TAPHONOMY ON RUSINGA ISLAND, KENYA

A DISSERTATION
SUBMITTED TO THE FACULTY OF THE
UNIVERSITY OF MINNESOTA
BY

KIRSTEN ELISE HOLT JENKINS

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

KIERAN McNULTY
MARTHA TAPPEN

AUGUST 2018

ACKNOWLEDGEMENTS

It took several villages to raise this dissertation.

In addition to the people and institutions below, I am grateful for the support of the National Museums of Kenya, the local communities on Rusinga Island, my committee in its multiple iterations—Kieran McNulty, Martha Tappen, Mike Wilson, and Ray Rogers- but also David Fox, Gil Tostevin, and Gilliane Monnier. The comradery from my communities of friends and mentors at the University of Minnesota's Department of Anthropology and in Nairobi helped me through every step of this research.

Kieran and Martha both took a very active role in my training, for which I am very grateful. Thank you for your years of advice, editing, teaching, listening, support, and friendship.

My family—my husband Austin Jenkins, my parents Tim and Leeann Holt, my in-laws John and Vicki Jenkins, and my daughter Leona -- has made this research possible with their love and support (both finical and moral). Thank you for supporting my Kenya habit and helping my helping my dreams become reality.

Acknowledgements for chapter 2

This work has been a multidisciplinary effort and portions of the synthesis presented here are the work of team members: This work was predicated on efforts lead by Kieran McNulty, Holly Dunswoth and Will Harcourt-Smith. Thomas Lehmann, Kieran McNulty, and Jack Conrad lead efforts on faunal IDs. Sheila Nightengale, Thomas Lehmann, and Sulemon Okayo assisted in leading excavations. Holly Dunsworth, Catya Maysef, Shelia Nightengale, and Lauren Michel all assisted in profile drawing. Geologists Dan Peppe, David Fox, Steven Driese and Lauren Michel all contributed their geologic interpretations and descriptions. Eddie Kadieda, Edwin Wandango, Elly Owino, Kennedy Oteino, Kellen Odira, Semekia Ponue, Victor Lare, Evans Siro, Martin Onoto, Moses Onwento, Fred Onyango, Charles Okongo, Dick Misasa, Kenneth Kaunda, Kennedy MIsiami, Edwin Siembo, Adam Cossette, Jack Conrad, Derek Nelson all diligently excavated the site. Blasto Oyango, Samuel Odhiambo, Joshua Siembo, and Ezra Kadieda provided support in the field. The total station was lent to the team for use by Christian Tryon. Students and team members conducted surface collections. Fieldwork and Museum research was conducted with support of the Emma Mbua, Fredrick Manthi, Kenya National Museum, and NACOSTI (exploration permits issued to Kieran McNulty, Holly Dunsworth and Will Hartcourt-Smith; and a research permit issued to myself

(NCST/5/002/R/605) with affiliation to the Department of Earth Sciences at the National Museum of Kenya. Fieldwork was funded by NSF grants to Kieran McNulty, Holly Dunsworth, and Will Hartcourt-Smith. Funding from the Leakey Foundation and University of Minnesota Doctoral Dissertation Fellowship and Department of Anthropology Block Grants supported taphonomic data collection in the museum. Samantha Porter stitched excavation photos using photogrammetry and assisted in producing figures. Field images were taken from a pooled collection of the team's photographs. Austin Jenkins assisted in creating the site map and collating total station data. Peter Andrews shared a copy of his 1972 report, which was critical to this research. This work was aided by many helpful conversations with Martha Tappen, Kieran McNulty, Dan Peppe, Sheila Nightengale, Lauren Michel, Jack Conrad, and Austin Jenkins. Kirsten is grateful for the support of her team, her advisors, the National Museum of Kenya, the Kaswanga community, anthropology community at the University of Minnesota, and her family.

Acknowledgements for chapter 4

This research was made possible by funding from the National Science Foundation, Leakey Foundation, and the University of Minnesota. Research on fossil specimens was conducted at the National Museums of Kenya under permits issued to K. Jenkins. I would like to thank the following persons for their helpful comments, ideas, and support during this research: Dr. Emma Mbua, Dr. Fredrick Manthi, and the curational staff at the National Museums of Kenya for their support of this research and making specimens available. Scott McGraw, Susanne Shultz, Bill Sanders, and John Mitani for making the Taï and Ngogo actualistic collections available for study and for helpful conversations about the predatory habits of raptors. Actualistic collections for the Ngogo nests collections were housed at the University of Michigan’s Natural History Museum and are now in the University of Michigan’s Department of Anthropology Collections. Actualistic collections for Taï nest sites were made available at the University of Ohio and are now housed in the S. Shultz Lab at the University of Manchester. Lars Werdlin, Matthew Borths, Thomas Lehman, Gerald Mayr, Kieran McNulty, Holly Dunsworth, Rutger Jansma for their expertise and helpful conservations about the carnivore, hyenadont, avian, and primate fossil records. Martha Tappen, Kay Behresmeyer, Linda Chisholm, and Aaron Armstrong all generously shared their own taphonomic comparative collections and expertise with the author and these conversations helped improve this paper and research design. The author is grateful to Austin Jenkins for assistance with figures. Lastly, the author would like to thank the numerous researchers and field assistances who have collected the many fossil primates from Rusinga Island through the decades.

Acknowledgements for chapter 6

Fieldwork was conducted under permits issued by the Kenya National Government and the Kenya National Museum. Funding was provided by National Science Foundation (BCS-1013199 and BCS-1013108), the Leakey Foundation, the National Geographic Society's Committee for Research and Exploration (8762-10), a graduate research grant from the Geological Society of America, the University of Minnesota, Baylor University, New York University, and the University of Queensland. This work would not have been possible if not for the support of the Kenya National Museum, Dr. Emma Mbua, Dr. Fredrick Manthi, Dr. Purity Kiura, and the always helpful museum staff in the Paleontology, Archaeology, Preparation Departments. The British Institute in East Africa, the Rusinga Island Lodge, Stephen Longoria, Matthew Macharwas, Julian Ogondo, Samuel Odhiambo, Lucyline Mbogori, Joshua Siembo, Adam Cosset, Jared Olelo, Breanne Clifton, and Myra Laird all provided exceptional support in the field. This work has benefited from helpful conversations with Martha Tappen, Gil Tostevin, Emily Beverly, Austin Jenkins, Reed Coil, Samantha Porter, Linda Chisholm, Phil Slater, Aaron Armstrong, Haley O'Brien, Katherine Hayes, and John Speth and from suggestions of four anonymous reviewers, an associate editor, and Sarah Elton. Samantha Porter and Austin Jenkins assisted with editing figures and Cornel Faith provided the artistic reconstruction of *Rusingoryx*. Lastly, we thank the Wakondo community on Rusinga Island and the excellent and skilled excavators for their support, hard work, and enthusiasm for this project: David Ochieng Miriga, Joseph Ochieng Oyugi, Robert Onkondoyo, Isayah Onyango, Samwel Odoyo, and William Ondongo Oyoro.

DEDICATIONS

To the communities and children on Rusinga Island who have been so generous, curious, and supportive of this research.

To my dear friend Joshua Seimbo – you are a true steward of Rusinga's prehistory.

To my daughter: Watching the world become new again through your eyes inspires me to keep exploring this big, ancient, and amazing planet.

To my husband: In the depths of my uncertainty, Austin Jenkins says to me, "I think our daughter will be very proud of you- I am". Thank you for your unwavering support and love.

ABSTRACT

Understanding taphonomy and site formation processes for fossil human and primate sites is central to testing hypotheses about paleoenvironments and the natural selection of various traits and behaviors in our lineage. Strong inferences about paleoenvironmental and behavioral reconstructions, however, rest on demonstrated associations between both fossil and sedimentary environmental proxies and taphonomic actualistic data. On Rusinga Island, Kenya, Miocene and Pleistocene fossils have been collected and studied for a century, yielding a rich assemblage of early Miocene stem hominoids and catarrhines—*Ekembo*, *Dendropithecus*, *Limnopithecus*, *Rangwapithecus,* and *Nyanzapithecus*. Numerous mammalian, avian, reptilian, invertebrate, and plant fossils are preserved alongside these primates. Pleistocene fossils on Rusinga are often in association with Middle Stone Age tools made my early Modern Humans. Despite the long history of collection, little consensus has been reached about the paleoenvironmental contexts in Miocene Rusinga, in part due to faunal mixing and lack of broad taphonomic studies. Furthermore, behavioral reconstructions of have been limited by not engaging with taphonomic surface modification data. Pleistocene deposits are generally understudied compared to the Miocene fossils and behavioral reconstructions have been similarly limited.

This dissertation examines taphonomic site formation processes of both time periods using archaeological style excavations, systematic surface collections and taphonomic data collection. Bonebed excavations and taphonomic data at Miocene R5-Kaswanga inform paleoenvironmental reconstructions and show that attritional predation and fluvial processes account for most of the bone accumulations. A survey of Miocene primate remains for trends in surface modifications suggest predation by creodonts, carnivores and avian raptors, indicating important selection pressures from predators. Bonebed excavations at Pleistocene Wakondo yield the first behavioral reconstruction of tactical hunting on Rusinga Island.

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CHAPTER 1 INTRODUCTION

In the 1930s, Dr. Louis Leakey set out to Rusinga Island on Lake Victoria, Kenya after hearing of vertebrate fossils there. He had hoped that new finds might renew international interest in his work; finding evidence of human evolution in East Africa in the wake of an extremely Eurocentric view of the fossil record (Kent, 1978; Andrews, 1981; Pickford, 1984; 1986a; Walker and Shipman, 2005). Fortuitously, Rusinga Island hosts fossils deposits from two important time periods in human evolution, separated by nearly 18 million years--the prolific and well known early Miocene hominoid assemblages and the less familiar mid-late Pleistocene Middle Stone Age sites left by early modern humans. Indeed, few paleontological sites outside of Europe can boast 100 years of research and collection. Over the course of the past century, more than 50,000 specimens have been collected from Rusinga Island resulting in a one of the most studied Miocene fossil assemblages in the world.

The Miocene primate assemblage includes at least 7 genera and has brought researchers to the Lake Victoria region, time and time again. In addition to the rich primate assemblage, large and small mammals, reptiles, birds, fish, insects, soft tissues, trace fossils, trees, and leaves are also preserved. Rusinga Island is well known for its fantastic fossil preservation and rich fossil communities giving context to the primate assemblage. Researchers have come, not only to collect fossils, but also to study the geology and paleoecology of these early Miocene deposits. However, despite the wealth of material and research, there is little consensus about the paleoenvironments themselves. The lack of detailed provenience and systematic taphonomic studies has left many paleoenvironmental reconstructions unreliable, and thus questions remain about the adaptive habitats of this important stem hominoid community.

The Pleistocene deposits on Rusinga have been much less popular and only sporadically collected through time. Sparser accumulations and slightly unimpressive preservation have made them less exciting to researchers, but this has led to less faunal mixing of the museum assemblages. Not to be outdone, a single early modern human humerus is now known from the Pleistocene deposits. Like the Miocene Rusinga, research questions have centered on understanding the paleoenvironmental contexts and chronostratigraphy, setting the stage for archaeological interpretation. However, despite preservation issues, critical land use and hunting behaviors can still be inferred from these sites with careful excavation and collection.

This dissertation explores the application of taphonomy to both Miocene and Pleistocene deposits so that we may better understand the adaptations and selections pressures of early Miocene stem hominoids and early modern humans. In 2011, I excavated two bonebeds—one at Miocene R5-Kaswanga and another at Pleistocene Wakondo. Archaeological style excavations, systematic surface collections, and taphonomic data collection and analysis were employed at each both sites to reconstruct biogenic and physical taphonomic processes. Taphonomic surface modifications were also surveyed on Miocene primate remains across localities to assess potential trends in selection pressures from predators. Findings from these taphonomic analyses inform our understanding of paleoenvironmental reconstructions and selection pressures for these early Miocene primate communities and ancient hunting techniques and land use patterns of early modern humans as they develop new and “modern” behavioral adaptations.

Miocene Background

Primates

Much of what we understand about the early Miocene of East Africa and the diversification of stem catarrhines and hominoids is based on the primate assemblages and deposits from Rusinga Island. *Ekembo*, *Dendropithecus*, *Limnopithecus*, *Nyanzapithecus*, as well as two different lorisoid genera (*Mioeuoticus* and *Komba*) are known from the Rusinga Island deposits--comprising a diverse fossil primate community. Holotypes, synonyms, important referred specimens, and dietary and locomotor reconstructions for the primate taxa are summarized in Table 1.1.

Ekembo — the primate formerly known as *Proconsul* (McNulty et al., 2015) — is perhaps the most important genus represented on Rusinga Island. It is known by two species, *E. nyanzae* and the smaller *E. heseloni. Ekembo* specimens are especially numerous on Rusinga and several partial skeletons and cranial elements known. *Ekembo* is thus a standard comparison for both early hominoids and hominins alike. Important specimens include the "pothole/tree trunk" partial *E. heseloni* skull and skeleton (KNM-RU-2036) from R114 (Napier and Davis, 1959; Walker et al., 1993; Walker, 2007), an accumulation of ten primates at R5—the Kaswanga Primate Site (KPS) (Walker and Teaford, 1988; Walker, 2007), and the largely complete "Mary Leakey" skull missing only the basal cranium (KNM-RU-7290) recovered from R106A (Le Gros Clark and Leakey, 1951).

There is no strong consensus as to phylogenetic relationship between *Ekembo* and the extant apes. While its taxonomic status has changed, many of the specimens now referred to as *Ekembo* have been used in previous phylogenetic analyses representing *Proconsul*. Indeed *Proconsul* was largely known from referred Kisingiri specimens (Rusinga and Mfangano Islands) now attributed to *Ekembo*, though the genus *Proconsul* is still recognized from Kenyan Tinderet and Ugandan localities (McNulty et al., 2015). Older analyses (Harrison, 1987; 2002; 2010) place *Proconsul* as a stem catarrhine and sister-group to cercopithecoids and hominoids. Others place *Proconsul* (*sensu lato*) as a hominoid or a stem hominoid (Rose, 1997; Feagle, 1999; Ward, 1991; Ward, 1997; Walker, 1993; Walker and Teaford, 1989). McNulty et al. (2015) deem *Ekembo* closely related to *Proconsul*, though more derived in the direction of extant apes.

Dendropithecus macinnesi, *Limnopithecus legetet*, and *Nyanzaepithecus vancouveringorum* and *Rangwapithecus gordoni* are all reconstructed as smaller stem catarrhines and generally considered more primitive than *Ekembo*. Several partial skeletons of *Dendropithecus* were recovered from R3 and thus it is relatively well understood. However, very few post-cranial elements are known from *Limnopithecus* or *Nyanzaepithecus* on Rusinga. *Ekembo heseloni*, *E. nyanzae*, *D. macinnesi* and *L. legetet* are commonly found at the same sites on Rusinga and may have been sympatric taxa. *Nyanzapithecus* specimens are much more rare in the collections.

Geologic Background

During the Miocene, Rusinga and Mfangano Islands were situated along the western margin of the Kisingiri stratovolcano, part of the Nyanza Rift arm of the East African Rift Valley. Accordingly, a significant proportion of the Miocene deposits there are volcaniclastic. Several other Miocene primate localities commonly discussed in conjunction with Rusinga also lie along the Nyanza Rift and Kavirondo Gulf; Karungu and Uyoma are also associated with the Kisingiri volcano complex and further north-east along the rift, Maboko, Koru, Fort Ternan, and Legetet are associated with the Tinderet volcano (Shackleton, 1951; McCall, 1958; Van Couvering, 1972; Pickford, 1984; 1986a; Drake et al., 1988; Bestland, 1991; Bestland et al., 1995).

Today, Rusinga and Mfangano Islands lie on the eastern edge of Lake Victoria. Much of the Kisingiri volcano has since been eroded to expose the Rangwa dome. Volcanic deposits make up much of the sediments on Rusinga and their unique geochemistry has greatly aided the preservation of fossils (Van Couvering, 1972). The western margins of Rusinga and Mfangano Islands have been down faulted into Lake Victoria. Lake Victoria, however probably filled to its current area during the Late Pleistocene/early Holocene (Tryon et al., 2012) and was not present during the early Miocene, nor much of the Pleistocene. Paleoenvironments and paleotopography are vastly different today than they were during fossil deposition in the Miocene (Kent, 1942)

The driving geologic research questions on Rusinga have centered on clarifying chronostratigraphy and obtaining absolute ages for the fossil bearing deposits (Kent, 1942; 1944; Shackleton, 1951; Whitworth, 1953; Van Couvering, 1972; Peppe et al., 2009; 2011; 2017). Two geologic groups are generally recognized; the older Rusinga Group, which was deposited in the volcanic depression, and the younger Kisingiri Group that was deposited evenly over the Rangwa dome during later growth of the volcano (Van Couvering, 1972). Recently, Peppe et al. (2011) took new samples from the Kibanga Member of the Hiwegi and Wayando for combined ^{40}Ar-^{39}Ar and paleomagnetism analyses. Their analyses showed that the Hiwegi Formation was deposited between 18-18.5mya and the Wayando Formation is at least 19.7mya. These results are consistent with historical interpretations suggesting the fossiliferous deposits on Rusinga and Mfangano do overlap with Koru, Napak and Songhor (Peppe et al., 2009; Peppe et al., 2011).

Geologists agree that the deposits on Rusinga and Mfangano represent basin filling at the Kisingiri volcano's margin. This basin formed as a result of faulting due to the growth of the volcano mastiff and was filled by alluvial fan/deltaic deposits fed by frequent volcaniclastic sediments and erosion (Van

Couvering, 1972; Pickford, 1986b; Bestland, 1991, Peppe et al., 2009). Both Pickford (1986b) and Retallack et al. (1995) suggest landscape-scale reconstructions where the different depositional contexts and beds can be related to common features and environments of distal volcanic basin filling. Pickford (1986b) suggests features such as lakes, drainages, and apron deposits are correlated with distance from the volcano's center and can explain variable deposits on Rusinga. Pickford goes on to suggest that both the Kulu Formation and portions of the Wayando could be distal lakes and that the Hiwegi Formation represents more medial floodplains and drainages. This hypothesis is generally consistent with basin filling processes and helps lay a foundation for understanding paleoenvironments. However, Pickford's model seems to suggest that the volcano's center moves unpredictably as no clear sedimentary patterns emerges with respect to the strata. On Rusinga, the Wayando Formation is the oldest, followed by the Hiwegi Formation, and then the Kulu Formation. As the basin is filled, we should expect the deposits to coarsen upwards (lake - channels - lake does not fit this pattern), however, continual growth of the volcano and faulting may cause irregular basin filling patterns.

The Problem with Paleoenvironments

Reconstructing the paleoenvironments of these catarrhine and hominoid taxa has been central to questions about dietary and locomotor adaptations and their subsequent evolutionary success or failure.

Numerous fossils from Rusinga and Mfangano preserve soft parts and are also associated with rapid burial by volcanism. A purported bird fossil preserving body and feathers (Pickford, 1984), a lizard head with scales and a tongue (Estes, 1962), several isolated insects and insect nests (Wilson, 1962; Thackray, 1994; Walker and Shipman, 2005), the endocast of a lorisoid (Le Gros Clark and Thomas, 1952), and fruits and leaves (Collison, 1983; Walker and Shipman, 2005; Collison et al., 2009; Maxbauer et al., 2013) are all examples of exceptional preservation. With fossils so richly preserved, environmental reconstructions should be clear, yet researchers have rarely agreed on the degree of tree cover, rainfall, or other environmental characteristics of Miocene Rusinga. Table 1.2 shows some of the many incongruent reconstructions.

Three underlying and often false or poorly justified assumptions plague multiple methods of paleoenvironmental reconstructions on Rusinga: (1) living assemblages were evenly preserved and collected as fossil assemblages, (2) fossil taxa in question are directly associated with the geologic contexts (isotopes, paleosols, sedimentology) or proxy taxa (modern analogs, ecomorphology, isotopes, dental wear) being studied, and (3) deposits on Rusinga are homogenous.

Rusinga, with its remarkable fossil preservation on the slopes of an ancient volcano has invoked the misguided assumption of a “Pompeii premise” site and approach to community and environmental reconstruction (see Asher, 1968; Schiffer, 1976; Binford, 1981). In the context of the Miocene, this assumption means that fossil preservation is unbiased and that no disorganization has naturally occurred since living populations were buried in place. Begun (2016) articulates what many assume about taphonomy when they embark upon paleoenvironmental reconstructions, “The ash beds at Rusinga have yielded fossil grasshoppers and grubs of various insects, as well as the bodies of chameleons, preserved as if they had died at Pompeii” (p. 41). However, Andrews et al. (1972) put it bluntly, “It can be little more than romanticism to theorize that the animals were killed in eruptions” (p. 15). While Begun is not incorrect, the majority of fossils are not of ash falls, but of reworked tephras in fluvial and lacustrine deposits and paleosols and the timing and frequency of eruptive episodes is still being researched by geologists. The assumption of the “Pompeii premise” site can be immediately falsified with evidence from R5, R106, R114, R117, R4, R3 and R1 for fluvial transport, predation damage on fossils, post-depositional fragmentation and time averaging of fossil assemblages. The task then becomes assessing how fossil assemblages are biased and what parts of the living assemblages are preserved via taphonomic reconstructions.

The second and third assumptions deal directly with provenience and association among fossils and geologic contexts and the history of the collections themselves. The majority of fossils housed in the National Museums of Kenya are from Leakey and Dr. Donald MacInnes’s East African Archaeological Expedition (E.A.A.E.) in the early 1940s and during the late 1940s and 50s with Leakey’s and Le Gros Clark’s British-Kenya Miocene Expedition (B.-K.M.E.) collections. This period of collection and research is often referred to as the “most prolific” or “intense” because approximately 20,000 fossil specimens were collected during this time and over 200 of those were primates (Andrews, 1978 p86; Pickford 1984). From these materials, Le Gros Clark and Leakey were able to describe a number of hominoid taxa (1950; 1951). Unfortunately, during these collections fossil provenience is only loosely recorded to R-numbered site names, and only roughly mapped (Le Gros Clark and Leakey, 1951 p. 9). Additionally, the geology was poorly understood during early collections and so fossils are rarely provenienced to beds, and sometimes not even to formations. Because of this, fossils and paleoecological reconstructions are often lumped as an analytical unit of “Rusinga”.

Much of Rusinga Island’s 5 square kilometers are fossiliferous. Rusinga’s Miocene deposits include 4 fossiliferous formations, spanning nearly 2.5 million years. Rusinga’s fossil assemblages have been continuously sampled for nearly 100 years and deposits have produced tens of thousands more fossils than any of the nearby and contemporaneous sites. A grouped Rusinga fauna is thus horrendously stratigraphically and spatially averaged. A grouped fauna is not an appropriate for ecological reconstructions, nor is it an appropriate comparison for examining faunal communities regionally.

Rusinga’s many localities can and should be examined individually if we are to better understand questions of local endemism, faunal influxes from Eurasia, and the evolution of the primate taxa themselves. Many have called for the type of collections methods needed to broadly reconstruct taphonomic site formation processes and thus ground paleoenvironmental reconstructions.

> The original collections of the fossils (referring to the Leakey collections, which represent the majority of the Rusinga fossils) were almost exclusively surface picked from where they had

> eroded out of sediments. Pickings from large areas were included under one site number. As many of the exposures occur in gully systems, one site number also included material from more than one stratigraphic level.
>
> *Collinson (1983; p. 5)*

> … data fall short of the kind of paleoecological study that could be achieved by more dedicated attention to the exact location of a large number of fossils.
>
> *Retallack (1991; p. 228)*

> … we lack the knowledge of exact horizons and localities of most of the specimens. Also unknown are possible biases of past collectors… This makes it impossible to determine such things as faunal differences between horizons, minimum numbers of individuals of different taxa, relative numbers of juveniles to adults, and relative numbers of skeletal analysis. Without this, analysis of the fauna and interpretation of associations is difficult.
>
> *Andrews et al. (1972; p. 16)*

Korlandt (1983) espouses a pessimistic view, “One can only hope that the mixing up of the plant fossils has resulted in a sample that represents a good average” (p. 475) as he laments the faunal mixing, a lack taphonomic considerations, and a lack of precise in reporting for Early Miocene sites paleoecological reconstructions.

Indeed several researchers embarked on research intended to help rectify these issues. Walker and Teaford collected some taphonomic data and published some maps of their finds from the Kaswanga Primate Site (Walker et al., 1988; Walker, 2007). Before Peter Andrews was known for his contributions to the field of taphonomy, he and colleagues published taphonomic observations at R5 (Andrews et al., 1972; Andrews and Van Couvering, 1975) and from R117, the Fruit and Nut Bed (Collison 1983; Collinson et al., 2009). However, other taphonomic assertions from Rusinga Island have been more anecdotal – R4

(Peppe et al., 2009), RU-2036 from tree trunk/pot hole (Walker, 2007), Wayando Formation (Pickford, 1984).

Miocene Research Questions

The need for detailed provenience, stratigraphic control, and taphonomic interpretations are clear. This dissertation thus builds on past and current research to carefully analyze individual sites so that those finding may inform the broader conversation on paleoecological contexts of early Miocene primates. In this vein, Chapter 2 examines the well-known R5-Kaswanga locality on Rusinga. Here, I test hypotheses of site formation with taphonomic data sets from systematic surface collections and a recently discovered bonebed. These findings are considered in light of other historic R5 excavations from the 1980s (KPS) and 1970s (Andrews et al., 1972) to assess how mixed surface collections may be and to reconstruct an a broader site formation processes.

The focus on paleoenvironments as a driver of ape evolution has been inescapable, but vegetation cover, rainfall, and seasonality would not have been the only selective pressures the Kisingiri Miocene primate community would have faced. In Chapter 4, I take individual primate remains from across Rusinga and Mfangano to assess trends in predation on the primate community. Assessments of surface modifications, grounded in actualism, show that *Ekembo*, *Dendropithecus*, and some lorisoids fell prey to a suite of creodonts, carnivores, and avian raptors. Such encounters can influence sociality, foraging behaviors, and body size and are an important regional consideration as new predators from Eurasia migrated into Africa during the early Miocene.

Pleistocene Rusinga Background

Much of what is understood about Middle Stone Age early modern humans is known from cave sites in South Africa with relatively little known from eastern Africa. However, East African Pleistocene sites are especially important for evaluating hypotheses as to why and how modern humans left Africa. Pleistocene deposits and fauna have long been known on Rusinga Island (Kent, 1942; Van Couvering, 1972; Pickford, 1984), but little attention had been paid to Rusinga's Wasiriya Beds until recently. Christian Tryon renewed research on Rusinga at the invitation the Miocene research team. Work by Tryon's team subsequently identified Middle Stone Age artifacts (Tryon et al., 2010; 2012), refined faunal reconstructions (Faith et al., 2011; Faith, 2013; O'Brien et al., 2015), assessed paleoenvironments via isotopes and faunal data (Tryon et al., 2010; 2012; Garrett et al., 2015), and clarified chronostratigraphy (Blegen et al., 2016). Behavioral and archaeological reconstructions of Middle Stone Age humans have been limited to regional artifact comparisons (Tryon and Faith, 2013). Only a single humerus fragment is attributed to anatomically modern humans on Rusinga Island (Peason et al., 2018), but more morphology is known from other roughly contemporaneous specimens in the region including Lukenya (Gramly and Rightmire, 1973; Tryon et al., 2015), Aduma, (Haile-Selassie et al, 2004; Yellen et al., 2005), Lake Eyasi (Domínguez-Rodrigo et al, 2008). Paleoenvironmental reconstructions show that during the mid-late Pleistocene, Lake Victoria was much lower than today and Rusinga and Mfangano Islands were merely high points in an expansive grassland. Tryon et al. (2012; 2016) hypothesize that resources and springs on the “islands” may have drawn Middle Stone Age (MSA) modern humans and fauna to the area and that lake levels fluctuated over time, but given the relatively low density of artifacts, it is unclear how important the area was to MSA peoples.

Pleistocene Research Questions:

Chapter 6 of this dissertation examines the site formation processes of the densest Pleistocene locality on Rusinga Island, Bovid Hill at Wakondo. At Bovid Hill a monospecific accumulation of the extinct bovid *Rusingoryx* is associated with a MSA lithic assemblage. Despite early modern humans’ large brains, a suite of behaviorally modern tool kits, the development of art and jewelry, and a large number of sites where hunting has been inferred (McBrearty and Brooks, 2000; McBrearty, 2013) scavenging is often still considered a default interpretation and must be ruled out for sites. However, taphonomic and faunal evidence at Bovid Hill suggest that MSA humans tactically hunted *Rusingoryx*. When considered regionally, Bovid Hill can be part of broad and seasonal land use reconstructions for early modern humans (Marean, 1997). These analyses together help inform our understanding of our species as they developed more recognizably “modern” behaviors (McBrearty, 2013).

Table 1.1: Brief Summary of the Primate Taxa on Rusinga Island.

	Taxon	Published Diagnoses	Dietary Reconstructions[1]	Body Size[2]	Locomotor Reconstructions[3]	Type specimen	Type Locality	Notable Referred Specimens	Synonyms
Catarrhines	*Ekembo nyanzae*	MacInnes 1943 McNulty et al 2015	soft fruit	28-40 kgs	above branch arboreal quadruped	BMNH M 16647 (CMA.2)	R1a	KNM-MW-13142	*Proconsul africanus,* *Proconsul major* *Proconsul nyanzae*
	Ekembo heseloni	Le Gros Clark, 1949 Walker et al., 1993 McNulty et al., 2015	soft fruit	10-20 kgs	above branch arboreal quadruped	KNM-RU-2036	R114	KNM-RU-7290, KPS	*Proconsul africanus,* *Dryopithecus africanus* *Proconsul heseloni*
	Dendropithecus macinnesi	Le Gros Clark and Leakey, 1950; 1951 Andrews and Simons, 1977	soft fruit, some folivory	5-9kgs	agile above branch arboreal quadruped	BMNH M 16650	Wakando (Kulu)	R3 skeletons	*Limnopithecus macinnesi*
	Nyanzapithecus vancouveringorum	Andrews, 1974 Kunimatsu, 1992	n/a	11-8 kg	n/a	KNM-RU 2058	R2 Nyamsingula (Hiwegi)	n/a	*Dryopithecus vancouveringi* *Proconsul vancouveringi* *Ragwapitheucs vancouveringi*
	Limnopithecus legetet	Hopwood, 1933 Le Gros Clark and Thomas,	soft fruit	5kgs	n/a	BMNH M 14079	Koru	n/a	n/a

		1951 Le Gros Clark, 1952							
Lorisiformes	*Mioeuoticus shipmani*	Phillips and Walker, 2000	n/a	n/a	quadruped	KMN-RU-2052 (complete cranium)	R105b (Fruit and Nut Bed)	n/a	*Progalago dorae*
	Mioeuoticus bishopi	Leakey ,1962	n/a	n/a	some leaping	NAP I.3.6/58	Napak I	n/a	*Progalago songhorensisi*
	Komba minor	Le Gros Clark and Thomas 1952	n/a	<200 g	leaping	KNM-SO-438	Songhor	n/a	n/a
	Komba robustus	Le Gros Clark and Thomas, 1952	n/a	>200 g	climbing, quadruped	KNM-SO-501	Songhor	n/a	n/a
	Komba walkeri	Harrison, 2010	n/a	<200 g	n/a	KNM-MF-100	A3 Mfangano	KNM-RU-1940 endocast	n/a

1 References for dietary reconstructions: Ungar et al, 2004; Shearer et al., 2015

2 References for body sizes: Ruff et al., 1989; Harrison 2002a; 2002b; Harrison 2010; Le Gros Clark and Thomas, 1952

3 Locomotor reconstructions: *Ekembo*-- Beard et al., 1993, Begun et al., 1994; Ward et al., 1993; Ward et al., 1995, Rafferty et al., 1995; Ward et al., 1997; Dunsworth, 2006. *Dendropithecus*-- Andrews and Simons, 1977; Rose, 1994. Lorisiforms—Gebo, 1986

Table 1.2: Paleoenvironmental Reconstructions for Miocene Rusinga

Bed	Site	Results: inferred habitat/paleoclimate/vegetation	Proxy	Author	Evidence/notes
Kulu	R4	evergreen forest	non-marine mollusca	Verdcourt, 1963	
Hiwegi	R3	colonizing forest	paleosols	Retallack et al., 1995	
Hiwegi	R3	evergreen forest, gallery forest and savanna	non-marine mollusca	Verdcourt, 1963	
Hiwegi	R3	forested	plant fossils	Michel et al., 2014	large fossil stumps and roots
Hiwegi	R1	colonizing woodland	paleosols	Retallack et al., 1995	
Hiwegi	R1	colonizing forest	paleosols	Retallack et al., 1995	
Hiwegi	R1	riparian forest	paleosols	Retallack et al., 1995	reports no fossil plants
Hiwegi	R1	angiosperm-dominated, humid-sub humid	fossil bee nest	Thackray, 1994	preferences and requirements of modern bee nests
Hiwegi	R1	dry evergreen forest, savanna or bush	non-marine mollusca	Verdcourt, 1963	
Hiwegi, Fossil bed member,	R1	variable habitats through time: open grassy riparian forest, colonizing forest, wet woodland, 479+/-282 mm MAP	paleosols	Retallack et al., 1995	Retallack paleosol typology and associated with modern analogs
Hiwegi	R1 Rhino Quarry	grassy riparian forest, well drained	paleosols	Retallack et al., 1995	
Hiwegi	R106	riparian forest	paleosols	Retallack et al., 1995	reports no fossil plants
Hiwegi	R107	forested- shrubs	chameleon fossil	Rieppel, et al. 1992	modern analogy

Hiwegi	R117	closed woodland	fossil plants	Colinson et al., 2009	climbing plants, trees, lack of grasses and few thorny bushes
Hiwegi	R117	gallery forest/disrupted woodland	fossil plants	Collinson, 1983	*in situ* collection of nuts, leaves and seeds. lack of fossil grasses and large forest trees, shrubs and woody climbers
Hiwegi	R117	colonizing woodland	paleosols	Retallack et al., 1995	
Hiwegi, Grit member	R5	tropical seasonal forest, MAP 100-160cm, MAT 30	fossil leaves	Maxbauer et al., 2013	leaf size and shape
Hiwegi	R5	forested	fossil community	Andrews and Van Couvering, 1975	forest dwelling taxa
Hiwegi	R5	riparian forest	paleosols	Retallack et al 1995	no fossil plants
Hiwegi	R5	evergreen forest and savanna	non-marine mollusca	Verdcourt, 1963	modern analogy

Table continued below

Bed	Site	Results: inferred habitat/paleoclimate/vegetation	Proxy	Author	Evidence/notes
Kiahera	R114 pot hole	semi-aquatic, riparian habitat	ecomorphology	Clos, 1995	fossil varanid
Kiahera and Hiwegi formations	unknown	disturbed by pyroclastic flows (not stream side), semi-arid, water stressed (no mock aridity)	paleosols, sedimentology, isotopes	Bestland and Krull, 1999	cross-bedding and large volcaniclastic sediments, inseptosols

Kiahera	Kiahera Hill- R126 or R123 appear to be the closest fossil localities	stream side, dry woodland or shrubby woodland, 550-750mm MAP	paleosols	Bestland and Retallack, 1993	Retallack paleosol typology
Kiahera	top of series?	swampy lakes, dry forest or savanna	non-marine mollusca	Verdcourt, 1963	modern analogy
Wayondo	Gumba	humid- sub humid	paleosols, geochemistry and isotopes	Forbes et al., 2004	paleosols show less weathering than Kiahera paleosols
Wayondo	R74-75	lake or river	non-marine mollusca	Verdcourt, 1963	modern analogy
Wayondo	Gumba	lakes and drainages	fossil mollusca	Kat, 1987	sedimentology and presence of fresh water mollusca

CHAPTER 2 EKEMBO IN CONTEXT: TAPHONOMY AND SITE FORMATION AT R5-KASWANGA

Introduction

Rusinga Island in southwestern Kenya is well known for its rich fossil primate and mammalian collections (Le Gros Clark and Leakey, 1950; Le Gros Clark and Leakey, 1951; Napier and Davis, 1959; Walker and Teaford, 1988; Walker and Shipman, 2005; Werdlin and Sanders, 2010; Andrews, 2016). Several important localities make up Rusinga's fossil assemblages, but R5-Kaswanga, central along the northern edge of the island, is among the richest. R5-Kaswanga is home to the Kaswanga Primate Site (KPS) where ten *Ekembo heseloni* partial skeletons were recovered in the 1980s (Walker and Teaford, 1988; Walker and Shipman, 2005; Walker 2007). Additionally, hundreds of mammalian and reptilian fossils compliment 51 more isolated primate specimens from this locality (Le Gros Clark and Leakey, 1951; Andrews et al., 1972; Andrews and Van Couvering, 1975; McNulty et al., 2007). With nearly 100 years of intermittent fossil collection, all of the Miocene primate taxa known from Rusinga as a whole are also known from R5-Kaswanga. R5-Kaswanga creates an excellent opportunity to examine the community structures and environmental contexts of the early Miocene catarrhines that lived on Rusinga.

There have been many attempts to reconstruct the environmental contexts of the Rusinga primates, many discordant of one another (see Chapter 1 for a review). Some potential reasons for these conflicting results include a failure to take into account the taphonomic histories of the fossil themselves, fossil assemblages mixed from both multiple localities or stratigraphic layers, and poor association between geologic methods of environmental reconstruction and the fossil organisms in question. Indeed, Rusinga Island is more than 5 square kilometers, with fossil deposits spanning approximately 3 million years (Evernden et al., 1964; Van Couvering and Miller, 1969; Drake et al., 1988; Peppe et al., 2009; Peppe et al., 2011; 2017). Properly documenting the paleoenvironments associated with these fossil deposits requires that localities such as R5-Kaswanga must be examined carefully and individually. Taphonomic reconstructions and careful field documentation that consider collection and preservation biases, depositional settings and processes, and spatial variability are needed to set the stage for careful environmental reconstructions. Without taphonomy, it is difficult to assess various paleoenvironmental reconstructions. Additionally, taphonomy can lend its own independent assessment of depositional environments and settings for fossils. This paper represents the first site-level synthesis of historic and recent work and taphonomic characterization of fossil deposits on Rusinga Island.

Environmental reconstructions that can be squarely associated with the fossils begin with detailed data collection in the field. Indeed, R5-Kaswanga has a long history of fossil collection and much of what is understood about the

Rusinga Island fauna and paleoenvironments has been generated from R5 datasets. In an effort to build a strong taphonomic foundation for paleoenvironmental reconstructions at R5-Kaswanga, I designed surface collection protocols to collect data for taphonomic sampling and led teams in archaeological style excavations across the site. During excavation, the team uncovered two previously unrecorded leave beds and a dense bonebed at Nyang Rise. While surface collections are stratigraphically averaged, taphonomic reconstructions of Nyang Rise and other previously reported accumulations at R5 suggest the site formed in a broad riparian habitat.

History of Study at R5

Miocene deposits and fossil wood were first reported on Rusinga Island in 1908 by Herbert Brentwood Maufe while he was surveying various locales of East Africa (Kent, 1944; Pickford, 1986). E. J. Wayland later was charged with conducting a geologic survey of Uganda and the Lake Victoria region for the British Empire in the early part of the century, and visited Rusinga and Mfangano Islands in 1929 reporting fossil vertebrates in 1930 (Pickford, 1986; Kent, 1978; Walker and Shipman, 2005). These findings caught the attention of Louis Leakey who, along with Donald MacInnes, organized the East African Archaeological Expedition (E.A.A.E.) to travel to Rusinga Island.

Louis and Mary Leakey often visited Rusinga Island for short fossil-hunting expeditions during Louis's appointment as senior curator at the Coryndon Museum (now the National Museums of Kenya) in Nairobi throughout the 1940s-50s under the British-Kenya Miocene Expedition project (B.-K.M.E.), which also focused efforts at Koru, Songhor and Karungu from 1947-1951 (Andrews, 1978). Like the E.A.A.E., the B.-K.M.E. was headed by Louis Leakey, but now British anatomist, W. E. Les Gros Clark, was co-directing the research. This period of collection and research is often referred to as “intense” or the “most prolific” because approximately 20,000 fossil specimens, including more than 200 primate specimens, were collected during this time (Andrews, 1978: 86; Pickford, 1986). From these materials, Le Gros Clark and Leakey were able to describe a number of new hominoid taxa (1949; 1950; 1951).

