from FLK North and 3 individuals from FLK Zinj.

Data Collection

The casts were scanned in the DeSantis Dietary Reconstruction and Ecological Assessments of Mammals (DREAM) lab using a Sensofar white-light scanning confocal profiler and SolarMap Universal software (Solarius Development, Inc) to render 3-dimensional microtopography. The surface scans sample and area of 204 x 276 µm^2 with a lateral sampling interval of 0.18µ and sub-nanometer vertical resolution. These scans are then run through ToothFrax and SFrax software packages (Surfract Corp.) for scale sensitive fractal analysis of the heterogeneity, which calculates the variation in feature complexity across the scanned surface at a variety of scales (Scott et al., 2005, 2006).



Complexity reflects food hardness. More complex surfaces have relief at more scales of measurement. This aspect of surface texture has two variables:

- **Complexity (*Asfc*)** - the roughness of a surface at multiple scales, which is defined by changes in the relative area between scales.
- **Scale of maximum complexity (*Smc*)** reflects the size of wear-causing particles.

Heterogeneity is thought to reflect differences in the size and variability of wear-causing particles. More heterogeneous surfaces have more variable textures across the measured surface.

- **Heterogeneity of Asfc *(HAsfc)*** is measured by splitting each scanned area into a grid of equally-sized cells

Figure 4.1. DMTA variables (Scott et al., 2006). Heterogeneity (right) is a used in the present study to examine variation in complexity (left) across the measured surface.

Enamel Facet Selection

Established protocol is to scan the same tooth facet on each specimen. This has developed from the observation that primates, which were among the first taxa to be studied using traditional dental microwear analysis, have differential directionality and force applied to different tooth cusps during a single power stroke in which teeth come into occlusion (Crompton and Hiiemae, 1970).

Phase I facets develop on those portions of the cusps that occlude during the power stroke, while Phase II facets are formed by the force of the cusps coming out of occlusion (Kaiser and Fortelius, 2003). In primates, the power stroke exerts greater force on Phase I cusps than is used to generate Phase II cusps, resulting in demonstrably different microwear signatures (Krueger et al, 2008). When studying bovids, researchers have focused on the mesio-buccal enamel band on the mesial cusp of the upper M1 and M2, and disto-buccal enamel band of the mesial cusp of the lower M1 and M2 (Teaford and Walker, 1984; Janis, 1990; Merceron et al, 2004; Scott, 2012). These facets occlude during power stroke (Janis, 1979; Merceron et al, 2004).

Bovids, particularly those that include a large portion of graze in their diet as *A. recki* and *P. altidens* are thought to have done (see Chapter 3), have evolved a chewing mechanism in which the Phase II facets were all but eliminated as the Phase I facets elongated to promote sheering tough and fibrous grasses (Janis, 1979). Each time the molars of an ungulate come into occlusion, it occurs as a single translatory stroke in which all the facets occlude sequentially (Janis, 1979). The MANOVA of facet and microwear in the sample of modern impala revealed no significant relationship (see Chapter 2). Therefore, facet selection in this sample of *A. reck* and *P. altidens* has focused on the traditional facets used in other ungulate studies, but does not rely on these exclusively when the archaeological samples are damaged in those locations.

Analysis

The median heterogeneity at multiple scales of the *A. recki* and *P. altidens* samples are compared between sites using the non-parametric Satterthwaite's *t*-test (also known as Welch's, Aspin-Welch, Welch-Satterthwaite, Aspin-Welch-Satterthwaite *t*-test) using the statistics software package SPSS. This test is appropriate for small samples sizes < 10, samples of unequal size, and samples of unequal variance (McDonald, 2014). Its purpose is to determine the probability that the compared samples belong to different populations, and the standard 95% confidence interval is used here. Scatter plots are presented to allow visualization of the data as well. DMTA values are reported in Appendices 6. and 7.

Results

The results for the Satterthwaite's t-tests comparing *A. recki* heterogeneity at multiple scales between FLK Zinj and FLK North indicate that the samples have a high probability of deriving from the same population (Table 4.3.). In the context of this analysis, this means that the heterogeneity values statistically reflect the same SOD at both sites. At the 3x3HAsfc scale, *A. recki* from FLK Zinj to have a range of variation skewed toward higher values relative to the FLK North sample (Figure 4.2.). However, the meaning of this distribution cannot be interpreted in terms of SOD given the currently available data.

Like *A. recki,* the Satterthwaite's t-tests comparing *P. altidens* heterogeneity at multiple scales between FLK Zinj and FLK North indicate that the samples have a high probability of deriving from the same sample (Table 4.4.). The sample size is small too small to assume that it is representative of the total sample from the sites. However, the graph of heterogeneity values at each site reveals that FLK Zinj falls near the mean values of FLK North at both larger (3x3HAsfc) and smaller (9x9HAsfc) scales (Figure 4.3.).

Satterthwaite's t-test for *Antidorcas recki*

Heterogeneity of Area-scale fractal complexity	Levene's Test for Equality of Variances		t-test for Equality of Means				
	F	Sig.	t	df	Sig.(2 - tailed)	Mean Difference	Std. Error Difference
2x2HAsfc	4.189	0.056	-0.758	9.647	0.466	-0.051	0.067
3x3HAsfc	2.178	0.158	-1.104	5.175	0.318	-0.146	0.133
4x4HAsfc	0.765	0.394	-0.889	5.499	0.411	-0.116	0.131
5x5HAsfc	1.546	0.231	-1.034	5.641	0.343	-0.186	0.180
6x6HAsfc	0.189	0.669	-0.970	6.604	0.366	-0.159	0.164
7x7HAsfc	0.077	0.785	-0.326	7.997	0.753	-0.052	0.161
8x8HAsfc	0.705	0.413	-0.742	5.985	0.486	-0.158	0.213
9x9HAsfc	0.007	0.935	-0.443	8.030	0.670	-0.110	0.249
10x10HAsfc	0.000	0.983	-0.317	8.032	0.760	-0.085	0.269
11x11HAsfc	0.348	0.563	0.291	16.719	0.774	0.133	0.456

Table 4.3. Results of a Satterthwaite's t-test comparing heterogeneity (HAsfc) at multiple scales between *A. recki* at FLK Zinj (n = 5) and FLK North (n = 14).

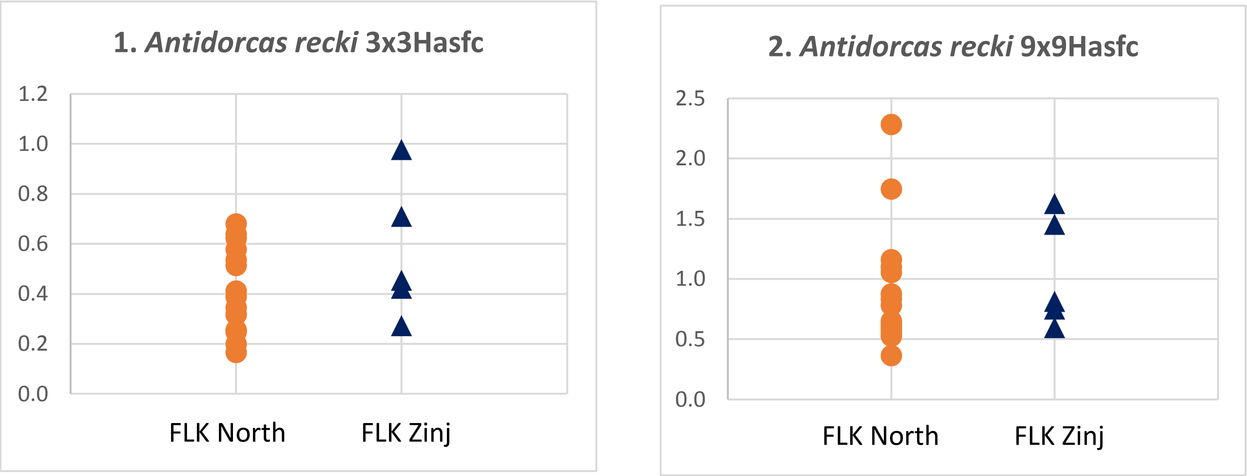


Figure 4.2. 1. Scatterplot of heterogeneity values for *A. recki* at the 3x3 scale for FLK North (n = 14) and FLK Zinj (n = 5). 2. Scatterplot of heterogeneity values at the 9x9 scale for FLK North (n = 14) and FLK Zinj (n = 5).

Satterthwaite's t-test for *Parmularius altidens209*

Heterogeneity of Area-scale fractal complexity	Levene's Test for Equality of Variances		t-test for Equality of Means				
	F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference
2x2HAsfc	3.041	0.107	1.394	6.100	0.212	0.057	0.041
3x3HAsfc	5.025	0.045	0.056	11.678	0.957	0.003	0.051
4x4HAsfc	5.361	0.039	0.207	11.360	0.839	0.008	0.041
5x5HAsfc	2.803	0.120	0.373	11.900	0.716	0.019	0.052
6x6HAsfc	2.705	0.126	0.505	12.000	0.623	0.028	0.055
7x7HAsfc	1.241	0.287	0.351	7.868	0.735	0.021	0.059
8x8HAsfc	1.206	0.294	-0.606	7.133	0.563	-0.032	0.052
9x9HAsfc	0.059	0.812	-0.363	3.547	0.737	-0.034	0.095
10x10HAsfc	0.029	0.867	-0.302	3.094	0.782	-0.032	0.107
11x11HAsfc	0.048	0.830	-0.357	3.507	0.742	-0.033	0.094

Table 4.4. Results of a Satterthwaite's t-test comparing heterogeneity (HAsfc) at multiple scales between *P. altidens* at FLK Zinj (n = 3) and FLK North (n = 11).

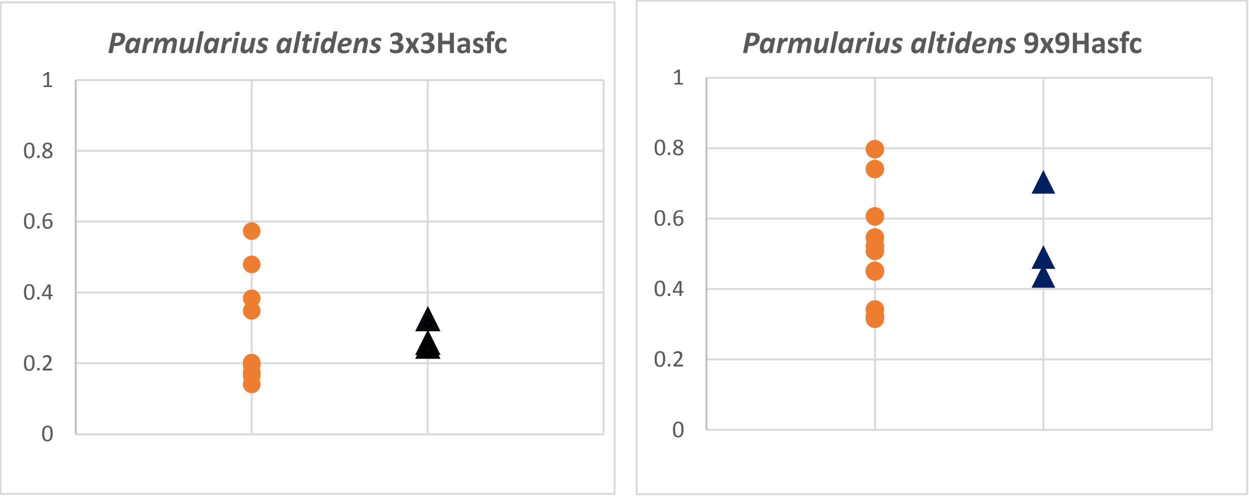


Figure 4.3. Left**:** Scatterplot of heterogeneity values for *P. altidens* at the 3x3 scale for FLK North (n = 11) and FLK Zinj (n = 3). Rigjt: Scatterplot of heterogeneity values at the 9x9 scale for FLK North (n = 11) and FLK Zinj (n = 3).

Discussion

Together, the dental microwear analysis of *A. recki* and *P. altidens,* and the presence of *K. sigmoidalis* newborns and *Connochaetes* sp. at FLK Zinj, support Hypothesis 3: hominins foraged for meat year round, in spite of seasonal variability in carnivore competition and prey distribution.

Antidorcas recki

The DMTA results suggest that hominins foraged and transported *A. recki* to FLK Zinj during the same range of seasons that the predators accumulated *A. recki* at FLK North. Leopards, which were present in Bed I at Olduvai Gorge, hunt prey like *A. recki* in woodlands year-round, and the *A. recki* assemblage at both sites is therefore inferred to reflect year-round accumulations. These results can be further interpreted to mean that seasonal changes in foraging habitat, phenology, and other influences on handling costs were insufficient to remove *A. recki* from the hominin menu. Whatever methods were used to acquire *A. recki*, they were an integral part of the hominin foraging strategy throughout the year.

Parmularius altidens

Unfortunately, the sample size of *P. altidens* from both sites is too small to be representative of either site. This is a problem that will be remedied in the near future through additional data collection and recasting. For the present, the range of heterogeneity values from FLK Zinj and FLK North is perhaps more revealing than the results of the Satterthwaite's t-test. Though only 3 individuals were analyzed from FLK Zinj, their values fall near the mean for the FLK North sample at both standard scales of analysis, suggesting that a future analysis of all 6 individuals from FLK Zinj would be weighted toward the apparent FLK North mean as well.

Speculating from the present data, this similarity in heterogeneity values appears to indicate the same behavioral pattern as is seen in the *A. recki* sample: hominins were acquiring *P. altidens* during the same season as lion-sized predators killed *P. altidens* at FLK North. By extension, hominins were not employing a seasonal strategy of avoidance when they took *P. altidens*, and FLK Zinj, like FLK North, may reflect a trend toward dry season acquisition in wooded environments, precisely when *P. altidens* is expected to have been present.

This pattern could reflect a number of strategic choices by hominins about when and where to transport the large *P. altidens* carcass. In the wet season, when *P. altidens* was dispersed in the grasslands, the energetic inefficiency of carrying a large and meaty burden to the FLK Zinj refuge may have outweighed the threat of predation while consuming meat in the open grasslands. This interpretation parallels the evidence thus far that hominins were not maximizing their opportunities for predator avoidance. Contrarily, it is possible that hominins foraged primarily in woodlands like those at FLK Zinj, and did not venture into open grasslands where plant foods were scarcer and large predators were abundant. In this case, they may only have had access to *P. altidens* during the dry season when it converged on the nearby spring. This interpretation casts hominins as more cautious members of the carnivore guild. Landscape archaeology at the FLK Zinj level has the potential to help distinguish between these interpretations. By sampling the broader paleo Olduvai basin, particularly those areas reconstructed as open to wooded grasslands, it may be possible to find evidence of hominin butchering activities in open environments, indicating a willingness to operate outside of woodlands. Until then, and without larger samples, the evidence is limited to an indication of dry season consumption of *P. altidens* by FLK Zinj hominins.

Other Bovids

There are additional speculations that can be made from comparing other large bovid samples between sites. *Kobus sigmoidalis*, which is present at FLK Zinj but not FLK North, is a relative of the extant waterbuck *K. ellipsiprymnus* (Tribe Reduncini). Of the 12 *K. sigmoidalis* individuals at FLK Zinj, 4 are newborn. The modern waterbuck is not a strongly seasonal breeder, but it does show peaks in births that coincide with rainfall and green grass availability in Uganda and South Africa (Melton, 1983; Spinage, 2012). In the Rwenzori National Park, Uganda, birthing seasonality was not as strong as predicted, but did follow the bimodal increase in rainfall (Spinage, 2012). Births peaked in the second half of the wet season, from January to March, during observations from 1977 – 1979 in Umfolozi Game Reserve in South Africa **(**Melton, 1983). Together, these studies suggest that the presence of 4 *K. sigmoidalis* newborns at FLK Zinj reflect some degree of wet season hominin foraging.

FLK Zinj also contains three wildebeest individuals (*Connochaetes* sp). Modern wildebeest are bulk short grass feeders that prefer open grasslands. In the wet season, they derive sufficient moisture from these habitats, but in the wet season they must remain within a daily commute of water (Estes, 1991). As an open grassland surrounding a playa lake basin, paleo Olduvai Gorge represents the preferred habitat of modern wildebeest. Thus, though not all extant wildebeest are migratory, their pattern of movement is dependent on water availability. Fossil *Connochaetes* would have been drawn to grasslands in the greater Olduvai basin, and to the springs near FLK Zinj and FLK North in the dry season. As a large, size 3B species, it is unlikely that hominins would have transported their carcasses over a greater distance than a day's commute radius around FLK Zinj. *Connochates* at FLK Zinj may well represent dry season foraging.

The wet season in the savanna sees the dispersal of prey animals and their predators into grasslands. During these times, woodlands continue to shelter residential bovids and leopards, but predation pressure eases as other carnivores follow prey biomass (Schaller, 1972; Pereira et al., 2014). The reduced carnivore competition would provide a meat foraging opportunity to subordinate, risk-averse hominins, but the reduction in prey abundance makes this a more difficult time to acquire bovids in woodlands (Hypothesis 1). The wet season is also a time when other resources were widely available, easing the dietary constraints hominins experienced. The dry season draws prey and predators back into the vicinity of enduring waterholes and the denser foliage they support, while the grassland dessicates. Carnivore competition in woodlands increases, as does the ease of acquiring prey (Woodburn, 19864; Bunn et al., 1988; Blumenschine, 1987). If hominins were only willing to compete with carnivores for prey in the dry season, it would be a nutritionally-driven strategy during a time of resource scarcity (Hypothesis 2).

The evidence for perennial meat foraging corroborates Hypothesis 3, that springs and associated woodlands were important resources for hominins throughout the year. This may have been because woodlands assisted meat foraging, perhaps by providing ambush opportunities (Bunn, 2007; Bunn and Pickering, 2010a; Bunn and Gurtov, 2014) or because they offered a range of important resources (Blumenschine and Peters, 1998; Sept, 2001). In either case, the DMTA results indicate that the FLK Zinj hominins did not avoid carnivores at the temporal scale of seasons, though they are certain to have operated diurnally like the subordinate members of the carnivore guild. This study of *A. recki* and *P. altidens* characterizes hominins as consistently competitive members of the carnivore guild at the dawn of persistent hominin carnivory.

Conclusion

Hominin meat eating appeared at a time of climatic cooling and instability, when the seasons themselves fluctuated in intensity and duration. Environmental unpredictability selects for a flexible organism, one that is not strongly specialized for any specific conditions, and which can respond strategically to a variety of selective pressures (Potts and Faith, 2015; Chiu et al., 2006; Woods et al., 2011). This is precisely what the paleoanthropological record reveals at 2.8 Ma with the evolution of *Homo,* and the concurrently mounting evidence for carnivorous behavior shortly after the eastern African climate cooled ~3.0 Ma (Villmoare et al., 2015; deMenocal, 2004; Harmond et al, 2015; McPherron et al., 2010; Thompson et al., 2015; Semaw et al., 2003; Dominguez Rodrigo et al., 2005). The climatic conditions for seasonal variability intensified again ~2.0 Ma, and the evidence for persistent hominin carnivory followed suit, and a hominin, *Homo erectus,* appeared (Wood, 1991).