During their expeditions, the Leakeys and their teams visited many fossil sites in the region and on Rusinga Island. They gave those fossil deposits from the Kaswanga area (historically referred to as “Kathwanga”) site designations such as “R5”. Le Gros Clark and Leakey (1951) indicate on their map that sites numbered R30-40 and R80-90 are also at Kaswanga Point. However, Van Couvering (1969) reported that the specific locations of sites R30-40 and R80-90 were no longer known nor used as site names. Given the complicated history site names, I refer to fossiliferous deposits from the entire Kaswanga Point area as “R5-Kaswanga” to encompass past names R30-40, R80-91, Andrew’s collections, KPS, and recent collections commonly referred to as “R5”. As of 1948, the B.-K.M.E. had collected 23 hominoid remains from the Kaswanga area (Le Gros Clark and Leakey, 1951). Multiple geologists and paleontologists also visited the site during the B.-K.M.E. years. Shackleton (1951) noted during his geologic surveys of the area that it was one of the more fossiliferous localities. Van Couvering (1972) undertook the detailed stratigraphic analysis of Rusinga’s fossil deposits, placing Kaswanga within the overall context of the island's geology, and as part of that study reported that several of the carnivore/creodont remains published in Savage's (1965) "Miocene Carnivora or East Africa" come from Kaswanga.

At the end of their tenure on Rusinga, Louis and Mary Leakey invited John Van Couvering, Peter Andrews, and Judy (nee Harris) Van Couvering to conduct systematic geologic and taphonomic surveys, and Kaswanga was the focus of these studies (Figure 2.1) (Andrews et al., 1972; 1975; Van Couvering, 1972). In total, Andrews' team dug 6 small excavations and approximately 16 square meters from the slopes along the Coryndon, Kent, Shackleton, Whitworth and Ndere Gullies in the southern portion of the Kaswanga locality (Figure 2.1). These were labeled KA, KB, KD, KE, KF, KG and KH and accompanied by gridded surface collections along the Kent Gully (site KA), Coryndon Gully (site KC) (Andrews and Van Couvering, 1975; Andrews et al., 1972; Andrews, unpublished notes 1972). Fossils recovered *in situ* were piece-plotted and orientation was measured (Andrews et al., 1972; Andrews and Van Couvering, 1975).

Peter Andrews, Judy Harris, and John Van Couvering's work at R5 became the basis for paleoenvironmental reconstructions projected too much of the Island's deposits. Fossils found in their excavations were attributed to various habitats through time (e.g. forest, "open", stream-side forest) based on taxon frequencies, leading to the conclusion that the associated Miocene primates were able to adapt to several types of habitats (Andrews and Van Couvering, 1975). Van Couvering (1972) references Andrew's and Harris's unpublished taphonomic study at R5 to note that fossil from the same individuals were in association of one another, but often disarticulated. This, as well as fine-grained sediments and the absence of soil horizons suggested to the team that "whole or partial corpses (had been) suspended in gentle currents" (p 174).

Despite the long history of research on Rusinga, it was the discovery of 10 partial skeletons of *Ekembo heseloni* (then referred to *Proconsul*) that made Kaswanga widely known in the paleoanthropological community (Walker and Teaford, 1988; Walker and Shipman, 2005; Walker, 2007). In 1984, Peter Nzube, working with a team headed by Alan Walker and Mark Teaford, discovered several *in situ* primate remains in an area that would become known as the Kaswanga Primate Site (KPS). The team promptly excavated and screened approximately 25m^2 of the shallow deposit (Walker and Teaford, 1988; Walker et al., 2007). These remains became the focus of several studies, clarifying the morphology and ontogeny of the genus (Ruff et al.,1989; Ward et al., 1991; Walker et al., 1993; Begun et al., 1994; Beyon et al., 1998; Nakatsukasa, et al., 2004; Dunsworth, 2006; Daver and Nakatsukasa, 2015).

The Kaswanga Primate Site is approximately 300 meters north of Andrews' and Harris's excavations. Primate remains were found in a fine-grained tuffaceous greenish and reddish silts and clays, just above the Grit Member. Walker's team recovered fruits, leaves, and limited vertebrate remains (lagomorph, small ruminant, carnivore/creodont, fish, bird, and crocodile remains) associated with the primate fossils (Walker and Teaford, 1988; Walker, 2007;

Jenkins unpublished field notes). Walker and Shipman (2005) disclose that Pickford noted the site as having crocodiles and leaves as well. Walker (2007) interprets the deposits as a possible creodont den, citing observed tooth pits, skeletal part representation reminiscent of C.K. Brain's (1981) leopard –baboon feeding experiments, and a sediment feature determined to be a den. However, I challenge this interpretation in chapter 2 and instead consider the KPS to be a raptor accumulation. Walker and colleagues (Walker and Teaford, 1988; Walker, 2007) also interpret sediments to have been laid down by low energy water, and bone orientations from primate remains are also suggestive of some reorientation by moving water.

Geology at R5

Early geologic work on Rusinga was largely driven by the need for chronostratigraphic control as Rusinga's fossil primates (Kent, 1942; 1944; Shackleton, 1951; Whitworth 1953). Shackleton (1951) conducted the first geologic research on deposits specific to the Kaswanga area. Van Couvering (1972) later refined this work and a team of geologists (Al Deino, David Fox, Steve Dreise, and Lauren Michel) led by Dan Peppe continues to advance our understanding of stratigraphic, sedimentological, and environmental reconstructions and dating of the site (Peppe et al., 2009; Peppe et al., 2011; Michel et al., 2014; 2017).

The Kaswanga deposits consist of three members of the Hiwegi Formation: Kaswanga Point Member, Grit Member, and Fossil Bed Member (Van Couvering, 1972). The Kaswanga Point Member rests at the base of the Hiwegi formation and lies unconformably above the Rusinga Agglomerate. It is made up of thin flaggy brown-greyish tuffs with accretionary lapilli and mica flakes, and is generally interpreted as a series of eruptive air fall deposits (Van Couvering, 1972). Fossils are rare. The deposits are best exposed on the northern edge of the Kaswanga area, near the lake, but are also known from R4, R107, and on Kiahera Hill (Van Couvering, 1972). The Kaswanga Point Member was placed at 14-17 Ma by early K-Ar dates (Evernden et al., 1964), but later K-Ar attempts dated the deposits to 18 Ma (Drake et al, 1988). In early research, the Kaswanga Point Member is referred to as the “Kathwanga Point Series” (Le Gros Clark and Leakey, 1951; Shackleton, 1951; Van Couvering, 1972).

The overlying Grit Member consists of fluvially deposited and thinly bedded red-grey clays, silts, and sands with some lapilli that are largely interpreted as reworked sediments from the Kaswanga Point Member and the more basal Rusinga Agglomerate (Van Couvering, 1972). While the Grit Member is generally not fossiliferous, some areas appear to be continuous with the Fossil Bed Member. Like the Grit Member, the Fossil Bed Member is also exposed at other important Hiwegi collection sites (R1, R5, R106, among others). The Fossil Bed Member consists of fluvially deposited silts to coarse-grained sands, pebbles and cobbles and contains reworked sediments from the Kaswanga Point Member and Rusinga Agglomerate as well (Van Couvering, 1972). Unlike the Grit Member, the majority of fossils at Kaswanga as well as the rest of the island are known from the Fossil Bed Member. Shacketon (1951) and colleagues (Le Gros Clark and Leakey, 1951) referred to the Grit Member as the “Lower Kathwanga

Series" and it is believed that most portions of the Fossil Bed Member would have been part of the Shackelton's (1951) "Upper Kathwanga Series" (Van Couvering, 1972).

Within the Fossil Bed Member at Kaswanga, Van Couvering, Harris, and Andrews further delineated strata, naming several marker beds in relation to a leaf layer near the base of the sequence. They anchored their excavations and surface collections with resistant sandstone marker beds (Andrews et al., 1972; Van Couvering, 1972; Pickford, 1984). Only one marker bed (IV) appears to have a published description as resistant sandstone of grey-green and coarse grained reworked volcanic tuffs (Van Couvering, 1972).

In 2009, Dan Peppe and David Fox dug a new geologic section (Figure 2.1) west-east across the "Main" collection area and delineated 33 beds, largely consisting of sands and silts that can be interpreted as fluvial channels (Peppe and Fox, 2009 unpublished field notes). This is consistent with Van Couvering's (1972) and Andrews et al., (1972) geologic interpretations of the Fossil Bed Member at Kaswanga. Peppe noted desiccation cracks throughout the sequence (2011; pers comm; Jenkins unpublished field notes). Steve Dreise and Lauren Michel collected samples for thin sections and observed that sediments appear to come from an erosive environment (unpublished data). These preliminary findings initially suggest that Kaswanga may have gone through a drying period during fossil deposition.

2006-2011 Collections

In 2006, Kieran McNulty, Holly Dunsworth, and Will Harcourt-Smith initiated new work on Rusinga with the goal of recovering additional fossils and examining the paleoecology of the Rusinga primates using a multi-disciplinary approach (McNulty et al., 2007). By refining the stratigraphy and applying the paleomagnetism and Ar^{39}-Ar^{40} dating technique, examining paleosols, carbon isotopes (Peppe et al., 2009; Peppe et al., 2011; Michel et al., 2014; Peppe et al., 2017), examining plant fossils (Maxbauer et al., 2013; Michel et al., 2014), uncovering new fauna (Conrad et al., 2013), reexamining taxonomic issues (Conrad et al., 2013; McNulty et al., 2015; Geraads, et al., 2016; Jansma et al., 2016) and assessing dental mircowear (Ungar et al., 2012) the team is in the process of revising and refining the paleoecological context for Rusinga's primate communities. From 2006-2010, informal surface collections took place at R5, but in 2011 the team conducted systematic archaeological style excavations there and used a Trimble total station to map surface finds with the goal of collecting data suitable for taphonomic reconstructions and evaluating stratigraphic averaging at R5.

Materials and Methods

Surface Collections

In 2006-2010, surface collections from the Kaswanga area focused on identifiable fossils and were provenienced with various levels of precision. Fossils included in this study are minimally provenienced to "R5-Kaswanga", while others are recorded as being from previously marked “sites” or sub-localities such as the “KPS” or “Coryndon Gully”. Traditional methods of fossil surface collection are generally insufficient for rigorous taphonomic analyses as they are likely to lack detailed provenience information and not include more poorly preserved specimens that may be unidentifiable but preserve important taphonomic signatures. Larger samples that are unbiased by preservation condition and identification are more likely to yield relevant surface modifications or breakage patterns that help illuminate the taphonomic history of a site. Given the collection bias inherent in previous collections, teams in 2011 used a Trimble total station with sub-centimeter precision to document the 3- dimensional surface position of *all* fossil finds 2cm or longer as well as all “identifiable specimens” (defined as having recognizable anatomy) regardless of size. Surface collections in 2011 focused on the areas around MacInnes, Corydon, Kent, and Shackleton Gullies and at the KPS—all areas geologically associated with the Fossil Bed Member (Figure 2.1). Crews systematically lined up approximately .5 m apart to flag fossils for collection (Figure 2.2). Fossils were first flagged and then shot in with the total station and given a unique field number generated by the total station that referenced its provenience. In total, 854 points with associated fossils (some with multiple fossils in very close association – within 5cm – were collected together) were collected using this method.

Excavation Methods

In order to assess the potential for stratigraphic averaging across the site and to collect data for taphonomic reconstructions, my team opened 16 m^2 of archaeological-style test excavations along the north side of Kent Gully and near Whitworth Gully (also known as the “Main Area”) (Figure 2.1). I placed test excavations along the rise between Coryndon and Kent Gulleys to maximize stratigraphic exposure and test topographically above areas that yielded denser surface accumulations during total station mapping. Excavation crews dug in arbitrary 5cm levels within visible stratigraphic layers. All bones larger than 2 cm were mapped on level forms. All excavated sediments were screened in 5 mm and 2 mm sieves. Each level had a small sample of sediment that was screened for mircofossils in .05-1mm sieves. Jack Conrad and Adam Cossette initiated a small quarry effort at Nyang Rise that was later expanded to formal excavations (Figure 2.1) (Conrad et al., 2013).

Faunal Identifications

The faunal identifications on the 2006-2011 material used in this study have been overseen by Thomas Lehmann with contributions from team members, the author, and taxon specialists. Fossils were identified to the highest level of taxonomic precision possible. A faunal list for R5 was generated using team catalogs (2006-2013), Andrews and Van Couvering’s (1975) excavation overview, and published reports (Le Gros Clark and Leakey, 1950, 1951; Pickford, 1984; Walker et al., 2007. Taxon names were updated according to Werdelin and Sanders (2010) as needed.

Taphonomic Data and Samples

Field teams sorted the 2011 surface collections for identifiable mammals or fossils that may be potentially accessionable in the National Museums of Kenya (unidentifiable, poorly preserved specimens, or excessively common fossils- such as crocodile fragments- are not traditionally stored in the museum collections). Taphonomic data were collected on a 50% random sample of the remaining “taphonomy surface collection” material (n= 672 fossils) as well as all identifiable surface collected specimens pulled for museum accessioning from 2011 (n=58 fossils), for a total 2011 surface collection sample of 740 fossils. Taphonomic data were also collected on all of the 2011 excavated fossil material found *in situ* and over 2 cm (n=997). However, not all data could be collected on every specimen. Some material from the early Nyang Rise Quarry had too much preparation consolidant to reliably collect surface data, but could be used in element counts for skeletal part frequencies. Material recovered from screening was surveyed for identifiable specimens and skeletal part frequencies, but not included in taphonomic analyses. Surface conditions were difficult to assess on turtle and textured crocodile cranial and osteoderms remains unless obvious modifications were present. Additionally, taphonomic data were collected from a limited sample of material from the identified 2006-2010 materials (n=27), and of some of the historic collections – namely primates from the KPS. Counts of these materials and taxa are included, but taphonomic data are not analyzed here.

Many types of taphonomic data were collected: surface modifications (including weathering, rounding, etching, and zoogenic pits, punctures, and grooves), breakage patterns, element portions present for skeletal part frequencies, size, and articulation and orientation patterns (for *in situ* excavated material). Bone pathologies were also recorded.

Several types of zoogenic surface modifications can be identified by their shapes and internal features and there are several potential modifiers from the fossil bearing deposits including a plethora of carnivores, creodonts, avian raptors, crocodiles, and invertebrates. Fossils were surveyed for surface modifications under a 10-20x hand lens and a 20-50x digital Dinolite microscope. Modifications were identified using criteria outlined in actualistic and experimental studies of animal tooth pits and gnawing (Binford, 1981; Haynes, 1983; Selvaggio and Wilder, 2001; Njau and Blumenschine, 2006; Pobiner et al., 2007; Pobiner, 2008; Domínguez-Solera and Domínguez-Rodrigo, 2008; Delaney-Rivera et al., 2009; Ferández-Jalvo and Andrews, 2010), avian raptor damage (see chapter 4) invertebrate damage (Behrensmeyer, 1978; Throme and Kimsey, 1983; Watson and Abbey, 1986; Tappen, 1994; Roberts et al., 2007), and rodent gnawing (Brain, 1981; Shipman and Rose, 1983; Kibii, 2009). Size, shape, internal morphology, and placement were recorded for surface modifications. Post-depositional surface modifications such as weathering (Behrensmeyer, 1978), fluvial rounding (Binford 1981; Tappen 1994; Domínguez-Rodrigo and Barba, 2006; Blumenschine et al, 2007;) root etching and bioerosion (Binford 1981; Tappen 1994; Domínguez-Rodrigo and Barba, 2006; Blumenschine et al, 2007;), and trampling (Behrensmeyer, 1988; Domínguez-Rodrigo et al., 2009; Domínguez-Rodrigo et al., 2010) were also recorded. Weathering stages were not assessed on crocodile osteroderms due to their unique surface morphology and lack of comparative data.

Breakage patterns were characterized according to Villa and Mahieu (1991) and notches were identified using criteria outlined by Capaldo and Blumenschine (1994) and Brain (1981). These were grouped into more conservative categories of pre-fossilization fresh breakage (largely consisting of green bone breakage, but also including extensive damage from gnawing in cancellous bone) and a lumped category of post-depositional (pre-fossilization) and post-fossilization breakage (dominated by straight, transverse breakage). While some post-fossilization and post-depositional breakage can clearly be differentiated by color of the break surface, or formation of crystals in the cracks, others are less obvious can only be attributed to a lumped category.

Orientation patterns were taken from the Nyang Rise bonebed using angle measurements taken in GIS on orthographic projections of the excavation area. These images were created using the photogrammetry software Agisoft PhotoScan. Orientations were taken along the long axis of the bone according to Dominguez-Rodrigo et al. (2012) and analyzed in PAST circular statistics (Hammer, 2015).

Results

Excavation Results

Subsurface testing at Kaswanga showed that nearly all the beds present between Coryndon and Kent Gullies are fossiliferous to various degrees. Geologic Beds 25-20 as well as an unnamed and laterally variable bed in between Beds 23 and 24 (now referred to as Bed 23.5) represent the upper-middle portion of the section at R5 (Beds 33-1) and were uncovered in test excavation Units 2, 3, 4, 5, 6, 7, 9 and units opened at Nyang Rise (Peppe and Fox unpublished field notes 2009) (Figure 2.3). Test Unit 1 near the top of the hill between Coryndon and Kent Gullies yielded only Pleistocene deposits (cf. Van Couvering, 1972), and Unit 8, while fossiliferous, showed intense bioturbation drawing into question the integrity of the fossils' geologic association.

From these excavations, two previously unknown fossil leaf beds were discovered and sampled for study by Dan Peppe from Unit 2, Bed 25 and Units 5 and 6 Beds 21 and 20 (with the densest collection at Unit 2. Fragmentary plant remains in the form of wood, leaf stems and fragments, root casts, seeds, and thorns where recovered in small numbers throughout the excavations and were often in association with a small number of bone fragments (Table 2.1). The variable preservation of plant remains throughout the site suggest that some plants parts may have been fluvially transported prior to deposition and burial, or may represent a local accumulation of surface litter. Other deposits with more complete specimens (Unit 2, Beds 25 and Bed 20, Unit 5) may have accumulated largely *in situ* (Collinson et al., 2009).

Vertebrate remains are scarce, but present from all beds that were screened across the excavation. The majority of fossils were recovered from screening efforts, but Beds 24 and 20 were so cemented that reliable screening was not possible. However, sediments from Bed 20 were broken with a hammer in order to recover plant fossils. Remains from the Main Area Test excavations were often too small and fragmentary for identification. Exceptions include two large mammal limb bones from Unit 7 Bed 23.5, lagomorph teeth from Unit 7 Bed 21, a varanid mandible from Unit 5 Bed 21, and scattered crocodile remains (Figure 2.3; Table 2.2).

Nyang Rise

Vertebrate remains are densest from Bed 22, a brown, laminated sandy-silt to clay-loam deposit present at the top of Unit 7, bottom of Unit 9 and Nyang Rise (see Figures 2.3 and 2.4). However, the majority of remains are derived from those units at the Nyang Rise excavation: especially Units A1-3 B1-2, B3/Jack's Quarry. Unit D2 also yielded fossils associated in this bed, but to a lesser extent. Excavations at Nyang Rise revealed a dense bonebed directly under Bed 23, a hard layer of grey tuffaceous sandstone. The bonebed itself was 10-30 cm thick and comprised mainly of crocodiles (*Brochuchus pigotti*; Conrad et al., 2013), but included several size classes of animals: large mammals such as anthracothere and rhinoceros, medium-sized taxa (*Anisinopa*, *Dorcotherium*, suids, and hyrax), as well as unidentified mirco-fauna (Tables 2.3 and 2.4). Vertebrate remains and limited plant fossils are also recovered from Bed 23.5), a greyish brown sandy-silt stone, stratigraphically above the bonebed at Nyang Rise. However, the majority of these are too fragmentary for identification to element or taxon with the exception of easily identified crocodile fragments. Further geologic work by Dan Peppe, Lauren Michele and Steven Dreise suggests that Bed 22 at Nyang Rise likely represents a slow moving fluvial deposit, and thin-sections show evidence of desiccation and erosion at the time of burial (Peppe, pers comm; Driese and Michel, unpublished data).

Nyang Rise Skeletal Parts

Skeletal part frequencies at Nyang Rise show that neither mammals nor crocodiles are complete (Tables 2.5 and 2.6; Figures 2.5 and 2.6). Whereas large mammals are present in the bonebed at Nyang rise, they are only represented by a few specimens of non-overlapping elements each (namely limbs or smaller elements, such as metapodials and other manual/pedal elements) and likely only represent an MNI of one per taxon. MNEs are calculated here using all specimens identified to “large mammal” which likely includes elements from known taxa represented in the excavation: a rhino, a chalicothere, an anthracothere, and a proboscidean. Remains identified to taxon show no overlapping elements and the most frequent element across the large mammal specimens - regardless of identification - are tibiae with an MNE of 4. Given the largest MNE of four and the number of identified taxa, it seems reasonable to assume that no more than four large mammal individuals, each a different taxon, are represented at the excavation.

Crocodile remains were much more numerous within the assemblage and %MAUs (percentage of the minimum number of animal units (Binford, 1981)) were calculated using the most dominant element (femora) to construct an MNI (13), and then scaled by the number of that element present in the body. Percent MAUs (Table 2.6; Figure 2.6) show that while osteroderms and vertebra appear to overwhelm the collections, they are in fact under-represented given an MNI of

13. Small elements such as vertebrae, osteoderms, and phalanges are generally under-represented, as is the case with flatter elements such as ilia, scapulae, and, again, osteoderms. Crania are generally fragmentary and difficult to assign to a specific cranial element, but basio-occipitals are particularly dense and frequent, as are larger and denser long bones such as femora, tibiae, and humeri.

Nyang Rise Taphonomy

Both crocodile remains (10% of the NISP) and large mammal remains (23% of the NISP) show evidence of predation or scavenging in the form of tooth pits and gnawing (Table 2.2; Figure 2.7). Several of the crocodile remains show clear crocodile tooth pits with bisected morphology (Njau and Blumenschine 2006; Domínguez-Rodrigo and Baquedano, 2018) on postcranial remains. Interestingly, pathology in the form of healed breaks and partially healed pits are present in the sample as well (Figure 2.7). Crocodile tooth pits can also exhibit shapes and interior morphologies indistinguishable from carnivore damage. The damage on the large mammal remains at Nyang Rise is neither obviously crocodilian nor mammalian (Figure 2.8). Pits attributed to avian raptors are scarce and identified on larger taxa and crocodiles and likely represent avian scavenging rather than predation. Limited invertebrate damage is present and likely from scavenging insects, but may also derive from aquatic invertebrates as well. The general lack of root damage, trampling, weathering, and rodent gnawing suggests that these remains were not exposed terrestrially prior to burial for any significant amount of time, if at all.

Most skeletal elements from the Nyang Rise excavation are not complete elements and show several types of breakage (Figure 2.9; Table 2.7). Only 22% of the mammalian specimens are complete and these are mostly manual and pedal elements. Some crocodile specimens may fragment more easily due to their suture patterns— vertebra and cranial elements have a greater number of less strongly fused surfaces than those of mammals and thus these specimens are the most fragmentary. Despite this, it is notable that a nearly complete crocodile mandible and cranium (not articulated) were recovered *in situ* (Conrad et al, 2013). Nearly all other crocodile post-cranial elements are also incomplete (with the exception of osteoderms). Most specimens show some post-depositional breakage and/or post-fossilization breakage. *In situ* crushing from sediment compaction is also common throughout the assemblage. Some fossils show high-angled and curved fracture patterns suggesting breakage while still fresh. Some irregular breakage in cancellous bone is also reminiscent of carnivore gnawing and breakage (Figure 2.10).

The surface conditions of the fossils from the Nyang Rise excavation are quite variable. Cortical surfaces range from showing pristine fresh bone surfaces to having variability pitted and decalcified, chalky surfaces; many (nearly 30% Table 2.8) show multiple post-depositional characteristics. However, when specimens were identifiable, chalky surfaces did not regularly prevent the identification of larger perthotaxic surface modifications such as tooth pits or gnawing. Low-stages of pre-fossilization weathering is limited to only 3 mammalian specimens. Behrensmeyer’s (1978) weathering categories were developed from mammalian taxa, and thus it is unclear if the thicker and denser cortical bone of crocodiles would behave similarly. Nevertheless, probable weathering in the form of transverse cracking along cortical bone grain is only noted in one crocodile specimen from the excavation. Crocodile remains exhibited a wide range of rounding patterns (Figure 2.12). Mammalian specimens were also variably rounded, but less severely than crocodile remains. Many specimens both mammalian and crocodilian (37%) yielded rounded fresh breaks, polishing, and exposed cancellous bone while other bone exhibited no rounding at all.

Nyang Rise Spatial Patterns

A small sample of measured bone orientations (n= 41) show a dominant NW-SE trend, with a nearly perpendicular secondary NNE-SSW trend (Figure 2.13). However, two tests of isotropy, Rayleigh's R (null hypothesis of a uniform data) and Rao's U (null hypothesis of non-parametric random distribution) indicated no statistical differences in the distributions (R = 0.19, $p = 0.26$; $U = 112.3$, $p = 0.70$). However, neither of these tests is well equipped to identify bimodal data, and thus it may be difficult to extrapolate anisotropy from them in this data set (Domínguez-Rodrigo, et al, 2014; Hammer, 2015). Watson's U^2 test against a von Mises normal distribution however and was significantly different ($U^2 = 0.15$, $p < 0.005$). Excavation revealed a cluster of bones with the dominant trend in the SW portion of Unit A2 of Nyang Rise that appeared to be adjacent to a possible large fossil root- evident from change in color and texture and identified by team geologist, Dan Peppe. It appears that much of the material in this cluster was pushed against the feature (Figure 2.4).

Surface Collections

The 2006-2011 surface collections produced a more diverse taxon list than the Main Test and Nyang Rise excavations did (Table 2.3). The majority of surface remains are small—under 4 cm in length (Table 2.9; Figure 2.14) — and bone surface conditions show high rates of rounding and pitting/corrosion (Table 2.8; Figure 2.11). Compared to excavated material, the surface collections have unsurprisingly undergone higher rates of post-fossilization weathering in the form of cortical surface cracking (Table 2.8; Figure 2.11). Breakage patterns are dominated by post-fossilization and/or dry breakage patterns, but nearly 30% of surface finds also show high-angled fresh bone breakage (Table 2.7; Figure 2.9). The surface collections showed a greater diversity in bone surface modifications than the excavated material, but the excavated material yielded greater proportions of tooth pits (Table 2.4).

Historic Excavation comparisons

Variable geologic descriptions between the recent and historic work make it difficult to compare excavation layers to one another. However, using sketch maps, topography and descriptions provided in Andrews et al., (1972) and Dan Peppe and David's Fox's 2009 unpublished field notes, the following seems likely: Van Couvering's Marker Bed II is captured in the 2011 excavations as Sand Stone Lens #1 in Bed 25 (Figure 2.3), and thus Andrews' excavation Units

KB and KH (grey silts and red clays) appear to be sampling the same strata tested in Main Test Excavation Units 2, 3, and 4 (Figure 2.1). Andrews' units are more fossiliferous, but did not capture a leaf layer present in Unit 2, suggesting that these faunal and leaf accumulations may not be continuous.

Van Couvering's (1972) Marker Bed I may be Sand Stone Lens #2 (Figure 2.3) that is largely deflated from the western exposure of R5 (Main Excavation Unit 7 and Nyang Rise) and may have been more easily identified in the eastern gully exposures (Figure 2.1). However, it is unclear if Andrews' Units KG and KF are equivalent to Beds 23.5 or 22 (the Nyang Rise Bone Bed). Unit KE appears to be topographically similar to deposits at Nyang Rise, but Andrews et al. (1972) report that this horizon is stratigraphically much lower than the leaf bed (presumed to be Beds 21 or 22, but may also possibly be the Maxbauer Leaf Bed). Alternatively, Andrews and Van Couvering's (1972) leaf bed may be an accumulation yet to be discovered by our team, or may no longer exist.

Given their similar elevation and relative close proximity, it is possible that Units KE and KF are part of the same deposit as Nyang Rise, and possibly an unexcavated area, "Croc Knob" (Figure 2.1). Indeed, all four areas are dense with crocodile remains (Andrews et al., 1972). Alternatively, they may represent repeating taphonomic processes throughout the sequence. The preferred relative stratigraphic sequence of excavations is summarized in Table 2.10.

The Kaswanga Primate Site is currently hanging in the stratigraphic sequence due to several volcanic dikes creating faulting at R5 (Figure 2.1). The KPS may be relatively low in the sequence near the bottom of the Hiwegi formation, as it appears to lie near the top of the Grit Member. Recent excavations in 2016 carried out by Thomas Lehman and Kieran McNulty may help to resolve this question.

Discussion

The paleoenvironmental setting, timing of deposition, and the behaviors that lead to the depositions should each be considered separately. At R5-Kaswanga, sediments within the Fossil Bed Member suggest successive deposits of low energy fluvial sediments (Van Couvering, 1972 Andrews et al., 1972; Peppe and Fox, unpublished field notes 2009). Andrews et al. (1972) suggest that numerous fossil accumulations may be within ponded areas of a larger alluvial channel system of braided streams. Andrews et al. (1972) and Andrews and Van Couvering (1975) recovered several relatively dense fossil pockets throughout the sequence. Alan Walker's KPS excavation likely represents another such pocket. The 2011 Main Test excavations revealed two previously unrecorded leaf beds, as did Maxbauer and Peppe's stratigraphically low leaf bed (Maxbauer, 2014). While the 2011 Main Area Test excavations did not expose any new bonebeds along Coryndon Gully, the presence of fossil material throughout test excavations further highlights that much of the sequence is indeed fossiliferous, but in discontinuous deposits. There are currently no sedimentary descriptions that indicate a depositional context other than a fluvial setting. Given the similarities of the sediments throughout the sequence it seems reasonable to assume that the majority of fossils are derived from ponded pockets of low energy fluvial sediments. Recent paleomagnetic dating by Dan Peppe shows that the deposits likely span 200-300k years (Peppe et al., 2017). As several small bonebeds are now known throughout the sequence, it is reasonable to assume that surface collections are stratigraphically averaged and represent 200-300k years of deposition. The excavated materials at Nyang Rise likely represent another such separate and localized bonebed within the sequence, but these inferences can be further assessed with additional taphonomic data. Fossils eroding from original contexts likely bear some characteristics of their taphonomic history and may help us understand if the majority of surface finds are related to the bonebed at Nyang Rise.

The surface collections have a greater taxonomic richness than the Nyang Rise excavation and greater richness in taphonomic surface modifications (Table 2.4). While surface collections from 2006-2010 were biased toward identifiable mammal elements, collections in 2011 contained nearly all specimens over 2 cm, regardless of preservation or identification. Fossils that were not collected during earlier seasons due to more restrictive collection criteria might have remained extant on the surface and been collected during the 2011 surface collections. However, the differences between these samples suggest that surface collections are derived from multiple horizons and not related to sample collection methods.

Coarse mammalian size classes reflect similarly low frequencies of large and medium sized taxa between the surface and excavated assemblages (Table 2.4). Surprisingly, small taxa are more frequent from the surface collections—an opposite finding of Andrews et al., (1972) and Van Couvering (1975). Both 5 mm and 2 mm screens were used to sieve materials at Nyang Rise and at the Main Test excavation. The general lack of small taxa from the excavations appears to be a real taxonomic or taphonomic bias and not a collection bias, further suggesting that the small mammals recovered by the 2006-2011 surface collections and Andrews' team are likely derived from other bonebeds not captured in the 2011 excavations.

The greater frequency of indeterminant specimens in the surface collections likely reflects the smaller sizes of these fossils and high rates of post-depositional/post-fossilization breakage (Figures 2.9 and 2.14). The high frequency of crocodiles in the excavated assemblage as compared to the surface collection (Table 2.4) also appears to be a real difference. Crocodile remains—even when not identifiable to element—can often still be identified as crocodile due to their thick cortical bone. Given the smaller sizes and more fragmentary nature of the surface collections, the frequency of crocodile remains is probably over estimated here compared to the excavated material. Thus, taxonomic differences between the surface and excavation assemblages do not reflect collection biases and support the hypothesis that the surface collections do not derive solely from the same depositional layers as Nyang Rise.

Surface conditions of the bones from the surface collections show high rates of rounding and polish (Figure 2.11), which likely reflect both the fluvial depositional environments and post-fossilization exposure. When compared to the excavated assemblage, higher rates of pitting/corrosion and concretions in the surface collections may obscure surface modifications and may explain the generally low frequencies of surface modifications on the surface collections. However, it would not explain the greater diversity of biogenic surface modifications observed on the surface collections. Taxonomic diversity and surface modification frequencies between the excavation and the surface collections further support a hypothesis that the surface collections do not derive from the Nyang Rise deposits alone.

Past excavations, geologic work, taxonomic diversity, and taphonomic characteristics suggest that Nyang Rise is one of many small bonebeds throughout R5. Rogers and Kidwell (2007) provide an important framework for interpreting taphonomic histories: assemblages should be considered in both in terms of their biogenic accumulators — resulting from the behavior of either the animals preserved themselves (intrinsic) or their collectors/hunters (extrinsic) and physical accumulators (hydraulic and sedimentological variables that lead to the assemblage accumulation and preservation. While several pockets of bonebed (KPS, Andrews and Harrison excavations, Nyang Rise) appear to be in similar fluvial depositional environments, it seems plausible that different extrinsic biogenic factors with variable post-depositional hydraulic influences contributed to their accumulations.

Nyang Rise Excavation interpretation

The several taphonomic variables from the excavation at Nyang Rise point to a complex taphonomic history. Crocodile behaviors, the accumulation of large and medium mammals and fluvial processes are all examined separately and appear to reflect a stream-side attritional accumulation.

Tooth pits, gnawing, and fresh bone breakage on both the larger mammals and crocodiles are indicative of early depositional processes. Additionally, many of the crocodile bones themselves have clear crocodile tooth pits, while other tooth pits cannot be assigned to an agent. Tooth pits by carnivores tend to be circular or semi-circular in outline with crushed and flattened interiors (Binford, 1981; Haynes, 1983; Pobiner, 2008). The diameter of a tooth pit can be related to the size of the tooth that made it, but large teeth can still produce small or shallow pits or punctures (Delaney-Rivera et al., 2009). Carnivore gnawing produces U-shaped grooves with crushed bone and is often concentrated on limb ends or on other locations with spongy bone (Haynes, 1983; Marean and Kim 1998). Bone breakage can be common with some carnivores and consumption may leave notches and curved breakage (Capaldo and Blumenschine, 1994).

However, crocodiles may also leave similar marks. As crocodiles capture and disarticulate prey, they often leave tooth pits on the cortical surfaces. These have a distinctive morphology, described as “bisected pits” reflecting the unique shape of many crocodile teeth. Bisected pits generally have a round outline, similar to a carnivore tooth pit, but often have two rays directed laterally out from and into the center of that pit or a more pointed-ellipse shape. These marks are produced by two sharp ridges, or carinae, along the length of the crown of crocodile teeth. Crocodiles can leave scores on bone similar to that of mammalian carnivores, but these are generally transversely oriented and often have a distinctive “hook shape” as opposed to long straight marks. However, crocodiles do not gnaw the ends of bone like mammalian carnivores do, but may leave drag marks on limb ends while holding on to joints. With their swift strong bite, crocodiles can also leave round or triangular punctures that penetrate the thick cortical bone of large mammal limbs. Actualistic studies have recorded crocodiles feeding and disarticulating carcasses by grabbing hold of the prey’s limbs and performing a “death roll” until the carcass breaks apart. Because of this, pits and punctures are likely to occur at great frequencies on distal limb ends (Njau and Blumenshine, 2006). Bisected marks are unmistakably crocodile, but not all tooth pits left by crocodiles are so distinctive. This is because crocodile teeth can be variable in morphology—despite their homodonty. As teeth wear, bite forces and location of the bite can affect the shape of the pit. Some tooth pits are remarkably similar to carnivore tooth pits because the bisection from carinae can be slight and difficult to see or because the carinae themselves were heavily worn.

Tooth pits, healed breaks, and partially healed pits found on the crocodile remains are indicative of aggression between conspecifics, which has been observed between juveniles and adults extant crocodiles when juveniles infringe on nesting grounds (Hunt, 1977) and among juvenile crocodiles during feeding and other social encounters (Morpurgo et al., 1993; Brien et al., 2013). Mortality profiles for the Nyang Rise crocodiles are unclear, but the presence of some unfused vertebral sutures suggests that at least some of these individuals may have been juveniles (Brochu, 1996; Conrad et al., 2013). Further studies of the suture patterns and femoral sizes may clarify ages of death for the crocodile assemblage. Crocodiles are known to be cannibalistic and will consume either hunted or killed conspecifics (Huchzermeyer, 2003). The crocodiles at Nyang Rise appear to have been aggressive with one another and likely cannibalized some of the individuals buried here.

Large mammalian remains also show tooth pits (not distinctly crocodilian) and medium sized taxa show probable avian damage as well. *Brochuchus pigotti* does not appear to have been a particularly large crocodile (approximately 2-2.5 meters in length) and it is unlikely that it would have regularly predated on larger taxa (Conrad et al 2013), so it is likely that tooth pits on these larger mammals may be the result of crocodile scavenging or from large creodonts or carnivores. Stream-side environments can serve as predation “hot spots” on the landscape as animals congregate near water (Tappen et al., 2007). Animal remains at these sites types of can represent attritional prey taxa of many different predators.

Crocodiles have tough leathery skin and osteoderms that help hold crocodile remains together longer than most mammalian carcasses and can prolong “bloat and float” stages of decay (Syme and Salisbury, 2014). However, at Nyang Rise very few crocodile remains are articulated (exceptions include some cranial elements, a small section of vertebrae, a section of 11 osteoderms (Conrad et al., 2013) and skeletal part frequencies show that whole carcasses were not deposited at Nyang Rise. Two hypotheses may explain the crocodile skeletal part profiles: 1) Nyang Rise represents a “drop zone” where more easily disarticulated portions such as heads and limbs become detached during decay whereas axial elements continue to bloat and float and are transported down stream, or 2) crocodile remains at Nyang Rise are largely lag deposits where less dense elements such as axial elements are transported away from the assemblage by fluvial action, leaving larger denser limbs. Although these hypotheses are not necessarily exclusive of one another, additional support in the form of fossil rounding — especially on vertebral elements — suggests that individual elements, rather than complete or partially complete carcasses, were winnowed from their primary depositional context and subsequently deposited at Nyang Rise. Denser crocodile elements may have been lag deposits, while less dense specimens may have been transported away from the area. Nyang Rise meets several of the criteria discussed in Voohies (1969) and Domínguez-Rodrigo et al. (2014) for assessing fluvially influenced assemblages: fluvial sediments, preferential orientation, presence of rounding and polish, and less dense bone—especially crocodile axial elements—is generally under-represented. Given the evidence for fluvial reworking and transport at Nyang Rise, it seems likely that the accumulation formed as a channel-lag assemblage, rather than a channel-fill concentration (Behrensmeyer 1988; Rodgers 1993) and thus Nyang Rise represents both allochthonous and parautochthonous material from an attritional stream-side predation hot spot.

Resolving site formation processes is often conducted with an end-goal of examining changes in faunal communities through space and time (Brickman et al., 2007). Portions of living assemblages may become preferentially deleted in a fluvial channel and time- and stratigraphic-averaging may affect our interpretations of fossil communities (Voohies, 1969; Behrensmeyer, 1988), yet these sedimentary settings also commonly preserve important plant and animal fossils (Behrensmeyer and Hook, 1992). Taphonomic interpretations that reflect a high fidelity of taxonomic representation from living communities are generally considered ideal for such reconstructions. However very few “types” of fossil assemblages will reveal all portions of a living community. Instead, different types of bonebeds are likely to capture specific portions of a faunal community and will be of variable use for questions about paleobehaviors or paleofaunal communities (Brickman et al., 2007).