The trend of increasing climatic instability, seasonality, and hominin carnivory are inherently related: the opportunity to acquire prey is dependent on the availability of resources to attract it. Resource availability in turn reflects seasonality, the intensity of which depends on broader climatic trends. The present study suggests that, despite highly variable, seasonally-mediated resource availability in Bed I Olduvai Gorge, the hominins who made FLK Zinj had the behavioral flexibility—or planning depth and tactical mobility—to take advantage of animal resources throughout the unpredictable year. Hominins had adapted to their changing environment morphologically, technologically, and behaviorally. They had mastered skill sets that enabled them to compete with carnivores for large prey animals, very likely by hunting for themselves (Bunn and Kroll, 1986; Bunn and Ezzo, 1993; Bunn, 2007; Bunn and Pickering, 2010a; Bunn and Gurtov, 2014).

One drawback to the design of this study is that the fossil bovids analyzed here cannot be compared with other bovid DMTA studies. Until recently, most DMTA analyses were conducted on an older confocal microscope model, including the test-of-method presented in Chapter 2. The dental microwear texture values generated by the old model cannot yet be calibrated with those from the newer Sensofar confocal microscope, which includes the present study of FLK Zinj and FLK North fossils. Planned future analyses of extant bovid species such as impala, waterbuck, and wildebeest on the new model confocal at the DeSantis Dream Lab will enable a direct comparison of DMTA values between fossil and modern samples. This will allow for additional analyses of untested fossil bovid diet as well as SOD of species not presented here. Furthermore, an algorithm for calibrating values between old and new confocals is currently under review and is expected to be published within the coming year (Arman, *pers comm*). These improvements will allow a more direct assessment of seasonal microwear values using modern samples with known dates of death, and may enable researchers to pinpoint SOD at isolated fossil sites without comparison with another comparable site. Until then, the seasonality of microwear samples collected from bovids that are present at FLK Zinj but not at FLK North cannot be interpreted because no extant or extinct baseline exists.

DMTA is nevertheless a very promising approach to studying hominin and carnivore foraging seasonality in the past. With breakthroughs in confocal calibration and new baseline studies, this method will allow exploration of hominin foraging strategies in a variety of environments and eras. Subjects of study can be expanded by applying DMTA to carcasses in modern savannas in order to develop a background baseline. With this baseline in place, it can be used in conjunction with landscape archaeology to compare anthropogenic sites with the contemporaneous environmental background. The present study provides a first look at hominin meat foraging seasonality at the dawn of archaeologically visible carnivory, and points the way forward for other Early Pleistocene sites.

Chapter 5. Conclusions

Key Insights

The contribution of meat to the diet of Early Pleistocene hominins, and *Homo* in particular, is a subject that attracts researchers across anthropology. Meat is implicated in the emigration of *Homo* out of Africa (Anton, 2003; Ehrlich 1989), in the elongation of the legs and expansion of the brain (Bramble and Lieberman, 2004; Pontzer et al., 2010; Aiello and Wheeler, 1995; Navarette et al., 2013), in the development of slow growth and long senescence (Bogin and Smith, 1996; Hawkes et al., 1997; Kaplan et al., 2000), and in a variety of social dynamics hypothesized to underlie modern human behavior (O'Connell et al., 2002; Speth 1987, 1989, 2012; Speth et al., 1991). It is notable that these critical developments originate not only with the earliest evidence for persistent hominin carnivory, but in the context of an increasingly seasonal and variable climate (Ferraro et al., 2013; Bunn and Kroll, 1986; Bunn and Pickering, 2010a; deMenocal, 2004; Magill et al., 2012a).

In Chapter 1, I outlined the ecological constraints on hominins as they entered a predatory niche in seasonal eastern African savannas. From the extensive actualistic, ecological, and paleontological research that has been conducted on the subject, it is evident that the large carnivore guild would have exerted both predation and competition pressure on meat-eating hominins (e.g. Potts, 1988; Van Valkenburgh, 2001; Rose and Marshall, 1996; Brantingham, 1998; Lewis, 1997). Based on the findings of these studies, I made the following observations about the hominin niche at FLK Zinj:

- At a maximum of 52-63 kg (McHenry, 1992), the FLK Zinj hominins were subordinate members of the carnivore guild; they are comparable in weight to wild dogs, which, due to their size, are subordinate members of the carnivore guild despite the use of group hunting tactics.
- Hominins and carnivores overlapped in both habitat and prey preferences.
- Hominins were omnivorous, providing additional, potentially seasonal, opportunities to avoid direct competition and predation from carnivores in wooded and watered habitats by resorting to plant foods in habitats less preferred by carnivores.

From these predictions, the following hypotheses for the FLK Zinj hominins are generated:

1. If meat eating was nutritionally driven, then it should occur in the dry season when plant foods require longer foraging times and are less nutritious.
2. If meat-eating occurred around a predator avoidance strategy, then it should take place in the wet season.
3. If meat-eating was an integral part of the foraging strategy of a carnivore-guild member, as it is for modern hunter-gatherers in similar environments, it will occur year-round.

To investigate hominin meat foraging seasonality at FLK Zinj and the penecontemporaneous carnivore site of FLK North, it was necessary to develop a new, non-destructive method for determining the season of death (SOD) of prey animals. Whereas stable isotopes and cementum rings track seasonality through incremental growth of the tooth, the former is only applicable to developing teeth and the latter is destructive. Dental microwear texture analysis (DMTA) is a relatively new method that is capable of identifying SOD in temperate bovids with seasonally-varying diets. I tested the ability of DMTA to distinguish wet and dry SOD of a sample of modern impala with known dates of death. As residential, ecotone, seasonal mixed-feeders, impala are good modern analogs for *Antidorcas recki*, an extinct bovid common to FLK Zinj and FLK North.

The results of this analysis, presented in Chapter 2, suggest that DMTA is indeed capable of tracking SOD. The effect is subtle but statistically significant in the heterogeneity of microwear features across the occlusal molar surface at several scales of analysis, with wet season samples more heterogeneous than dry season samples. This pattern is unexpected, given the greater variability of food textures in the dry season impala diet, and is interpreted to reflect an increase in atmospheric grit in the dry season, as grit particles are known to homogenize microwear (Schulz et al., 2013). These results bode well for the ability of DMTA to identify SOD in arid environments.

Several previous studies have attempted to ascertain the seasonality of Early Pleistocene sites using taphonomic analyses. Contrary to observations of modern hunter-gatherers in arid savannas, who have their greatest hunting success in the dry season, Speth (1987) has suggested that bovids are too fat-depleted to be a nutritional resource to early hominins in the dry season. According to this perspective, dry season sites in an African savanna would be located near water and have relatively few faunal remains, most of which derive from species, individuals, and skeletal elements that best retain fat in the lean season. As a large bovid assemblage dominated by the fattiest elements and located near a waterhole, FLK Zinj is not immediately identifiable to season using Speth's (1987) predictions.

In Chapter 3, I evaluated evidence for seasonality at FLK Zinj based on the criteria presented in Speth (1987) by reviewing ecomorphological, isotopic, and DMTA analysis of the extinct bovids from FLK Zinj and identifying modern analogs. From the diet and habitat preferences of the modern analogs, as well as their ranging and reproductive behavior, I determined that no clear seasonal signal can be identified from the species composition at FLK Zinj. Demographics from each modern analog are present in wooded and ecotone habitats like FLK Zinj throughout the year, though more individuals aggregate in the dry season than in the wet season due to presence of a freshwater spring in the vicinity. The demographic distribution of the fossil assemblage ranges from young to old and includes males and females, encompassing a broad range of physical conditions in both wet and dry seasons. The presence of several infants at FLK Zinj, while suggestive of the wet season, cannot be directly attributed to any season given the absence of restricted birthing seasons of bovids living in this highly unpredictable environment. The failure to identify a predominant season of activity from species composition and demographics at FLK Zinj is reflected in taphonomic studies of skeletal element representation. In analyses of limb marrow fat retention in extant bovids and the relative proportion of limb elements at FLK Zinj, researchers came to opposite conclusions about hominin selectivity for individuals in prime condition. In sum, Chapter 3 indicates the need for a new method, like DMTA, to analyze hominin foraging seasonality at FLK Zinj.

In Chapter 4, I apply DMTA to anthropogenic FLK Zinj and the slightly younger carnivore site FLK North. Both sites accumulated during phases of maximum aridity (Magill et al., 2012a) in wooded habitats within 200 m of freshwater springs, located in the broader lightly-wooded grassland of the paleo Olduvai Basin (Ashley et al., 2010a, 2010c; Barboni et al., 2010). Both sites contain similar faunal assemblages dominated by extinct bovids *Parmularius altidens* and

Antidorcas recki. Using DMTA analysis, I compared mean heterogeneity at multiple scales between FLK Zinj and FLK North. This research design accounts for the possibility that microwear heterogeneity reflects seasonality differently from the pattern observed in modern impala, and investigates whether hominins were operating during the same time(s) of year as peneconemporaneous carnivores.

The results of the analysis revealed no statistically significant differences in heterogeneity between sites, suggesting that hominins were not employing seasonal strategies to avoid carnivores when foraging for meat. Despite being physically subordinate members of the carnivore guild, hominins had apparently developed behavioral and possibly technological strategies that enabled them to compete for animal resources during the same seasons and in the same places that leopards, lions, and extinct sabertoothed cats were operating (Treves and Treves, 1999; Rose and Marshall, 1996; Brantingham, 1998). In conjunction with the evidence for increasing body size and brain size, and the development of the Acheulean (Diez-Martin et al., 2015), the present analysis of prey SOD at FLK Zinj appears to reflect a hominin rapidly-adapting to membership in the carnivore guild during a time of increasing climatic instability and seasonality. The results further suggest that meat and other animal resources had become an integral part of the foraging strategy of a carnivore-guild member, as it is for modern hunter-gatherers in similar environments (Hypothesis 3).

Future Directions

There are some significant constraints on the types of analyses that could be conducted in this study. At present, it is not possible to compare DMTA results that were run on the old and new

Sensofar confocal microscopes. As a result, the impala microwear presented in Chapter 2, which was analyzed on an old confocal, could not be compared with that of *Antidorcas recki* analyzed on a new confocal, for which it is used as a modern analog. The research design of Chapter 4 alleviates the need for direct comparisons with modern analogs, but future research should evaluate the diets of FLK Zinj bovids in order to better identity potential modern analogs. Such a study would improve the interpretive power of Chapter 3, in which modern analogs for three extinct bovids were determined primarily from ecomorphological studies and no direct microwear analyses were possible. Should the diets of the FLK Zinj bovids differ significantly from the modern analogs, it weakens the subsequent analysis of seasonality at FLK Zinj. It is very likely that this comparison will be possible following the publication of a calibration algorithm for old and new confocal microscopes in the coming year (Arman, *pers comm*).

A second problem is sample size, and it is one that will be corrected in future iterations of these chapters. By and large, the problem results not from the number of modern and fossil specimens, but from problems in the casting process that affected the molds irrevocably. By remolding and recasting, it is very probable that the sample sizes can be increased, particularly for FLK North bovids. The modern impala sample size will also increase once new specimens currently housed at the National Museum in Dar es Salaam, Tanzania, are analyzed. Together, these augmented samples will increase the statistical power of the analyses presented in chapters 2 and 4.

Despite these limitations, DMTA has proved promising for investigating SOD, particularly where airborne grit is seasonally present, as in environments like FLK Zinj and FLK North. Future studies can expand upon this method in several ways. First, DMTA studies of SOD should be conducted on a variety of extant ungulate taxa in eastern and southern African taxa with known dates of death. This will create a baseline against which fossil bovids can be compared, allowing for better behavioral interpretations of extinct taxa. This may also enable direct comparisons of SOD between extant and extinct bovids, but equivalence cannot be ensured without additional methods. One such would be to apply the more invasive methods of stable isotope analysis (in developing teeth), cementum analysis, and DMTA to determine how these are correlated in fossil and modern samples. Finally, landscape archaeology can provide a “background” signal of non-anthropogenic SOD against which anthropogenic assemblages can be compared. This would determine if hominin meat foraging activity reflects the timing of greatest bovid vulnerability. Together, these approaches will greatly improve the efficacy of DMTA for studying hominin and bovid predator-prey dynamics.

Today we face a new challenge of climatic instability and increasing seasonality across the globe. While this study cannot speak directly to the strategies that we modern hominins will employ, the subject matter of savanna seasonality is highly relevant to the survival of our carnivore colleagues. Eastern Africa is experiencing enormous population growth among pastoralists, and the home ranges of carnivores and their prey are shrinking, portioning, and dessicating (Fratkin, 2001). Waterholes are overtaken by cattle, and grasslands are grazed down to dust. This is the case in the beautiful Ngorngoro Conservation Area, where Olduvai Gorge is found, and along Lake Eyasi, home of the Hadza. As water becomes an ever more precious resource in these places and around the world, it is my sincere hope that we will recall that we are members of this great and dynamic community.

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Appendices

Appendix 1.

Total Sample of Impala

Catalog Number	Element	Season	Age Class	Collection Year	Facet	Known Associations
BA 029 21	Right M_2	Wet	Subadult	1986	5	1
BA 029 1	Right M^2	Wet	Early Prime Adult	1986	7	2
BA 029 1	Right M^1	Wet	Early Prime Adult	1986	1	2
NSL 460	Left M^2	Wet	Subadult	1998	6	3
NSL 536	Right M^1	Wet	Subadult	1998	1	3
NSL 537	Left M_2	Wet	Subadult	1998	1	4
NSL 977	Left M^2	Wet	Subadult	1998	1	5
NSL 95	Right M_1	Wet	Subadult	1998	7	6
NSL 1187	Right M_2	Wet	Early Prime Adult	1998	5	7
NSL 444	Right M_1	Wet	Early Prime Adult	1998	1	8
NSL 503	Left M^1	Wet	Early Prime Adult	1998	1	9
NSL 532	Right M^1	Wet	Early Prime Adult	1998	1	9
NSL 508	Left M^2	Wet	Early Prime Adult	1998	6	10
NSL 524	Left M_1	Wet	Early Prime Adult	1998	1	11
NSL 527	Left M^2	Wet	Early Prime Adult	1998	1	12
NSL 534	Left M_2	Wet	Early Prime Adult	1998	1	13
NSL 538	Right M_2	Wet	Early Prime Adult	1998	2	13
NSL 547	Right M_2	Wet	Early Prime Adult	1998	4	14
NSL 498	Right M^1	Wet	Early Prime Adult	1998	1	15
NSL 498	Right M^2	Wet	Early Prime Adult	1998	1	15
NSL 934	Left M^1	Wet	Early Prime Adult	1998	1	16
NSL 533	Left M_2	Wet	Early Prime Adult	1998	5	17
NSL 531	Right M^1	Wet	Late Prime	1998	3	18
NSL 7	Right M_2	Wet	Subadult	2007	1	19
NSL 7	Left M_1	Wet	Early Prime Adult	2007	1	20
OB-14	Left M^2	Wet	Early Prime Adult	2009	6	21
UK 023 26	Right M_2	Wet	Early Prime Adult	2009	4	22
UK 023 35	Left M_2	Wet	Early Prime Adult	2009	5	23
UK 023 9	Left M_2	Wet	Early Prime Adult	2009	2	24
UK 023 9	Left M_1	Wet	Early Prime Adult	2009	3	24
UK 023 - 20	Right M_2	Wet	Late Prime	2009	1	25
UK 023 - 7	Right M_1	Wet	Late Prime	2009	1	25
SN 1403	Left M_2	Dry	Early Prime Adult	1984	1	26
SN 5304	Right M_2	Dry	Early Prime Adult	1984	1	26
SN 1553	Right M^1	Dry	Early Prime Adult	1984	1	27

Catalog Number	Element	Season	Age Class	Collection Year	Facet	Known Associations
SN 3080	Right M^2	Dry	Early Prime Adult	1984	3	28
SN 3080	Right M^1	Dry	Early Prime Adult	1984	2	28
SN 600	Left M^1	Dry	Early Prime Adult	1984	1	28
SN 600	Left M^2	Dry	Early Prime Adult	1984	1	28
SN 4585	Right M^2	Dry	Early Prime Adult	1984	7	29
SN 4585	Right M^1	Dry	Early Prime Adult	1984	5	29
SN 2356	Right M_1	Dry	Late Prime	1984	3	30
SN 2356	Right M_1	Dry	Late Prime	1984	1	30
SN 4080	Left M_2	Dry	Late Prime	1984	1	30
SN 1110	Right M^1	Dry	Late Prime	1984	4	31
SN 1309	Left M^2	Dry	Late Prime	1984	4	32
SN 4861	Left M^1	Dry	Late Prime	1984	1	33
SN 5821	Right M^2	Dry	Late Prime	1984	1	33
SN 4865	Right M^1	Dry	-	1984	2	34
SN 6095	Left M^2	Dry	Late Prime	1984	2	35
SN 6095	Left M^1	Dry	Late Prime	1984	1	35
SN 5474	Right M_2	Dry	Late Prime	1984	6	36
SN 6800	Right M_2	Dry	Late Prime	1984	4	37
SN 714	Right M_2	Dry	Late Prime	1984	1	38
BA2	Left M_2	Dry	-	1986	2	39
BA2 113	Left M^2	Dry	Early Prime Adult	1986	1	40
BA2 62	Right M^1	Dry	Early Prime Adult	1986	1	40
BA2 1210	Left M^2	Dry	Late Prime	1986	1	41
BA2 712	Left M_1	Dry	Late Prime	1986	1	41