Peter Andrews, Judy Harris, and John Van Couvering’s (1972; 1975) work on Rusinga began pioneering work joining site formation and community analysis. Their test excavations sought to examine changes through time, but Andrews et al. (1972) noted that not all of their *in situ* fossil finds were appropriate for comparison across assemblages. Units KA, KD, and KE were either too fragmentary or had too few taxa. Unit KF was clearly fluvially reworked and thus may include taxa transported from further away. Units KB and KG were deemed more comparable in nature—both yielded several specimens of well-preserved and identifiable fauna. Andrews et al. (1972) notes that Unit KB may have included remains of owl pellets or other avian raptor prey and that Unit KF may represent a stream-side environment. Later, Andrews and Van Couvering (1975) suggest their findings represent at least three separate paleo-communities— a stream-side fauna, a forest community, and a more open community. However, Andrews et al. (1972) also acknowledge that comparisons across fossil assemblages can be “fraught with dangers, even to the wary” (p.16) and consider that winnowing likely played a role the preservation of size selection fauna.

In this vein, I suggest that the fossil deposits across R5 (Nyang Rise, Andrew’s test excavations, and KPS) do not reflect distinct and changing environmental conditions, but instead represent different snap shots of a broad riparian environment of braided streams within an alluvial fan. Likely raptor accumulations such as KPS and Unit KB would capture the prey preferences of the predator, which may or may not reflect a specific habitat. However, raptor accumulations are generally dropped from nests or perches, which are likely to be in trees— and in this case, overhanging water. Indeed, even these probable raptor accumulated assemblages appear to be deposited in slow moving fluvial deposits as evidenced by sedimentology and orientation patterns. We should not necessarily expect small taxa to be present in the same fluvial environments that larger taxa are preserved— the absence of “forest fauna”, likely dominated by size selected raptor kills, in other deposits should be considered a very localized taphonomic bias and not reflective of overall conditions. Water-dependent crocodiles present across the site (KPS, Nyang Rise, Units KF and KE) suggest that water was available year-round and numerous leaf beds indicate the presence of trees along the water. Larger taxa generally associated with more open habitats may have been periodic visitors to this wetter landscape or may have been transported from further up-steam—potentially representing an entirely different habitat— but appear to reflect the overall attritional nature of the deposits. Large taxa generally have large home ranges (Harestad and Bunnell, 1979; Gomper and Gittleman,1990) and thus caution should be used when reconstructing their preferred habitats with depositional setting alone. The presence of desiccation cracks, high erosion, and sediment loads may have less to do with broad changing environmental conditions, than reflect expected meandering stream evolution— where ox-bows periodically form and dry as fluvial systems flood and change course on an immature alluvial fan dominated by volcanic sediments. Such a system would be ideal for small pockets of fossil preservation on a dynamic, but largely uniform landscape.

In order to test a hypothesis of broad environmental change overtime at R5 using fossil fauna, additional excavations would need to reveal isotaphonomic bonebeds from multiple horizons, allowing for the examination of taxa from contemporaneous assemblages together. This is not to say that faunal community comparisons are a futile endeavor. Indeed, few fossil sites such as R5-Kaswanga can boast such a rich history of collection and study, which conventional wisdom suggests should be ideal for such analysis. However, the alluvial nature of R5-Kaswanga is such that it has the potential to capture many types of biogenetically biased fossil sites simultaneously within the same landscape. Considering these current findings, lumping the fauna from R5's many collections as an analytical unit is probably most appropriate for community analysis against Rusinga's other localities that are similarly understood. More precise stratigraphic resolution and the recovery of additional bonebeds may allow for future analysis within the R5 locality.

Conclusions

The *Ekembo* remains from the KPS are arguably the most studied early Miocene primate assemblage in eastern Africa and R5-Kaswanga is currently the best known and understood fossil site from Rusinga. Our understanding of R5 is largely due to its history of detailed collection methods from the 70s and onward. Taphonomic inferences rest on important observations such as *in situ* geologic context, bone spatial and orientation patterns, and the collection of non-identifiable specimens to gather important surface modification data. No other fossil site on Rusinga has had so many published archaeological style excavations where detailed taphonomic data were gathered. The work conducted in 2011, as well as Walker's 1984 KPS excavations and Andrew's and Van Counvering's 1971 excavations have helped to paint a picture of a diverse riparian environment where *Ekembo* appears to have been the dominant primate genus. The 2011 Main Area test excavations and the Nyang Rise excavation demonstrated that pockets of bonebed still exist throughout the sequence and that most other beds are fossiliferous to varying degrees. Taphonomic assessment of the surface collections suggests that these fossils are likely stratigraphically mixed from multiple bonebeds. The recently discovered bonebed at Nyang Rise yields an attritional fluvial deposit, sampling surrounding faunas that survived the winnowing process. The suite of excavations together show variable biogenic processes with hydraulic over-printing are present throughout the site—further suggesting that surface assemblages may be derived from several taphomonically variable assemblages within a larger alluvial system. Assessments of changing environmental conditions based on *in situ* faunal assemblages at R5 are likely premature, despite the wealth of data.

While several primate taxa are known from R5, *Ekembo* is the most numerous. If interpretations of a sustained riparian habitat at R5 are correct, *Ekembo* may have been better adapted to this type of habitat or lived in larger social groups than other catarrhine taxa on Rusinga. Alternatively, behaviors relating to *Ekembo*'s preferred substrate, sociality, or activity patterns may have led to it becoming the preferred prey taxon of a larger avian predator. The work on R5-Kaswanga materials shows that *Ekembo* and other stem hominoids shared riparian habitat with numerous taxa in an alluvial setting, likely for over 300k years.

Table 2.1: Screen Finds by Bed.

Bed	Screen Counts	Plant Fossils	Notable Screen Finds	Units	M^2 Excavated	Scaled by Bed[1]
25	98	x	Wood and leaves, beebroods, fish tooth, small turtle, gastropods, mammal tooth	2, 3, 4	3	32.7
24	not screened	-	-	3, 4, NR	7	NA
23.5	584	x	Wood and leaf frags, crocodiles, hedgehog tooth	3, 4, NR	7	83.4
23	289	x	Crocodiles, enamel frags, small animal post-crania	9, NR	6	48.2
22	3191	x	Bone Bed at NR; crocodiles, leaf stems, *Afrohyrax*, small animals	7, 9, NR	7	455.9
21	183	x		5, 6, 7	3	61.0
20	not screened	x	Leaf bed	5, 6, 7	3	NA

Screen finds include material recovered from both 5mm and 2mm sieves. [1] "Scaled by bed" is the number of finds scaled by the number of square meters that were excavated from that bed and shows represents a relative density among beds.
X=present
NR=Nyang Rise

Table 2.2: Main Area Test Excavations in situ Mammal Remains.

Unit	Bed	Taxon	Element
2	25	*Dorcatherium parvum*	M1
4	24.5	*Kelba*	tooth
7	24.5	*Paraphiomys*	molar
7	22	Perissodactyl	radius
7	22	Perissodactyl	ulna

Table 2.3: R5-Kaswanga Faunal List by Collection.

			NISP Counts		*Presence/Absence**					*NISP Counts***
			Recent work		**Walker**	**Andrews and Harris**				**Vault Hominoids**
			2006-2011 Surface	2011 Excavation	KPS	KB	KH	KG	KF	Leakey, Walker, and Andrews Collections
Afrotheria	Ptolemaiidae	*Kelba quadeemae*	1	1	-	-	-	-	-	na
	Macroscedlidae	indet	3	-	-	-	-	-	-	na
		Myohyrax oswaldi	-	1	-	-	-	-	-	na
		Miorhynchocyon clarki	-	-	-	X	-	X	X	na
	Tubulidentata	Orycteropodae	1	-	-	-	-	-	-	na
		Myorcteropus africanus	4	-	-	-	-	-	-	na
	Hyracoidea	indet	4	-	-	-	-	-	-	na
		Afrohyrax championi	13	3	-	-	-	-	-	na
	Proboscidea	indet	3	6	-	-	-	-	-	na
		Prodeinotherium hobleyi	2	-	-	-	X	-	-	na
Euarchontoglires	Primates	indet	1	-	-	-	-	-	-	4
		Ekembo indet	1	-	-	-	-	-	-	-
		E. heseloni	1	-	10 MNI	-	X	X	-	12
		E. nyanzae	2	-	-	-	-	-	-	10
		Limnopithecus legetet								3
		Dendropithecus macinnesi	1	-	-	-	-	X	-	10
		Komba minor	-	-	-	-	-	X	-	na
		Komba robustus	-	-	-	-	-	X	-	na
		Progaligo songhorensis	-	-	-	X	-	-	-	na
	Rodentia	indet	38	-	X	X	X	X	-	na

	Rodentia, cont.	Anomaluridae	-	-	-	X	-	X	-	na
		Kenyamys	1	-	-	-	-	-	-	na
		Myophiomys	-	-	-	X	X	X	X	na
		Megapedetes pentadactylus	4	-	-	-	X	-	-	na
		Diamantomys luederitzi	32	-	-	-	X	X	-	na
		Simonimys genovefae	1	-	-	-	-	-	-	na
		Paraphiomys indet	11	1	-	-	-	-	-	na
		P. pigotti	10	-	-	-	-	-	-	na
		P. stromeri	6	-	-	X	-	X	-	na
	Lagomorpha	indet	1	-	Partial Skeleton	-	X	-	-	na
		Kenyalagomys indet	22	-	-	-	-	-	-	na
		K. rusingae	11	-	-	-	-	-	-	na
		K. minor	1	-	-	-	-	-	-	na
Laurasiatheria	Carnivora/Creodonta indet		35	3	X	X	-	X	X	na
	Creodonta	*Anasinopa leakeyi*	1	-	-	-	-	X	-	na
		Hyaenodontidae	7	-	-	-	-	-	-	na
		Hyainailouros	-	-	-	-	X	-	-	na
	Carnivora	Barbourofelidea (*Afrosmilus* sp.)	2	-	-	-	-	-	-	na
		Amphicyonidae	2	-	-	-	-	-	-	na
		Cynelos	1	-	-	-	-	-	-	na
	Insectivora	(Erinaceidae)	2	0	-	X	-	-	X	na
		Gymnurechinus leakeyi	0	1	-	-	-	X	X	na
		Lanthanotherium	-	-	-	-	-	X	X	na
	Chiroptera	*Tadarida rusingae*	1	0	-	-	-	-	-	na

	Pholidota	Manidae	1	-	-	-	-	-	-	na
	Chalicotheriidea	*Butleria rusingense*	5	3	-	-	-	X	X	na
	Rhinocerotridae	Indet	11	7	-	-	X	-	-	na
		Rusingaceros leakeyi	2	-	-	-	-	-	-	na
		Brachypotherium snowi	1	-	-	-	-	-	-	na
Artiodacyla	Ruminantia	indet	15	-	-	-	-	-	-	na
	Tragulina	*Dorcatherium* indet	18	-	X	-	-	-	-	na
		D. pigotti	17	-	-	-	X	X	X	na
		D. songhorensis	21	-	-	-	-	-	-	na
		D. chappuisi	11	1	-	-	-	-	-	na
		D. parvum	2	1	-	-	X	X	X	na
	Giraffidae	*Canthumeryx sirtensis*	5	-	-	-	-	-	-	na
	Pecora	indet	2	4	-	-	-	-	-	na
	(infraorder)	*Walangania africanus*	8	-	-	-	-	-	-	na
	Suidae	indet	13	-	-	-	X	-	-	na
		Kenyasus indet	1	-	-	-	-	-	-	na
		Kenyasus rusingensis	3	-	-	-	-	X	X	na
		Kenyasyus africanus	1	-	-	-	-	-	-	na
		Libycochoerus jaenelli	1	-	-	-	-	-	-	na
		Nguruwke kijivium	2	-	-	-	-	-	-	na
	Anthrocotheriidea	indet	9	3	-	-	-	-	-	na
		Bracyodus aequatorialis	7	2	-	-	X	-	-	na
	Hippopotamidae	indet (*Kulutherium*)	1	-	-	-	-	-	-	na

X present
- not present

* Published in Andrews and Van Couvering (1975), Walker 2007 and updated using taxonomies published in Werdelin and Sanders (2010). Some KPS remains were identified by Jenkins.

** Identifications from vault counts are from K. McNulty and provenienced using field numbers and site name synonyms published in Pickford (1984).

Table 2.4: Excavation and Surface Collection NISP counts and Associated Surface Modifications.

			Tooth Pits		Gnawing		Invertebrate		Avian		Rodent Gnawing		Root Damage		Digestive Etching		Trampling	
	NISP Total	% NISP Total	N	%NISP	N	%NISP	N	%NISP	N	%NISP	N	%NISP	N	%NISP	N	%NISP	N	%NISP
Excavation																		
crocodiles	859	89.3%	87	10.1%	47	5.5%	6	0.7%	2	0.2%	0	0.0%	2	0.2%	0	0.0%	0	0.0%
chelonia	4	0.4%	0	0.0%	0	0.0%	1	25.0%	0	0.0%	1	25.0%	0	0.0%	0	0.0%	0	0.0%
large mammals	48	5.0%	11	22.9%	12	25.0%	5	10.4%	1	2.1%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
medium mammals	15	1.6%	1	0.1%	0	0.0%	0	0.0%	2	13.3%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
small mammals	3	0.3%	0	0.0%	0	0.0%	2	66.7%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
indet	33	3.4%	2	6.1%	1	3.0%	4	12.1%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
Total Excavation	**962**	**-**	**101**	**10.5%**	**60**	**6.2%**	**18**	**1.9%**	**5**	**0.5%**	**1**	**0.1%**	**2**	**0.2%**	**0**	**0.0%**	0	0.0%
Surface																		
crocodiles	326	41.2%	8	2.5%	6	1.8%	20	6.1%	0	0.0%	0	0.0%	2	0.6%	6	1.8%	3	0.9%
chelonia	46	5.8%	0	0.0%	0	0.0%	3	6.5%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
large mammals	53	6.7%	3	5.7%	3	5.7%	6	11.3%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
medium mammals	42	5.3%	1	2.4%	1	2.4%	1	2.4%	2	4.8%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
small mammals	80	10.1%	9	11.3%	0	0.0%	2	2.5%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
indet	230	29.0%	7	3.0%	6	2.6%	13	5.7%	0	0.0%	1	0.4%	0	0.0%	1	0.4%	3	1.3%
reptiles	12	1.5%	1	8.3%	0	0.0%	1	8.3%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
amphibian	1	0.1%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
aves	1	0.1%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
hymenoptera	1	0.1%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%	0	0.0%
Total Surface	**792**	**-**	**29**	**3.7%**	**16**	**2.0%**	**46**	**5.8%**	**2**	**0.3%**	**1**	**0.1%**	**2**	**0.3%**	**7**	**0.9%**	**6**	**0.8%**

Table 2.5: Skeletal Part Frequencies (MNE) for Excavated Large Mammal Remains at Nyang Rise.

Element	MNE
Cranial-Dental	1
Scapula	1
Humerus	1
Radius	2
Ulna	2
Vertebra	4
Rib	0
Pelvis	1
Femur	1
Tibia	4
Fibula	1
Metapodial	5
Manual/Pedal	8

MNEs are raw frequencies and include all large mammal specimens identified to element. The most frequent element is the tibia, with 4 overlapping elements at the midshaft.

Table 2.6: Skeletal Part Frequencies (%MAU) for Crocodile Remains at Nyang Rise.

Element	%MAU
Basio-occiptial	92
Dentary	96
Coricoid	39
Scapula	31
Humerus	42
Radius	4
Ulna	4
Osteoderm	11
Vertebra	11
Rib	4
Illium	31
Femur	100
Tibia	50
Fibula	8
Metapodial	5
Phalanx	2

%MAUs are scaled by the MNI, defined by the most frequent element. An MNI of 13 crocodile individuals from Nyang Rise are known from overlapping portions of femora.

Table 2.7: Breakage Patterns on Specimens from Excavation and Surface Collections.

Breakage Type	Surface Collections n=596		Nyang Rise Excavation n=338	
1	169	28.4%	49	14.5%
2	331	55.5%	152	45.0%
3	4	0.7%	5	1.5%
1 & 2	59	9.9%	70	20.7%
1, 2, & 3	4	0.7%	13	3.8%
1 & 3	9	1.5%	43	12.7%
2 & 3	20	3.4%	6	1.8%

1=Fresh breakage, 2=Post-depositional/Post-fossilization breakage, 3= Post-fossilization deformation or cracking. Breakage counts do not include crocodile osteoderms and cranial specimens or specimens recovered from the Nyang Rise Quarry.

Table 2.8: Bone Surface Conditions for Nyang Rise Excavation and Surface Collections.

Surface Conditions of Bone	Nyang Rise Excavation n=312	% of NR Ex. Assemblage	2011 Surface Collections n=656	% of Surface Assemblage
Fresh Bone Surfaces	83	26.6%	84	12.8%
Rounded, Polished, or Eroded edges	116	37.2%	428	65.2%
Dissolution - Chalky	70	22.4%	35	5.3%
Pitting and Corrosion	106	34.0%	494	75.3%
Weathering	13	4.2%	41	6.3%
Concretions	16	5.1%	2	0.3%
Differential Preservation	12	3.8%	32	4.9%
Surface Cracking	0	0.0%	128	19.5%
Fossils with Multiple Conditions Present	91	29.2%	464	70.7%

Table 2.9: Specimen Sizes of the Nyang Rise Excavation and Surface Collections.

Size	**Nyang Rise Excavation n=236**	**Surface Collections n= 602**
2.1-4cm	23.7%	83.1%
4.1-6cm	29.7%	14.6%
6.1-8cm	14.4%	1.8%
8.1-10cm	10.2%	0.3%
Over 10cm	22.0%	0.2%

Counts only include specimens larger than 2cm due to differential collection procedures between excavations and surface collections. Does not include crocodile vertebrae from the excavation, the majority of which fall within the 2.1-4cm and 4.1-6cm size categories and so these categories are underrepresented with respect to the excavated material by approximately 100 specimens. The largest specimen from the excavation was 26cm in length. The largest specimen from the surface collections was 16cm in length.

Table 2.10: Proposed Sequence of 2011 and Historic excavations at R5-Kaswanga.

	Excavation	**Taphonomic Interpretation**	**Characteristics**
Marker Bed III			
	Unit KD	N/A	Rodents, gastropods, and hyrax skeleton
Marker Bed II/SS Lens #1			
Possibly Sampling Same Horizons	Unit KB	Possible raptor accumulation	Small mammals (lorisoid and rodents) and reptiles, several partial skeletons, unimodal orientation pattern
	Unit KH	N/A	Large taxa, very fragmentary, random bone orientation
	Units 2, 3, 4	N/A	Leaf Bed in Unit 2, low density and fragmentary fossils
Marker Bed I/ SS Lens #2			
	Unit KG	Fluvially reworked	Small mammals-medium sized mammals, unimodal bone orientation
Possibly Sampling Same Horizons	Unit KF	Stream-side deposition— likely attritional	Fragmentary crocodiles (2-5 individuals, large-small mammal sizes classes represented, fossil rounding and pre-fossilization exposure), bimodal bone orientations, same horizon as *E nyanzae* 1967 mandible
	Nyang Rise	Attritional streamside accumulation of prey remains	Crocodiles and large-medium sized mammals, fossil rounding, tooth pits
	Units 5 & 6	N/A	Leaf Bed
	Unit KE	Stream-side deposition	Fragmentary crocodiles and large - medium sized mammals
	Maxbauer Leaf Bed	N/A	Leaf Bed
Unknown	KPS	fluvially reworked raptor predation assemblage	10 *E. heseloni* partial skeletons, possible raptor damage, bi-modal orientation patterns, capped by a leave and fruit bed

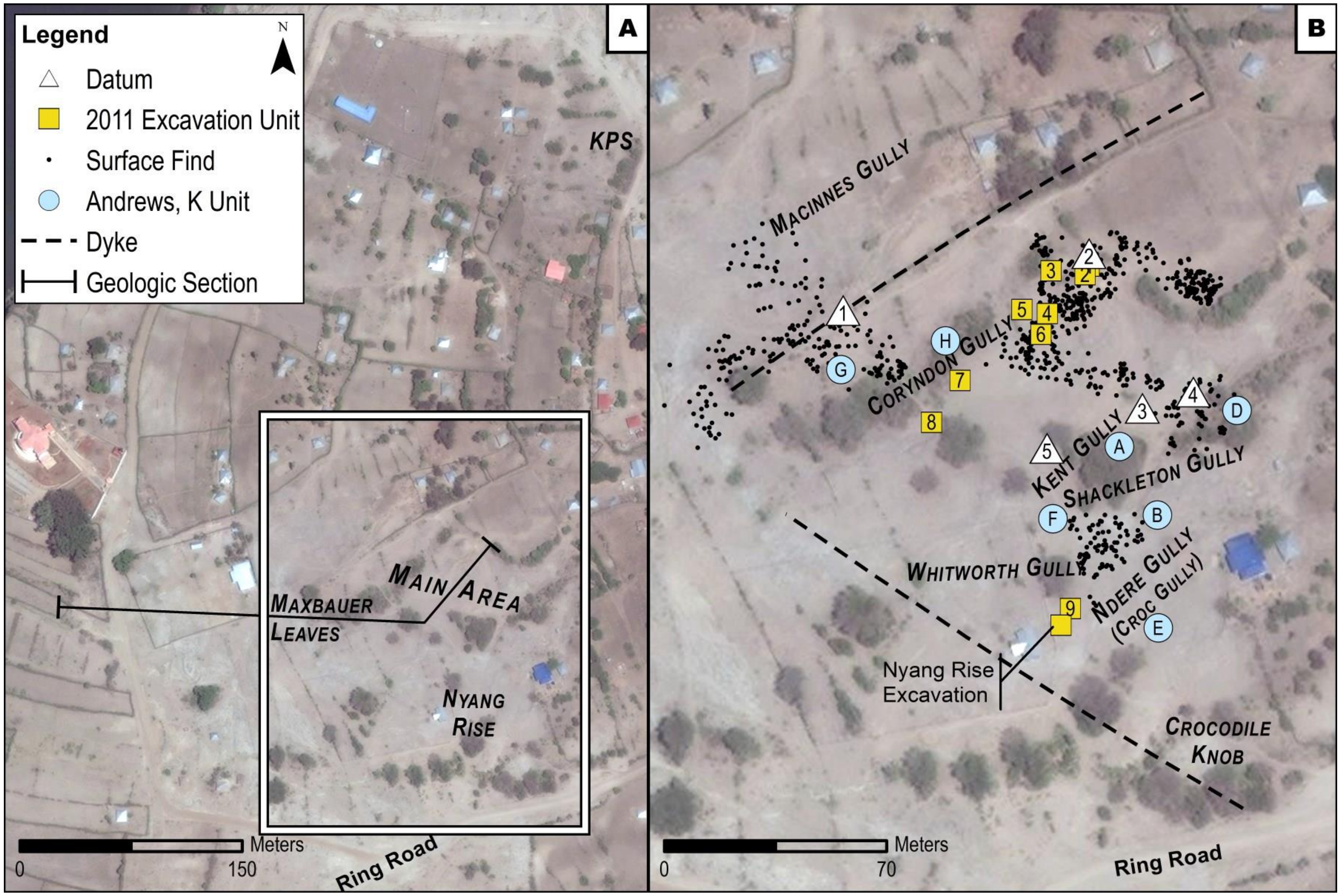

Figure 2.1: Site Map of R5-Kaswanga, Rusinga Island.

A) Kaswanga Point collections areas: KPS (Kaswanga Primate Site, Main Area, Nyang Rise, and Maxbauer Leaf site. Geologic section by Dan Peppe and David Fox. (B) Main Collection Area and Nyang Rise. Andrews et al. (1972) excavation units and gully names are approximated. Dots are the spread of surface collected fossils collected with the total station. Aerial photographs from Digital Globe Inc. under license by University of Minnesota.

Figure 2.2: Main excavation area.

(A) Crews conduct surface crawls placing flags at fossils to be shot in with a total station at the top of the rise between Coryndon and Kent Gully's. Photo faces South. (B) View of Main excavations area facing west toward Lake Victoria prior to the placement of excavation units. (C) View of crews excavating. Photo facing east of rise between Coryndon and Kent Gullies,.

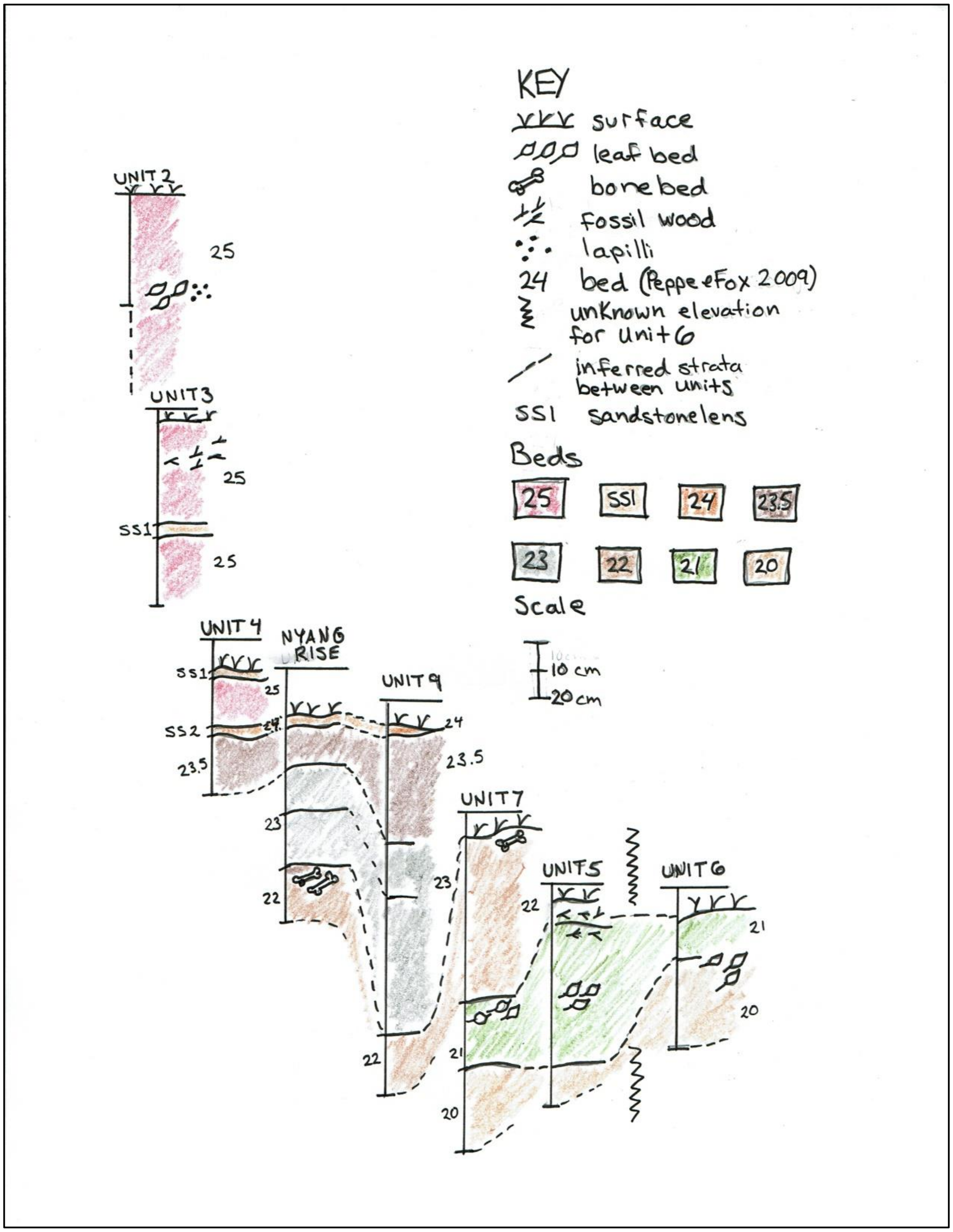

Figure 2.3: Stratigraphic Correlations between 2011 Main Area Excavation Units and Nyang Rise.

Depths and relative heights are to scale. Beds are named using Peppe and Fox's 2009 stratigraphic profile.

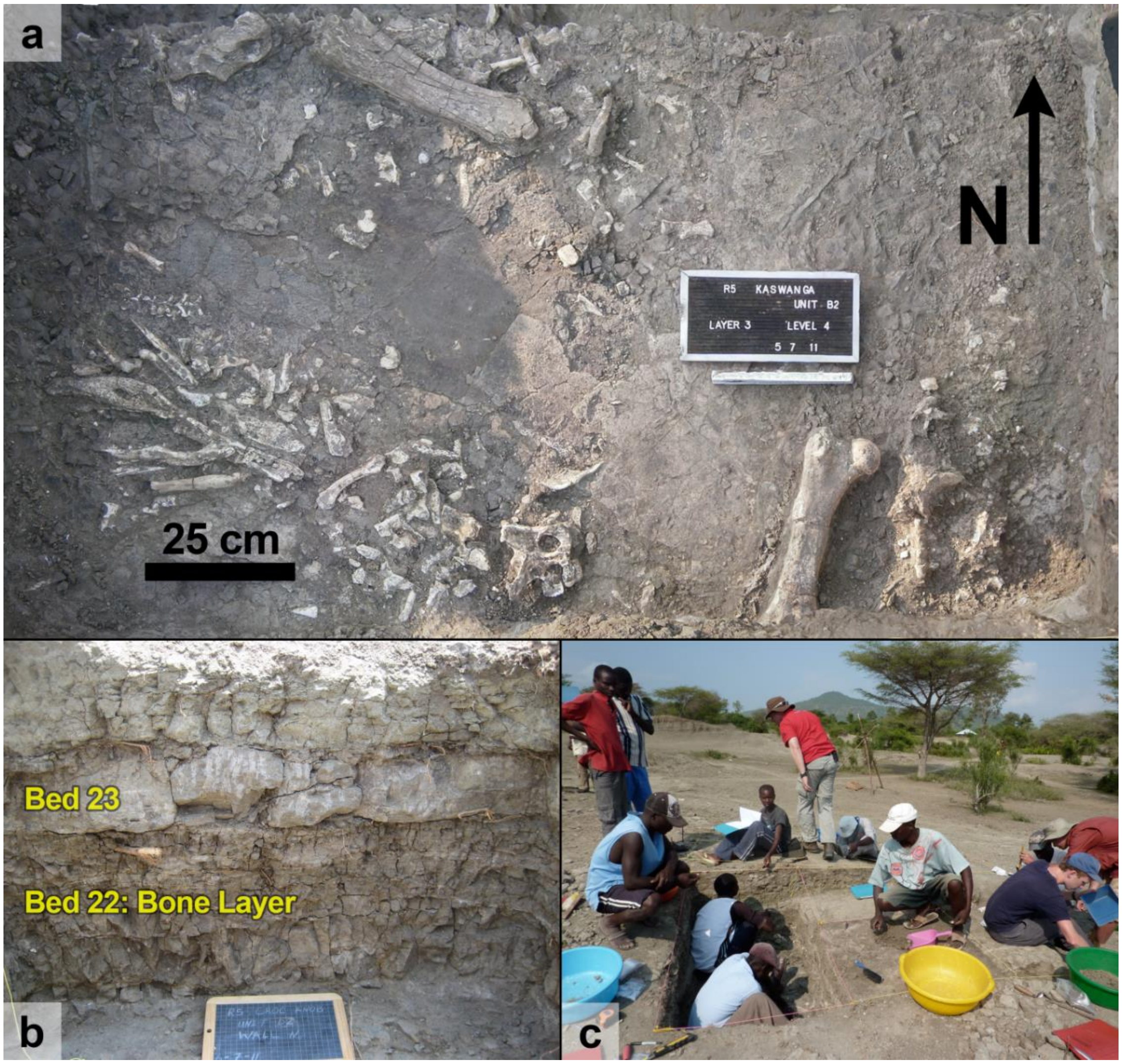

Figure 2.4: Nyang Rise Excavation.

(A) Photo showing a portion of the bonebed at Nyang Rise in Bed 22 from Units B1 and B2. Cluster of bones in the SW portion are mostly crocodile remains and appear to have been pushed against a fossil root directly south of the cluster. (B) Photo illustrative of the Nyang Rise profile from Unit D2. Bonebed comes from Bed 22. (C) Facing east, showing four square meters open; Units A1, A2, B1, and B2. Quarry effort along a slight slope to the south later becomes Unit A3. Unit D2 was later opened in the background.

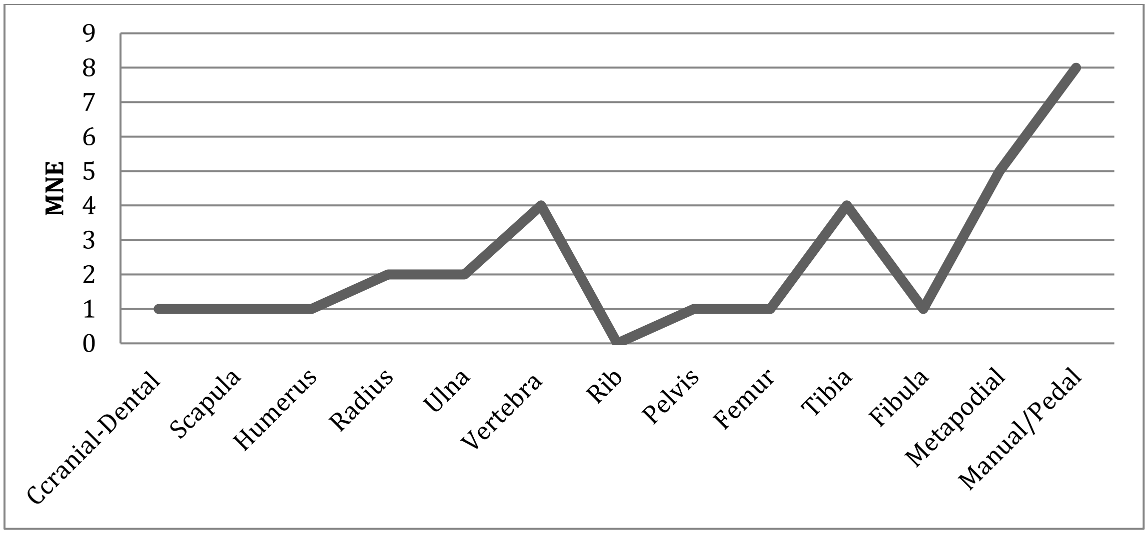

Figure 2.5: Large Mammal MNE Counts for the Nyang Rise Excavation.

Raw MNE values are shown Counts reflect at least 4 different taxa— Anthrocotheridea, Chalicotheriidea, Rhinocerotridae, and Probocidea. Raw counts of smaller elements and limbs dominate the large mammal assemblage. Reference Table 2.5.

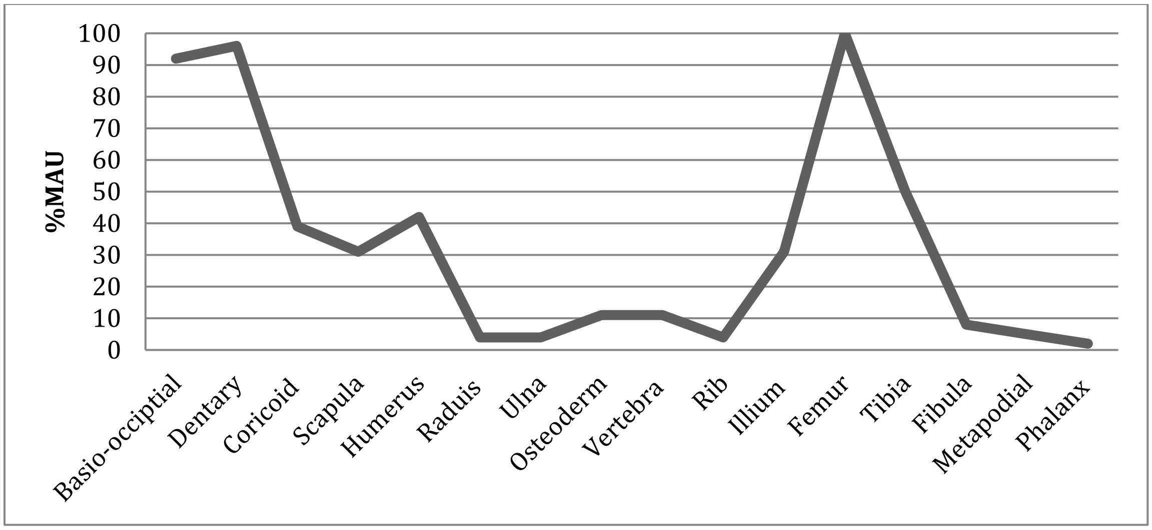

Figure 2.6: Crocodile %MAU for Nyang Rise Excavation.

%MAU (Minimum number of Animal Units) is scaled by the an MNI (minimum number of individuals) of 13, based on overlapping portions of femora. Percent MAUs are dominated by larger and denser limbs (femur, tibia, humerus) and skull elements. Reference Table 2.6.

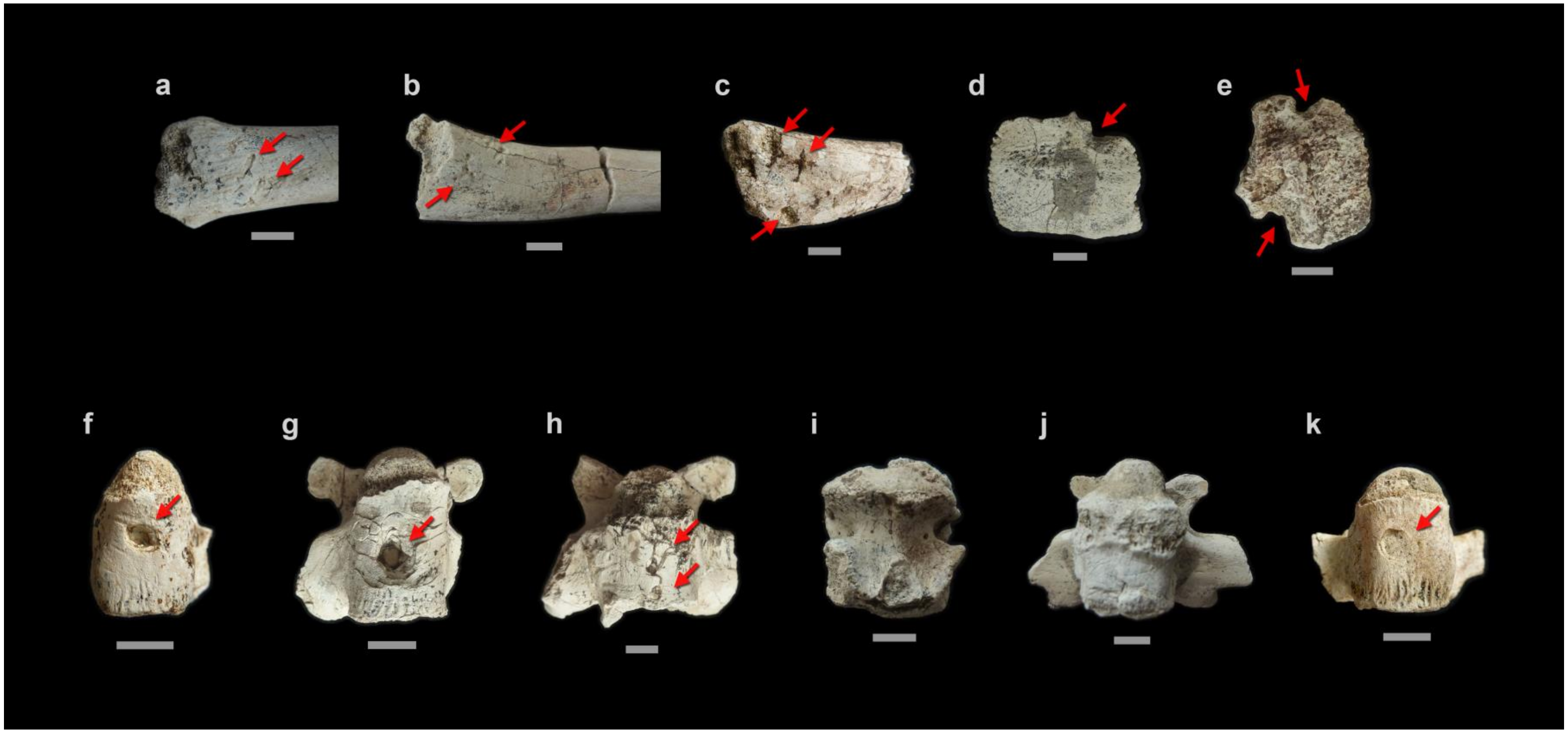

Figure 2.7: Damage and pathologies on crocodile remains at Nyang Rise.