Appendix 2. MNI Sample of Impala DMTA Results

Catalog Number	Asfc	epLsar	Smc	Tfv	Ftfv	2x2 HAsfc	3x3 HAsfc	4x4 HAsfc	5x5 HAsfc	6x6 HAsfc	7x7 HAsfc	8x8 HAsfc	9x9 HAsfc	10x10 HAsfc	11x11 HAsfc
SN 6800	3.965	0.000766	0.152234	14774.23	21811.83	0.206	0.235	0.233	0.294	0.286	0.300	0.317	0.366	0.396	0.474
SN 714	2.191	0.006201	0.268428	-	-	0.472	0.453	0.495	0.792	0.649	0.734	0.844	0.969	0.950	1.044
SN 2356	2.492	0.001720	0.268824	14669.12	20434.82	0.239	0.332	0.341	0.432	0.399	0.430	0.507	0.487	0.566	0.608
SN 1553	4.311	0.002756	0.150292	17593.83	25790.02	0.295	0.329	0.326	0.375	0.373	0.391	0.436	0.446	0.489	0.468
SN 600	2.362	0.002791	0.209603	17606.58	23884.45	0.358	0.472	0.476	0.574	0.556	0.626	0.619	0.720	0.689	0.727
BA2 1210	4.189	0.003503	0.152225	14802.46	20667.96	0.341	0.312	0.286	0.351	0.399	0.417	0.471	0.479	0.510	0.513
BA2 113	2.957	0.002482	0.150683	15813.63	22060.07	0.127	0.351	0.293	0.402	0.430	0.569	0.529	0.663	0.725	0.685
SN 4585	8.957	0.000649	0.150681	19023.69	24637.30	0.162	0.194	0.217	0.261	0.267	0.310	0.331	0.368	0.394	0.431
SN 5474	2.671	0.006396	0.151413	11706.91	18670.62	0.263	0.455	0.414	0.487	0.470	0.534	0.558	0.577	0.613	0.665
NSL 538	4.735	0.001126	0.154289	13847.06	21195.15	0.278	0.333	0.396	0.469	0.498	0.599	0.611	0.667	0.792	0.894
UK 023 9	-	0.001555	0.155784	14429.60	21192.90	0.177	0.239	0.276	0.377	0.396	0.388	0.420	0.458	0.463	0.526
NSL 524	5.243	0.001339	0.150335	15538.53	22800.13	0.319	0.287	0.281	0.354	0.366	0.444	0.469	0.535	0.578	0.585
NSL 537	7.170	0.001802	0.150540	14579.07	21669.16	0.197	0.191	0.210	0.253	0.246	0.285	0.295	0.303	0.320	0.353
NSL 444	4.421	0.004284	0.152942	13501.87	17624.69	0.337	0.481	0.602	0.752	0.702	0.873	0.998	1.079	1.033	1.023
NSL 1187	2.350	0.004442	0.150297	12494.73	18884.74	0.567	0.497	0.516	0.591	0.641	0.682	0.724	0.754	0.785	0.836
NSL 95	3.544	0.002139	0.149878	-	-	0.419	0.428	0.492	0.521	0.572	0.635	0.625	0.738	0.723	0.793
NSL 531	2.074	0.002997	0.212207	16145.91	23694.11	0.311	0.465	0.566	0.545	0.500	0.762	0.769	0.729	0.714	0.785
NSL 7	3.306	0.005640	0.149933	7109.06	10539.25	0.303	0.345	0.422	0.440	0.472	0.510	0.615	0.690	0.695	0.714
NSL 7	2.440	0.004062	0.151671	12431.24	19710.37	0.297	0.409	0.454	0.465	0.514	0.603	0.611	0.646	0.687	0.764
UK 023 20	3.983	0.001006	0.150257	14527.39	21571.41	0.145	0.232	0.263	0.322	0.292	0.319	0.377	0.465	0.438	0.502
UK 023 26	2.843	0.001435	0.149948	13417.76	20225.67	0.262	0.395	0.477	0.517	0.673	0.788	0.780	1.035	1.064	1.173
UK 023 35	3.213	0.001603	0.150242	15697.23	23080.08	0.348	0.422	0.511	0.551	0.634	0.701	0.729	0.820	0.868	0.919
BA 029 21	2.556	0.003056	0.150860	17296.79	25064.33	0.421	0.455	0.480	0.605	0.598	0.651	0.674	0.752	0.757	0.754
OB-14	2.008	0.001097	1.670944	13380.04	20453.39	0.248	0.340	0.375	0.394	0.423	0.467	0.510	0.577	0.511	0.667
BA 029 1	7.614	0.000780	0.150798	16123.49	22756.22	0.236	0.368	0.352	0.484	0.486	0.613	0.652	0.690	0.701	0.669
NSL 498	1.517	0.002783	0.208384	13973.58	18635.59	0.460	0.737	0.723	0.954	1.004	1.030	1.222	1.635	1.695	2.204
NSL 934	1.450	0.003154	0.208448	13409.73	19856.08	0.230	0.322	0.360	0.458	0.495	0.549	0.619	0.686	0.668	0.751

Catalog Number	Asfc	epLsar	Smc	Tfv	Ftfv	2x2 HAsfc	3x3 HAsfc	4x4 HAsfc	5x5 HAsfc	6x6 HAsfc	7x7 HAsfc	8x8 HAsfc	9x9 HAsfc	10x10 HAsfc	11x11 HAsfc
NSL 977	1.615	0.004240	0.834040	15025.64	21434.41	0.239	0.346	0.403	0.468	0.507	0.509	0.496	0.572	0.575	0.590
NSL 547	3.272	0.002679	0.151027	7746.96	12712.43	0.427	0.438	0.503	0.549	0.672	0.848	0.729	1.276	0.994	1.143

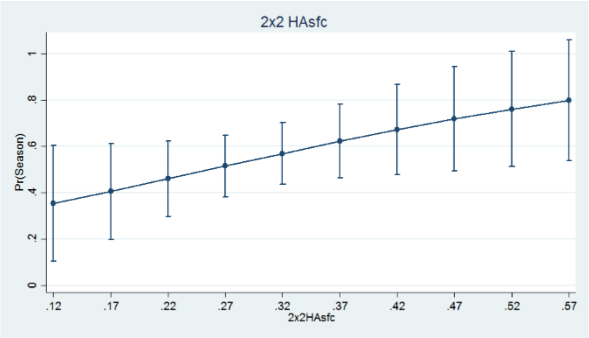
Appendix 3. Total Sample of Impala DMTA Results

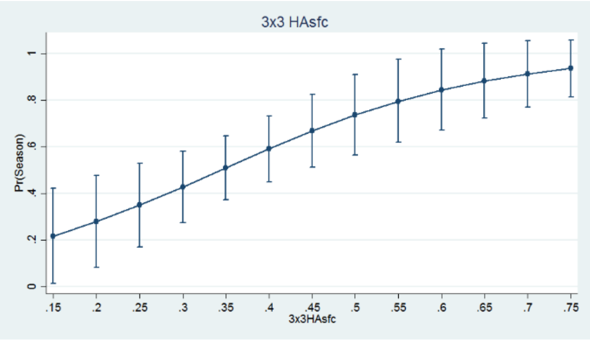
Catalog Number	Asfc	EpLsar	Smc	Tfv	Ftfv	2x2 HAsfc	3x3 HAsfc	4x4 HAsfc	5x5 HAsfc	6x6 HAsfc	7x7 HAsfc	8x8 HAsfc	9x9 HAsfc	10x10 HAsfc	11x11 HAsfc
BA 029 1	7.614	0.000780	0.150798	16123.49	22756.22	0.236	0.368	0.352	0.484	0.486	0.613	0.652	0.690	0.701	0.669
BA 029 1	5.348	0.000538	0.150208	12732.53	18058.06	0.315	0.765	0.541	0.901	0.871	1.019	1.009	1.117	0.970	1.129
BA 029 21	2.556	0.003056	0.150860	17296.79	25064.33	0.421	0.455	0.480	0.605	0.598	0.651	0.674	0.752	0.757	0.754
BA2	2.901	0.001455	0.152728	7368.69	15803.30	0.310	0.367	0.399	0.415	0.455	0.553	0.646	0.639	0.678	0.686
BA2 113	2.957	0.002482	0.150683	15813.63	22060.07	0.127	0.351	0.293	0.402	0.430	0.569	0.529	0.663	0.725	0.685
BA2 1210	4.189	0.003503	0.152225	14802.46	20667.96	0.341	0.312	0.286	0.351	0.399	0.417	0.471	0.479	0.510	0.513
BA2 62	2.854	0.001746	0.149968	7875.86	13980.01	0.269	0.379	0.342	0.425	0.532	0.626	0.562	0.753	0.798	0.753
BA2 712	3.270	0.002784	0.149891	14534.38	20508.15	0.151	0.227	0.239	0.327	0.346	0.343	0.412	0.423	0.470	0.544
NSL 1187	2.351	0.004442	0.150297	12494.73	18884.74	0.567	0.497	0.516	0.591	0.641	0.682	0.724	0.754	0.785	0.836
NSL 444	4.421	0.004284	0.152942	13501.87	17624.69	0.337	0.481	0.602	0.752	0.702	0.873	0.998	1.079	1.033	1.023
NSL 460	4.928	0.001235	0.151027	14378.71	22238.63	0.199	0.202	0.265	0.290	0.362	0.414	0.447	0.447	0.486	0.565
NSL 498	1.959	0.001827	0.149913	7623.42	15181.25	0.415	0.558	0.476	0.742	0.726	1.002	1.101	1.235	1.182	1.362
NSL 498	1.517	0.002783	0.208384	13973.58	18635.59	0.460	0.737	0.723	0.954	1.004	1.030	1.222	1.635	1.695	2.204
NSL 503	2.377	0.001249	0.150043	13004.76	21411.81	0.141	0.249	0.272	0.380	0.367	0.445	0.491	0.520	0.532	0.576
NSL 508	1.357	0.004736	0.150993	12055.22	18776.22	0.429	0.457	0.678	0.731	0.788	0.921	1.066	0.949	1.104	1.186
NSL 524	2.226	0.008733	0.150242	15805.40	23621.33	0.345	0.638	0.583	0.681	0.693	0.747	0.764	0.833	0.790	0.852
NSL 527	2.228	0.005079	0.153107	17538.19	23581.52	0.422	0.479	0.456	0.543	0.582	0.662	0.649	0.684	0.664	0.801
NSL 531	2.074	0.002997	0.212207	16145.91	23694.11	0.311	0.465	0.566	0.545	0.500	0.762	0.769	0.729	0.714	0.785
NSL 532	2.475	0.003466	0.266904	12525.87	20080.85	0.355	0.431	0.435	0.552	0.577	0.641	0.659	0.734	0.756	0.827
NSL 533	2.612	0.001958	0.150156	14945.73	21461.62	0.404	0.528	0.545	0.607	0.670	0.826	0.863	1.041	0.959	1.077
NSL 534	3.290	0.003265	0.208832	12404.81	20173.45	0.424	0.643	0.664	0.658	0.599	0.635	0.724	0.880	0.786	0.901
NSL 536	2.703	0.001156	0.150248	8440.76	14867.80	0.314	0.621	0.570	0.649	0.741	0.748	0.791	0.882	0.933	0.896
NSL 537	7.170	0.001802	0.150540	14579.07	21669.16	0.197	0.191	0.210	0.253	0.246	0.285	0.295	0.303	0.320	0.353
NSL 538	4.735	0.001126	0.154289	13847.06	21195.15	0.278	0.333	0.396	0.469	0.498	0.599	0.611	0.667	0.792	0.894
NSL 547	3.272	0.002679	0.151027	7746.96	12712.43	0.427	0.438	0.503	0.549	0.672	0.848	0.729	1.276	0.994	1.143
NSL 7	3.306	0.005640	0.149933	7109.06	10539.25	0.303	0.345	0.422	0.440	0.472	0.510	0.615	0.690	0.695	0.714
NSL 7	2.440	0.004062	0.151671	12431.24	19710.37	0.297	0.409	0.454	0.465	0.514	0.603	0.611	0.646	0.687	0.764

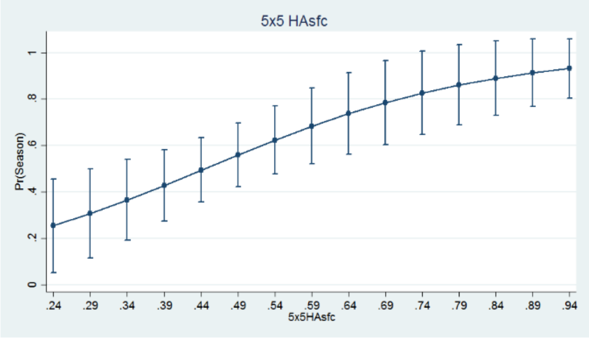
Catalog Number	Asfc	EpLsar	Smc	Tfv	Ftfv	2x2 HAsfc	3x3 HAsfc	4x4 HAsfc	5x5 HAsfc	6x6 HAsfc	7x7 HAsfc	8x8 HAsfc	9x9 HAsfc	10x10 HAsfc	11x11 HAsfc
NSL 934	1.450	0.003154	0.208448	13409.73	19856.08	0.230	0.322	0.360	0.458	0.495	0.549	0.619	0.686	0.668	0.751
NSL 95	3.544	0.002139	0.149878	-	-	0.419	0.428	0.492	0.521	0.572	0.635	0.625	0.738	0.723	0.793
NSL 977	1.615	0.004240	0.834040	15025.64	21434.41	0.239	0.346	0.403	0.468	0.507	0.509	0.496	0.572	0.575	0.590
OB-14	2.008	0.001097	1.670944	13380.04	20453.39	0.248	0.340	0.375	0.394	0.423	0.467	0.510	0.577	0.511	0.667
SN 1110	7.156	0.005156	0.266459	17253.36	24706.34	0.194	0.192	0.250	0.320	0.402	0.474	0.641	0.628	0.742	0.887
SN 1309	3.395	0.001929	0.151082	13590.71	19450.62	0.254	0.359	0.358	0.417	0.460	0.552	0.548	0.559	0.617	0.687
SN 1403	2.707	0.002229	0.149975	1853.02	9059.15	0.299	0.316	0.315	0.375	0.365	0.481	0.550	0.513	0.596	0.657
SN 1553	4.311	0.002756	0.150292	17593.83	25790.02	0.295	0.329	0.326	0.375	0.373	0.391	0.436	0.446	0.489	0.468
SN 2356	2.492	0.001720	0.268824	14669.12	20434.82	0.239	0.332	0.341	0.432	0.399	0.430	0.507	0.487	0.566	0.608
SN 2356	5.083	0.001284	0.149999	18821.08	24962.21	0.234	0.263	0.360	0.403	0.444	0.508	0.558	0.559	0.660	0.750
SN 3080	7.003	0.001264	0.154590	12088.24	17967.41	0.193	0.205	0.214	0.259	0.273	0.309	0.324	0.370	0.380	0.398
SN 3080	3.504	0.006944	0.149950	17584.88	24967.24	0.362	0.337	0.348	0.394	0.382	0.455	0.453	0.570	0.588	0.658
SN 4080	2.218	0.002225	0.267220	14174.22	20426.89	0.288	0.356	0.368	0.445	0.464	0.553	0.596	0.602	0.633	0.614
SN 4585	8.957	0.000649	0.150681	19023.69	24637.30	0.162	0.194	0.217	0.261	0.267	0.310	0.331	0.368	0.394	0.431
SN 4585	7.608	0.001307	0.151752	15323.83	22740.34	0.339	0.355	0.395	0.469	0.421	0.514	0.560	0.637	0.671	0.766
SN 4861	4.156	0.001767	0.150890	16476.45	23724.63	0.301	0.478	0.527	0.595	0.664	0.807	0.718	0.810	0.852	0.901
SN 4865	3.937	0.001403	0.150054	15311.75	22145.75	0.460	0.413	0.527	0.784	0.809	0.789	1.180	1.038	1.005	1.266
SN 5304	3.152	0.001390	0.150247	14150.81	21492.18	0.140	0.154	0.215	0.245	0.280	0.306	0.322	0.417	0.402	0.446
SN 5474	2.671	0.006396	0.151413	11706.91	18670.62	0.263	0.455	0.414	0.487	0.470	0.534	0.558	0.577	0.613	0.665
SN 5821	4.723	0.001000	0.151403	14721.68	21007.38	0.264	0.287	0.279	0.331	0.361	0.381	0.441	0.452	0.500	0.495
SN 600	2.499	0.005404	0.150557	14181.09	21869.85	0.254	0.249	0.375	0.421	0.515	0.577	0.667	0.706	0.782	0.832
SN 600	2.362	0.002791	0.209603	17606.58	23884.45	0.358	0.472	0.476	0.574	0.556	0.626	0.619	0.720	0.689	0.727
SN 6095	3.993	0.003977	0.150059	14285.30	21778.98	0.253	0.316	0.293	0.368	0.422	0.530	0.497	0.557	0.577	0.608
SN 6095	2.436	0.006590	0.266724	17014.94	23846.72	0.412	0.428	0.485	0.538	0.665	0.639	0.654	0.724	0.760	0.868
SN 6800	3.965	0.000766	0.152234	14774.23	21811.83	0.206	0.235	0.233	0.294	0.286	0.300	0.317	0.366	0.396	0.474
SN 714	2.191	0.006201	0.268428	-	-	0.472	0.453	0.495	0.792	0.649	0.734	0.844	0.969	0.950	1.044
UK 023 - 20	3.983	0.001006	0.150257	14527.39	21571.41	0.145	0.232	0.263	0.322	0.292	0.319	0.377	0.465	0.438	0.502
UK 023 - 7	7.601	0.000979	0.150107	18862.97	25633.33	0.207	0.201	0.240	0.317	0.289	0.375	0.354	0.380	0.463	0.442

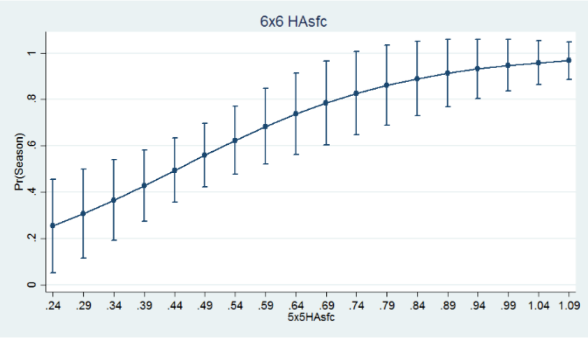
Catalog Number	Asfc	EpLsar	Smc	Tfv	Ftfv	2x2 HAsfc	3x3 HAsfc	4x4 HAsfc	5x5 HAsfc	6x6 HAsfc	7x7 HAsfc	8x8 HAsfc	9x9 HAsfc	10x10 HAsfc	11x11 HAsfc
UK 023 26	2.843	0.001435	0.149948	13417.76	20225.67	0.262	0.395	0.477	0.517	0.673	0.788	0.780	1.035	1.064	1.173
UK 023 35	3.213	0.001603	0.150242	15697.23	23080.08	0.348	0.422	0.511	0.551	0.634	0.701	0.729	0.820	0.868	0.919
UK 023 9	-	0.001555	0.155784	14429.60	21192.90	0.177	0.239	0.276	0.377	0.396	0.388	0.420	0.458	0.463	0.526
UK 023 9	3.266	0.002216	0.150221	10359.31	17712.69	0.231	0.322	0.330	0.468	0.459	0.517	0.510	0.557	0.678	0.646

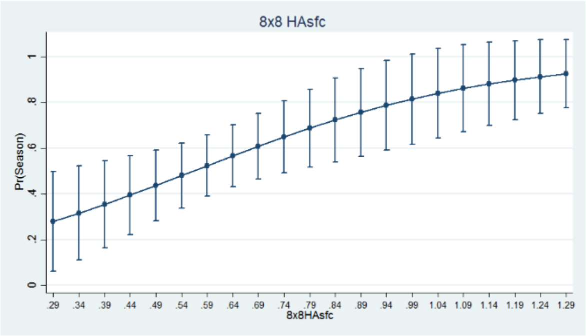
Appendix 4. Logistic graphs for Heterogeneity of the Total Sample of Impala values at various scales.