(A) tooth drags/gnawing on a distal tibia. (B) femur showing characteristic crocodile tooth drags/gnawing and pits (red arrows). (C) proximal humerus showing characteristic crocodile tooth pits (D) smooth/interior view of osteoderm with fresh break/notch (red arrow). (E) smooth/interior view of osteoderm with fresh breaks/notches (red arrows). (F) anterior view of a vertebra with a clear crocodile tooth pit on the vertebral body; such pits and placement are common on crocodile vertebrae from Nyang Rise. (G) anterior view with a clear crocodile tooth pit on the vertebral body and associated crushing. (H) anterior view with tooth pits on the vertebral body(red arrows); (I) dorsal view of a vertebral body showing severe remodeling at the articular head of the vertebra (J) anterior view of a vertebral body showing pathological bulging- possibly due to a partially healed fracture (K) anterior view of a vertebral body showing partially healed pit (red arrow).

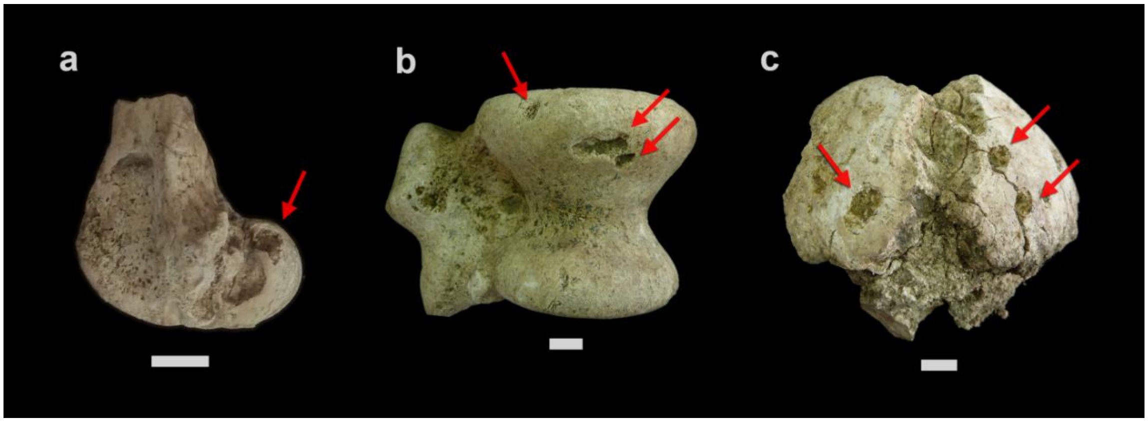

Figure 2.8: Damage on Mammalian Remains from Nyang Rise.

(A) lateral view of a *Dorcatherium* distal femur with crushed in pits on the condyle (B) Anthracothere astragalus showing crushed in tooth pits and gnawing (C) Fragmentary humeral head of a large mammal showing pits on the articular surface (red arrows).

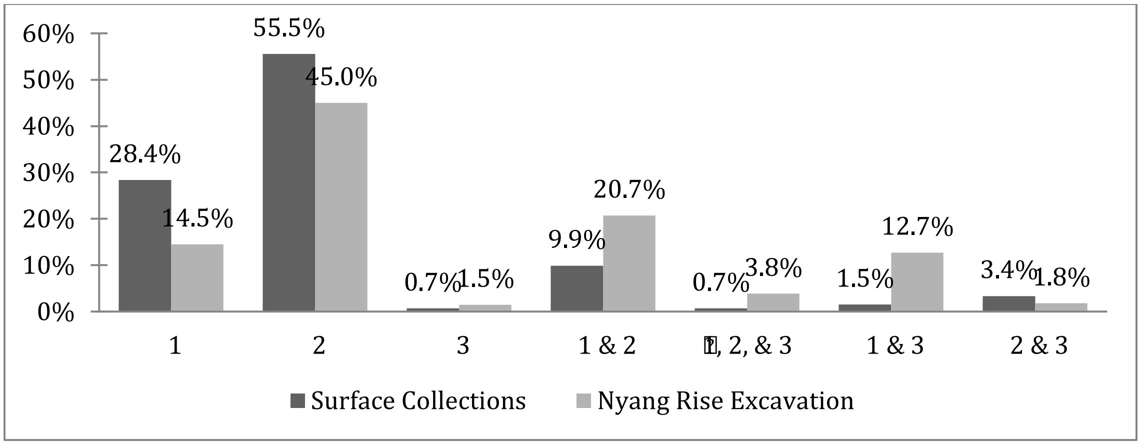

Figure 2.9: Breakage Patterns % Frequencies for the Surface and Nyang Rise Excavation Assemblages.

1= Fresh Breakage, 2= Post-depositional/Post-Fossilization Breakage, 3= Post-Fossilization Distortion, Expanding Matrix, and Crushing. Reference Table 2.7.

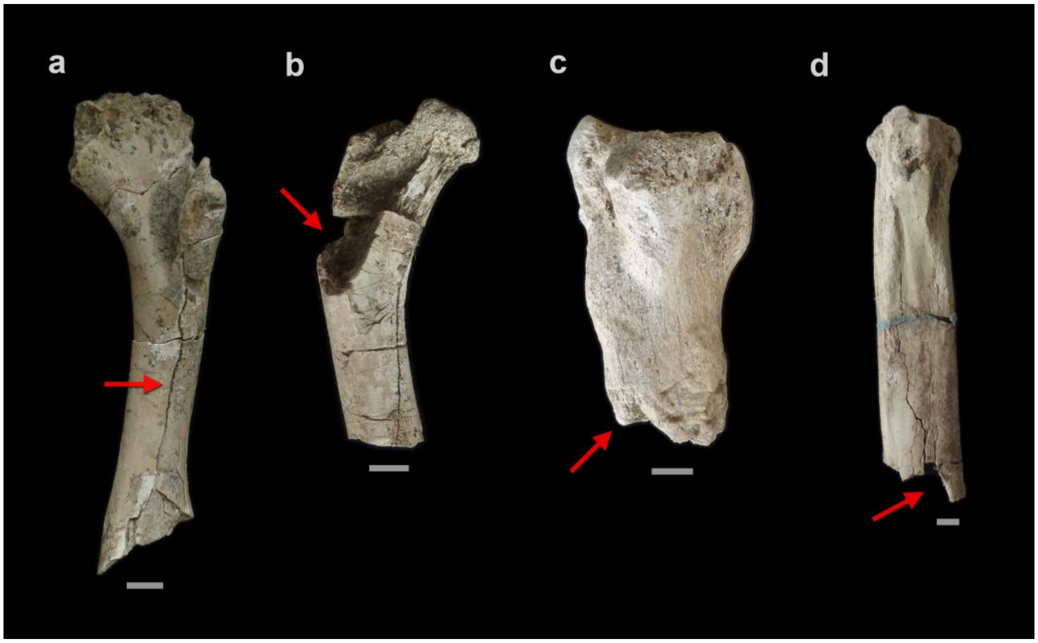

Figure 2.10: Breakage Examples from the Nyang Rise excavation.

(A) Crocodile femur showing post-depositional/fossilization longitudinal cracking (red arrow) — pitting and gnawing is present on the proximal end (B) crocodile femur showing a mix of high angled fresh breakage (red arrow) and post-depositional/fossilization transverse breakage midshaft (C) proximal end of an anthracothere metapodial with eroded and rounded jagged and transverse fracture mid-shaft (red arrow). Break appears to be associated with pitting and gnawing, but erosion diminishes the confidence of the identification for these marks (D) Large mammal metapodial showing post-depositional/fossilization step fractures (red arrow). Pits and gnawing are also present on the proximal articular surface.

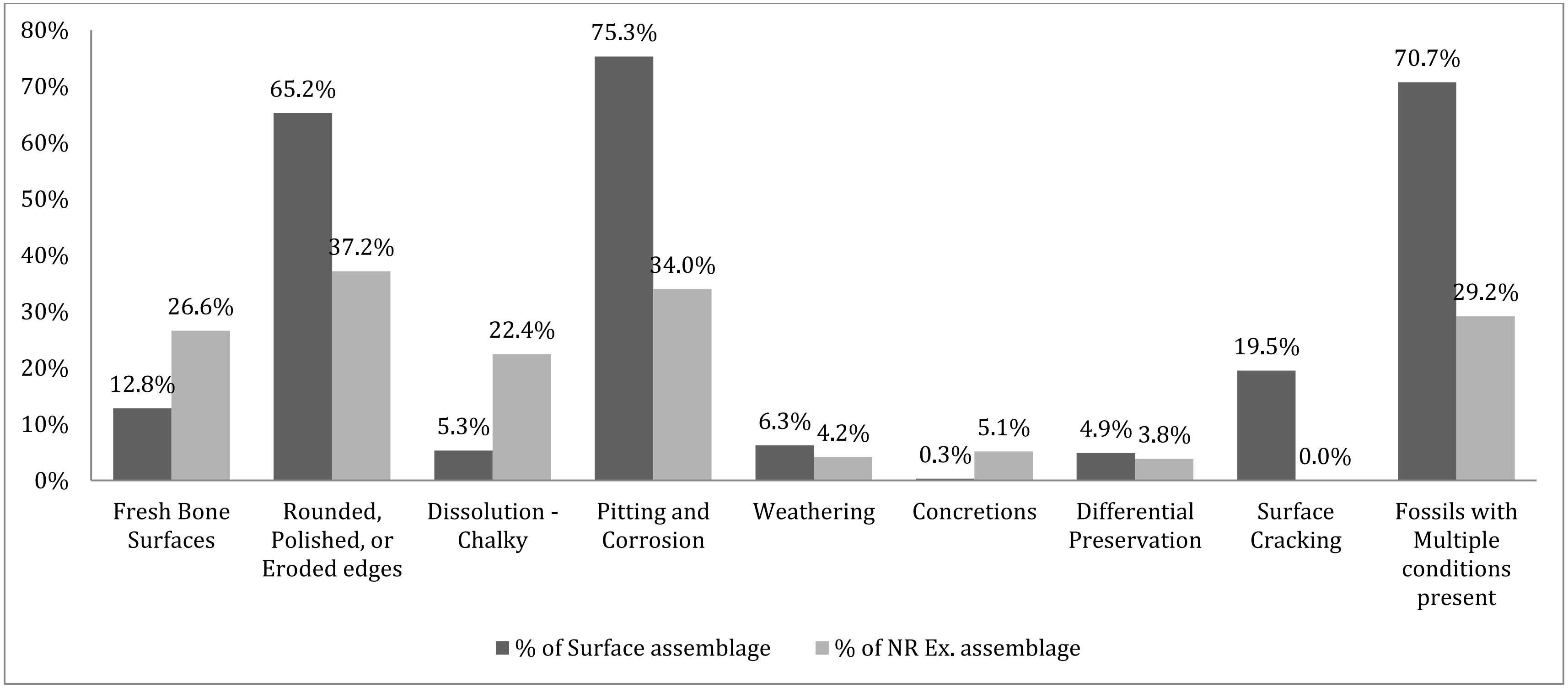

Figure 2.11: Bone Surface Conditions of the Surface Collections and Nyang Rise Excavation.

Reference Table 2.8.

Figure 2.12: Crocodile vertebrae showing severe erosion and rounding from the Nyang Rise Excavation.

(A) vertebral bodies with cancellous bone exposed and smoothed. (B) transverse and spinal processes showing rounded breaks and polish.

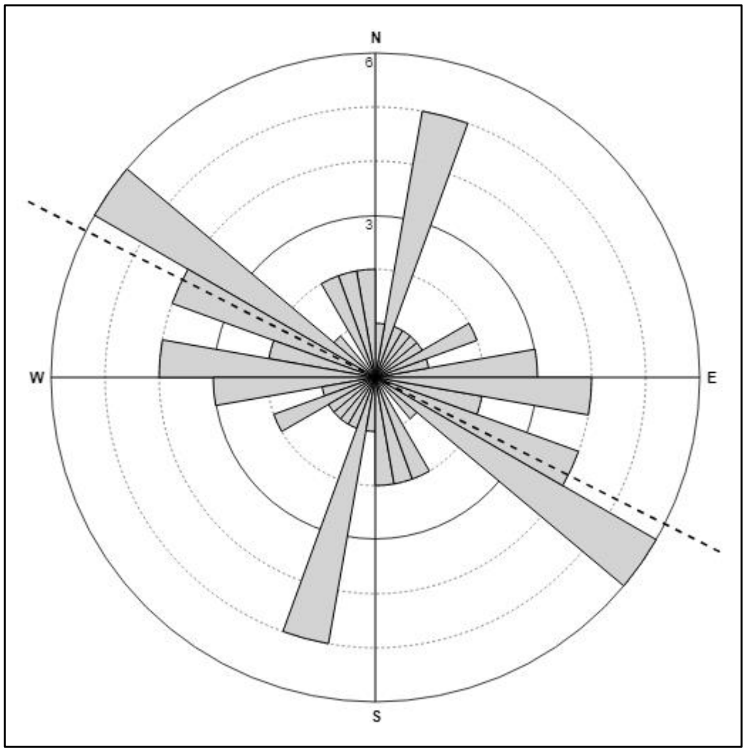

Figure 2.13: Rose Diagram for Nyang Rise.

Orientation patterns are not statistically isotropic, but appear to show a bimodal distribution with a NW-SE trend and secondary perpendicular direction of NE-SW. N=41.

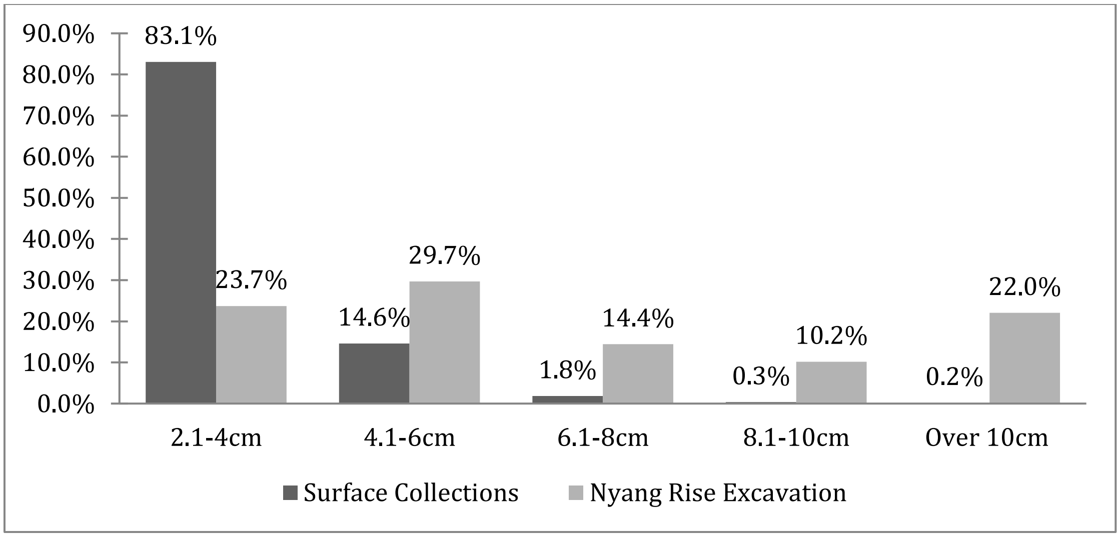

Figure 2.14: Proportion of Specimen Sizes for the Surface Collections and 2011 Excavated Collections.

Specimens from the surface collections are generally smaller. Surface Collections n=236, Nyang Rise Excavation n= 602. See Table 2.9.

CHAPTER 3 BRIDGING STATEMENT FOR CHAPTERS 2 AND 4

In the previous chapter, I give the primates and other fauna at R5-Kaswanga a strong taphonomic reconstruction from which to base paleoecological reconstructions from. New surface collections, excavations, and taphonomic signatures show that the R5 surface collections are likely stratigraphically averaged, but that most fossil deposits are derived from fluvial contexts, suggesting an overall riparian environment. While paleoecology is generally limited to isotopes, sedimentology, paleosols, plant fossils, and faunal communities relatively little attention has been paid to reconstructing interactions between fauna. Chapter 4 assesses predator-prey relationships between the Rusinga many carnivores, creodonts and primate community. New actualistic data from avian raptor predated monkey assemblages from the Taï (Ivory Coast) and Ngogo Forests (Uganda) are used to identify the first inference of raptor predation on Rusinga. Here, I show that large birds of prey, as well as medium sized creodonts/carnivores likely hunted both *Dendropithecus macinnesi* and *Ekembo heseloni* and the larger *Ekembo nyanzae*. Reconstructing predator-prey relationships allows for additional hypotheses about natural selection of these primate communities.

CHAPTER 4 IDENTIFICATION OF RAPTOR ACCUMULATED PRIMATE ASSEMBLAGES AND THE RECORD OF PREDATION ON EARLY MIOCENE PRIMATES OF RUSINGA ISLAND, KENYA

Introduction

Predation is a powerful selection pressure that continually affects morphological (Isabel, 1994), ontological (Hill and Dunbar, 1998) and behavioral (van Schaik,1983; Stanford, 1998; McGraw, 1998; Miller, 2002) adaptations among modern primates. Presumably, predator-prey relationships also helped shape primate evolution in the past and including that of our own lineage, but predation trends in the fossil record are poorly understood, often anecdotal, and rarely synthesized (but see Hart and Sussman, 2005). An understanding of the predatory guild of any primate, extant or extinct, provides an important criterion for differentiating sympatric primate niches and for interpreting behaviors and adaptive morphology.

While reptiles, snakes, and larger hominoids are known to predate on primates, avian raptors and mammalian carnivores are the most frequently reported predators of extant primates. Leopards are reported to stalk and consume chimpanzees or monkeys in the Taï Forest (Jenny and Zuberbühler, 2005; Zuberbühler and Jenny, 2007) and Mahale Mountains National Park in

Tanzania (Nakazawa et al., 2013). Large cats are important predators for baboons as well (Cowlishaw, 1994). Buss (1980), Brain (1981), and Pickering et al. (2011) report that leopards will take baboons and Cowlishaw (1994) notes that leopards will prey on males more frequently than males. Lions appear to rely on surprise attacks when hunting baboons at the Tana River Reserve, Kenya (Condit and Smith, 1994) and in the Moremi Wildlife Preserve in Botswana (Buss, 1980). The euplerid fossa, *Cryproprocta,* hunts several different lemur taxa and has been described as a lemur specialist (Dollar et al., 2007; Wright et al., 1997). Small carnivores have been implicated in the predation of galagos in South Africa, which display predator avoidance behaviors in the vicinity of jackals, genets, and domestic cats (Bearder et al., 2002).

Large bodied hominoids such as chimpanzees and orangutans have also been documented predating on smaller primates. Chimpanzees have notoriously focused their hunting efforts on red colobus monkeys (Stanford, 1998), but are equipped to capture other cercopithecoids (Watts and Mitanai, 2015) and strepsirrhines (Pruetz and Bertolani, 2007). While orangutans are not habitual predators, wild Sumatran orangutans have been observed eating slow lorises on multiple occasions as well (Utami and van Hooff, 1997; Hardus et al., 2012).

Predation on primates by avian raptors is also widespread; several avian taxa are known to regularly hunt small- to medium-sized primates in Africa, South and Central America and in Asia (for a review see Miller, 2002; McGraw and Berger, 2014). For example, cercopithecoids are the dominant prey taxon of crowned hawk eagles of equatorial Africa (McGraw et al., 2006; Struhsaker and

Leakey, 1990; Trapani et al., 2006, Mitani and Sanders, 2001; Sanders et al., 2003). While hominoids have not been observed as prey of avian raptors, gibbons nevertheless exhibit avoidance and altered behavior in the presence of raptors, suggesting at least occasional predation or predation in the taxon's recent past (Uhde and Sommer, 2002). Presumably, this dynamic between large birds of prey and small or juvenile hominoids, monkeys, tarsiers, and lemurs has persisted for millions of years, yet little physical evidence of these encounters has been documented.

Taphonomic signatures of raptor predation

Identifying predatory agents in the fossil record relies on two primary lines of evidence: site formation studies and careful surveys of bone surface damage. Each should be firmly based in modern actualistic studies and observations, and requires careful data collection in the field and laboratory. When these methods are employed together, the likelihood that a predation signal can be detected in the fossil record is substantially improved.

The taphonomic signatures for identifying predation by mammalian carnivores from bone assemblages are well documented: rounded and crushed-in tooth pits (Binford, 1981; Pobiner, 2007); U-shaped tooth scores (Binford, 1981; Hayes, 1983). Depending on bone portion and density, tooth pit diameters may or may not be proportional to the predators' body size (Delaney et al., 2009). Carnivores often break bones during consumption and leave characteristic fractures (Capaldo and Blumenschine, 1994; Brain 1981; Pickering et al., 2003; Pickering et al., 2011). Carcass processing by carnivores can lead to the complete consumption of less dense elements that results in digestive thinning and etching of bone fragments in scat (Andrews and Nesbit, 1983; Carlson and Pickering, 2003). Actualistic studies specific to primates are particularly important as a taxon's body plan can influence how and what carnivores choose to consume (Brian, 1981; Kerbis et al., 1993; Carlson and Pickering, 2003; Pickering and Carlson 2004; Pickering et al., 2011; Nakazawa et al., 2013). As a result, it is not difficult to identify mammalian predation in the primate and hominin fossil record (see Hart and Sussman, 2005 for a review).

The frequency with which avian raptors hunted primates throughout primate evolution and the evolutionary outcomes of these interactions remain poorly understood. However, a few key studies have laid the foundation for identifying raptor predation in the primate fossil record. For example, Berger and Clarke (1995) suggest avian raptors as the accumulating agent of the holotype of *Australopithecus africanus*, the Taung Child, employing taphonomic observations to support this conclusion. They present five criteria derived from Brain's (1982) actualistic study of modern avian nests and bone accumulations and from their own actualistic observations to aid in the identification of raptor-accumulated specimens. (1) Body sizes should be relatively homogenous and small (<20kg). Predator accumulations of any taxon, mammalian or avian, will reflect the prey preferences of that taxon, and these are determined in part by body size, the locomotor and habitat preferences of the prey, and thus the predator's ability to capture said taxon. (2) Raptor accumulations of primates have generally yielded a high proportion of relatively complete crania. Unlike carnivores, avian raptors are unlikely to completely destroy less dense or smaller cranial remains with chewing and gnawing. Raptors are, however, likely to puncture and tear cranial remains to access the brain, leaving behind small “v-shaped” marks on the cranium. (3) Tortoise remains may be present as they have been reported as preferred prey for some raptors. (4) Egg shell may be present suggesting nesting activity. (5) Accumulations should occur within topographic or geographic surrounding likely to facilitate nesting (i.e. caves or cliffs). Berger and Clarke (1995) advocate a holistic approach that relies on actualistic observations while considering both the content of the larger assemblage and bone surface modifications.

Sanders et al. (2002), Trapani et al. (2006) and McGraw et al. (2006) detail additional criteria for diagnosing raptor accumulations based on analyses of modern collections of monkey prey from crowned hawk eagle (*Stephanoaetus coronatus*) nests in the Ngogo and Taï Forests. These studies highlight damage to the crania and scapulae likely related to actual capture and subsequent consumption of the monkey prey. V-shaped nicks and “can-opener” marks (Sanders et al., 2002) are reported for both assemblages and appear to be a function of curved shape of both beaks and talons. These authors also report taxon lists and skeletal part frequencies from multiple nests. The specific prey taxa vary between the sites, but body sizes are consistently between 11 to >1kg. Likewise, skeletal part frequencies vary among nests and sites, but a predominance of cranial elements is relatively consistent (Sanders et al. 2002; McGraw et al. 2006).

Despite availability of these diagnostic criteria, very few instances of raptor-predated primates have been identified in the fossil record. Notable exceptions are Gilbert et al.’s (2009) cercopithecid remains from Humpata Cave, Angola, *Aegyptopithecus* remains from the Fayum, Egypt (Sanders 2012; Gebo and Simons 1984), and the *Australopithecus* and cercopithecid remains from the Buxton-Norlim Limeworks, Taung, South Africa, (Berger and McGraw, 2007).

The general lack of evidence for raptor predation in the fossil record is likely a function of (1) under reporting of taphonomic signatures that can be used to infer predator-prey relationships (2) the difficult and time consuming nature of identifying those taphonomic markers and distinguishing them from carnivore marks, and (3) the nature of most fossil primate assemblages and collection methods.

Most fossil primates are not recovered from cave deposits, but rather from open-air settings such as paleosols, fluvial, alluvial, or lakeside deposits and have complex taphonomic histories (for example: Rudabanya-Andrews and Cameron, 2010; Pasalar-Anderws and Ersoy, 1990; Fort Ternan-Shipman et al., 1980; Maboko- Andrews et al., 1980; Barranc de Can Vila 1- Caranovas-Vilar, et al., 2008; Rusinga-Walker, 2007; Jenkins, 2014). This presents difficulties for identifying raptor damage since open air settings are (1) less likely to preserve complete crania or scapulae from which raptor damage is most clearly identified, and (2) are less likely to yield multiple primate individuals or specimens that are clearly associated. The situation is exacerbated when the primary mode of fossil collection is by surface survey, whereby seemingly isolated elements have eroded from their original depositional contexts. Site formation variables and collection procedures can hinder the identification of any predator accumulation in the fossil record, but the taphonomic signatures of raptor accumulations are especially susceptible in this regard because they are most easily identified by their unique surface modifications on fragile elements and by their skeletal part frequencies.

To further aid in the identification of raptor-accumulated assemblages, this paper details surface modifications present on post-cranial elements of raptor-predated monkeys previously recovered from the Taï and Ngogo. These elements are more likely to preserve in the fossil record, but exhibit raptor damage that differs somewhat of that on cranial elements. Using these actualistic assemblages as a comparison, bone surfaces modifications from the Rusinga and Mfangano Island primate collections are surveyed for damage and that can be used to infer predator prey relationships.

The Rusinga and Mfangano Fossil Assemblages

The early Miocene deposits of Rusinga and Mfangano Islands, in southwestern Kenya (Figure 4.1 MAP) are well known for their copious remains of fossil primates and present an excellent opportunity to examine possible instances of raptor and carnivore predation in the fossil record. Stem hominoids, (*Ekembo heseloni* and *Ekembo nyanzae* (formally known as *Proconsul*; McNulty et al., 2015)); stem catarrhines (*Dendropithecus macinnesi*, *Limnopithecus legetet*, and *Nyanzapithecus vancouveringorum*), as well as four lorisoid taxa (*Komba minor*, *Komba robustus*, *Komba walker, Progalago songhorensis*, and

Mioeuoticus shipmani) are known from these assemblages (Table 4.1). Potential predators are also recovered from the fossil deposits on Rusinga and Mfangano Islands, including hyenadonts, carnivores, crocodiles, snakes and monitor lizards (Table 4.2).

Rusinga and Mfangano's large primate and faunal assemblages are the result of nearly a century of fossil collection by multiple teams (Le Gros Clark and Leakey, 1951; Le Gros Clark and Thomas, 1951; Napier and Davis, 1959; Pickford, 1986; Walker et al., 1994; Shipman and Walker, 2005; McNulty et al., 2007). As such, this material is commonly used for base line regional and temporal comparisons of biodiversity, paleoecology, morphology, and phylogeny. To date, no large-scale taphonomic studies have assessed how preservation conditions or predation trends may influence and inform such interpretations. Several specific observations of predation damage have been noted (Ward et al., 1997; Walker and Pickford, 1983; Walker, 2007), however, and these are revisited in light of new actualistic data presented here.

Materials and Methods

The Actualistic Assemblages

Prey remains from beneath two crowned hawk eagle nests from Ngogo Forest, Kibale National Park, Uganda (Mitani et al., 2001; Sanders et al., 2003; Trapani et al., 2006) and from 16 nests in the Taï Forest, Ivory Coast (McGraw et al., 2006; Shultz 2003; Shultz et al., 2004) were systematically collected for the purpose of understanding modern predator-prey relationships and for taphonomic studies of eagle predation. At both sites, remains were largely represented by cercopithecoid monkeys, though other mammalian, reptilian and avian remains were also found associated with raptor nests. The Ngogo and Taï collections were housed at the Museum of Paleontology at the University of Michigan and the McGraw Laboratory at The Ohio State University, respectively, and made available for further taphonomic data collection. Taï collections now reside at Oxford University. Additional information on the field sites and collection protocols are reported elsewhere (Mitani et al., 2001; Sanders et al., 2003; McGraw et al., 2006; Shultz 2003; Shultz et al., 2004).

Samples and Surface Modifications

Two collections from Ngogo nests and five from Taï nests were examined to establish criteria for diagnosing raptor damage on cercopithecoid long bones. Bone surfaces were examined under a 10-20X hand-lens or 50x microscope. For all identified surface modifications, size, location on the element, shape, internal morphology and association with other surface modifications was recorded. Lengths and widths of modifications were measured with digital calipers. Length was defined by the longest extension of the mark, while width was measured perpendicular to the length. The shapes of modifications were first described and sketched, and then grouped according to common shapes observed across the collections. Interior morphologies of the modifications were also characterized by texture and symmetry. Bone specimens had not undergone intentional cleaning since their original collection.

The Rusinga and Mfangano primate collections housed at the National Museums of Kenya were surveyed under 10-50% magnification for taphonomic markers that would indicate predation, such as pits, punctures, or scratches and the morphology and location of these modifications were noted. In some instances, breakage patterns and skeletal part frequencies can be used to assess predation when specimens have known associations.

Post-Cranial Avian Raptor Damage

In addition to the marks left of cranial remains, described by McGraw et al. (2006) and Sanders et al. (2003), several surface modifications including pits, punctures, scratches and digestion were identified on postcranial elements from these collections. All observed specimens were in weathering stage zero, and some elements still had small pieces of flesh attached and were found associated with hair. There was no evidence of trampling (Behrensmeyer, 1978; Dominguez-Rodrigo et al., 2009), carnivore gnawing or tooth pits (Binford, 1981; Delaney et al., 2009; Selvaggio and Wilder, 2001), rodent gnawing (Brain, 1981; Rose and Shipman, 1983), insect damage (Blackwell et al., 2012; Tappen, 1994), root etching or bioerosion (Blumenschine et al, 2007; Tappen 1994). Lacking evidence for significant post-depositional alteration, all surface modifications recorded here are presumed to be the direct results of crowned hawk eagle hunting and feeding.

Pits and Punctures

Punctures are defined as marks that penetrate the cortical bone through to the medullary cavity or cancellous bone, whereas pits only partially penetrate or depress the cortical bone. Both pits and punctures range in diameter from 1-4 mm, have a variety of irregular shapes, and are often clustered together. For the purposes of description and identification, the majority of these marks are described as V- or can-opener shaped, ellipse, hour-glass, or tailed (Figure 4.2). These marks are generally asymmetrical or irregular in cross-section with flaps or flakes of bone surrounding the exterior of the mark or within the pit or puncture itself (Figure 4.3). Additionally, larger patches of bone were occasionally removed and appear to be tightly clustered pits and punctures (Figure 4.4).

Scratches

Here, scratches are defined as thin linear marks 2mm or longer. They are rare in the collections (estimates of <10% of postcranial bones per nest) and often associated with mid-shaft breaks. Of the 12 sets of scratches identified from both collections, only 3 were unassociated with breaks. Scratches were generally short (<5mm in length) and tended to be roughly perpendicular to the long axis of the bone, though some specimens showed more random scratch orientations (Figure 4.5). Scratches also tended to vary in thickness and exhibited both U- and V-shaped cross-sections, with no visible internal morphological features such as striations.

Etching

Etching is the processes by which bone surfaces become chemically corroded by digestive acids. Among mammalian predators, recognizable bones can be in scat or from regurgitated meals. However, in avian predators bones are only regurgitated or completely dissolved. Trapani et al. (2005) report that several small elements were recovered from crowned hawk eagle hair boluses at Ngogo. While crowned hawk eagles have not been observed swallowing larger elements (Shultz, Mitani, pers comm), several additional long bone elements showed evidence of digestive etching, with thinned and porous cortical surfaces. Partial long bones also yielded digestive etching and thinning, exaggerated along breaks, cracks and pitting on epiphyseal ends (Figure 4.6). In these specimens, little cancellous bone was preserved. Some long bone fragments with etching were as long as 10cm in length.

Tearing and Breakage

In addition to the tearing described on the crania and scapula reported by McGraw et al. (2006) and Sanders et al., (2002), vertebrae were commonly torn on the processes and vertebral body. Thinner long bones such as the fibula or distal ulna also exhibit tearing and fraying. These breaks show plastic deformation from bending and splintering of bone marked by jagged, feathered edges (Figure 4.7). Other long bones were broken mid-shaft or in thicker cortical bone (Figure 4.8). These breaks are similar in appearance to “wet spiral breaks” and or damage that may be expected of carnivores, with high angled breakage planes (Pickering et al., 2005).

Damage Profile

Within the complete nest assemblages, roughly 20% of postcranial specimens exhibited some degree of observable damage. Approximately half of the specimens that exhibited any type of damage had more than one mark or type of damage (e.g. scratches/breaks, scratches/pits, or multiple pits/punctures). Among both collections, pits and punctures commonly occurred on the epiphyseal ends of long bones where cortical bone is thin and penetrated into cancellous bone. Pits also occurred near epiphyseal ends, but with less frequency and where cortical bone was generally thicker. No punctures or pits were recorded mid-shaft. Damage most commonly occurred on the femur and tibia, whereas the humerus and distal limb bones had relatively few breaks, pits, punctures, or scratches inflicted upon them (Table 4.3). Deep grooves repeatedly appeared around the head of the femur.

Marks appear to coincide with tendon and muscle attachment sites. Damage on the proximal femur is common on the head, neck, greater trochanter, and to a lesser extent, the lesser trochanter. Pits and more extensive punctures are common on the femoral condyles. On the tibia, pits and punctures were largely confined to the proximal end; along the edges of the tibial plateau and along the tibial tuberosity. Marks on other elements were only found on the epiphyseal ends unless they were associated with a midshaft break.

Predation on the Early Miocene Primates of Rusinga and Mfangano Islands

Le Gros Clark and Leakey (1951) suggested that many of the primates from Rusinga and Mfangano had fallen victim to the many carnivores and hyenadonts known from the same deposits. However, with the exception of individuals from the Kaswanga Primate Site (hereafter, KPS), and three other partial skeletons of *Ekembo* (KNM-RU 2036, KNM-MW 13142, KNM-RU 5872), the hundreds of primate specimens collected from Rusinga and Mfangano have not been described in the context of predation damage. The vast majority of the primate assemblage is made up of isolated surface finds recorded at varying levels of provenience. Historic collections by the Louis and Mary Leakey and by Alan Walker and Mark Teaford are generally recorded with site numbers or names, and in some cases stratigraphic horizon. In special circumstances, more specific localities are noted. Andrews' team employed an extensive grid system at some localities to better provenience both surveyed and excavated specimens. More recently, teams lead by McNulty, Dunsworth, Harcourt-Smith, Lehmann, Peppe, and Jenkins have used a variety of techniques, including systematic excavations and advanced survey equipment for precise three-dimensional coordinates as well as more generalized prospecting. Excepting the KPS and tree trunk site (R114), the direct association of most primate specimens with other fossils is difficult to confirm, making assemblage-level taphonomic analyses difficult.

An additional challenge for identifying taphonomic agents in the accumulations of primate remains is that important specimens may go unrecognized and uncollected. Unidentifiable specimens can be key to taphonomic analysis because these specimens may yield diagnostic damage, such as pits or gnawing that are especially useful when in association with identifiable remains. While such damage may obscure important morphological information, it is key for reconstructing depositional contexts. Moreover, whereas the postcrania of *Ekembo* and *Dendropithecus* are well known from associated partial skeletons, no postcrania can be reliably assigned to *L. legetet* or *N. vancouveringorum*. Most postcranial specimens have been assigned on the basis size, yet body sizes of *E. heseloni*, *D. macinnesi*, *L. legetet*, and *N. vancouveringorum* would have overlapped considerably (Harrison, 2014; see Table 4.1).

Many specimens from the historic collections have been lacquered and prepared in accordance with 20th century curational standards. In some cases, these processes may have destroyed slight modifications or hinder taphonomic diagnosis, but it does not always render surface modifications unidentifiable. Similarly, specimens in later stages of weathering or characterized by post-depositional rounding exhibit more obscured morphology of some surface modifications. In these cases, modifications were described as best as possible given visibility and preservation. Despite these limitations, taphonomic trends are still visible and provide an opportunity to examine predation on this important fossil primate community.

The curated primate assemblage is dominated by isolated teeth, hand and foot elements. This is likely in part due past research focus on these elements, but also due to the relative frequency of these elements in the body (i.e. %MAU) and their relative density aiding in their preservation. While hand and food elements are often swallowed by both carnivores and raptors, they may be less likely to yield diagnostic pits due to digestive etching (Brain, 1981; Boesch, 1991; Trapani et al., 2006; Nakazawa et al., 2013). Digestive acids reduce density and thereby make them less likely to survive subsequent post-depositional processes to fossilization (Andrews, 1990). The majority of the collection, which is derived from multiple sub-localities, shows little identifiable damage, and should be considered an under-representation of actual instances of predation as not all carcasses are likely to become part of the fossil record.

Damage on *Ekembo nyanzae*

E. nyanzae is the largest fossil primate from Rusinga and Mfangano Island, similar in size to a female chimpanzee and reconstructed as a generalized arboreal quadruped (Le Gros Clark and Leakey, 1950; 1951; Andrews, 1978; Walker and Pickford, 1983; Ward et al., 1997; McNulty et al., 2015). It is best known from sites within the Hewegi formation and from the partial skeleton discovered on Mfangano Island (KNM-MW-13142; Ward et al., 1997; Shipman and Walker, 2007). Surface modifications associated with this species are described in Table 2.4 and pictured in Figure 4.9 and modifications on partial skeletons are described below.

KNM-RU 5872

The partial skeleton, KNM-RU 5872, from R3 consists of distal femur fragment, a distal tibia with shaft, fibula shaft, 6 metatarsals, 3 phalanges, 5 tarsals, a calcanium, and several associated fragments. Walker and Pickford (1981) briefly noted carnivore damage on the specimen, and it is described here in detail. The distal femoral fragment and calcanium show probable carnivore gnawing and subsequent insect damage (Roberts et al., 2007). A tooth pit visible on one of the unidentifiable fragments associated with the skeleton is shallow, crushed in, and round with 3.5 mm diameter. Grooves on these specimens are also approximately 3.5mm wide suggesting the taphonomic agent was a medium-sized hyenadont/carnivore. Furthermore, 5 of the 6 metatarsals are missing their distal articular heads and show pre-fossilization breaks, suggesting they may have been chewed off.

KNM-MW 13142

The partial skeleton from Mfangano, KNM-MW 13142, initially described by Ward et al. (1997), preserves carnivore and probable raptor damage. The specimen includes the right and left femora, right *os coxa*, right talus, right calcanium, five vertebrae, and some additional appendicular element fragments. Carnivore or hyenadont gnawing noted on the sacrum, all five vertebrae, and calcanium is consistent with observations made by Ward et al. (1997). Small irregular marks and extensive damage are noted on the distal femur may be attributed to either mammalian carnivores or avian raptors. Whether carnivores/hyenadonts or avian raptors were predator or scavenger is not distinguishable, but it is likely that both were involved in the consumption of the carcass.

Natural disarticulation patterns have not been studied in as much depth for non-human primates as they have for large ungulates (Hill, 1979; Behrensmeyer and Hill). However, comparisons for KNM-MW 13142 can be drawn from Kerbis et al.'s (1993) study of chimpanzee remains in the Kibale forest. At Kibale, carcasses were often separated into two or more clusters of bone; of the eight carcasses described in detail, two appeared to have been disarticulated at the lower back, with lumbar vertebrae associated with pelves, sacrum and portions of the hind limbs, possibly by the jaws of scavengers (Kerbis et al., 1993). While caution must be exercised when examining skeletal part patterns in the fossil record (e.g. elements can be lost to post-fossilization erosional processes), the skeletal element profile for KNM-MW 13142 is consistent with modern tropical forest disarticulation processes where carnivores or scavengers are be involved.

While larger body sizes may prevent a raptor from flying away with live prey, it does not hinder its ability to ambush prey on the ground or knock prey from a branch, then killing and disarticulating prey into manageable pieces on the ground. Baboons from Angola of similar size to *E. nyanzae* have been interpreted as raptor kills (Gilbert et al., 2007), and the biggest modern raptors have been observed killing even larger ungulates (Kerley and Slaght, 2013). Raptor damage on the hands and feet was not consistently observed in actualistic collections, but several hand and foot fossil specimens show possible raptor damage. In this case, body size differences may impact the degree and location of raptor processing. In the actualistic collections from the Tai and Ngogo Forests, the largest monkey prey taxa are estimated to be just over 10kg (male *Colobus gueresa*, *Piliocolobus badius, Cerococebus atys*), which is on the low end of *Ekembo heseloni* size estimates (Table 4.1) (Harrison, 2002a; Harrison 2010a, 2010b). The monkeys of the Taï and Ngogo Forests may not be the best analogy for the location and frequency of raptor surface modifications for the larger (28-40kg) *E. nyanzae*.

Damage on *Ekembo heseloni*

E. heseloni is the most frequent primate recovered from Rusinga. Similar to the larger *E. nyanzae*, it is also reconstructed as an above branch quadruped, but with smaller body sizes (1-20kg) (Table 4.1). Patterns of damage on *E. heseloni* specimens are similar to those noted for *E. nyanzae*; isolated specimens show damage consistent with both avian raptors and carnivores or hyenadonts (Table 4.4; Figure 4.10). Well-known specimens of *E. heseloni*, such as the R106 skull recovered by Mary Leakey (KNM-RU-7290), the KPS individuals and the type specimen KNM-RU 2036 also warrant further discussion.

Kaswanga Primate Site

The Kaswanga Primate Site (KPS) is made up of ten *E. heseloni* individuals, identified by Roman numeral I-X, nine of which are represented by partial skeletons (Walker et al., 1993; Walker 2007). Walker (2007) suggested that the site was a hyenadont accumulation by virtue of observed surface modifications and comparison of skeletal part frequencies to C.K. Brain's (1984) leopard feeding experiments. Much of KPS has suffered plastic deformation and cortical flaking making diagnosis of surface modifications difficult. Furthermore, Individuals I, II, I, VI, VII, and VIII are juveniles/sub-adults and have missing and unfused epiphyses. Carnivores are likely to leave tooth pits both midshaft and at the epiphyses and often produce high angled breaks on long bones (Marean and Kim, 1998).

In this reexamination of the KPS, possible predation related pits were observed on both identified primate material and associated unidentified fragments. These include an oblong crushed-in depression on the distal epiphysis of the KPS I femur, a small heart-shaped mark on the pelvic fragment of KPS VI, and several small punctures on the femur of KPS VII. Several instances of surface damage previously diagnosed by Jenkins (2010) and Walker (2007) as tooth pits, however, I reassess these marks here as insect damage. Species of beetles and termites excavate pits and grooves in bone that can appear similar to carnivore tooth pits and gnawing marks (Roberts et al., 2007; Tappen, 1994; Throme and Kimsey, 1983; Watson and Abbey, 1986). The interior morphology of insect pits differs from carnivore pits in that insect pits do not show crushing and may exhibit radial patterns or grooved interiors. This is consistent with the morphology of pits observed on specimens I (ulnar shaft), III (L femoral neck and femoral head, R femoral head, radial shaft), and VIII (radial shaft), and therefore these instances are considered to represent insect damage. None of KPS specimens exhibits high-angled or “wet” fractures.

It is unlikely that a medium-sized carnivore or hyenadont capable of transporting and disarticulating *E. heseloni* would leave so little damage on the remaining elements (Pickering et al., 2011). Raptors, however, are generally more fastidious eaters and leave fewer marks – usually on limb ends. Unlike, the skeletal part profiles of raptor predated monkeys from Taï and Ngogo, the KPS yields little cranial material, but the presence of teeth from nearly all individuals attests that some cranial material was indeed present at the time of deposition. The general lack of tooth pits and wet/curved breakage patterns at the KPS is inconsistent with carnivore or hyenadont accumulation, and hence may be better interpreted as the remains of raptor kills that accumulated beneath a nest.

KNM-RU 2036

The Tree Trunk Site (R114) where the type specimen of *E. heseloni* (KNM-RU 2036) was discovered has also been interpreted as a hyenadont den (Walker, 2007; Walker and Pickford, 1983), and is largely supported by important contextual evidence. Namely, the juvenile *E. heseloni* specimen was thought to be the unfortunate victim of a medium-sized hyenadont and deposited in the trunk of a hollowed out tree (Walker, 2007; Walker and Pickford, 1983). This is consistent with the discovery of several other similarly-sized individuals associated in the dense assemblage: a monitor lizard, medium-sized snake, lagomorph and two small tragulids, Walker (2007) also reported tooth pits on KNM-RU 2036, but these are not confirmed here. The matrix in which these specimens were consolidated is exceedingly hard, and preparation of the RU 2036 left many grooved marks and destroyed much of the bone surfaces. Given the context and presence of other similarly sized animals, a predator accumulation seems likely. However, without the clear tooth pits or gnawing, a raptor hypothesis should not be ruled out for the tree trunk assemblage. Careful preparation of the associated non-primate specimens may clarify whether a mammalian or avian predator was the taphonomic agent.

KNM-RU 7290

Perhaps the most diagnostic characteristic of a raptor accumulation are the can-opener marks on crania with the basio-occipital regions torn out (McGraw et al, 2006; Sanders et al., 2003). The KNM-RU 7290 skull is a well-preserved specimen that lacks the basio-occipital region, but yields no additional evidence of raptor damage. All of the breaks are clearly post-depositional (e.g. right angles) and there is no evidence of tearing that accompanies damage from raptor feeding. No other marks or scratches were observed. Unfortunately, the region that would be most likely to preserve diagnostic damage is missing and thus no accumulating agent can be assigned.

<u>Damage on *Dendropithecus*</u>

R3 Dendropithecus

Le Gros Clark and Thomas (1951) described a dense cluster of bones “somewhat more than a cubic foot in volume” from the red limestones of R3 (See Figure 4.1 (map) and Figure 4.12) that are referred to *Dendropithecus macinnesi* (then grouped with *Limnopithecus*);. They report at least 4 individuals (1 juvenile, 1 young adult, 2 adults) represented by dental and postcranial remains in close association. Many of the postcranial specimens yield damage characteristic of consumption (Table 4.5). Pits are frequent and several long bones have gnawed epiphyseal ends with rounded irregular breakage and grooves. (Figure 4.11). Pits are generally round, 1-2 mm in diameter and damage is heavier on limb ends. Damage on limb ends could be carnivore gnawing or more extensive raptor fraying/tearing, but the absence of more irregularly shaped pits suggests the modifier was likely a carnivore or hyenadont. Additional details that would help distinguish raptor from mammalian carnivore modifications such as plastic deformation, interior morphology, bone splintering, have been obscured by post-depositional rounding and lacquer. The possibility of bone fraying is relevant because, while not commonly observed on the raptor-predated cercopithecoids reported here, it is characteristic of larger prey taxa from Verreaux's eagle (*Aquila verreauxii*) assemblages (Armstrong, 2014). Bone fraying is also a common taphonomic characteristic in chimpanzee prey remains (Pobiner et al., 2007; Tappen and Wrangham 2006). However, since chimpanzees and other primates are not known to accumulate bones, it is unlikely that the R3 assemblage represents an early instance of primate-primate predation. Long bones and cranial/dental elements are the more frequent (%MAU) than axial elements, which is consistent with both actualistic raptor studies (McGraw et al., 2006; Sanders et al., 2002) and baboon-leopard feeding experiments (Carlson and Pickering, 2003). However, given the lack of irregularly shaped marks, the surface modification trends are more consistent with that of a medium-small carnivore/hyenadont than an avian raptor.

Damage on Indet. Catarrhines

Given the overlap in body size of the smaller catarrhines, several specimens are not currently diagnosed to the genus level, yet still show recognizable damage (Table 4.4). It is possible that these specimens include the lesser known *Limnopithecus* or *Nyanzapithecus* and that these specimens may be further diagnosed in the future.

RU-2009-1506 is a femoral head within the size range of *E. heseloni* or *D. macinnesi* with four irregular shaped marks and tearing/excavation around the neck. A small mark is a “c-shaped can opener” mark on the head. It is adjacent to longer (7.5 x 2.7mm) irregularly shaped puncture with pressed-in cortical bone. Two additional crushed-in punctures are present on the edge of the head. All of these marks are consistent with raptor damage more so than mammalian carnivore damage.

Damage on Lorisoids

The Lorisoid collection dominated by cranial and dental specimens and has a very limited postcranial assemblage. A talus, KNM-RU-3424, was recovered from Andrews’ excavations at R5 (Kaswanga) in the 1970s. The specimen has a single round pit, less than 1mm in diameter, which I interpret as a small carnivore/hyenadont tooth pit. Additionally, a left distal humerus fragment from Mfangano Island (RU-2007-284) is associated with several small mammals remains yields two pits on the posterior side, approximately 0.6mm in diameter and 4mm apart (Figure 4.13). Given their morphology, I interpret these pits being created by small carnivores/hyenadonts, but it should be noted that they are not outside the range variation that should be expected for avian raptors based on Andrews (1990) actualistic studies as well.

The small body size of Miocene lorisoids makes them ideal prey for the numerous small mammalian carnivores and raptors. The small body size of the lorisoids does not necessarily mean that their elements are less likely to preserve (Andrews, 1990). However, these samples are likely limited due to the difficulty in recovering and identifying small specimens. Both Gully 15 and Andrews’ excavations at R5 have yielded multiple small mammal taxa and it is possible that these areas represent predator accumulations (Andrews and Van Couvering, 1975).

Discussion

Relationship between raptor surface modifications and specific behaviors

Avian raptors have been observed snatching monkeys from trees and bringing back both complete and incomplete carcasses to their nests. Hunting appears to be opportunistic as raptors ambush prey (Shultz, 2002). Crowned hawk eagles often take freshly killed monkey prey to the ground and disarticulate portions of the body into presumably more manageable pieces, usually individual limbs. A raptor may make multiple trips back to the kill site to bring back additional pieces of the carcass within 1-2 days (Shultz pers. com.). These choices appear to reflect prey size and maneuverability within the forest and the need to reduce time spent on the forest floor where raptors are at a disadvantage with other predatory taxa.

In the modern collections from the Taï and Ngogo nests, marks left on postcranial remains by avian raptors can be directly related to consumption and disarticulation. Damage on the modern femora, proximal tibiae, and proximal humeri is consistent with observed disarticulation behaviors at Taï and Ngogo. Surface modifications with irregular and asymmetrical interior morphologies are consistent with curved talons and beaks piercing into bone while ripping through ligaments. Hourglass shaped marks appear to be formed by both the maxillary and mandibular beak pecking. Triangular marks with asymmetrical cross sections on long bones are morphologically similar, though reduced in size, to the “can opener” and “V” shaped marks that Sanders et al. (2002) describe on crania, suggesting similar processes and mechanics produce the marks. Without interfering in the natural feeding process, it would be nearly impossible to absolutely link these marks with either claw or beak damage for actualistic study. However, it is likely that the majority of punctures and pits near joint surfaces are the result of disarticulation processes by repeated pecking and ripping.

Raptors use their feet to grasp and hold carcasses, creating resistance as they strip meat from bones and disarticulate limbs. Tearing observed on vertebrae is likely the result of disarticulation processes at the spine. Scratches observed on the mid-shaft of some long bones likely reflect manipulation from the talons or from beaks repeatedly stripping meat from the bone or intentional bone breaking in order to access marrow or swallow smaller pieces. Larger raptors are strong enough to break smaller, less dense bones.

Trapani et al. (2006) recovered and described pellets and hair boluses containing small bone fragments, but crowned hawk eagles have not been observed swallowing complete or partial monkey long bones. However, digestive etching on elements suggests that they do on occasion swallow and subsequently regurgitate larger pieces of bone. This is not extraordinary as pellets belonging to the similarly sized Verreaux's eagle have been observed containing tortoise plastron fragments as large as 8cm (Brain, 1981). Skeletal part frequencies from nests generally yield low frequencies of smaller, less dense elements, suggesting that these elements may have been consumed (Sanders et al., 2002; Trapani et al., 2006; McGraw et al., 2006). Eagles, unlike owls, do not routinely produce pellets with identifiable bone preserved (Andrew, 1990).

Comparison of surface modification to carnivores and other raptors

The damage caused by crowned hawk eagles on monkeys is not dissimilar from that of other avian raptors on small mammals such as lagomorphs and small ungulates or smaller avian taxa. Lloveras et al. (2009), Hocket (1991), Bochenski and Tornberg (2003), Montalvo et al. (2011), Erlandson et al. (2007), and Armstrong (2014) note the presence of small punctures and perforations on uneaten prey remains of lagomorphs, rodents, and birds from the eagle owl (*Bubo bubo*), northern harrier (*Circus hudsonius*), gyrfalcon (*Falco rusticolus*), crested caracara (*Caracara cheriway*), and bald eagle nests (*Haliaeetus leucocephalus*). Bochenski and Tornberg (2003) document small punctures left by gyrfalcons on the humeri of grouse prey and appear irregular and "v-shaped" in outline. Furthermore, Erlandson et al. (2007) document similar punctures and tearing on avian sternal elements, and Sanders et al. (2002), McGraw et al. (2006), Trapani et al., (2006), and Andrews (1990) document this tearing on cercopithecoid and small mammal crania and scapulae. Photo documentation suggests raptors with similar beak and talon morphologies lead to similar feeding processes and surface modifications. However, skeletal parts and surface modification frequencies can be quite variable, presumably due to the body sizes and plan of prey taxa (Armstrong, 2014), density of raptors, and whether or not the accumulation is produced at a breeding pair's nest or an individual perch.

Marks left by crowned hawk eagles fall within the range of variation of carnivore tooth pits. Carnivore tooth pits are generally round, show crushing in and around the pit, and have a U-shaped interior (Binford, 1981; Delaney-Rivera et al., 2009; Haynes, 1983; Pickering et al., 2011; Pobiner, 2008; Selvaggio and Wilder, 2001). However, tooth pit morphology can vary considerably; producing asymmetrical cross-sections and irregular outlines, especially as an animal engages in gnawing behavior. Furthermore, carnivore damage on primates is likely to be concentrated at long bone epiphyseal ends (Pickering et al., 2011), similar to marks left by crowned hawk eagles. Damage from large carnivores such as leopards, lions, hyenas, or reptilian predators are unlikely to be mistaken for avian raptor damage because of differences in the size of the pits. Large predators will commonly leave many tooth pits several millimeters in diameter, whereas raptor damage tends to be much smaller. From a collection of leopard predated baboons, Pickering et al. (2011) identified at least one tooth pit or puncture on 80% of long bones, compared to approximately 20% left by avian raptors. Similarly large predators are likely to completely destroy bones of prey by crunching or swallowing them whole.

As is a familiar problem to taphonomists, mark shape and size can be deceiving. Raptors will repeatedly peck in the same location, creating a larger mark that could be mistaken for a larger carnivore's tooth pit. However, larger marks by raptors are likely to be irregular in outline, unlike a single carnivore tooth pit. Grooves and scoring on limb ends from small carnivores and raptors have the potential to also appear very similar. While toothpits and gnawing from smaller carnivores may be within the size range of avian raptor damage, subtle differences exist in pit morphology. Raptor damage is more likely to be more asymmetrical and have v-shaped or irregular outlines. Carnivore pits are likely to have rounder outlines with u-shaped cross-sections. The frequency of marks may also help differentiate between carnivore and raptor; in this study, raptors left marks on only 20% of the postcranial material where carnivores may mark as much as 80% of the assemblage (Pickering et al., 2011).

Predation Trends on Rusinga

Modification Trends: Surface modifications provide clear evidence of predation on the Rusinga/Mfangano primate guild by carnivores, hyenadonts and avian raptors. Both species of *Ekembo* and *Dendropithecus* fell prey to avian raptors and mammalian carnivores. While caution should be exercised when extrapolating predator body sizes from tooth pits (Delaney et al., 2009), some carnivores and hyenadonts may have been specialized hunters; tooth pits on *E. nyanzae* generally range from 2-5 mm size range, while tooth pits on *E. heseloni* and *Dendropithecus* are somewhat smaller (1-3mm), suggesting body size preferences among the different predators. Unsurprisingly, pits preserved on the lorisoid material are smallest (sub-millimeter). It is tempting to match tooth pits to taxa; however, with such diverse sets of carnivores and hyenadonts preserved on Rusinga and Mfangano, any such designations would be fraught with equifinality (Delaney et al., 2009). Medium-sized hyenadonts such as *Anisinopa leakeyi*, *Leakitherium hiwegi*, *Metapterodon*, or carnivores such as *Herpestides aequatorialis* may have all been catarrhine predators.

Today, when raptors hunt primates, they generally do so from the trees. Discussions about the degree of tree cover around Miocene Rusinga have generated much debate in the past (Bestland and Kroll, 1999; Retallack, 1995; Andrews, 1997; Walker and Pickford, 1983; Harris and Van Couvering, 1995). However, preserved leaves from the R5 locality (Maxbaurer et al., 2014) and a recently discovered fossil forest from R3 (Michel et al., 2014), both of the Hewegi Formation, have added to the previously known fossil tree trunks at R114 showing that forests likely persisted in places on Rusinga (Andrews, 2015). Whether densely wooded or not, raptor predation associated with trees should not be surprising given the inferred substrate preference of these primates.. Furthermore, it may suggest that both *Ekembo* and *Dendropithecus* shared a similar or overlapping niche space (social behavior or preference within the canopy) that left them vulnerable to hunting by raptors. Unfortunately, little is currently understood about the ecomorphology and preferred habitats of the Miocene hyenadonts or carnivores, and that information could shed additional light on to the niche spaces occupied by these primates. It is possible that the larger hyenadonts and carnivores were terrestrial and that smaller ones may have had some arboreal adaptations.

The Avian Fossil Record from Rusinga and Mfangano

Despite clear taphonomic evidence for raptors interacting with these early Miocene catarrhines, the overall record of avian fossils is exceedingly poor compared to the rich mammalian assemblages of Rusinga and Mfangano. The few avian taxa known include a smaller stork (*Ciconia minor*) and a medium-sized hawk (*Accipiter tachiro*). The Kulu formation at the R4 locality is the richest avian site with a possible mass death assemblage of flamingos (Harrison and Walker, 1976; Rich and Walker, 1983; Dyke and Walker, 2008; Peppe et al., 2009). While *Accipiter* may have been capable of hunting rodents and lorisoids, it would not have been large enough to dispatch of larger primates such as *Ekembo*. Additional birds of prey (vultures, owls and hawks) are known from roughly contemporaneous deposits from Songhor and Legetet Hill. However, it is unlikely that larger birds of prey were absent in the early Miocene of Mfangano and Rusinga and this lack of fossils should be attributed to preservation bias and spatial density of raptors on the landscape. Avian remains are notoriously fragile and while their cortical bone is actually denser than that of mammals, it is thin and can easily break into unidentifiable fragments (Higgins, 1999). Furthermore, actualistic studies show that avian remains may weather more quickly than mammalian remains in terrestrial environments (Behrensmeyer et al., 2003).

As asocial predators, modern raptors are relatively rare on any given landscape (Shultz, 2002; Seavy and Apodaga, 2002. Breeding pairs can keep individual territories of several square miles (Shultz, 2002). With raptors potentially spaced so widely in a forest, the odds of recovering them in the terrestrial fossil record may be low. Furthermore, they are unlikely to be the preferred prey of carnivores. There are few agents or processes known to accumulate large numbers of birds of prey. One exception is natural traps or tarpits such as LaBrea (Stock and Harris, 2001). While the odds of raptors preserving in the fossil record are not high, taphonomic evidence of their presence is much more likely to be preserved in the numerous prey they consume throughout their life span, as demonstrated above.

Identification of raptor accumulated or modified fossil sites

Using the criteria outlined by Brain (1981), Andrews (1980), Clark and Berger (1995), and the actualistic observations described here and by McGraw et al. (2006), Sanders et al. (2002), and Trapani et al. (2006), raptors and their ecological impacts on primates can be visible in the fossil record. Given the behaviors associated with raptor feeding and hunting, there is potential to recover three types of raptor accumulated “sites” in the fossil record: nest sites similar to those described from Taï and Ngogo (McGraw et al., 2006; Sanders et al., 2002), perch sites, and isolated kill sites.

Nest sites are produced by breeding pairs that bring portions of prey back to the nest. Nests are not used continuously throughout the year, but only when a pair is breeding and raising hatchlings. Large avian raptors such as the crown hawk eagle often prefer to nest in emergent trees or trees near the edges of forest so that they have room to maneuver, and some nests may be repeatedly used (Malan and Shultz, 2002). Cliffs can also be attractive nesting sites for other large birds of prey (Brain, 1981). Below the nest, uneaten prey remains are discarded and are generally found within a 5m radius (McGraw et al., 2006). Beneath the annually used nests at Taï, older prey remains were buried in organic matter and specimens were found several centimeters deep in soils developed on fluvial sediments (Shultz, pers com).

Perches are localities where a raptor will habitually visit to safely eat, disarticulate, or watch for prey. Perches can be trees, cliffs, or other high structures where prey remains can accumulate below. Behaviorally, these sites are differentiated from nesting sites because food is not being cooperatively brought to a central location for the sake of offspring. Brain (1981) reports on several black eagle perches and notes that they reflect the dominant prey of the eagle, similar to nests. However, it is likely that nests and perches sites would be nearly indistinguishable except for the potential presences of egg shell at nests.

Isolates/Kill Sites are defined here as single episodes of feeding or prey disarticulation. As discussed above, raptors will generally take freshly killed prey to the ground to quickly disarticulate it for transport. While raptors may return for the rest of the carcass, some carcasses are abandoned, leaving the potential for portions of partially articulated carcasses to be preserved with characteristic surface modifications near disarticulation points. Additionally, many raptors have been known to “stash” portions of prey for later consumption near perches or other localities. A stash is likely to be an isolated and disarticulated element with characteristic surface modifications.

Raptor accumulations can be identified within karst systems by examining associated remains of similarly sized animals with associated surface modifications. Caves make ideal localities for identifying raptor accumulations because important elements are more likely to be preserved in a more protected environment; the most common diagnostic criteria of avian prey remains is characteristic damage to fragile crania and scapulae (Andrews, 1990; McGraw et al., 2006; Sanders 2002). Open-air sites, where trampling, scavenging and other post-depositional processes are more likely to destroy crania and other less dense elements pose a potential problem for identifying raptor accumulated sites from cranial damage and skeletal part frequencies alone. Nevertheless, most modern raptor accumulations occur outside for karst systems.

Identifying an open-air fossil raptor accumulation requires (1) detailed examination for trends in surface modification morphology and (2) detailed and systematically collected provenience data. It would be difficult to positively identify a single postcranial mark to raptor or other agent because some raptor damage overlaps in morphology and size with small carnivore damage. Assemblages, rather than isolated bones, should be examined for trends when possible. However, assemblages require large samples of associated fossils which can be difficult to amass when surface collecting only those fossils that have eroded out of context. In such cases, recording precise locations so that finds recovered over the course of several field seasons can be grouped together can produce an associated assemblage for analysis. Additionally, archaeological style excavations (i.e. not quarrying) can provide contextual evidence for depositionally associated remains. By using careful field methods and detailed documentation of surface modification, predation by raptors or carnivores on primates can be confidently identified.

Recommendations

Site formation studies are particularly difficult to draw strong conclusions from when samples lack detailed provenience. The majority of fossil primate sites are open air and some are exceedingly large with fossils littering a vast landscape. In many instances, 100% collection from the surface is simply not logistically possible given time and space constraints. Behrensmeyer and Barry's (2005) bone walk survey methods help collect taphonomic samples and data relative to strata and involve trained taphonomists and geologists mapping out sampling transects and recording frequencies of taxa, fragments, and taphonomic variables in the field. However, multiple trained taphonomists are not always available and stratigraphy is not always worked out prior to fossil collection. Given these constraints, I have developed a sampling protocol that can be used for future field work to collect small, but useful taphonomic samples from localized deposits that can be quickly implemented during scouting and generalized surface collections. The method involves identifying a deposit or exposure of interest, noting general topographic features and basic geologic context, and laying down a small surface grid in which 100% of fossils are collected by square. This information allows a taphonomist to generate hypotheses about small-scale site formation processes that are often missing from interpretations of fossil sites. A small and localized sample of 100% collection also allows for examination of associated unidentified fragments that may have important surface modifications that can shield light on to predation patterns.

Rusinga's rich primate assemblage poses a unique problem where similarly sized taxa are primarily understood from presumed predation assemblages. *Dendropithecus* is largely known from the R3 block and the type specimen of *E. heseloni* is from the tree trunk assemblage at R114 and supplemented by the KPS assemblage. Both carnivores and raptors are likely to select prey by body size and preferred substrate. *E. heseloni*, *Limnopithecus*, *Dendropithecus* and *Nyanzapithecus* would have overlapped in body sizes and are all thought to have been arboreal quadrupeds. However, the diagnosis of postcrania is based on the association of cranial dental remains without considering the nature of that association. In instances where multiple individuals are represented, caution should be exercised when remains are not explicitly articulated, as raptors have been shown to accumulate multiple taxa, but not necessarily overlapping body elements when only portions are brought back a nest site. While predators are excellent at accumulating primate remains, they may also severely damage important limb ends, making diagnosis of postcrania even more difficult. Taxonomic identifications should consider the nature of the depositional settings and be strongly rooted in morphology, rather than just association.

Using a holistic approach to understanding site formation- including actualistic comparisons of surface modifications, breakage patterns, skeletal part frequencies and fossil associations- is the most rigorous method for examining predation patterns. As evident from the Rusinga and Mfangano material, surface modifications or skeletal part frequencies alone cannot always be diagnosed to a specific predator and specimens out of context are of limited value. However, as paleoanthropologists, we work with the available record to observe visible trends. An understanding of predation behaviors can inform hypotheses about selection pressures, biogeography, and paleo-communities. The early Miocene primates of Rusinga and Mfangano likely faced predation threats from both the trees and the ground and would have evolved mechanisms to limit these threats. Traits such as body size, evasive locomotor behaviors and morphology, social behaviors, inter-birth intervals, and substrate preferences are often adaptations to predation and during the early Miocene, catarrhines faced a suite of predation threats. These adaptations need to be incorporated into discussions of evolutionary trajectories and can be examined through time with respect to taxon and environment with larger samples.

Table 4.1: Primate taxa from Rusinga and Mfangano Island and body size estimates (Harrison, 2002a; 2002b; 2010a; 2010b).

Primate Taxa	**Body Size Estimates**
Catarrhines	
Dendropithecus macinnesi	5-9 kg
Limnopithecus legetet	5 kg
Nyanzapithecus vancouveringorgum	8 kg
Ekembo heseloni	10-20 kg
Ekembo nyanzae	28-40 kg
Lorisoids	
Komba minor	60g
Komba robustus	266
Komba walkeri	266
Progalago songhorensis/Mioeuopithecus bishopi	266-465
Mioeuoticus shipmani	600-1600g

Table 4.2: Hyenadonts and Carnivores known from Rusinga and Mfangano Island.

Hyenadonts
Anasinopa leakeyi
Hyainailouros napakensis
Hyainailouros nyanzae
Isohyaenodon andrewsi
Isohyaenodon matthewi
Isohyaenodon pilgrimi
Leakitherium hiwegi
Megistotherium osteothlastes
Metapteordon kaiseri
Metapterodon zadoki
Teratodon spekei
Carnivores
Amphicyonidae
Cynelos euryodon
Cynnelos macrodon
Ursidae
Hemicyon sp
Nandiniidae and Viverridae
Herpestides aequatorialis
Stenopleisictis muhoronii
Herpestidae
Kicherchia zamanae
Kicherchia sp.
Leptoplesictis mbitensis
Leptoplesictis rangwai
Barbourofelidae
Afrosmilus africanus

Table 4.3: Actualistic monkey postcrania were sampled from nests for surface modifications. Femora, tibiae, and fibulae were most commonly modified by larger punctures.

		Observed occurrences of types of surface damage by element				
Element	**Number of specimens with damage**	**Pits**	**Puncture**	**Scratches**	**Breakage**	**Average number of mods per element**
clavicle	1	0	0	1	1	2.0
scapula	3	0	2	0	2	1.3
humerus	5	2	6	2	1	2.2
radius	3	0	2	0	1	1.0
ulna	6	0	6	3	3	2.0
manual elements	3	0	0	0	3	1.0
vertebrae	4	0	2	0	0	0.5
femur	22	19	40	3	6	3.1
tibia	25	7	35	5	3	2.0
fibula	13	0	10	0	4	1.1
pedal elements	3	2	2	0	0	1.3

Table 4.4: Isolated primate specimens with damage attributed to predation damage.

Specimen	Element	Site	Modification	Location of damage	Dimensions (mm)	Description	Probable Modifier
Isolated E. *nyanzae* specimens							
KNM-RU-1896	talus	Rusinga	2 pits	head	3.7 x 1.0; 1.0 x 1.0	irregular; round	indet
KNM-RU-3105	talus	Rusinga	pits	trochlea	2.6 x 2.0	round pit and with prefossil irregular breaks	indet
KNM-RU-3688	femoral shaft	Rusinga	gnawing	proximal and distal articular surfaces	n/a	n/a	carnivore/ hyenadont
KNM-RU-18383	phalanx	R1	pit	proximal shaft	2.5 x 2.2	Heart-shaped/ asymmetrical	raptor
KNM-RU-14230	talus	R106	pit and groove	head and neck	2.0 x 2.0	round	indet
KNM-RU-18381	proximal 1st metacarpal	R106	pit	distal shaft, near head	4 x 3.5	tailed and crown shaped	raptor
KNM-RU-5527	femur	R106	pits and punctures	head; pateller surface	n/a	proximal end: irregular and triangular shaped punctures; distal end: oval and irregular shaped punctures	raptor
KNM-RU-7696	distal humerus fragment	R106	3 pits	posterior side of the medial epicondyle and trochlea	7.8 x 3.7	round; triangular and crushed; oval	carnivore/ hyenadont
RU-2007-002	proximal 3rd phalanx fragment	R106	possible digestion	n/a	n/a	pitting and irregularly thinned bone	indet
RU-2007-093	talus	R106	grooves	trochlea	n/a	irregular cross section, associated with	indet

						breakage	
KNM-RU-1786	proximal ulna fragment	R3	pit; groove	trochlear notch; olecranon process	3.1 x 1.4	oval	raptor
KNM-RU-5940	talus	R3	2-3 pits, head gnawed off	trochlea	1.5 x 2; 3.5 x 2	irregular, c-shaped	indet
KNM-RU-1809	distal metacarpal fragment	R5	2 pits	articular surface and side	2.0 x 2.0	round	carnivore/ hyenadont
KNM-RU-1743	talus	R73	pit	head	2.4 x 2.4	round	carnivore/ hyenadont
Isolated specimens of *E. heseloni*							
KNM-RU-1755	calcaneus	Rusinga	possible gnawing	calcaneal tuberosity gnawed off	n/a	prefossil irregular breaks	carnivore/ hyenadont
KNM-RU-14277	distal femur fragment	R106	3 pits	patellar surface		oval/irregular with crushed in cortical bone	raptor
RU-2006-068	proximal 3rd metatarsal	R3	gnawing, pit, and possible etching	proximal shaft	6 x 4mm	oval pit with crushed in cortical bone	carnivore/ hyenadont
RU-2006-547	distal tibia fragment	R106	3 pits	edges of distal articular surface	6.4; 6.7; 6.8 wide; post-dep. compression	elongated irregular shape, asymmetrical cross sections	raptor
RU-2008-014	2nd pedal phalanx	R016	possible etching	n/a	n/a	pitting and bone thinning	indet
RU-2008-122	femoral head	R3	pits/gnawing	head	6.0 x 2.9 mm	grooves and breakage associated with irregular punctures with asymmetrical cross sections and cortical flakes	raptor
RU-2010-823	astragalus	R5	irregular grooves	head and body	n/a	irregular grooves	indet
Isolated indet catarrhine specimens							
KNM-RU-5724	distal phalanx	Rusinga	pits, possilbe etching	proximal shaft	2.5 x 4; 3.3 x 4.7mm	C-shaped, round,	carnivore/ hyenadont

	frag					asymmetrical cross section	
KNM-RU-5944	thoracic centrum and vertebral arch	Rusinga	pit	transverse process	4.8 x 4.8	round	carnivore/ hyenadont
KNM-MW-17380	talus	Mfangano	groove/gnawing	neck and head	3mm wide	irregular and jagged edges	raptor
KNM-MW-17385	talus	Mfangano	irregular break/gnawing	n/a	n/a	n/a	indet
RU-2009-1506	femoral head	Rusinga	3 pits/punctures	head	3.1 x 2.4; 7.5 x 2.7; 2.3 x 1.5	bisected pit; irregular oval with pressed in cortical at one end; diamond shaped asymmetrical cross-section and pressed in cortical.	raptor

Table 4.5: R3 Dendropithecus specimens with damage.

Specimen	Element	Modification	Location	Dimensions (mm)	Description
KNM-RU-1637	distal femur and shaft	gnawing	distal end	n/a	rounded and grooved breakage at distal epiphysis
KNM-RU-1638	distal femur	gnawing	distal end	n/a	irregular damage and rounded possible fraying
KNM-RU-1640	femoral head	gnawing and tooth pit	pit	2.0 x 2.0	round
KNM-RU-1641	tibia shaft	gnawing	proximal end	n/a	
KNM-RU-1642	fibula shaft	pit	shaft	1.5 x 1.5	round, sediment inside pit
KNM-RU-1645	distal humerus shaft	gnawing	distal shaft	n/a	rounded and grooved breakage with crush cortical bone
KNM-RU-1660	calcaneus fragment	pits/gnawing	lateral and medial sides	2.0 x 6.2	
KNM-RU-1663	talus	pits and gnawing	lateral malleoloar surface	3 x 1.5	tailed pit
KNM-RU-2097	humerus	gnawing	proximal end	n/a	rounded and grooved breakage
KNM-RU-2098	radius	possible pits	shaft	n/a	obscured with glue
KNM-RU-2099	proximal ulna and shaft	gnawing	proximal end	n/a	rounded and grooved breakage

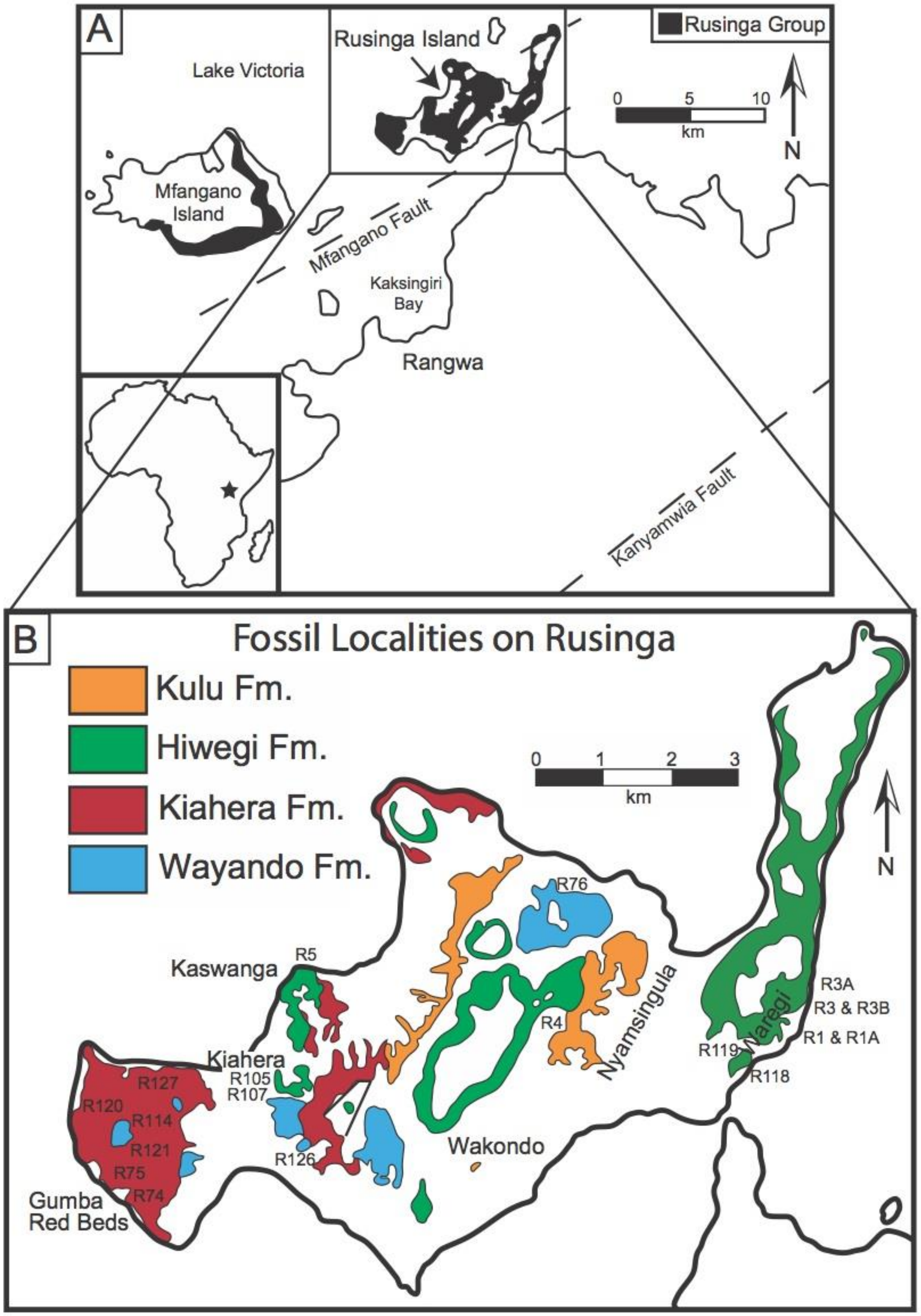

Figure 4.1: Map of Rusinga Island and important localities.

Credit: Dan Peppe

Figure 4.2: Drawings of common shapes of pits and punctures from crowned hawk eagles.

A) c/v-shaped marks or can-opener marks. B) ellipse or oval pits and punctures. C) figure-eight or hour-glass shapes. D) round, tailed pits and punctures.