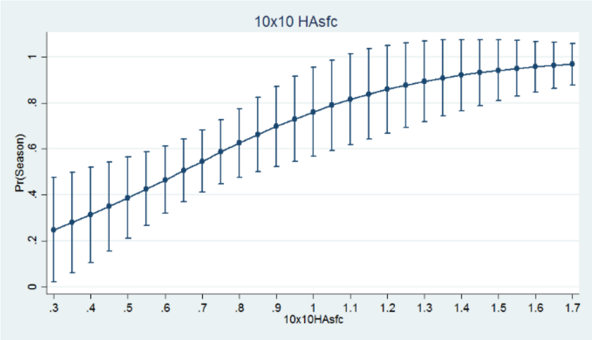


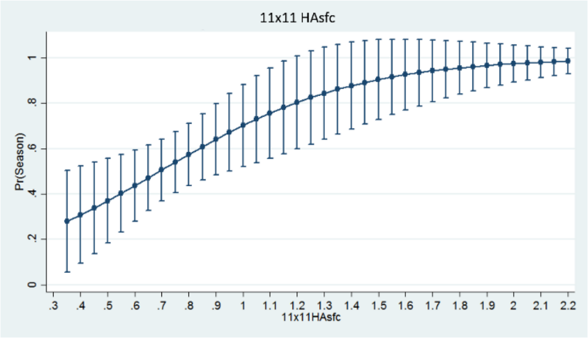












Appendix 5. Modern referents for extinct bovids at FLK Zinj

Antidorcas marsupialis (analog for *A. recki*): The antilopine springbok is the only extant representative of its genus, evolving about 0.1 Ma from *A. recki* (Vrba, 1973). It is a size 2 bovid with females 20 – 44 kg and makes 25 – 48 kg. They are currently found in southwestern Africa where they inhabit a broad range of arid habitats from the South African Highveld at 2000 m altitude to sea level, and with annual rainfall between 750 mm in savannas to < 100 mm in the Namib Desert. Their primary requirements are firm footing and semi open habitats. They are therefore not found in rocky hills, mountains, or dense woodlands (Estes, 1991). **Water dependence:** Springbok are capable of subsisting indefinitely without drinking water so long as their forage retains at least 10% moisture, and are adapted to tolerate water with high mineral content (Estes, 1991). **Mobility and Diet:** To maintain sufficient water intake from plant foods, springbok switch between a grazing diet during rainy seasons to one that is primarily browse during dry seasons (Estes, 1991; Kingdon, 1997; Gagnon and Chew, 2000). Springbok are a territorial species in which males defend regions of varying size depending on water accessibility and resource richness. In order to maintain their territories, males must remain within them even when high rainfall increases vegetation density and predation, or when low rainfall decreases plant food quality (Jackson et al., 1993). Territorial males exclude non territorial males and bachelor herds, but allow females and calves to move freely. The latter do not have home ranges per se, and associate in herds of < 300 without significant social interactions (Estes, 1991). Generally, springbok buck the typical bovid seasonal distribution pattern, aggregating in the wet season in green grasslands and dispersing into small groups during the dry season. Important exceptions to this pattern occur when waterholes are available, and when prolonged drought precipitate a phenomenon known as the trekbokken, in which springbok migrate *en masse* to wetter regions. Despite their water-independent subsistence adaptations, springbok will drink when water is available, particularly during the dry season (Estes, 1991; Jackson et al, 1993). Waterholes are capable of exerting a strong force of female distributions within their ranges, and on male sexual selection, such that several hundred females and calves will drink from isolated waterholes during the dry season (Ritter and Bednekoff, 1995). When dry season foliage withers and falls as a result of insufficient rainfall, springbok are known to gather in herds of many thousands of individuals and trek to more favorable regions hundreds of kilometers away (Child and Le Riche, 1969; Crowe and Liversidge, 1977). **Reproduction**: Springbok are aseasonal breeders. Jackson and colleagues (1993) attribute this to the unpredictability of springbok environmental conditions. Instead, they breed opportunistically, with rutting peaks early in the dry season while individuals are in peak condition after the growing season (Estes, 1991). These can result in large nursing herds of females and their calves six to seven months later, just before the rainy season begins, which remain separate from other social groups for several weeks (Estes, 1991). **Body condition:** Visually-assessed springbok body condition tracks both age and rainfall, such that body condition deteriorates over the course of the lifespan and improves at the peak of the growing season, approximately two months after the commencement of the rainy season (Turner et al, 2012). Late pregnancy and lactation are also associated with a decrease in adult female body condition (Turner et al, 2012).

Aepyceros melampus (analog for *A. recki*): Impala are the only extant member of the genus *Aepyceros* in the subfamily *Aepyceroptini* which evolved approximately 4 million years ago in southeast Africa (Kingdon, 1997), though there are two subspecies of which the common impala, *A. m. melampus* is more numerous and will be the subspecies considered here (Lorenzen et al, 2006). Impala range in size from 30 – 60kg for females and 40 – 80 kg for males (Gagnon and

Chew, 2000). They are currently found throughout eastern and southern Africa in open woodlands and grasslands of low to medium height. **Water dependence**: Unlike springbok, impala are reliant upon water in the dry season when they cannot extract sufficient moisture from foliage (Estes, 1991.) **Mobility and diet:** They are almost exclusively grazers in the wet season, and switch to browsing in the dry season. This requires a shift in habitat usage within their range, from grasslands in the wet season to woodlands near waterways in the dry season (Kingdon, 1997). These ranges are typically less than 2 km^2 and used by "clans" of 30 – 120 loosely associated females which overlap significantly at their edges with other female clans (Jarman, 1979; Murray, 1981; Estes, 1991; Kingdon, 1997). Males may be territorial during the wet season or breeding season, which varies between southern and eastern Africa as a result of climatic differences, with the size of the territory reflecting habitat quality, individual defensive prowess, population density, and season (Estes, 1991). During the dry season or non-breeding season, territorial males exert dominance over other males but are less active in expelling them or retaining females (Estes, 1991). Bachelor male herds rarely exceed 10 individuals and move independently of female ranges or territorial male boundaries. **Reproduction:** Eastern African impala are aseasonal breeders with minor birthing peaks occurring at the end of the long dry season and into the early short wet season (Ogutu et al, 2014). **Body condition:** In southern Africa, impala are largely able to maintain their body condition in response to seasonal changes by switching between grazing and browsing with the exception of nursing females, whose fat stores decline in the dry season (Gallivan et al, 1995) and post-rut males. Only at the end of the dry season are impala of all demographics in poorer physical condition, with adults in increasingly poor condition as they age (Gallivan et al, 1995). Body condition on eastern African impala is not as extensively studied but would presumably follow similar patterns.

Beatragus hunteri (analog for *P. altidens*): Modern hirola are limited in their distribution to the border between Kenya and Somalia and are the only living member of the genus *Beatragus* in tribe Alcelaphini. They range in size from 73 – 118 kg at the high end of size group 2. **Water dependence:** Hirola are arid-adapted species that can forgo drinking water indefinitely (Bunderson, 1981; Dahiye, 1999). In one long-term study with 674 observations, hirola were only seen to drink on 10 occasions, each of which occurred in the peak of the dry season (Andanje, 2002). During more than half of these observations, however, hirola were selectively grazing on green grasses at waterholes, presumably to maintain sufficient moisture intake (Andanje, 2002). **Mobility and diet**: Hirola are primarily grazers, though browse may contribute a small but important component to their diet in the dry season (Gagnon and Chew, 2000). Within their range, single males defend territories of several km. Non-territorial males form bachelor herds that range from 2 – 38 individuals. Females and calves form larger groups of 5 – 40, often in association with a male (Kingdon, 1997), and roam across multiple territories (Andanje, 2002). Hirola are typical of bovids in dispersing in the wet season throughout their range of open woodlands and bushy grasslands, and aggregating in the dry season where grasses remain green longer. This is particularly true toward the end of the season when herds of mixed demographics > 300 individuals are drawn to isolated green grass patches (Andanje, 2002). **Reproduction:** Hirola breed seasonally, with strong birth peaks at the beginning of the short wet season that follows the long dry season (Kingdon, 1997; Andanje, 2002). Calves are extremely vulnerable to predation from carnivores and disease, with nearly 70% dying within the first six months of life (Andanje, 2002). **Body condition:** The same long-term study mentioned above did not find visual evidence of seasonal changes in body condition (Andanje, 2002; Probert, 2011). However, pre-parturition females were in poorer condition, and often lagged behind the rest of the herd (Andanje, 2002), from which it is inferred that lactating females continue to be fat-depleted. Females are also reported to show reproductive senescence (Andanje, 2002), which likely reflects declining physical condition.

Kobus ellipsiprymnus (analog for *K. sigmoidalis*): Waterbuck is a size group 3 bovid, with males weighing 198–262 kg and females 161–214 kg, and are found throughout sub-Saharan Africa. **Water dependence:** Waterbuck are present throughout sub-Saharan Africa but are extremely limited in their distribution by the physiological requirements of large quantities of water (Taylor et al, 1969). A study by Taylor and colleagues (1969) determined that the waterbuck requires three times as much water as the arid adapted oryx, and 25% more water than the domesticated Hereford steer, which is considered to be highly water dependent. **Mobility and diet:** The waterbuck is a territorial species that organizes into a variety of social groups, including territorial male singletons, non-territorial male singletons, bachelor male groups of 4 – 6 individuals, and female and immature groups of variable size that increase as the seasons change from rainy to dry (Tomlinson, 1981). This social organization and territoriality dictates access to both water and food. Female and immature groups associate loosely as they range across male territories (Tomlinson, 1981), while bachelor male groups are relegated to habitats with lower quality plant foods (Wirtz and Oldekop, 1991). Though there is variability between social groups, the general trend is for feeding to occur predominately on grasses in woodlands during the wet season and primarily along waterways in the dry season (Tomlinson, 1980). When grasses desiccate in the dry season, waterbuck will supplement their protein intake by incorporating browse species during up to 21% of their feeding time (Tomlinson, 1980; Spinage, 2012). **Reproduction:**

Reproduction is perennial among some equatorial waterbuck, and highly variable throughout the species' range, though there is an increase in calving during the wet season when lactation energy budgets are more easily met (Spinage, 2012; Estes, 1991). In order to protect newborns from predation, mothers isolate themselves in woodland thickets shortly before parturition and remain there for several weeks thereafter in order to conceal calves (Estes, 1991). This provides one exception to the seasonal mobility trend, in which females and calves may find themselves in woodlands during the dry season as well as the wet season. **Body condition:** Females do not appear to correlate body condition with season of parturition, as measured by the kidney fat index. Nor do pregnant and non-pregnant females differ significantly in their kidney fat index, although there is a significant difference between females at the beginning and end of pregnancy, with the latter more fat depleted. Females do experience significant variability in body fat between seasons, with peaks that trail behind the wet seasons (Spinage, 2012). Females also have a higher kidney fat index than males throughout most of the year. More broadly, waterbuck body fat declines during the dry season, but this species remains in better condition than other bovids during years with typical seasonal variance (Child and Von Richter, 1969).

Appendix 6. *Antidorcas recki* from FLK North and FLK Zinj DMTA Results

Catalog Number	Asfc	epLsar	Smc	Tfv	Ftfv	2x2 HAsfc	3x3 HAsfc	4x4 HAsfc	5x5 HAsfc	6x6 HAsfc	7x7 HAsfc	8x8 HAsfc	9x9 HAsfc	10x10 HAsfc	11x11 HAsfc
FLKNorth 067-339	2.124	0.003196	0.34445	12102.15	19583.38	0.18	0.17	0.22	0.25	0.30	0.33	0.33	0.37	0.37	0.39
FLKNorth 067-402C	1.448	0.005064	0.420229	8654.523	15541.29	0.59	0.51	0.59	0.64	0.66	0.76	0.80	0.84	0.86	0.89
FLKNorth 067-402D	2.283	0.002005	0.220448	16744.63	23532.39	0.16	0.20	0.22	0.36	0.38	0.44	0.49	0.58	0.62	0.67
FLKNorth 067-414	4.209	0.006022	0.172225	12723.52	20280.23	0.54	0.54	0.69	0.88	1.03	1.33	1.42	2.28	2.51	6.12
FLKNorth 067-459B	2.591	0.002646	0.220448	8080.39	15747.94	0.29	0.26	0.29	0.40	0.39	0.46	0.53	0.55	0.62	0.64
FLKNorth 067-463	2.388	0.004159	0.282449	16140.61	22050.48	0.26	0.32	0.44	0.55	0.58	0.68	0.80	0.88	0.96	0.99
FLKNorth 1045	2.176	0.004034	0.282449	10848.06	17811.8	0.31	0.39	0.43	0.42	0.45	0.54	0.52	0.60	0.60	0.64
FLKNorth 1152	1.238	0.004734	0.220448	12343.32	18786.01	0.49	0.68	0.78	1.06	1.16	1.10	1.32	1.16	1.30	1.25
FLKNorth 1281	2.131	0.003088	0.496008	8457.057	15324.21	0.52	0.62	0.75	1.09	1.19	1.37	1.25	1.75	1.82	1.95
FLKNorth 1511	1.344	0.005258	0.420229	14322.72	21517.54	0.22	0.25	0.31	0.37	0.40	0.46	0.48	0.53	0.55	0.59
FLKNorth 503	1.793	0.002552	0.220448	12715.06	20687.01	0.56	0.58	0.59	0.61	0.65	0.68	0.76	0.78	0.85	0.89
FLKNorth 627	2.185	0.003662	0.34445	10512.13	16966.18	0.47	0.64	0.65	0.95	0.91	1.04	1.12	1.10	1.13	1.18
FLKNorth 7266	5.074	0.001243	0.172225	13630.09	21729.53	0.30	0.41	0.52	0.67	0.72	0.92	0.93	1.06	1.14	1.18
FLKNorth NoNum	-	0.001055	3.754505	14493.34	21369.84	0.20	0.32	0.40	0.53	0.54	0.63	0.63	0.65	0.92	0.92

Catalog Number	Asfc	epLsar	Smc	Tfv	Ftfv	2x2 HAsfc	3x3 HAsfc	4x4 HAsfc	5x5 HAsfc	6x6 HAsfc	7x7 HAsfc	8x8 HAsfc	9x9 HAsfc	10x10 HAsfc	11x11 HAsfc
FLKZinj B119	1.354	0.0036	0.344450	9824.18	16998.99	0.25	0.27	0.31	0.43	0.48	0.52	0.53	0.60	0.66	0.68
FLKZinj B188	2.932	0.0029	0.282449	13936.10	20781.50	0.39	0.42	0.56	0.70	0.67	0.72	0.81	0.81	0.94	0.90
FLKZinj B492	2.052	0.0012	0.496008	11467.19	19146.24	0.41	0.45	0.43	0.54	0.66	0.59	0.68	0.75	0.70	0.80
FLKZinj D154	7.173	0.0016	0.344450	14560.43	22396.69	0.45	0.71	0.74	1.23	1.11	1.10	1.54	1.63	1.82	1.95
FLKZinj D35	5.741	0.0028	0.861125	11445.80	19009.23	0.57	0.98	0.99	1.18	1.22	1.17	1.31	1.45	1.40	1.54

Appendix 7. *Parmularius altidens* From FLK North and FLK Zinj DMTA Results

Catalog Number	Asfc	epLsar	Smc	Tfv	Ftfv	2x2 HAsfc	3x3 HAsfc	4x4 HAsfc	5x5 HAsfc	6x6 HAsfc	7x7 HAsfc	8x8 HAsfc	9x9 HAsfc	10x10 HAsfc	11x11 HAsfc
FLK North 067/1096	1.121	0.0050	0.496008	12018.35	19067.68	0.107	0.140	0.188	0.215	0.250	0.273	0.278	0.323	0.334	0.371
FLK North 841	1.711	0.0050	0.509786	14706.98	22355.12	0.386	0.573	0.457	0.708	0.742	0.654	0.616	0.741	0.721	0.797
FLK North 128	1.737	0.0047	0.881792	13342.87	20845.50	0.196	0.174	0.248	0.333	0.340	0.416	0.421	0.450	0.507	0.517
FLK North 265	2.449	0.0065	0.358228	11541.19	19211.76	0.332	0.479	0.523	0.620	0.708	0.738	0.673	0.797	0.845	0.815
FLK North 8045	1.467	0.0034	0.998905	11721.17	17939.52	0.316	0.348	0.405	0.434	0.491	0.490	0.496	0.523	0.582	0.616
FLK North 38	1.156	0.0071	-	13705.34	21066.30	0.205	0.195	0.280	0.275	0.412	0.491	0.481	0.606	0.604	0.639
FLK North 7798	0.749	0.0070	0.496008	11359.64	18542.31	0.171	0.196	0.251	0.408	0.381	0.435	0.483	0.452	0.554	0.527
FLK North 7933	1.057	0.0070	0.496008	14014.86	20700.42	0.262	0.202	0.270	0.350	0.396	0.470	0.454	0.508	0.551	0.581
FLK North 10144	0.944	0.0047	0.496008	11314.69	17741.23	0.178	0.168	0.207	0.217	0.278	0.279	0.325	0.316	0.328	0.338
FLK North 8728	1.018	0.0038	0.496008	12096.98	19494.07	0.348	0.383	0.406	0.411	0.475	0.508	0.583	0.546	0.550	0.582
FLK North 1099	0.996	0.0038	0.585565	12247.32	19364.80	0.144	0.164	0.183	0.236	0.268	0.293	0.324	0.342	0.361	0.404
FLK Zinj D42	1.920	0.0064	0.344450	12958.24	20103.65	0.169	0.253	0.275	0.335	0.362	0.369	0.471	0.437	0.449	0.537
FLK Zinj G361	1.492	0.0039	0.220448	13016.49	20192.95	0.140	0.242	0.288	0.399	0.438	0.505	0.570	0.704	0.760	0.756
FLK Zinj D111	1.903	0.0024	0.344450	12039.96	19866.12	0.241	0.320	0.343	0.356	0.410	0.440	0.455	0.490	0.507	0.495