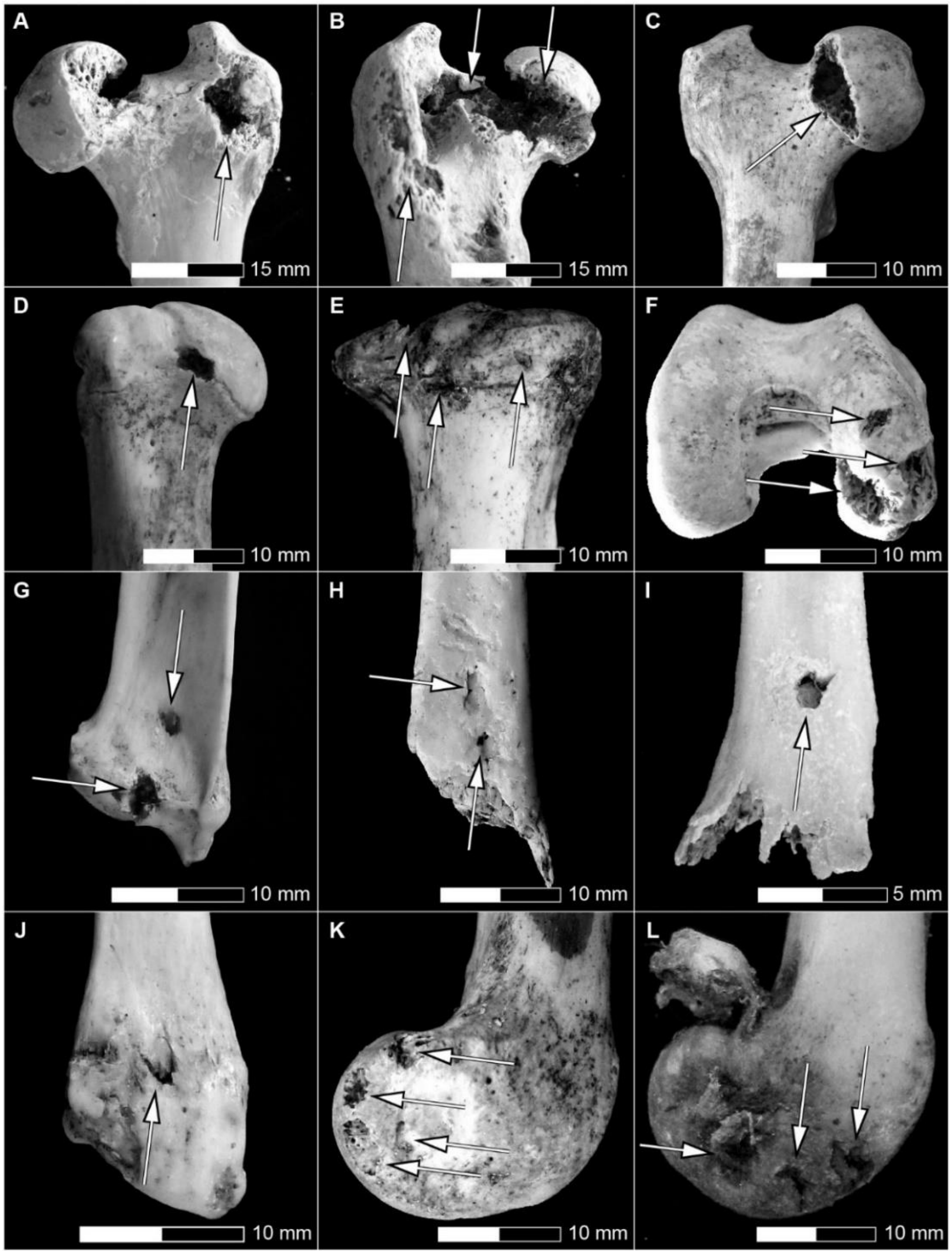

Figure 4.3: Modern monkey postcrania.

From the Taï and Ngogo Forests showing pits and punctures characteristic of crowned hawk eagle damage. A-B) proximal femur with punctures excavated portions around the neck. C) proximal femur with excavation portion from multiple punctures around the neck. D) proximal humerus with “figure 8”- shaped puncture. E) multiple irregular and elipse shaped marks around the tibial plateau. F) irregular and ellipse shaped marks on a distal humerus. G) C-shaped/can-opener and irregular punctures on a distal ulna. H) can-opener and figure –eight punctures associated with scratches on a long bone shaft fragment. I) “tailed” puncture associated with frayed bone breakage on a long bone shaft fragment. J) V-shaped -opener mark on a fibula. K-J) distal femurs with irregular punctures

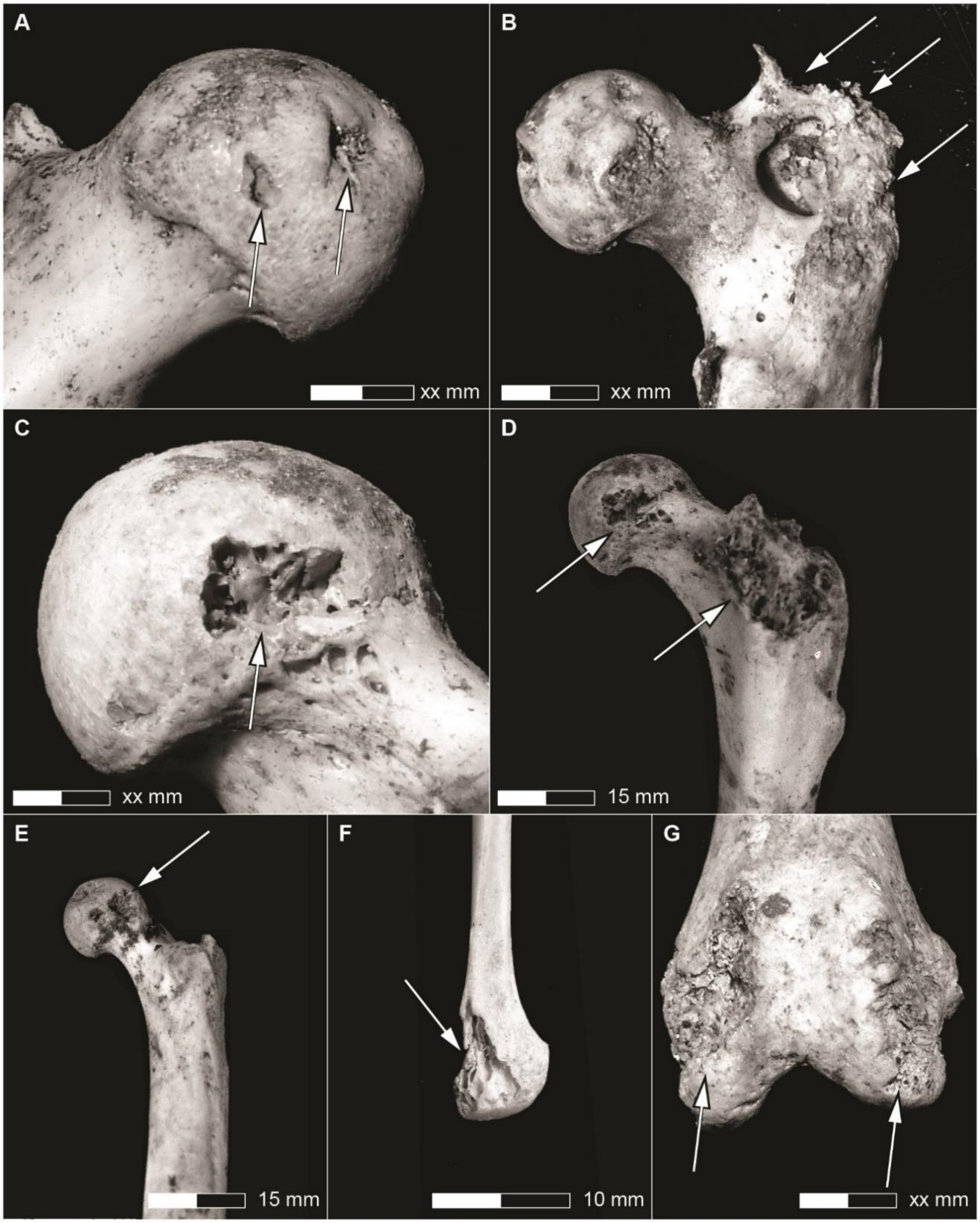

Figure 4.4: Modern monkeys from crowned hawk eagle nests.

A) femoral head with crushed in punctures and pits. B) proximal femur with large portions of the greater trochanter removed. C) crushed in irregularly shafted puncture in the cancellous bone on the femoral head. D-E) femoral heads with large portions removed. F) Fibula with large portion removed. G) distal femur with large portions of the condyles removed.

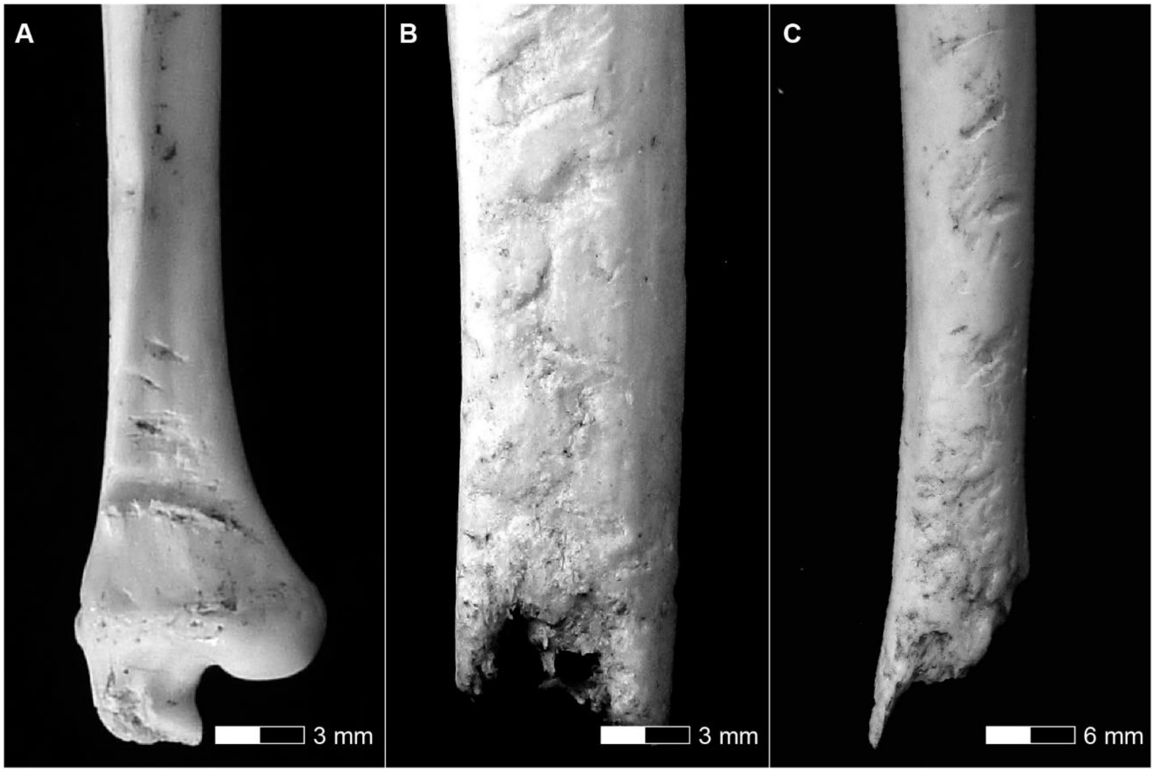

Figure 4.5: Modern monkey postcrania.

From the Taï and Ngogo forests with multiple scratch marks on long bone shafts characteristic of crowned hawk eagle damage. A) distal ulna. B-C) long bone shafts with articular surfaces torn off.

Figure 4.6: Partially digested monkey bones.
With thinned cortical surfaces and etching.

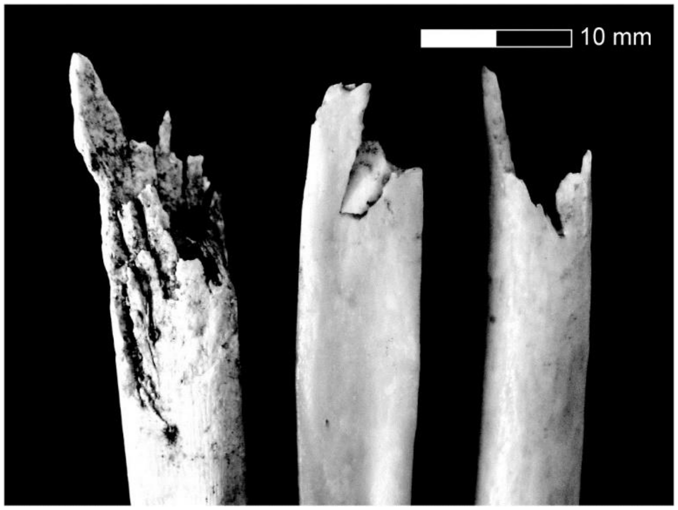

Figure 4.7: Modern torn and frayed monkey bones.
From crown hawk eagle nests.

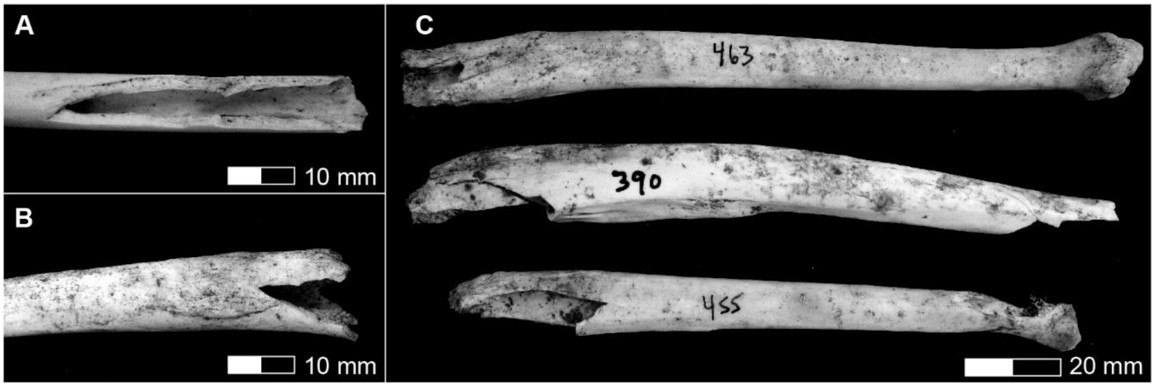

Figure 4.8: High angled breaks on modern monkey postcrania.

From the Tia and Ngogo Forests.

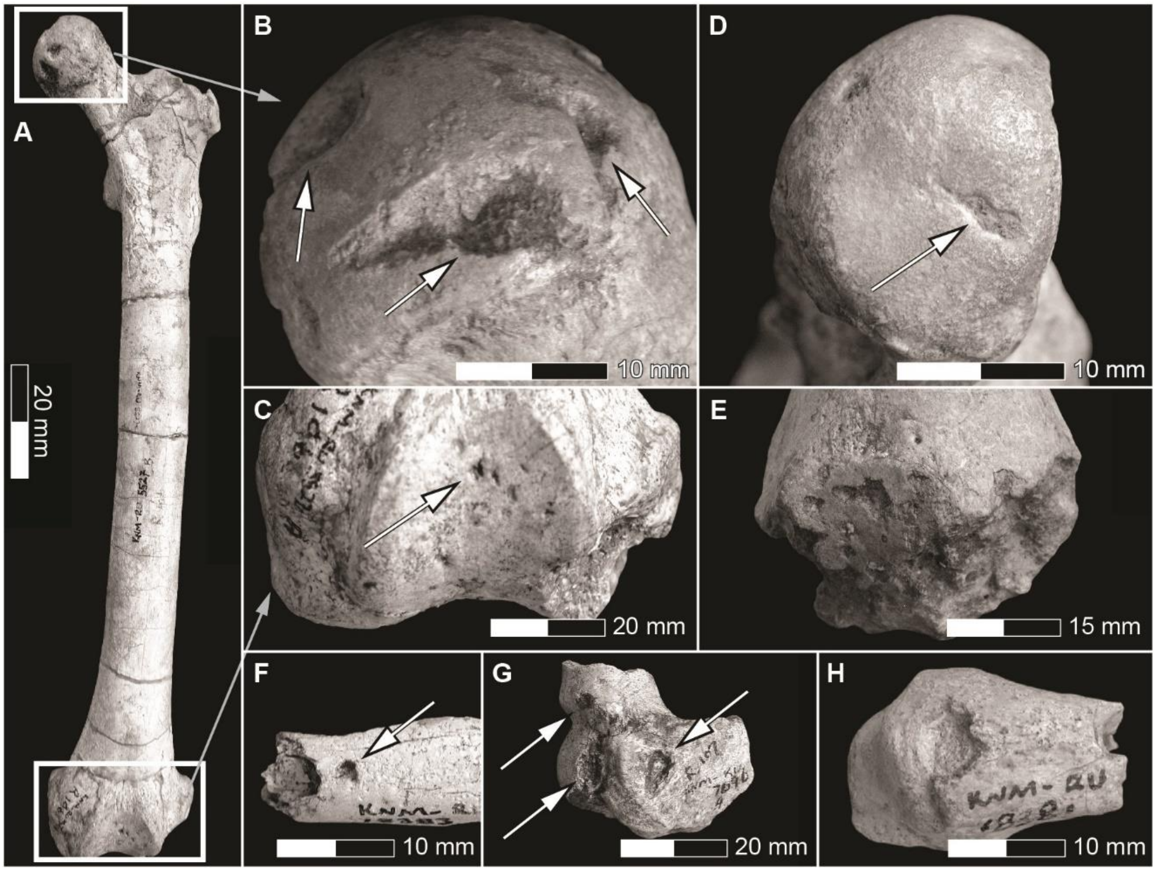

Figure 4.9: *Ekembo nyanzae* specimens with probable raptor damage.

A-C) KNM-RU 5527 B) femoral head with large tailed pits C) distal femur with multiple small v-shaped marks on the patellar surface. D) femoral head with tailed figure-eight shaped pit E) KNM-MW 13142 distal femur with extensive damage and small irregular marks. F) KNM-RU 18383, phalanx with “heart-shaped” pit, similar to avian damage recorded by Bochenski and Tornberg (2003). G) KNM-RU 7696 distal humerus with irregular/ellipse shaped punctures. Specimen lacks other taphonomic damage generally attributed to carnivores such as gnawing or additional crushing H) KNM-RU 18381, metacarpal with tailed/irregular pit.

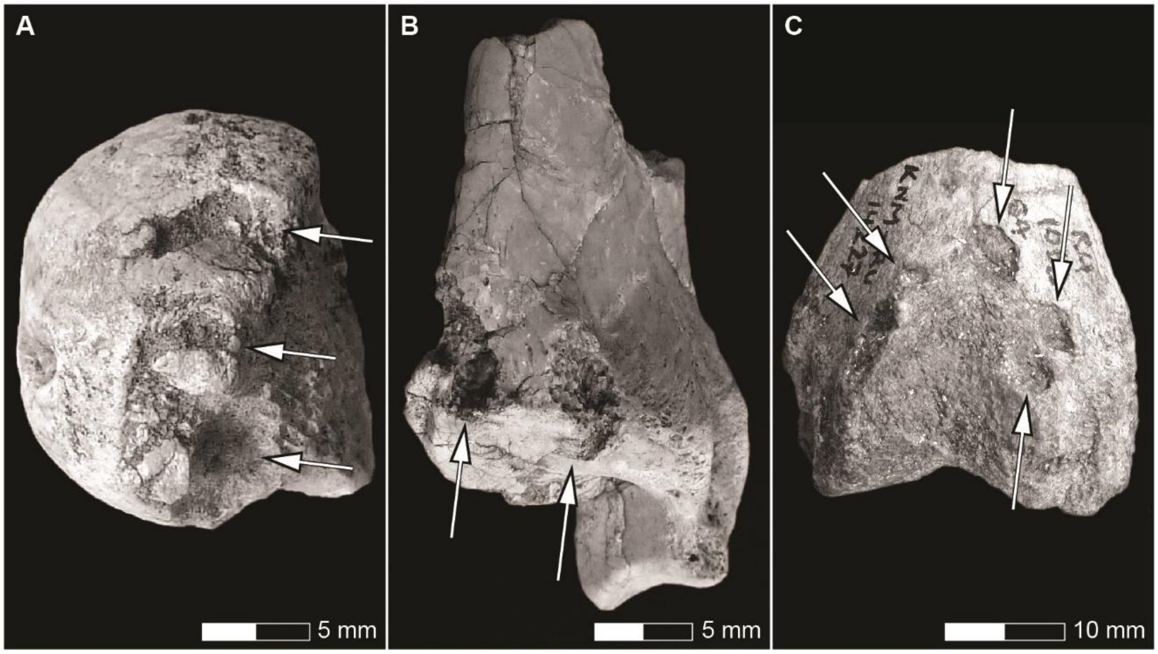

Figure 4.10: *Ekembo heseloni* specimens with probable raptor damage.

A) RU-2008-122, femoral head with irregular crushed in marks B) RU-2006-547, distal tibia with irregular punctures along the edge of the articular surface C) KNM-RU-14277, distal femur with ellipse-shaped pits along the patellar surface.

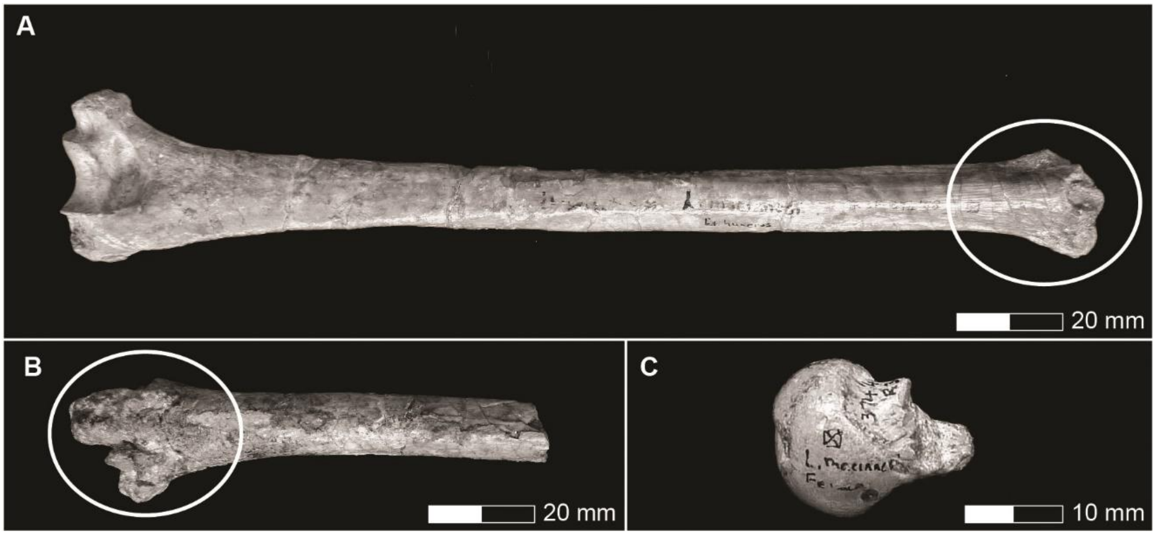

Figure 4.11: *Dendropithecus* specimens from the R3 block with damage.

A) KNM-RU- 2097, gnawed off proximal humerus. B) KNM-RU-1638, frayed distal femur shaft. C) KNM-RU-1640, femoral head with round pit.

Figure 4.12: R3 *Dendropithecus* block elements in situ. Republished from Le Gros Clark and Thomas (1951).

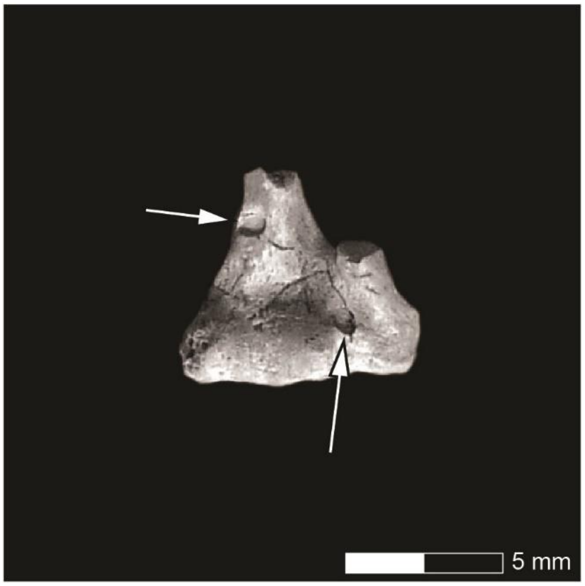

Figure 4.13: RU-2009-284.

Lorisoid distal humerus with two small, round, and crushed-in pits.

CHAPTER 5 BRIDGING STATEMENT FOR CHAPTERS 4 AND 6 AND CO-AUTHOR CONTRIBUTIONS FOR CHAPTER 6

In the previous chapter, predator-prey relationships are reconstructing using actualistic models of surface modifications on the Rusinga primates. In the later Pleistocene deposits, predator-prey relationships are reconstructed again. Data at Bovid Hill, Wakondo on Rusinga Island indicate that early modern humans hunted the extinct bovid *Rusingoryx*. At Bovid Hill I excavated a bonebed using similar methods to the bonebed at R5 in Chapter 2. While both bonebeds were deposited in fluvial contexts, Bovid Hill accumulated much more rapidly. While frequent surface modifications on the primate assemblage made inferences about predator-prey relationships possible, inferences of hunting at Bovid Hill rely more heavily several additional lines of evidence: age classes, stone tools, sedimentology, and other types of taphonomic data. These inference of tactical hunting at MSA Bovid Hill helps inform hypotheses about regional movement and seasonal occupation of early modern humans in eastern Africa.

The following paper has been published in the *Journal of Human Evolution* with several co-authors. Their contributions are as follows:

Sheila Nightingale served as a crew chief helping to oversee daily excavation procedures. She also conducted preliminary analysis of the artifacts, sketched the artifacts, and produced the map using the total station data. Tyler Faith identified *Rusingoryx*, provided taxon counts from previous seasons and collected dental wear stage data, which I analyzed. Dan Peppe provided the geologic context for the Wakondo area. Lauren Michel helped identify paleosols in the field and collected samples for micro morphology. Steve Driese and Lauren Michel analyzed sediment samples for micromorphology, providing additional geologic context. Kieran McNulty provided support in the field, research permits and countless edits. Christian Tryon provided further analysis of the artifacts, dates, and funding for the project. All team members provided editorial comments.

I designed and lead excavations, and collected taphonomic data. The taphonomic analysis, the synthesis of the many types of data, and the ideas presented in this paper are my own and were approved by my co-authors.

CHAPTER 6 TACTICAL HUNTING IN THE MIDDLE STONE AGE: INSIGHTS FROM A BONEBED OF THE EXTINCT BOVID, *RUSINGORYX ATOPOCRANIUN*

Introduction

Middle Stone Age (MSA) archaeological sites have long been of interest for interpreting the development of modern foraging behaviors especially dietary breadth, prey preferences, and modes of procurement e during the transition to and early diversification of anatomically modern humans (McBrearty and Brooks, 2000). The foraging behavior of MSA humans is best known from the butchered faunal remains of well-stratified South African cave sites, and such findings have shown MSA peoples to be capable and savvy hunters, employing a variety of methods to procure diverse game resources. Recent research suggests that South African foragers likely utilized multiple hunting techniques (hafted points, snares, and ambush and mass or tactical hunting methods) to obtain both large and small animal resources, including gregarious ungulates (Lombard, 2005; Clark and Plug, 2008; Faith, 2008; Klein, 2009; Wadley, 2010; Thompson and Henshilwood, 2011; 2014; Armstrong, 2016; Clark and Kandel, 2013). However, the limited geographic sampling of cave sites combined with the restricted range of activities performed inside them means that only some aspects of MSA behavioral diversity are well documented from these contexts. To capture fully the variability of MSA foraging behavior across Africa's diverse biogeographic zones, multiple regions in Africa need to be represented better. Open-air sites provide a complementary perspective on MSA behaviors and can help illuminate specific aspects of hunting and foraging strategies across the broader landscape; they have the potential to inform our understanding of hunting methods, primary butchery techniques and the stone tools associated with them, placing these behaviors in specific landscape and environmental contexts (Sharon et al., 2014). Unfortunately, open-air sites are far less likely to contain well-preserved faunal assemblages than caves or rockshelters.

In an effort to reconstruct MSA foraging behaviors in the Lake Victoria Basin, we report on a new MSA sub-locality, Bovid Hill at Wakondo on Rusinga Island, Kenya. Bovid Hill joins the small number of Late Pleistocene MSA eastern African sites with associated fauna, including Porc-Epic Cave (Assefa, 2006), sites at Aduma in Ethiopia (Yellen et al., 2005), sites at Lukenya Hill in Kenya (Marean, 1997; Tryon et al., 2015), Loiyangalani, Nasera, and multiple localities near Lake Eyasi (Bower et al., 1979; Mehlman, 1987, 1989; Thompson, 2005; Domínguez-Rodrigo et al., 2007, 2008), and perhaps Olduvai Gorge in Tanzania (Eren et al., 2014). We describe our 2011 excavation of an assemblage of the extinct bovid, *Rusingoryx atopocranion*. The excavated bonebed includes cut-marked specimens and an associated MSA Levallois blade-based artifact industry excavated from a channel deposit dated to 68 ± 5 ka via optically stimulated luminescence (OSL; Blegen et al., 2015). Data from Bovid Hill suggest that Late Pleistocene MSA for- agers may have taken advantage of natural topographic features such as seasonally swollen stream channels to target herds of *R. atopocranion* through active use of fluvial channels to corral, slow down, and dispatch disadvantaged herd members. Importantly, Bovid Hill provides evidence corroborating observations from Lukenya Hill (GvJm-22 and GvJm-46) (Marean, 1997) that mass capture techniques were part of the hunting repertoire of Late Pleistocene eastern African hominin populations, consistent with similar evidence from southern African and Eurasian sites during this time. Together, this evidence may indicate a key shift in foraging strategies practiced by Late Pleistocene human populations.

Wakondo and the Pleistocene Wasiriya Beds of Rusinga Island

History of research

Sparse artifacts and abundant fauna from open-air sites on Rusinga Island, Kenya, highlight the association of MSA humans with a diverse and arid-adapted ungulate community (Tryon et al., 2010, 2012, 2014, 2016; Faith et al., 2011, 2013, 2014, 2015, 2016; Tryon and Faith, 2013; Blegen et al., 2015; Beverly et al., 2015a, b; Garrett et al., 2015). The Wakondo locality is one of three main Pleistocene collecting areas on Rusinga, and lies on the south-eastern slope of the island (UTM: 36M 0630458, 9953261), ~20 m above the modern lake level of Lake Victoria (Figure 6.1 A and B). Whereas Wakondo is better known for its early Miocene fossils, including the type specimen of the catarrhine primate *Dendropithecus macinnesi* (Andrews and Simons, 1977), the locality is also associated with abundant faunal remains and lithic artifacts derived from the Pleistocene Wasiriya Beds (Pickford and Thomas, 1984; Pickford, 1986; Tryon et al., 2010, 2012, 2014; Faith et al., 2011). Kent (1942) provides one of the first written observations of Rusinga's Pleistocene deposits, but the earliest formal description was published by Van Couvering (1972), and this work was later extended by Pickford and Thomas (1984) as context for the holotype of the extinct alcelaphin bovid, *R. atopocranion*. Lithic artifacts and Pleistocene fauna had been noted casually by previous researchers, but not extensively collected (Pickford, 1986), prior to the work by the current research team beginning in 2007.

Our recent work on Rusinga's Pleistocene localities (primarily Wakondo, Nyamita, and Nyamsingula; Figure 6.1B) is part of a broader research program reconstructing paleoenvironments, faunal com- munities, and hominin landscape use around the eastern shores of Lake Victoria (Tryon et al., 2010, 2012, 2014, 2016; Faith et al., 2011, 2015, 2016; Blegen et al., 2015; Beverly et al., 2015a, b; Garrett et al., 2015). The research in Wakondo's Pleistocene deposits was initiated through limited surface collections and rescue excavations conducted by Miocene paleontological researchers (McNulty et al., 2007; Peppe et al., 2009), who discovered three partial bovid skeletons eroding from sediments at the sub-locality at Wakondo referred to as “Bovid Hill” (Figure 6.1D). From these 2007 collections we identified the first recorded cut marks from the Wasiriya Beds (Tryon et al., 2010), and the Wakondo locality then became the focus of systematic surface collections in 2009 and 2010, which increased the sample of

MSA lithic artifacts and confirmed high densities of *Rusingoryx* fossils at the Bovid Hill sub-locality. During collections in 2010, two partial *Rusingoryx* crania were recovered in situ which, together with a large sample of surface-collected horn cores and dental remains, confirmed its generic distinction from *Megalotragus* (Faith et al., 2011). Furthermore, test excavations

(4 m2) at another sub-locality at Wakondo, approximately 50 m NW of Bovid Hill, demonstrated the presence of in situ artifacts (n 11) and fauna (Tryon et al., 2010). Based on these initial results, we opened 19 m2 for excavation at Bovid Hill in 2011 with the results of that work described below.

Geologic and paleoenvironmental context

At Wakondo, Pleistocene sediments of the Wasiriya Beds are <10 m thick and unconformably overlie early Miocene deposits (Figure 6.1C). The deposits vary somewhat in thickness, depending in part on the Miocene paleotopography, and are roughly contemporaneous with the other major Wasiriya Beds exposures on Rusinga Island, the Waware Beds on nearby Mfangano Island, and unnamed Pleistocene deposits near Karungu on mainland Kenya (Tryon et al., 2010, 2012, 2014; Blegen et al., 2015; Faith et al., 2015). The Wasiriya Beds are dominated by cut-and-fill fluvial deposits of poorly sorted, medium-to-coarse grained sandstones and conglomerates with variably reworked tephra deposits that are carbonate- cemented and paleosols comprising fine-grained sandstones, silt-stones, and mudstones. The sediments represent a semi-arid, relatively unstable landscape characterized by episodic erosion and fluvial and alluvial sedimentation (Tryon et al., 2010, 2012, 2014; Garrett et al., 2015; Beverly et al., 2015a, b). Specifically at the Bovid Hill excavation, fossil-bearing sediments are comprised of fine-to coarse-grained sandstones and pebble- to cobble-sized conglomerates (Figs. 1C, 2A), the latter interpreted to be fluvial channel deposits. Lateral to and below the stream deposits is a partially eroded paleo-Vertisol, reflecting a more stable land surface that was subsequently eroded by the fossil-bearing stream channel. The minimum age estimate for the Wasiriya Beds at Wakondo is approximately 33-45 ka. These dates are based on accelerator mass spectrometry (AMS) radiocarbon dating of intrusive, burrowing gastropods (*Limicolaria* cf. martensiana) from the nearby Nyamita locality, which is correlated to Wakondo by shared tephra deposits that are stratigraphically below the Bovid Hill excavation (Tryon et al., 2010). This minimum age is further supported by a direct40Ar/39Ar date of 35.62+/- 0.26 ka on deposits of the Menengai Tuff, the uppermost tephra in the local depositional equivalents of the Wasiriua Beds (Blegen et al., 2015). Maximum age estimates for the Wasiriya Beds of ~100 ka are based on tephrostratigraphic correlations at Wakondo and Nyamita with known eruptions from the East African Rift Valley volcanoes (Tryon et al., 2010; Blegen et al., 2015) and from U-series dates of 94.0 +/- 3.3 to 111.4 +/- 4.2 ka on tufa at Nyamita at the base of the Wasiriya Beds sequence (Beverly et al., 2015a). The excavated deposits at Bovid Hill are further constrained by OSL ages of 68 +/- 5 ka on the fossiliferous channel sands (Blegen et al., 2015), providing the best age estimate for the collections reported here. Paleoenvironmental and landscape reconstructions suggest that Rusinga and Mfangano Islands, as well as the remains of the nearby Kisingiri Volcano on the mainland (Figure 6.1A), represented high points on a Pleistocene landscape dominated by open and semi-arid grasslands. Lake bathymetry and faunal communities indicate that Lake Victoria was at least 20 m lower than today, and that both islands would have been connected to the mainland (Tryon et al., 2012, 2014). Dental carbon isotopes, dental mesowear, and faunal remains dominated by extinct grassland specialists are all consistent with a widespread semi-arid grassland environment (Faith et al., 2011, 2015, 2016; Tryon et al., 2012, 2014, 2016; Garrett et al., 2015). However, multiple stream and spring deposits, as well as the presence of wetland fauna such as hippopotamuses and reduncin bovids at the Nyamita locality, indicate that free-standing water was likely available year-round on Rusinga Island (Tryon et al., 2010, 2014; Beverly et al., 2015a, b). These locally wetter environments, some spring-fed, would probably have drawn humans and animals to the area in an otherwise dry setting (Tryon et al., 2014; Beverly et al., 2015a; Garrett et al., 2015). The first- or second-order streams evident from fluvial deposits at Bovid Hill flowed primarily southward, and were likely seasonally rain fed from Rusinga's highlands in the center of the island, a maximum of 300 m above and 1 km away from Wakondo (Figure 6.1B).

Materials, Methods and Results

Excavations at Bovid Hill

In 2011, we piece-plotted and collected all fossil specimens 2 cm in length and all lithic artifacts (regardless of size) from the surface at Bovid Hill with a Trimble M3 total station relative to an arbitrary datum. Based on surface distributions, previous years' findings, and modern topography, we set three excavation trenches (totaling 19 m2) to test for subsurface in situ remains (Figure 6.1D). Grids 1 and 2 were set back from a productive gully and fossils were recovered subsurface. Grid 3 was set over the area where fossil cranial material and other fossils had been collected eroding from the surface. All excavation finds were likewise piece-plotted with the total station, sketched, and photographed. Materials 5 cm were plotted with multiple points to capture dip and orientation, following McPherron and Dibble (2002). In some cases, multiple fossils were cemented together rather than separated by matrix, and these had to be plastered and transported back to the National Museum of Kenya (NMK) for preparation. Hence, only those fossils that were visible prior to preparation have associated orientation data. Excavated sediments were screened consecutively through 5 mm and 2 mm sieves and then further sampled with a 0.5 mm sieve to recover additional microfauna or microdebitage. Special attention was paid to potential sedimentary changes as evidence of multiple deposi- tional layers. Within stratigraphic layers, the site was dug in 10 cm arbitrary levels, and small (500 g) bulk sediment samples were collected within each of these levels. From the south wall of Grid 3 (Figure 6.1D), a larger sediment column was consolidated in the field using polyester resin and transported back to the laboratory for micromorphological study. This column was later subdivided into smaller samples and impregnated with epoxy for thin-sectioning.

Sedimentology

Fossiliferous deposits and the sterile deposits that pre- and post-date occupation at Wakondo indicate an overall dynamic fluvial landscape, subject to seasonal variability in hydrology. Cross-bedded, coarse-grained, sub-angular sands dominate all fossil-bearing depths sampled at Bovid Hill, with larger cobbles common in Grid 2, and present in small numbers in Grid 3 (Figure 6.1D). These sediments were sampled using large-format (5 7 cm) thin sections prepared commercially by Spectrum Petrographics, Inc., from selected stratigraphic intervals. Thin-sections were examined at Baylor University using an Olympus BX51 research microscope equipped with a 12.5 MPx digital camera and both standard transmitted light and UV fluorescence. Micromorphological descriptions follow FitzPatrick (1993) and Bullock et al. (1985). Sediment thin-sections reveal a significant amount of detrital pedogenic rhizoliths and carbonates, possibly reworked from pre- existing soils upslope. Some carbonates are Fe-stained, coated and impregnated, suggesting variable hydrology or drainage in the soil carbonate systems and, therefore, repeated cycles of soil aeration and saturation (Figure 6.2C-E). The presence of unstable mineral grains, such as pyroxenes, Ti-oxide minerals and plagioclase feldspar, which show variable weathering and degrees of alteration, probably indicates the erosion of both pre-existing soil mantles containing weathered materials, as well as exhumation of fresh, unweathered parent materials; these could also reflect periodic input of tephra deposits on the landscape, and its redistribution by fluvial and pedogenic processes.

A sterile and partially eroded paleo-Vertisol was identified with an undulating subsurface below the fossil- and artifact-bearing fluvial sediments in Grids 1 and 3. However, there is no sedimentary or fossil evidence (e.g., fossil shearing associated with slickenside planes) that the paleosol affected artifact placement or fossil distribution post-depositionally (cf. Driese et al., 2013 for an example of the assessment of Vertisol shrink-swell effects on stratigraphic integrity of lithic artifacts). Although the paleo- Vertisol predates the occupation at Bovid Hill, it provides additional paleoenvironmental context for the site. Vertisols are clay- rich soils characterized by the presence of vertic features such as slickensides and gilgai that form from seasonal water surpluses and deficits (e.g., Buol et al., 2003; Southard et al., 2011). The paleo- Vertisol found at Bovid Hill was a mudstone with both slicken- side planes and mukkara (subsurface expressions of gilgai surface topography) present, indicating seasonally wet and dry conditions. Sterile sediments were also identified in the eastern portion of Grid 3 (Figure 6.1D) and represent a later cut-and-fill into the underlying archaeological/fossiliferous fluvial deposits.

Faunal Identification and Analysis

We examined 577 fossil specimens from the excavation (Number of Identified Specimens [NISP] 450). Taxon identifications were made with the aid of comparative collections housed in the osteology and paleontology sections at the National Museums of Kenya (Nairobi). The size class III (Brain, 1981) extinct alcelaphin bovid *R. atopocranion* is the only identified taxon represented in the excavated sample at Bovid Hill, although small numbers of additional taxa were identified from earlier surface collections (Table 6.1). Specimens belonging to other ungulate species are found scattered throughout the Bovid Hill surface and are represented almost exclusively by isolated teeth, with the exception of a mandibular fragment with P3eP4 that belongs to *Connochaetes taurinus* (blue wildebeest). In contrast, the dental remains of *Rusingoryx* collected from the surface frequently include partial mandibles and maxillae (26/95 specimens 27%), are associated with postcranial remains (likely of *R. atopocranion*), and are localized around the excavated channel deposits yielding the *R. atopocranion* bonebed. Based on these conspicuous taphonomic differences, it is probable that surface-collected specimens belonging to other taxa represent limited stratigraphic or time-averaged deposits unrelated to the deposition of the excavated bonebed at Bovid Hill, whereas the surface-collected specimens of *R. atopocranion* likely eroded from the bonebed itself.

Rusingoryx is most closely related to the modern wildebeest, *Connochaetes*, and its massive Pleistocene counterpart, *Megalotragus* (Faith et al., 2011; O'Brien et al., 2016). It is notable for its enlarged nasal cavity, which may be related to production of loud, low-frequency calls (Figure 6.3) (O'Brien et al., 2016). Mesowear, ecomorphology, and stable carbon isotopes show that Rusingoryx was a specialized grassland grazer that fed primarily on C4 grasses (Faith et al., 2011, 2015; Garrett et al., 2015). Likewise, *Rusingoryx* is associated throughout the Wasiriya Beds with an arid-adapted faunal community e including Grevy's zebra (*Equus grevyi*), blue wildebeest (*C. taurin*us), hartebeest

(*Alcelaphus buselaphus*), and *Damaliscus hypsodone* that is very different from those seen during the Holocene of eastern Africa or in the Pleistocene of South Africa. *Rusingoryx* was likely gregarious and seasonally migratory, similar to the modern wildebeest (Faith et al., 2011; O'Brien et al., 2016).

The 2011 excavations yielded an MNI (minimum number of individuals) of 11 *Rusingoryx* (based on cranial material), with an MNI of 27 derived from the combined excavated and surface- collected samples. Ages of death were estimated using eruption and wear patterns following Bunn and Pickering (2010) using a blue wildebeest analogy as well as the criteria outlined by Stiner (1990). Given that *Rusingoryx* shares a close phylogenetic relationship with blue wildebeest and is similar in body mass eruption schedules are likely to have been comparable, and thus wildebeest are the most appropriate analogy. The *Rusingoryx* assemblage at Bovid Hill includes both juvenile and adult specimens, but is dominated by prime-aged adults.

Drawing upon Schaller's (1972) observations, Bunn and Pickering (2010) estimate that the mesial infundibulum of the M_1 is lost in Serengeti wildebeest at approximately 13-15 years of age (approximately 75% of the maximum life expectancy), thus marking the boundary between prime and old. Using this scheme, the mortality profile for the sample at Bovid Hill is 8 juveniles, 13 prime adults, and 6 old adults. This scheme produces slightly more old adults than does Stiner's widely used aging scheme (8 juveniles, 15 prime adults, 3 old adults; e.g., Stiner, 1990; Steele, 2005), but we rely on the former, more conservative age profile to ensure comparability with Bunn and Pickering's (2010) relevant data on wildebeest mass drownings and living herds.

A finer breakdown of tooth wear patterns in the *Rusingoryx* sample reveals important insights into the age structure of the fossil population. Table 6.2 presents the frequencies of mandibular and maxillary dP4s and M1-3s according to the qualitative wear scheme developed by Payne (1973, 1987) and refined by Zeder (2006; Zeder's codes used here). All of the dP4s and M1s are in active wear or late wear. Using Attwell's (1980) eruption schedule for blue wildebeest, this corresponds to animals >12 months of age. We also note that none of the M3s has progressed to late or final wear, and only a few M2s (n 3) have progressed to late wear, underscoring the lack of older individuals in the assemblage and dominance of prime age adults. The dominance of M1s in Zeder's (2006) wear stage 17 (active wear) is consistent with blue wildebeest aged between 3 and 7 years (Attwell, 1980) (maximum longevity: 18-21 years), although the more hypsodont teeth of *Rusingoryx* could have extended the duration of this wear stage beyond that of wildebeest. Extant alcelaphins, including blue wildebeest, are known to form both harem and bachelor herds, the latter comprising of males >12 months in age (Skinner and Chimimba, 2005; Kingdon and Hoffman, 2013). To the extent that the blue wildebeest analogy is appropriate, this may suggest that the *Rusingoryx* bonebed represents an all-male bachelor herd and this hypothesis is supported further by a general lack of sexual dimorphism in the Bovid Hill *Rusingoryx* sample (O'Brien et al., 2016). Alternatively, it may indicate that the very youngest individuals are under-represented in our sample due to taphonomic processes that disproportionately affect juveniles, such as winnowing (Kaufmann et al., 2011).

We compared the Bovid Hill age profiles to both hypothetical and idealized mortality models developed by Steele (2005). The age distribution from Bovid Hill (Figure 6.4) differs significantly from the expected distribution of an attritional mortality profile (following Bunn and Pickering, 2010: $\chi^2 = 12.40$, $p < 0.01$), but is comparable to a hypothetical catastrophic mortality/living profile ($\chi^2 = 0.125$, $p = 0.94$; expected values derived from Steele, 2005, and scaled to MNI 27). The dominance of prime age adults, however, is also consistent with Stiner's (1990) prime-dominated profile, which she links to interception of prey herds and selective culling of prime adults.

Using actualistic mortality data of mass drownings, hunted assemblages, and predator kills presented by Bunn and Gurtov (2014), we further compared the Bovid Hill mortality profiles in ternary diagrams with 95% confidence intervals using software provided by Weaver et al. (2011) (Figure 6.5). Compared with mortality profiles of wildebeest drownings from Lake Masek, the Bovid Hill assemblage is statistically different. Moreover, the Bovid Hill assemblage overlaps with living ages of a wildebeest herd and ethnographic mortality data from Hadza hunts of impala and kudu (Bunn and Gurtov, 2014) and with mortality data from the Middle Stone Age sites at Lukenya Hill, which are interpreted as mass hunts of *D. hypsodon* (Marean, 1997), although we note that the confidence limits of these samples are quite broad. Traditional ternary diagrams after Stiner (1990) can be problematic when interpretive emphasis is placed on the zoning within the diagram with respect to hypothetical outcomes (e.g., “L-shaped living profiles” or “U- shaped attritional” profiles) or when zones do not account for adjusted age categories of unequal distribution (Discamps and Costamagno, 2015). However, this potential misstep is largely avoided when relevant actualistic data are incorporated, so long as taphonomic biases can be accounted for.

Driver and Maxwell (2013) suggest adjusting mortality models to account for the fact that young juvenile ungulates can be dispatched quickly by carnivores prior to any given catastrophic event, thus altering the living profile of a group and subsequent death assemblage. Additionally, juveniles are more likely to be preferentially deleted by a number of different taphonomic processes such as post- depositional winnowing, trampling, sediment compaction, or carnivore consumption (Munson, 2000; Kaufmann et al., 2011). These factors together suggest that a comparison restricted to prime and old categories (rather than young, prime, and old) is the most conservative approach to interpreting mortality profiles in this context. Hence, we also statistically assessed the ratio of prime-to-old adults with the expectation that the ratio of prime-to-old in natural deaths (predator hunts, mass drowning) should be much smaller than in human- hunted assemblages or herd structures (Bunn and Gurtov, 2014: Table 6.3). Comparing the Bovid Hill ratio to the examples cited in Bunn and Gurtov (2014) using a one-tailed Fisher's exact test, our assemblage was statistically indistinguishable from a living herd in the Serengeti, mass drownings at Lake Masek, and hunted assemblages from the Hadza ($p > 0.05$). Despite our small sample sizes, these comparisons show that the mortality profile at Bovid Hill is prime- dominated. Whereas many processes — both natural events and various human hunting techniques — can lead to prime-dominated assemblages (Gaudsinski, 2005; Bunn and Gurtov, 2014; Discamps and Costamagno, 2015), they are most commonly associated with unselective catastrophic mortality events and human hunting, rather than carnivore activity (Stiner, 1990; Driver and Maxwell, 2013).

Taphonomy

Skeletal part representation

Skeletal elements were tallied using Lam et al.'s (1999) bone density of wildebeest scan sites using skeletal element portions (Tables 6.4 and 6.5). Subsequent skeletal element profiles were derived from these counts and used to generate minimum animal unit (MAU) values (Binford, 1978; Lyman, 1994). Much discussion has centered on the importance of long bone shaft fragments in calculating skeletal part frequencies (Marean and Kim, 1998; Marean et al., 2001) and so identifiable shaft fragments were included using Lam et al.'s (1999) bone portions. Using Lam et al.'s bone mineral density (BMD) portions was an expedient method for collecting skeletal element portion data on an assemblage that was dominated by post-fossilization breakages (e.g., transverse/straight). Lam et al.'s (1999) bone density values of blue wildebeest (*C. taurinus*) were compared against the Bovid Hill excavated sample in order to determine whether skeletal part frequencies were altered by density-mediated taphonomic processes, such as trampling or carnivore ravaging. We used Lam et al.'s (1999) wildebeest bone mineral density two (BMD2) values for long bones and their BMD1 values for all other element portions. BMD2 values exclude medullary cavities for measures of bone density that might otherwise artificially lower densities values, whereas BMD1 values do not exclude medullary cavities. Given the fluvial sedimentation at Bovid Hill, %MAU values were compared with Voorhies' Fluvial Transport Groups (Voorhies, 1969) to assess the potential for bone winnowing. Given the presence of stone tools at Bovid Hill, Blumenschine and Madrigal (1993) wildebeest marrow indices were also used to examine potential patterns in long bone frequencies for preferential marrow processing.

The skeletal part profile at Bovid Hill (Table 6.4; Figure 6.6) shows high proportions of cranial and mandibular elements, followed by intermediate and lower limb elements (radio-ulnae, tibiae, and metapodia). Axial and upper limb elements are represented in lower frequencies than expected for complete animals (Figure 6.6). Correlation of skeletal element frequencies with BMD values shows a weak but significant relationship (r_s 0.30, $p < 0.005$), suggesting that bone density and attritional taphonomic processes only partially explain the skeletal part representation at Bovid Hill.

Preferential fluvial transport can be investigated using Voorhies Transport Groups (Voorhies, 1969). In Voorhies' flume experiments, crania and mandibles were most often left behind as lag deposits while other elements were more easily transported downstream by fluvial action. More recent studies have shown transport groups can vary somewhat when wet versus dry bone or articulated versus disarticulated bone is taken into account (Coard and Dennell, 1995;

Coard, 1999). However, the majority of elements from Bovid Hill are disarticulated and not in anatomical association (with the exception of a partially articulated and associated juvenile skeleton visible in Grid 3). Coard and Dennell's (1995) experimental outcomes with disarticulated specimens were broadly comparable to Voorhies' (1969). However, some aspects of natural fluvial systems are difficult to model in a flume setting, such as variation in sediment floor or bones catching on vegetation debris, point bars, large cobbles, or other deposited bones (Hanson, 1980; Todd and Frison, 1986). Aslan and Behrensmeyer's (1996) experiment in the East Fork River of Wyoming tested transport distances of various elements in a natural river system, finding that long bones often traveled an average of 200 m downstream, whereas skulls were transported very little, if at all. Acknowledging the likelihood for variable depositional factors, we do not use Voorhies Groups (1969) for statistical comparison, but rather as a guide from which transport may be estimated. With these caveats, we note that Voorhies lag group elements at Bovid Hill are disproportionally represented (Tables 6.4 and 6.6; Figure 6.7). Skeletal element profiles closely resemble those of known wildebeest mass drownings at the Mara River, Kenya and Masek Lake, Tanzania, where cranial and mandibular elements dominate assemblages and there are fewer elements from Groups I-II (Figure 6.7) (Dechant-Boaz, 1982; Capaldo and Peters, 1995) due to post-depositional winnowing. Similar profiles would also be expected from winnowed assemblages derived from any unselective catastrophic mortality event, including large-scale human hunting.

Voorhies Transport Group II includes all long bones, with the implication that different long bone elements are not expected to be transported differentially. However, in our excavated sample from Bovid Hill, upper limb bones (femur and humerus, MAU 11) are present at significantly lower frequencies than are intermediate (tibia and radio-ulna, minimum number of elements [MNE] 25) or lower limb bones (metapodials, MAU 15), which is inconsistent with a simple fluvial transport model (Table 6.4). A chi-square test for goodness of fit indicates a significant difference ($\chi^2 = 5.051$, $p = 0.025$) between observed frequencies of upper limb bones and lower and intermediate limb bones compared to their expected frequencies (i.e., all elements equally represented), suggesting that differential representation of limb elements may be behaviorally meaningful. Limb bone frequencies can vary for a number of reasons at archaeological sites, such as transport, in situ destruction via attritional processes or marrow processing, and/or issues surrounding the identification of shaft fragments (Marean et al., 2000). Given the dearth of shaft fragments at Bovid Hill, we believe our skeletal element counts are representative of the preserved assemblage. There is no significant correlation between marrow indices and the frequency of limb bones (r_s 0.2, $p > 0.05$), as might be expected for preferential transport for marrow processing. Specifically, tibiae (%MAU 45) and radio-ulnae (%MAU 68) together are more frequent than lower marrow-yielding metapodials (%MAU 34) (Table 6.4; Figure 6.6), and therefore it is unlikely that preferential transport away from Bovid Hill for marrow processing explains the long bone frequencies (Blumenschine and Madrigal, 1993). Upper limbs have a greater meat yield than intermediate and lower limbs and thus these elements may have been transported away from Bovid Hill by humans for additional processing, sharing, and consumption off site (Binford, 1978, 1981). Unfortunately, evidence for winnowing at Bovid Hill makes these hypotheses difficult to fully test. Fluvial transport models may be inadequate for examining long bone frequencies in this context and any elements that may have been heavily processed and produced fragments were likely to have been subsequently winnowed away (Pante and Blumenschine, 2010). Transport for marrow processing does not appear to explain the long bone frequencies as upper limb bones generally have less marrow than intermediate limbs (Blumenschine and Madrigal, 1993), but rather we tentatively suggest that the large amount of meat on the upper limb bones may explain their general scarcity in the assemblage.

Surface modifications

Fossils were examined for surface modifications under a 10e20 hand lens and a 20-50 digital microscope. Modifications were identified using criteria outlined in actualistic and experimental studies of animal tooth pits and gnawing (Binford, 1981; Haynes, 1983; Selvaggio and Wilder, 2001; Pobiner, 2008; Delaney-Rivera et al., 2009), cut marks (Shipman and Rose, 1983; Behrensmeyer et al., 1986; Domínguez-Rodrigo et al., 2009, 2010, 2012a), hammerstone percussion marks (Blumenschine and Selvaggio, 1988), and weathering (Behrensmeyer, 1978). Post-depositional processes such as fluvial abrasion and edge rounding were taken into consideration when assessing surface modifications (Shipman and Rose, 1983; Fernández-Jalvo and Andrews, 2003; Thompson, 2005; Chisholm et al., 2014).

Bone surface preservation at Bovid Hill is variable, but many specimens lack well-preserved cortical surfaces. While weathering patterns show little diversity (99% of specimens are attributed to weathering stage 0 or 1; Behrensmeyer, 1978), post-depositional chemical dissolution and surface abrasion has affected nearly all cortical surfaces. Furthermore, fluvial sediments are cemented to the majority of the assemblage (96% of specimens from the excavated assemblage have sediments adhering to at least a quarter of the specimen). Fossils that were recovered in close proximity to the modern ground surface (largely from Grid 3) have cortical surfaces that are more heavily obscured by cemented sediments than those that were more deeply buried. Experimental studies by Daniel and Chin (2010) have shown that sediments can become cemented to bone surfaces post-depositionally as bacteria form microbial mats and consume carcasses or bone collagen in watery environments. The pattern of adhered sediments at Bovid Hill suggest that *Rusingoryx* remains were submerged in a watery setting post-depositionally while still relatively fresh and that this process appears to have affected only the uppermost fossils. Bone surface modifications are rare on the Bovid Hill assemblage. Fossils from the 2011 excavation as well as the 2007 rescue excavation were surveyed for modifications. One unidentified bone fragment yielded a likely invertebrate burrow with smooth semi- circular excavated marks -

possibly termite damage. Two specimens show likely trampling damage with shallow and short striations.

Three specimens exhibit cut marks (Figure 6.8). A largely complete, though post-depostionally broken, left radio-ulna has three clusters of surface modifications. On the distal end and lateral edge of the capitulum, four linear and parallel marks are present. In cross-section, these marks are deep and narrow with an asymmetrical V- shaped cross section at the edge of the bone and widen into a U- shape towards the medial termination of the mark. On the mid- shaft, six short and shallow marks are clustered tightly together and run perpendicular to the long axis of the bone. On another mid- shaft fragment of the same radio-ulna, a 7 mm mark with a straight trajectory runs oblique to the long axis of the bone. This mark is V- shaped and symmetrical, with slight shoulder effect and internal striations along the interior of the walls. Associated with this mark is a small, shallow and dense cluster of unidirectional micro- striations. This specimen was found in situ from Grid 3. A second specimen, a tibial shaft fragment recovered from the northwestern corner of Grid 3, shows 12 straight and parallel marks. These marks are narrow and mostly V-shaped in cross section, though some are more U-shaped. Many have barbs and forks and although they do not exhibit shoulder flaking, the outer edges of these marks show what appear to be shoulder-flake scars, or the negative space left after shoulder flakes have eroded away. These marks run perpendicular to the long axis of the tibia and some are truncated by a post-depositional longitudinal dry break. The bone surface of this specimen has undergone some chemical dissolution with pitting and some manganese staining; small concretions and dissolution are visible inside these marks attesting to their antiquity. Last, a lower cervical vertebrae fragment (pedicle) recovered from the 2007 rescue excavation and published in 2010 (Tryon et al., 2010) shows three parallel, straight, deep, and long V-shaped marks on a corroded bone surface. An isolated mark on the same specimen is a similarly straight, deep and V-shaped mark with shoulder flake scars.

The deep V-shaped marks occurring on the distal radio-ulna and on the cervical vertebra are diagnostic of anthropogenic disarticulation and are interpreted as chop marks at the distal forelimb and base of the neck. Additional marks on the radio-ulna and tibia may reflect butchery for meat or cleaning of periosteum for marrow processing. The small cluster of striations on the radio-ulna is reminiscent of hammerstone percussion (Blumenschine and Selvaggio, 1988), but given that this specimen can be refitted from fragments with dry breaks, it seems unlikely that the mark represents an instance of attempted marrow access. Instead, this mark is likely a scrape from a stone tool.

Breakage Patterns

Breakage patterns were categorized according to Villa and Mahieu (1991) and break angles were measured when break characteristics suggested fresh or green breakage (Pickering et al., 2005; Alcántara García et al., 2006). Notches were identified using criteria outlined in Capaldo and Blumenschine (1994). The majority of long bones from the excavation are complete, but many exhibit in situ post- depositional, straight, and transverse breaks. A small sample of long bone shaft fragments exhibit high break angles (>110o), V- shaped or curved outlines, notches, or bone flakes consistent with fresh bone fractures due to either hammerstone percussion or carnivore breakage (n=6) (Figure 6.9).

Although fresh breaks are rare in the collection, cut marks suggest that humans may have filleted fresh bones and processed some elements for marrow on site. We observe no conclusive carnivore damage (gnawing or tooth pits) on any of the Bovid Hill material. Low-density long bone epiphyses are frequently pre- served (MNE 51 long bones, 90% have at least one epiphysis preserved; Table 6.5), which is inconsistent with substantial bone consumption by carnivores (Haynes, 1983). Furthermore, when limb ends are missing, breaks are clearly post-depositional or post- fossilization and do not show rounded, curved, or irregular breaks characteristic of carnivore damage. Given that many fossils were recovered near or at the surface, it is unsurprising that some limb ends may have become disassociated from the in situ material.

Spatial patterning

The fossils and lithic artifacts were found in close association within the same deposit (Figures 6.1D, 6.10). For example, material recovered during the 2010 rescue excavation yielded an artifact sandwiched between two skulls. Articulated fossils are rare in the excavated sample with the exception of a partial juvenile skeleton and three crania with articulated mandibles (Figure 6.10). Most fossils are complete, with breaks occurring post-fossilization and in situ. Articulated skulls suggest that some elements were quickly buried after deposition (Hill and Behrensmeyer, 1984, 1985).

Orientation patterns can be useful for distinguishing undisturbed archaeological deposits from water transported fossils and artifacts; sites that show anisotropic bone orientations are generally interpreted as being fluvially transported or reoriented by water action (Coard and Dennell, 1995; Domínguez-Rodrigo et al., 2014). Domínguez-Rodrigo and García-Pérez (2013) and Domínguez-Rodrigo et al. (2012b, 2014) demonstrate that bone orientation measurements can vary significantly depending on the shape of the bone and the method of measurement, and that using the symmetrical longitudinal axis (SLA) is the best approach. We measured bone orientations for fossils >5 cm in length along the SLA using total station plots. At Bovid Hill, the majority of fossils are complete long bones with orientations that can be measured with little ambiguity. Additionally, the provenience of oblong fossils such as skulls or scapulae was recorded using multiple points to capture the SLA. We excluded from the analysis of orientation elements from the partially articulated juvenile in Grid 3, because anatomical position dominates the orientations of those bones (Figure 6.10), as well as excluding fossils that were under 5 cm in length, round, or had similar length and width. Rayleigh's and Rao's tests of uniform distribution were performed in PAST (Hammer et al., 2001) to examine trends in bone orientation. Both test against a null- hypothesis of randomly distributed circular data. Additionally, Watson's U2 was computed to test the goodness-of-fit for von Mises distribution against the null-hypothesis of random distribution.

Bone orientations at Bovid Hill were anisotropic, or non-random ($n = 182$; Rayleigh's R = 0.28, $p < 0.05$; Rao's U = 158.2, $p < 0.05$; Watson's $U^2 = 2.39$, $p <$

0.05) and show a dominant NNW-SSE orientation, with a secondary perpendicular trend, consistent with post-depositional channel reorientation of the fossil assemblage (Figure 6.11). While anisotropy is often interpreted as fluvial transport, Cobo-Sánchez et al. (2014) note that anisotropy does not always represent an allochthonous assemblage. Given the abundance of lag elements in the Bovid Hill assemblage (Figure 6.7), it is unlikely that these larger fossils were transported long distances after initial deposition, but instead were simply reoriented by fluvial action. However, together with the skeletal part profiles, this evidence for fluvial processes strongly suggests that many smaller elements (and artifacts) may have been transported away from the site.

Nuances of any given depositional setting, such as channel shape and size or flow velocity, must also be taken into account when assessing spatial patterning (Hanson, 1980; Todd and Frison, 1986). At Bovid Hill, fossils generally lie flat except when overlying one another, in which cases dips became more variable. In Grid 3 and the south end of Grid 1, fossils were densely piled. Skulls, heavily present in both areas, probably formed obstacles and sediment traps to other elements (Schick, 1986).

Lithic artifacts

Excavations at Bovid Hill recovered 24 lithic artifacts (blades, flakes, fragments, and retouched pieces), supplemented by 82 lithic artifacts collected from the surface of Bovid Hill from 2009 to 2011 (Tryon et al., 2010, 2012). In situ artifacts are made from a variety of locally available lavas and chert, and a single obsidian artifact was collected from the surface. Two artifacts were recovered in situ during the 2010 salvage excavation of two *R. atopocranion* crania eroding from what was later established as Grid 3. Flakes from the excavation are generally fresh with sharp edges, suggesting minimal transport. The excavated artifact sample has a modal size class of 5 (40.0-49.9 mm in maximum dimension), with artifact maximum dimension ranging from 34.9 to 110.6 mm. Large average artifact size, plus a lack of cortical flakes and small elements suggests that either knapping occurred elsewhere or that smaller elements from artifact production have been winnowed away by fluvial processes (Schick, 1986; Petraglia and Potts, 1994). No refits were found among the excavated material, though similarities in material type and the reduction method suggest several artifacts may have come from the same cobble. No cores were present, but small (<4 cm) tested cobbles with 1-2 flakes removed were recovered during the excavation (n 1) and surface collections (n = 3).

The in situ material, and to a lesser extent the surface material, is notable for the dominance of laminar elements (some > 7 cm) apparently produced by Levallois and other methods (Figure 6.12). The Bovid Hill blades and blade fragments have facetted, dihedral, and plain striking platforms that are relatively broad and thin (platform width:length ratio of 3.2 ± 0.7), with multiple dorsal scars that parallel blade margins. Dorsal scar patterns indicate removal from uni- (Figure 6.12A, D, G) and bi-directionally (Figure 6.12B, C, E, F) flaked cores. Latitudinal and longitudinal profiles of elongated flakes and blades are relatively flat, suggesting removal from a large and broad flake release surface. Retouched blades (Figure 6.12A, B, D, F) exhibit retouch on one or both lateral margins, with retouched edge angles varying from ~45 to 60o. When compared to totals for other artifact localities across Rusinga Island published in Tryon et al. (2014), blades are significantly more abundant at Bovid Hill ($\chi^2 = 11.74$, $p < 0.001$), indicating the unique nature of this site and activities performed there, with primary butchery being the favored interpretation.

Discussion

Site Formation at Bovid Hill

There are multiple site formation scenarios that could potentially explain the assemblage of *Rusingoryx* specimens at Bovid Hill. In the discussion that follows, we consider several alternative, but not mutually exclusive, interpretations for the formation of the Bovid Hill bonebed. These group into two types of accumulations: single mass-mortality events (including mass drowning, severe drought, or tactical hunting), or a time-averaged palimpsest (of natural deaths, carnivore accumulations, and/or human hunting activities). We consider multifarious taphonomic agents (primary, post-depositional, post-fossilization) that may have contributed to the taphonomic history of the sub-locality, relying on the following lines of evidence to interpret site formation processes at Bovid Hill: 1) a fluvial geologic setting, high on the landscape; 2) an in situ monospecific *Rusingoryx* assemblage; 3) a prime-dominated mortality profile; 4) three cut-marked specimens; 5) 24 MSA lithic artifacts in situ and 82 associated surface artifacts; 6) specimens (albeit limited) with wet bone breakage with high fracture angles; 7) minimal variance in bone surface conditions throughout the assemblage (i.e., little weathering or rounding); 8) a dominance of lag deposit elements for both fauna and artifacts; and 9) in situ anisotropic bone orientation patterns, with few articulated re- mains. None of these characteristics alone is diagnostic of a single taphonomic explanation for Bovid Hill. Nevertheless, when considered as a whole, the evidence favors human tactical hunting over other possible, but less likely explanations.

Mass-mortality Event versus Time-averaged Accumulation

Monospecific prime-dominated mortality profiles provide an important line of evidence for determining mass mortality events in both archaeological and paleontological contexts. Gaudsinski (2005) recognizes that single species-dominated assemblages need not be the result of mass hunts, but may also represent time-averaged hunting efforts at a favorable hunting locality. Evidence that can help differentiate between a single event and a time-averaged accumulation includes knowledge of the sociality of the taxa present and other taphonomic markers for time-averaging such as variable weathering, abrasion, or trampling (Gaudsinski, 2005).

At Bovid Hill, the seasonal fluvial sedimentary context, coupled with a dominance of lag elements and anisotropic bone orientation patterns, demonstrates that the bonebed was deposited and reworked in an active fluvial environment. Behrensmeyer (1982) has shown that fluvial systems may accumulate time-averaged fossils over thousands of years in the same bonebed. However, if this were the case at Bovid Hill we would expect to see greater taxonomic diversity (i.e., greater representation of other large mammals known from proximate Wasiriya Bed deposits) and more diverse bone weathering and rounding patterns than are present. Furthermore, bones clustered tightly together in a high sediment output environment point to little to no time-averaging. Both of these taphonomic indicators point to a single event rather than time-averaged accumulation. Furthermore, if *Rusingoyx* had behavioral patterns similar to its closest living relative — the modern wildebeest, a highly gregarious and migratory alcelaphin bovid — it is plausible that *Rusingoryx* would have occasionally died together in groups, by whatever means. Hence, we favor the hypothesis that the excavated Bovid Hill assemblage records a single catastrophic event and not a time-averaged accumulation.

Catastrophic death assemblages: drought, drowning or hunting?

"Catastrophes" are a diverse set of phenomena and may include death during drought conditions, by drowning, or through mass hunting events. Given the fluvial setting at Bovid Hill, all types of catastrophes must be considered.

During severe droughts, animals congregate around the few vestiges of wet or vegetated environments in an attempt to avoid starvation; the ephemeral stream at Wakondo might have been such a place. The taphonomic signatures of drought vary depending on the paleo-community structure and landscape setting, but some common features include evidence of scavenging, possibly more young than prime and old individuals, and trampling if remains are concentrated around water (Shipman, 1975; Weiglt, 1989; Rogers, 1990; Gates, 2005; but see Behrensmeyer et al., 2012a, b; Western and Behrensmeyer, 2009). During a severe drought in Amboseli, Behrensmeyer and colleagues (2009, 2012a, b) found that ungulates had extensive tooth wear as a result of their grittier and fallback diet. None of these characteristics fits the Bovid Hill assemblage. There is little evidence of extensive trampling or scavenging by carnivores, juveniles are not over-represented, and the dental remains do not show excessive wear. The lack of desiccation-related features that would be characteristic of drought conditions, such as deep vertical mudcracks and mudcrack polygons in the strata enclosing the bones at Bovid Hill, can be explained simply by the paucity of clay and abundance of silt, sand, and gravel sediments, which would not shrink and form desiccation features. The formation of evaporite minerals such as gypsum or halite would require evaporation of a long-standing water body containing dissolved salts, which is also not present at the site. Therefore, an explanation of severe drought is inconsistent with evidence from Bovid Hill.

Given the fluvial setting at Bovid Hill, actualistic observations of mass drownings are also directly relevant to taphonomic interpretations. Most herd catastrophes are presumed to produce living group mortality profiles, but this assumption may not hold for all large culling events. Specifically, large numbers of wildebeest drown in Lake Masek and the Mara River during seasonal migrations in the Serengeti (Dechant-Boaz, 1982; Capaldo and Peters, 1995; Bunn and Gurtov, 2014), but these events disproportionately yielded more old individuals when compared to samples of a living herd (Bunn and Gurtov, 2014). Bunn and Gurtov (2014) further note the general absence of juveniles from the Lake Masek drowning skeletal assemblage, despite reports of their demise

(Dechant-Boaz, 1982; Capaldo and Peters, 1995); those authors reasonably attribute some of this loss to subsequent carnivore scavenging of washed-up carcasses or to bachelor herd structures wherein juveniles were never present. Moreover, young individuals would be more easily transported away and dissociated from the mass drowning, which would be expected given the prevalence of skeletal elements in Voorhies' lag group recovered from these drownings (Voorhies, 1969; Dechant-Boaz, 1982; Capaldo and Peters, 1995; Kaufmann et al., 2011). During a drowning event, it appears that older individuals and juveniles alike may lack the physical strength and agility to swim across the water in chaotic situations. Thus, mass drownings may largely fall outside of the traditional “catastrophic” or “living” profile, with biased representation across age categories, and further potential taphonomic bias due to carcass winnowing.

The only published mortality profile for mass drowning of wildebeest comes from Lake Masek. When this is compared to the mortality profile for Bovid Hill the differences are statistically significant: young and older adults are more evenly represented at Bovid Hill. However, if only prime and old adults are compared — mitigating the potential bias against juvenile representation — the two mortality profiles are not significantly different. Therefore, based solely on mortality profiles, mass drowning cannot be ruled out as the primary accumulating agents for the Bovid Hill assemblage. Nevertheless, we consider mass drowning to be less likely than other explanations. The ancient stream at Wakondo was an ephemeral first- or second-order stream, up-slope from the surrounding plains with a source at most 1 km distant in the uplands of Rusinga

Island. It seems unlikely to have caused major or repetitive drowning events for large-bodied animals similar to those that occur in much larger bodies of water in the Serengeti today. That is, the geomorphological setting of the stream at Wakondo differs dramatically from that of the Mara River, which is fed by numerous tributaries that drain the highlands of central Kenya before draining into Lake Victoria. Both the size of the river and the steepness of its banks (upwards of 2 m) appear to contribute to the regular wildebeest drownings observed there. In contrast, the Wakondo channel was situated less than 1 km from Rusinga's highlands and was likely a small seasonal stream that was almost exclusively rain-fed. This conclusion is supported by the paleo- Vertisol, which has features indicative of seasonal wet and dry periods that would cause variable stream output. Furthermore, the absence of water-dependent hippopotamuses and crocodiles (with no apparent taphonomic biases against such taxa) suggests that the Wakondo stream was not large or deep enough to support such taxa. It is probable that the Wakondo stream could slow down groups of *Rusingoryx*, but not regularly drown them.

A third type of catastrophe to consider is a mass hunting event by Late Pleistocene humans. Lubinski (2013) provides criteria for distinguishing mass hunting events in archaeological contexts from paleontological herding accidents, and calls for a holistic approach using multiple lines of evidence to demonstrate anthropogenic accumulation of catastrophic assemblages, including the presence of artifacts and culturally modified bone surfaces as markers of primary depositional modifiers, natural or man-made landscape features that may aid in large-scale hunts (such as cliffs or drive lanes), and the use of taphonomic data to demonstrate a lack of time-averaging (weathering and articulation patterns, sedimentary context). This type of approach cannot rule out alternative explanations, at least based on the evidence available from Bovid Hill, but it provides a basis for assessing the relative likelihood of different scenarios. Taking into account the landscape context, additional taphonomic data, and the presence of artifacts and cut marks on bones, we favor mass hunting over drowning to explain the Bovid Hill assemblage, as detailed below.

Timing and Degree of Human Involvement

Whereas the taphonomic data do not exclusively endorse one explanation for the Bovid Hill assemblage, the archaeological evidence does provide unambiguous evidence of human activity at Bovid Hill. The excavated assemblage has yielded 24 in situ MSA cutting tools, supplemented by 82 surface artifacts and cut-marked bone specimens. Direct evidence for human interaction with *Rusingoryx* is not overwhelming — three cut-marked bones, a handful of specimens with green fracture patterns, and no angular punctures or tears characteristic of projectile damage from wooden- or stone-tipped spears (Smith, 2003; Smith et al., 2007; Letourneux and Petillon, 2008; Churchill et al., 2009; O'Driscoll and Thompson, 2014) — but these low numbers are consistent with the post-depositional processes observed at Bovid Hill. It is difficult to model the extent to which primary depositional processes (butchery/carnivore action) should be observable in the record when post-depositional processes are known to obscure their visibility. Controlled actualistic experiments are generally conducted on fresh bone, providing some of the most rigorous and extensive comparisons for taphonomic signatures. However, the taphonomic histories of many fossils from open-air assemblages are long and complex, thus an understanding of how post-depositional processes are likely to affect observations of various surface modifications is necessary for adjusting expectations and site interpretations.

At Bovid Hill, the fluvial setting is well established, both geologically and taphonomically. Post-depositional fluvial and chemical processes almost certainly contributed to the scarcity of anthropogenic marks, as sediment abrasion from fluvial processes, chemical weathering, and microbial processes will obscure delicate surface modifications such as cut marks. Hence, we would not expect to observe many cut marks, especially as these surface modifications are generally light and shallow. Whereas the Bovid Hill fossils do not show strong evidence of fluvial rounding (cf. Fernández-Jalvo and Andrews, 2003), studies have shown that sediment abrasion can obscure or destroy cut marks (Shipman and Rose, 1983) even before fossils show evidence of rounding at their ends and in less than 50 h in a fluvial environment (e.g., flume) (Chisholm et al., 2014). Carnivore damage, unlike cut marks, is typically more conspicuous. Tooth marks tend to be deeper and wider than cut marks, and thereby less easily obscured by slight sediment abrasion. They are also more frequent in assemblages where carnivores have played a significant role. Carnivore gnawing will lead to irregular and jagged limb ends (Haynes, 1980). While fluvial processes would also affect the identification of carnivore activity, we would not expect it to be completely obliterated in an assemblage where human butchery is still evident. At Bovid Hill, no unambiguous carnivore damage was observed on any of the fossil material examined, suggesting that if carnivores had any role in the accumulation or destruction of the assemblage, it was minimal.

Nevertheless, the scarcity of surface modifications makes it difficult to assign a primary accumulating agent to the Bovid Hill assemblage or to determine who may have had primary access to carcasses. Post-depositional winnowing would have also played an important role in deleting portions of the record, and remaining bone fragments resulting from wet breakage (possibly due to marrow processing) at Bovid Hill are likely to have been transported away by fluvial processes early in the taphonomic history of the site (Pante and Blumenschine, 2010). Anthropogenic spear damage is also expected to be rare in any assemblage, but most likely to be preserved on axial elements such as scapulae, ribs, and vertebrae (Smith, 2003; Smith et al., 2007; Letourneux and Petillon, 2008; Churchill et al., 2009; O'Driscoll and Thompson, 2014) —elements that are poorly represented at Bovid Hill and appear to have been preferentially winnowed. Similarly, smaller lithic artifacts and flaking debris may have also been winnowed away from the site, and fluvial processes may therefore account for low artifact counts (Schick, 1986; Petraglia and Potts, 1994), though Garrett et al. (2015) point out that these artifact densities are nevertheless within the range of other important open-air sites.

It is notable that the only surface modifications that are clearly diagnosable are cut marks, and that, despite the occurrence of post- depositional processes known to delete important anthropogenic modifications, their presence along with many lithic artifacts is unambiguous. Given these findings, we believe that MSA humans likely had primary or early access to the *Rusingoryx* carcasses.

Hunting versus Scavenging

Despite evidence for human butchery at Bovid Hill, definitive direct evidence for hunting is lacking. No projectile points have been recovered, and no surface modifications characteristic of projectile damage (e.g., punctures or tears to the ribs, vertebrae or scapulae; Smith, 2003; Churchill et al., 2009) were identified. Therefore, it is currently impossible to rule out scavenging as a means to meat procurement.

Until more refined taphonomic methods were developed, scavenging was considered the default mode of meat procurement during the Middle Stone Age and Middle Paleolithic (for a review see Domínguez-Rodrigo, 2003). Whereas we now understand Middle e Late Pleistocene hominins to have been savvy and capable hunters (Marean, 1997; McBrearty and Brooks, 2000; Lombard, 2005; Assefa, 2006; Clark and Plug, 2008; Faith, 2008; Klein, 2009; Wadley, 2010; Thompson and Henshilwood, 2011, 2014; Armstrong, 2016; Clark and Kandel, 2013; McBrearty, 2013), there is little evidence to suggest they would have been disinterested in fresh and easily accessible carcasses. Aside from relatively rare projectile damage, the taphonomic signatures for hunting and early access scavenging of a mass mortality event are virtually indistinguishable. The availability of scavengable carcasses as a reliable resource on the landscape has been hotly debated (Tappen, 1995; Domínguez-Rodrigo, 2003). However, Capaldo and Peters (1995) and Dechant-Boaz (1982) have shown that mass drownings can occur seasonally as migratory ungulates cross dangerously swollen rivers and drainages. Bone studies along the Mara and Masek Rivers, as well as local oral histories indicate that these recurring events consistently deposited carcasses on the same beaches over the course of several years (Capaldo and Peters, 1995). Such a scenario is a possible explanation for the Bovid Hill assemblage, but is not favored here based on the topographic placement of the stream and its seasonal rain-fed nature: the stream at Wakondo was un- likely to be deep or the current strong enough to cause a downing event and present an opportunity for scavenging.

Tactical Landscape Use

Given the evidence outlined above for a single catastrophic death assemblage (prime-aged-monospecific mortality profile of a likely gregarious bovid, little variation in post-depositional weathering or rounding), the evidence of human butchery (cut- marked specimens, associated stone tool assemblage), and the geomorphological context of the stream setting (first- order stream, unlikely to have been a regular location of accidental drowning occurrences), we believe that Bovid Hill most likely records an instance of tactical hunting. Marean (1997) defined tactical hunting as the large-scale procurement of a single species, likely using some aspect of the landscape (natural or modified) to aid in hunting. At Bovid Hill, this could have been undertaken by a small group of hunters (reflected by low artifact densities). In addition to taphonomic, faunal, and artifact data, the association of a procurement site with a culturally modified landscape or kill facility (drive lanes, blinds) is an important aspect for identifying mass hunting events in archeology (Lubinski, 2013). Although Bovid Hill is not associated with any known cliffs or culturally modified landscapes, we suggest that the ancient stream in which the bonebed was deposited likely served as such a kill facility. Ethnographic examples have shown that rivers and other bodies of water make excellent landscape features where humans can hunt gregarious herds. Large ungulates are particularly vulnerable while swimming or wading and individual animals can be easily trapped among water, hunter, and herd. Binford (1991) described traditional Nunamiut hunting techniques where hunters would drive herds of caribou (*Rangifer tarandus*) into Tulugak Lake and into streams draining into the lake, subsequently spearing them from both kayaks and the shore. The Murle of South Sudan traditionally hunted kob (*Kobus kob*) at the confluence of the Pibor and Kengen Rivers near Pibor Post, killing 100-200 kob in a day during the migration season. Hunters were able to stand in the shallow river and spear kob as they attempted to cross while carcasses were collected and processed downstream (Lewis, 1972; Langley, 1985; Arensen, 1997). Lubinski (1999) cites historic ethnographic accounts of Native American Arikara hunters taking pronghorn (*Antilocapra americana*) during migrational crossings on the Missouri River, killing 58 individuals in total. More generally, prehistoric Native American groups appear to have used similar methods in dry river beds or arroyos to kill bison (Bison bison) (Driver and Maxwell, 2013). In these recent and modern examples, caribou, kob, and pronghorn were easily dispatched while in the water, and such a strategy could have been similarly effective for MSA foragers.

In a tactical hunting scenario at Bovid Hill, herds of *Rusingoryx* may have been actively driven into a deeper or treacherous portion of the stream, likely during the wet season, upstream from where the bonebed is found today. Alternatively, individuals within a group may have been targeted as they waded into calmer, shallower sections or near a riverside hunting blind where water may not have been deep or swift enough to lose control, but restrictive enough to make the bovids easy prey for hunters. This interpretation presents a new opportunity to explore Marean's (1997) hunter- gatherer foraging models for tropical grasslands. With respect to tactical hunting, Marean proposed three foraging models: 1) a generalized grassland model, where hunter-gatherers relied heavily on plant foods, supplemented by opportunistic encounters with prey without tactical hunting; 2) a specialized grassland model, where larger groups of hunters routinely used tactical and communal large-scale hunts of a limited number of prey species; and 3) a seasonal grassland model, which is a combination of both the generalized grassland model and the specialized grassland model where hunters utilized tactical hunting to capture herds of gregarious ungulates on a seasonal basis (e.g., during seasonal migrations of grassland ungulates) and relied on ambush methods during other times of the year (Marean, 1997).

Properly testing these models would require multiple contemporaneous sites demonstrably produced by the same social group e a degree of resolution that is rare in the archaeological record. However, when all of the evidence from Bovid Hill is considered, use of the fluvial system as a kill facility in the aid of tactical hunting is most consistent with Marean's (1997) seasonal grassland model. Landscape reconstructions show Rusinga as a high spot in an open and arid grassland that may have drawn MSA foragers for a range of resources such as water, wood, and high-quality stone raw material (Tryon et al., 2014). Hence, if the ancient stream at Bovid Hill rep- resents a natural kill facility, it is unlikely to have made an effective obstacle to large ungulates year-round. Likewise, artifact distributions are sparse around Rusinga and nearby Mfangano Island, suggesting that the region may not have supported the large hu- man populations predicted for the specialized grassland model (Tryon et al., 2010, 2012). Nearby Nyamita, where faunal diversity is high and several retouched points have been recovered, may have been a favored ambush site near a spring and watering hole (Tryon et al., 2012; Beverly et al., 2015a; Blegen et al., 2015).

The use of tactical landscapes to exploit large numbers of ungulates is well suited to gregarious and migratory taxa, as is inferred for *Rusingoryx*. The precise location of such animals can be unpredictable both spatially and temporally, but careful observation combined with group efforts to corral or drive herds towards natural or constructed features make these strategies effective and optimal in highly seasonal environments. Topographically high areas on Rusinga would have allowed hunters to spot prey and plan hunts at relatively low costs, as animals congregated at seasonal water sources. Knowledge of the landscape, *Rusingoryx* herding behavior, and seasonality would have been crucial for exploiting large groups of animals and may represent a type of soft technology not visible in the archaeological record (Kelly, 2013).

Within eastern Africa, only GvJm-22 and GvJm-46 at Lukenya Hill show evidence for the mass exploitation, in both cases of the size class 2 alcelaphin, *D. hypsodon* (Marean, 1997; Faith et al., 2012), indicative of tactical hunting strategies. At Porc-Epic Cave, Ethiopia, MSA hunters exploited a diverse group of species (Assefa, 2006), and artifacts and fauna from the Aduma sites in Ethiopia suggest possible hunting and processing of water dependent fauna, but bone surfaces are generally poor and so conclusions are limited (Yellen et al., 2005). Loiyangalani in Tanzania also lacks consistently well-preserved bone surfaces that are ideal for interpretations of human behaviors, but the presence of surface modifications, even in low frequencies, demonstrates that humans were involved in the accumulation of some fauna at lake shore or marsh environment (Bower et al., 1979; Thompson, 2005). Fauna and artifacts are associated with archaic *Homo sapiens* remains from Lake Eyasi, Tanzania, but taphonomic histories and thus behavioral interpretations are currently not well published (Mehlman, 1987; Domínguez-Rodrigo et al., 2008). None of these sites, however, with the exception of those from Lukenya Hill, is dominated by a single gregarious taxon and thus they are more suggestive of ambush or encounter hunting rather than tactical hunting. Across eastern Africa, a seasonal grassland model - with its use of both tactical landscape and other hunting techniques - may have been common for Late Pleistocene MSA and LSA hunters. Alternatively, individual groups employed different methods and current data represent a diversity of landscape use methods.

Conclusions

Excavations at Bovid Hill, Wakondo revealed both in situ lithic artifacts and a dense bonebed accumulation of the extinct alcelaphin bovid *Rusingoryx*. The taxonomic dominance of *Rusingoryx*, a prime-dominated mortality profile, fluvial setting, cut-marked bone, and lithic artifacts are suggestive of a tactically hunted herd assemblage. Middle Stone Age lithic artifacts, bone surface modifications, and bone breakage patterns suggest primary human butchery at the site, but post-depositional processes have likely deleted portions of this record. Sedimentology, bone orientation patterns, and skeletal part frequencies are consistent with a fluvially reworked bone deposition. Evidence from Wakondo demonstrates that the stream itself may have played a role as a hunting facility for tactical landscape use.

Although post-depositional processes such as winnowing and abrasion can hinder the interpretation of sites, the multiple lines of evidence used here can bolster inferences. The best preserved sites with the densest artifact accumulations can yield a wealth of in- formation. Yet these localities tend to occur only in specific con- texts: caves and rock-shelters used as habitation sites, where bones and artifacts are shielded from the elements. Such sites are spatially dissociated from procurement areas, and thus unlikely to document the full diversity of foraging strategies employed by MSA humans.

Our results highlight the importance of rivers and streams in the procurement of large groups of gregarious ungulates for MSA foragers, and are suggestive of a seasonal grassland model of foraging and mobility. Paleoenvironmental and landscape reconstructions indicate that the region that makes up Rusinga Island today was relatively resource-rich in an otherwise open and arid grassland during the later Pleistocene. Seasonal fluvial environments at Wakondo clearly added to the desirability of the area for mobile hunter-gatherers, and ancient streams, such as the one present at Wakondo, were likely part of a seasonal and tactical landscape used by MSA foragers.

If the inference of tactical landscape use at Wakondo is correct, this site joins a growing number of Late Pleistocene (<126 ka) MSA and LSA sites in sub-Saharan Africa suggestive of tactical landscape use: monospecific and catastrophic mortality profiles of *D. hypsodon* at GvJm-46 and GvJm-22 at Lukenya Hill (Marean, 1997; Faith et al., 2012; Tryon et al., 2015), and a catastrophic mortality profile of gregarious eland (Taurotragus oryx) at Klasies River Mouth (Klein, 1978; Klein and Cruz-Uribe, 1996). Similar patterns are reported from several Late Pleistocene Middle Paleo- lithic sites across Eurasia including La Quina (Chase et al., 1986), Grotte XVI (Grayson and Delpech, 2003), Mauran and Les Pradelles (Rendu et al., 2012) in France, Salzgitter-Lebenstedt in Germany (Gaudzinski and Roebroeks, 2000), Starosele in Crimea

(Burke, 2000), Il'skaya I in Russia (Hoffecker et al., 1991; Hoffecker and Cleghorn, 2000), Ortvale Klade in the Republic of Georgia (Adler et al., 2006), and many others where the culling of herds can be inferred. White et al. (2016) suggest that tactical hunting of herd animals may have been a preferred Neanderthal technique. Inferences of tactical hunting are rare or non-existent in the Early Stone Age and Lower Paleolithic, with the possible exception of Schöningen (Voormolen, 2008; van Kolfschoten, 2014). This may suggest a shift in foraging strategies and new techniques across hominin taxa (e.g., African *H. sapiens* and Neanderthals) by the Late Pleistocene, and gives further evidence to refute hypotheses that MSA hunters were incapable of procuring large and difficult ungulate taxa (see McBrearty and Brooks, 2000; Faith, 2008 for reviews). Data from across Africa show that MSA foragers regularly employed new and adaptive techniques to exploit a variety of environments (McBrearty and Brooks, 2000; McBrearty, 2013). Whereas caves and other long-term habitation sites record a palimpsest of hunting events accumulated throughout their occupation, open-air sites such as Wakondo paradoxically sample a narrower time interval, thus providing insight into the wide range of foraging strategies used by Pleistocene hominins.

Table 6.1: Taxonomic list of specimens (Number of Identified Specimens [NISP] and Minimum Number of Individuals [MNI]) collected from Wakondo Bovid Hill (2007-2013).

Taxon	Common name	Surface collections		Excavated
		NISP	MNI	MNI (2011)
Leporidae cf. *Lepus*	Rabit/hare	1	1	0
Equus grevvi	Grevy's Zebra	2	1	0
Reduca arundinum/ Kobus kob	Southern reedbuck or Kob	3	1	0
Alcelaphini cf. *Alcelaphus buselaphus*	Hartebeest	1	1	0
Connochaetes taurinus	Blue wildebeest	1	1	0
Damaliscus hypsodont	Extinct blesbok	3	1	0
Megalotragus sp.	Giant wildebeest	1	1	0
Rusingoryx atopocranion	Extinct wildebeest	118	16	11

Table 6.2: Frequencies of mandibular and maxillary teeth according to Zeder's (2006) wear scheme.

General wear	**Zeder (2006)**	**dP_4**	**M_1**	**M_2**	**M_3**	**dP^4**	**M^1**	**M^2**	**M^3**
Eruption	6	-	-	-	1	-	-	-	1
	7	-	-	-	-	-	-	-	-
	8	-	-	-	-	-	-	-	2
Early wear	9	-	-	3	-	-	-	3	-
	10	-	-	1	-	-	-	-	-
	11	-	-	2	1	-	-	-	1
	12	-	-	-	-	-	-	-	-
Active wear	13	-	-	-	-	-	-	-	-
	14	-	-	1	1	-	-	-	-
	15	-	-	-	-	-	-	-	-
	16	-	3	3	3	-	-	1	1
	17	-	23	16	18	6	17	12	12
Late wear	18	-	1	-	-	-	-	-	-
	19	1	-	-	-	-	-	-	-
	20	2	2	-	-	-	-	-	-
	21	1	-	-	-	-	-	-	-
	22	-	1	3	-	-	-	-	-
	23	2	-	-	-	-	-	-	-
	24	-	-	-	-	-	-	-	-
Final wear	25	-	6	-	-	-	2	-	-
	26	-	-	-	-	-	-	-	-
	Total	6	36	29	24	6	19	16	17

Table 6.3: Mortality profiles at Bovid Hill compared to a living herd structure, mass drowning, and to ethnographic hunting accounts.[a]

	Juveniles	Prime	Old	Ratio of Prime:Old	Fishers Exact Test
Bovid Hill	8	13	6	2.2:1	
Serengeti Wildebeest Living Herd	82	104	17	6:1	0.06
Wildebeest Drowning at Lake Masek	8	100	67	1.5:1	0.32
Hunting Hadza Impala	15	31	4	7.75:1	0.08
Hunting Hadza Kudu	6	10	2	5:1	0.31

[a] Due to the likelihood that juveniles will be disproportionally deleted in the taphonomic record due to taphonomic processes, we examine the ratio of prime to old adults using Fisher's exact test, following Bunn and Gurtov (2014). When the prime-old ratio from the Bovid Hill sample is compared to the mass drowning at Lake Masek, a wildebeest living herd, and ethnographic data on Hadza hunts, none is statistically different ($p > 0.05$) from the Bovid Hill assemblage. Data taken from Bunn and Gurtov Tables 6.1 and 6.2 (2014).

Table 6.4: Skeletal element frequencies from the excavated sample of Bovid Hill.[a]

Element	MAU	%MAU
Cranium	11	100.00%
Hemi-mandible	17	77.3%
Atlas	1	9.1%
Axis	0	0.0%
Vertebra	24	8.4%
Rib	42	14.7%
Innominate	6	27.3%
Scapula	8	36.4%
Humerus	5	22.7%
Radius/Ulna	15	68.2%
Metapodial	15	34.1%
Femur	6	27.3%
Patella	1	4.5%
Tibia	10	45.5%
Astragalus	4	18.2%
Calcanium	5	22.7%
Navi-Cuboid	1	4.5%
1st Phalanx	11	12.5%
2nd Phalanx	12	13.6%
3rd Phalanx	10	11.4%

[a] MAU - minimum animal unit. Binford's MAUs (1981) were calculated using portions present as defined by Lam et al. (1999). %MAU is a scaled by the MNI (minimum number of individuals), which is based on the most frequent element, crania (n = 11).

Table 6.5: Skeletal part frequencies generated using Lam et al. (1999) bone mineral density portions (BMD).[a]

Element	Portion	BMD	Frequency
Humerus NISP 8 MAU/NISP .63	HU1$_1$	0.32	3
	HU2$_2$	0.49	1
	HU3$_2$	1.1	2
	HU4$_2$	1.03	3
	HU5$_1$	0.51	5
Radius/Ulna NISP 26 MAU/NISP .58	UL1$_1$	0.46	10
	UL2$_2$	0.85	10
	RA1$_1$	0.51	15
	RA2$_2$	1.02	14
	RA3$_2$	1.07	14
	RA4$_2$	0.96	12
	RA5$_1$	0.47	12
Metacarpal NISP 9 MAU/NISP 1.0	MC1$_2$	0.72	9
	MC2$_2$	1.12	9
	MC3$_2$	1.15	8
	MC4$_2$	0.83	6
	MC5$_1$	0.56	6
	MC6$_1$	0.62	6
Femur NISP 12 MAU/NISP .50	FE1$_1$	0.41	5
	FE2$_2$	0.51	2
	FE3$_2$	0.92	3
	FE4$_2$	1.16	4
	FE5$_2$	0.66	3
	FE6$_1$	0.38	6
	FE7$_1$	0.31	2
Tibia NISP 10 MAU/NISP .91	TI1$_1$	0.42	3
	TI2$_2$	0.91	8
	TI3$_2$	1.12	10
	TI4$_2$	1.09	7
	TI5$_2$	0.59	8
Metatarsal NISP 6 MAU/NISP 1.0	MR1$_2$	0.83	6
	MR2$_2$	1.11	6
	MR3$_2$	1.14	6

MR4$_2$	0.84	4
MR5$_1$	0.54	4
MR6$_1$	0.65	3

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[a] MAU - minimum animal unit; NISP - number of identified specimens. Bone portions from Lam et al., 1999. Subscripts under the portion column denote where BMD$_1$ or BMD$_2$ values were used. BMD$_2$ values are used when available and for bone shafts.

Table 6.6: Average %MAU values by Voorhies Group.[a]

Transport group	Bovid Hill	Lake Masek	Mara River
Float 1	10.32	20.59	25.52
Intermediate 1.5	36.36	29.17	36.36
Gradual 2	37.52	34.38	36.36
Lag 3	88.65	64.58	95.45

[a] Bovid Hill, as well as wildebeest mass drownings in the Serengeti, is dominated by elements from Voorhies group 3, when scaled by %MAU. This comparison suggests that winnowing likely took place at all sites and that additional morality comparisons between the sites are valid. Data from Lake Masek and Mara River taken from Dechant-Boaz (1982) and Capaldo and Peters (1995).

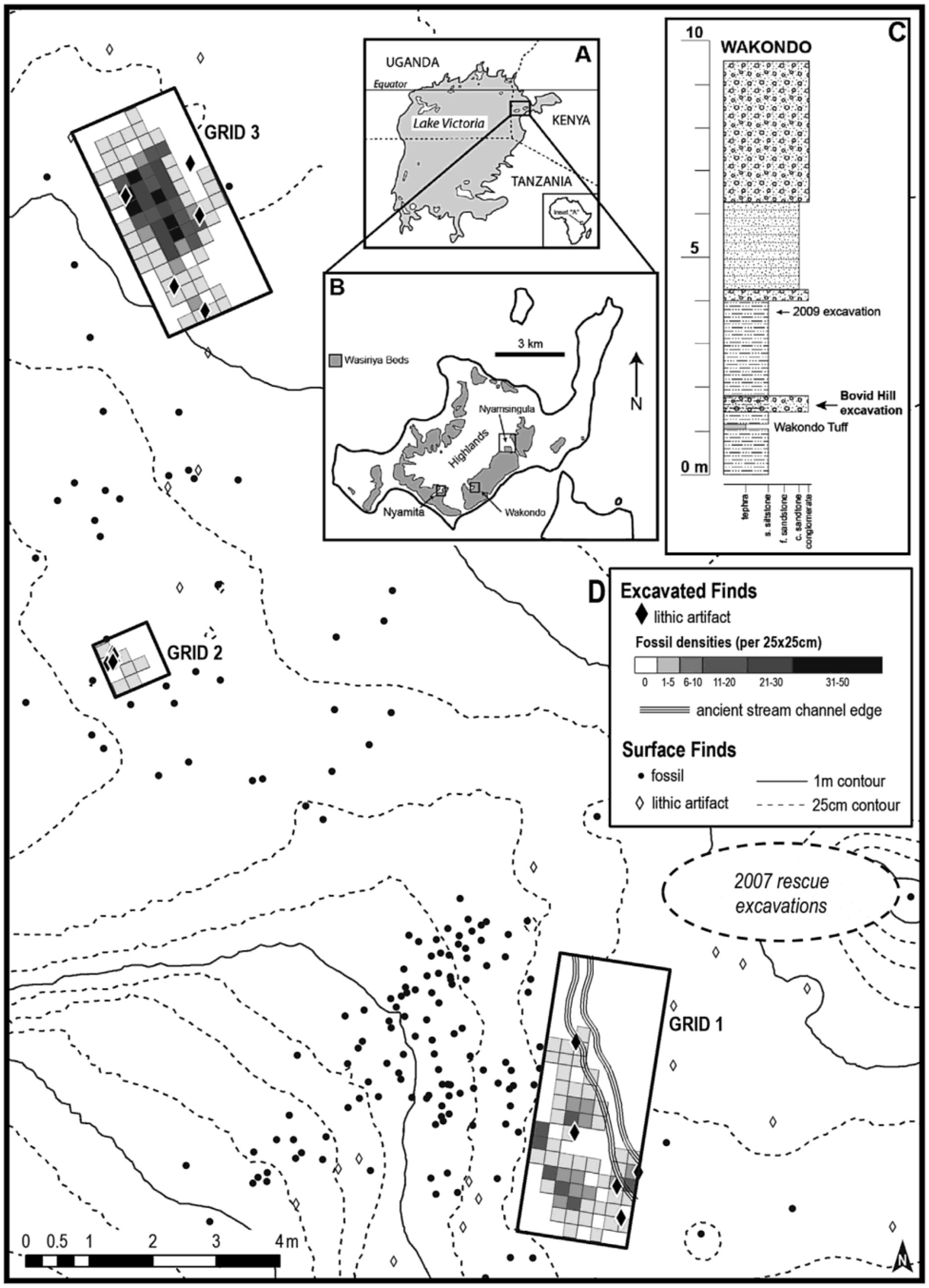

Figure 6.1: Location and site map, and lithostratigraphy of Wakondo locality. A. Location map of Rusinga Island in Lake Victoria, Kenya. B. Pleistocene exposures of the Wasiriya Beds on Rusinga Island with the three major fossil localities, Wakondo, Nyamita, and Nyamsinguala, indicated. C. Stratigraphy of the Wakondo locality showing the stratigraphic position of the Bovid Hill excavation and a preliminary excavation in 2009 (Tryon et al., 2010). The presence of the Wakondo Tuff allows the correlation of the Wakondo site to all other localities on Rusinga (Tryon et al., 2010; Blegen et al., 2015). D. Bovid Hill sub-locality at Wakondo. Three trenches were opened in 2011, totaling 19 m^2.

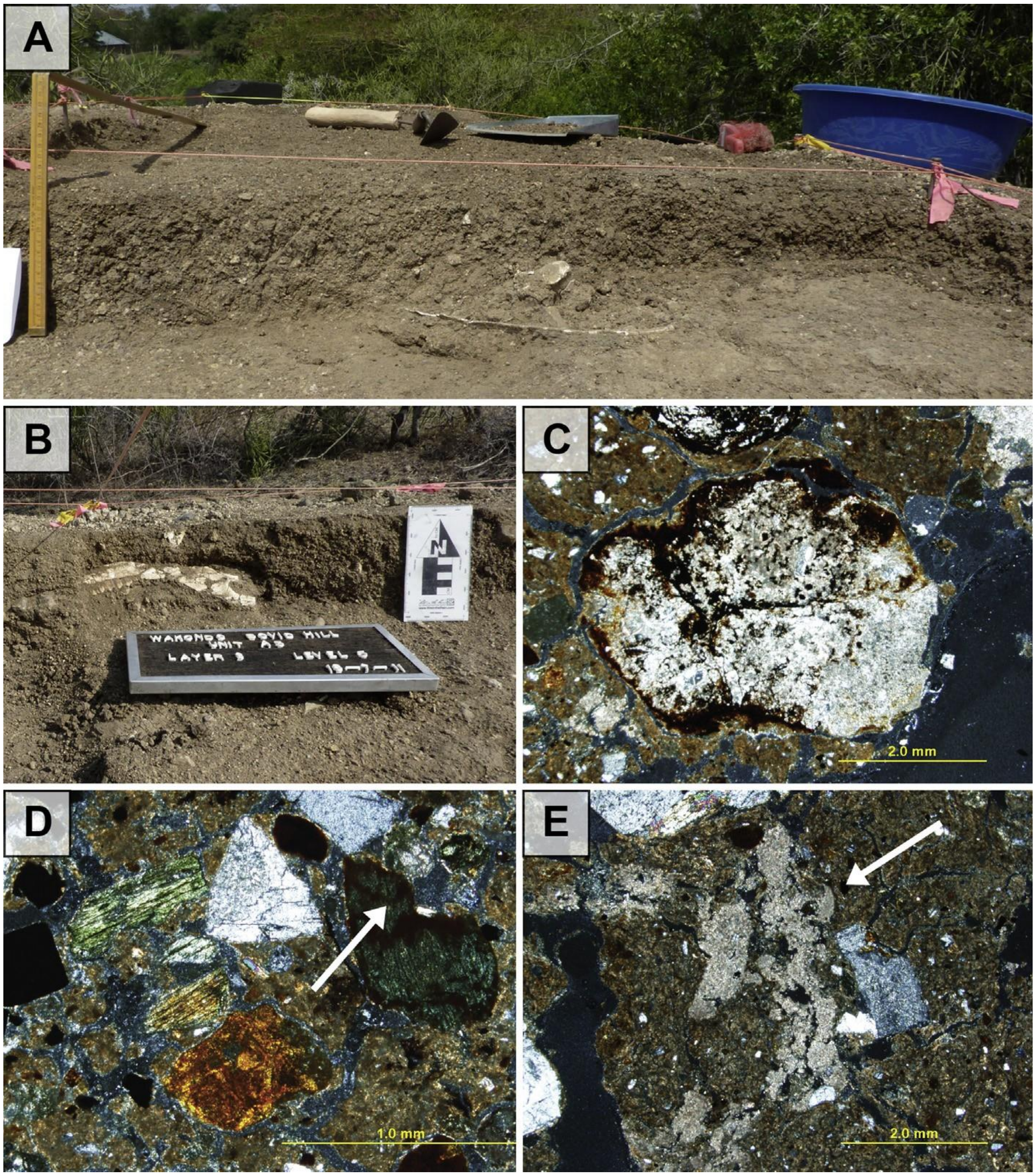

Figure 6.2: Field photographs of the coarse grained, fossil bearing sediments and associated micrographs of the Bovid Hill excavation, Grid 1. A. Conglomeratic sands in excavation wall. B. Coarse grained sandstone and conglomerates preserving in situ fossil material C. Thin-section micrograph of iron-impregnated soil carbonate nodule in cross-polarized light (XPL). D. Thin-section micrograph showing volcaniclastic sand grains (XPL). White arrow indicates a weathered pyroxene clast. E. Thin-section micrograph of the paleo-Vertisol adjacent to the excavation showing the paleosol matrix (XPL). White arrow indicates soil carbonate rhizoliths formed around roots. Color images available online.

Figure 6.3: Artistic reconstruction and cranium of *Rusingoryx*, (KNM-RU-52572) size 3 alcelaphin bovid. Art by Cornel Faith.

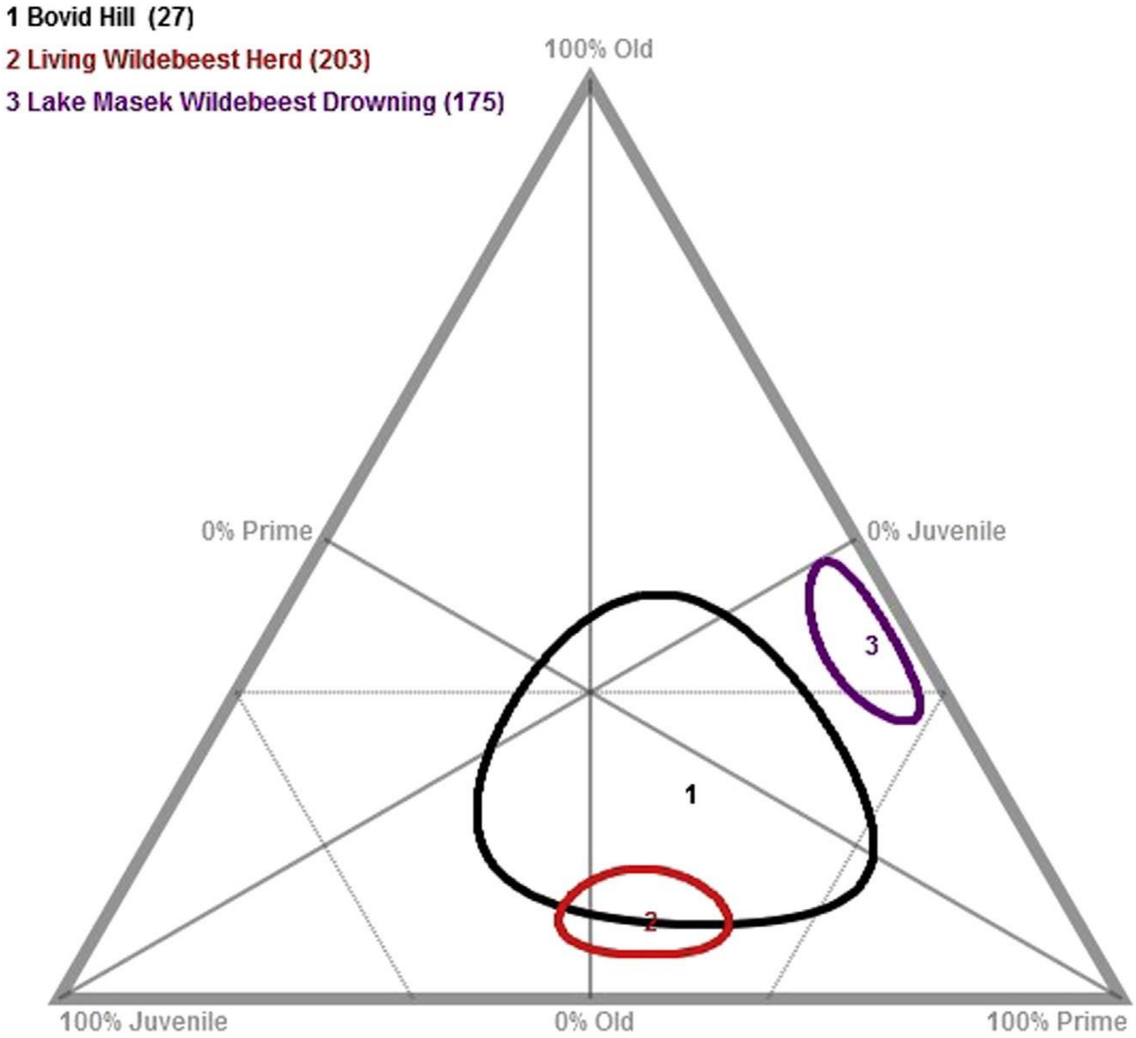

Figure 6.4: Modified triangle plot showing the age profiles of (1) *Rusingoryx atopocranion* specimens from the excavations and surface collections at Bovid Hill (MNI ¼ 27 Individuals; see Table 6.2) compared to the age profiles of (2) a mass drowning of wildebeest at Lake Masek, and (3) a living population assemblage of wildebeest (Bunn and Gurtov, 2014). Ellipses indicate 95% confidence intervals. The *Rusingoryx* age profile differs significantly from a theoretical attritional age profile ($\chi2 = 12.4$, $p < 0.01$) but it is indistinguishable from the age structure of a modern wildebeest herd (methods following Steele, 2005 and Weaver and Steele, 2011).

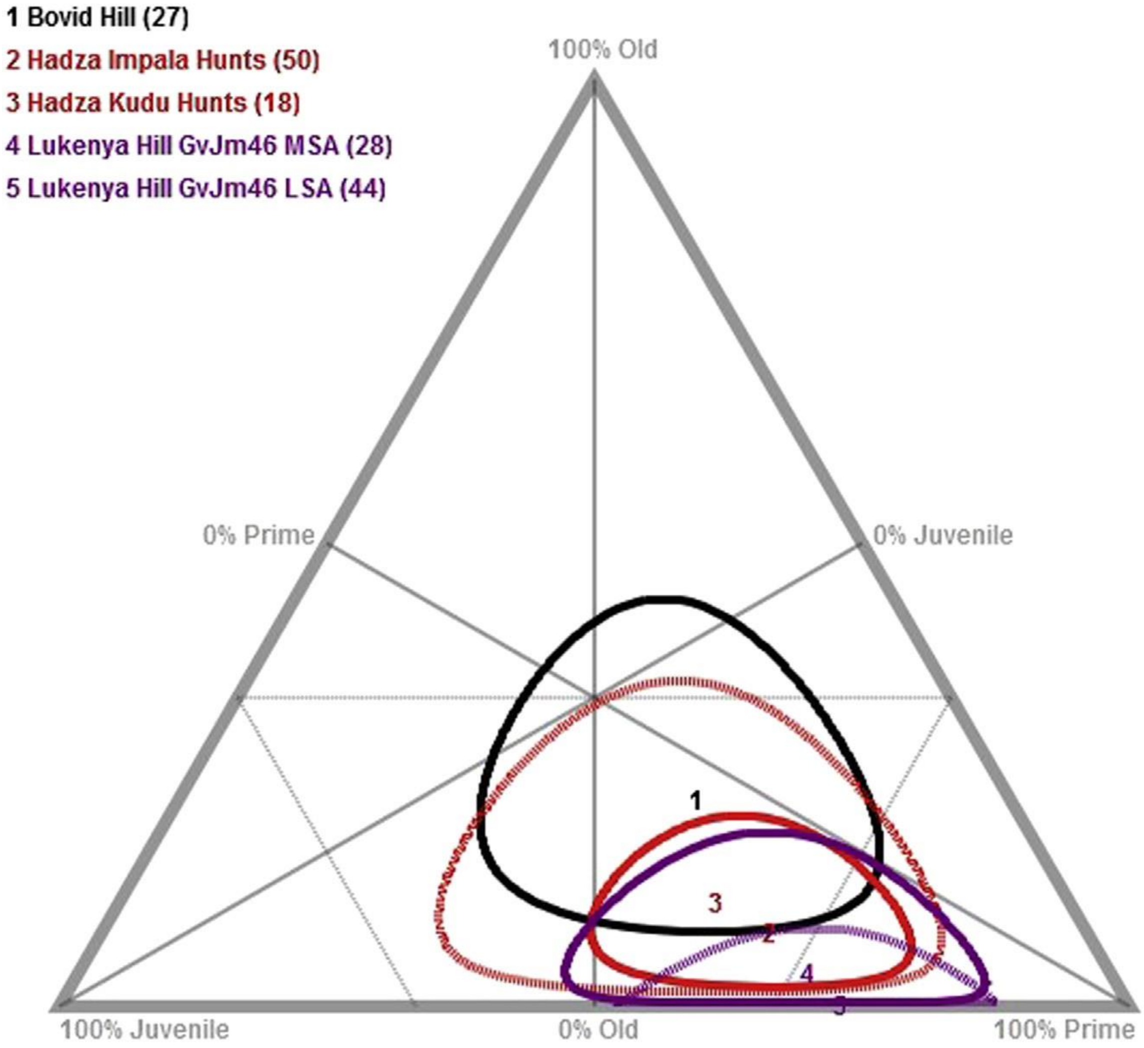

Figure 6.5: Modified triangle plot showing the age profiles of *Rusingoryx atopocranion* at Bovid Hill (Table 6.2) and mortality data of kudu and impala hunted by Hadza (Bunn and Gurtov, 2014). Bovid Hill is also compared to data from MSA and LSA layers at Lukenya Hill (Marean, 1997). Ellipses indicate 95% confidence intervals. Assemblages at Lukenya are hypothesized to represent mass hunts, similar to Bovid Hill. Ethnographic data from the Hadza, archaeological data from Lukenya Hill and Bovid Hill all show prime-dominated mortality profiles with overlap in a hypothetical living structure/catastrophic profile at a 95% confidence interval (methods following Weaver and Steele, 2011).

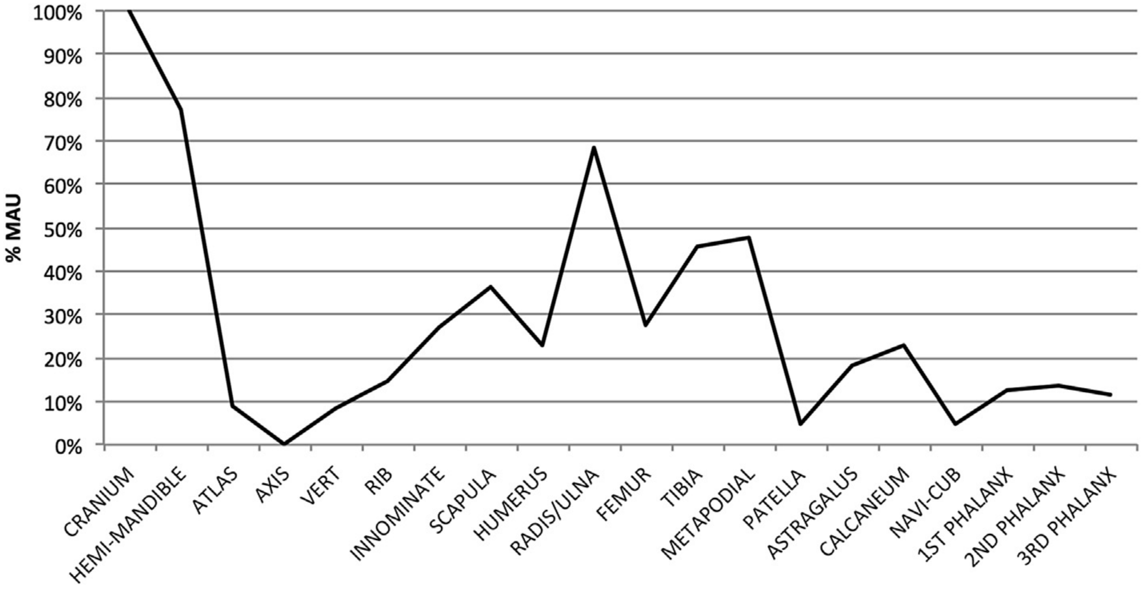

Figure 6.6: Percent MAU (minimum animal units) values for the 2011 excavated Bovid Hill sample.

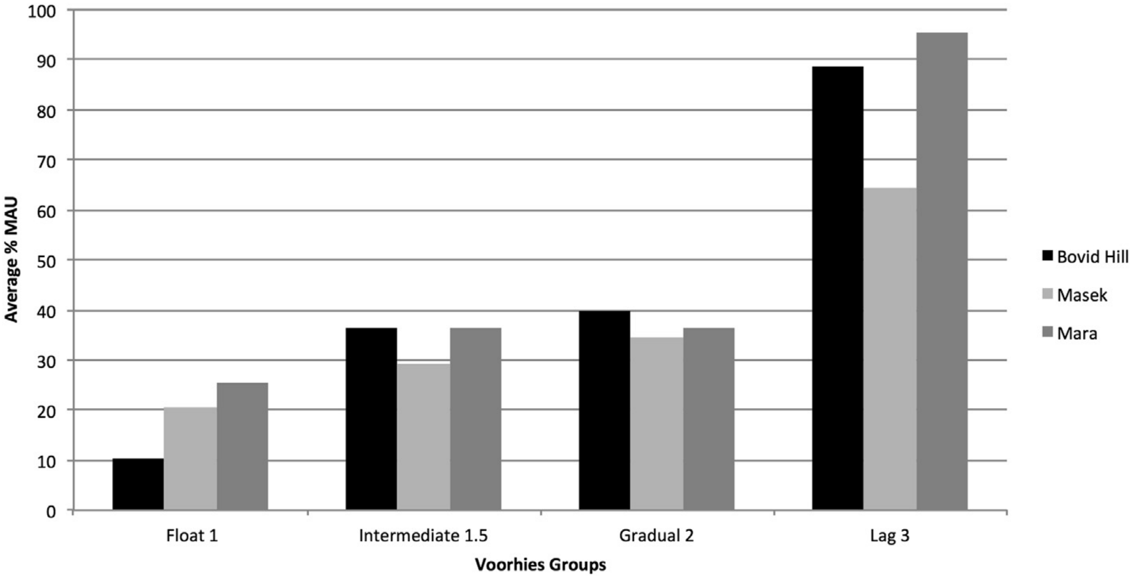

Figure 6.7: Voorhies' (1969) Fluvial Transport Groups at Bovid Hill. Average % MAUs from Bovid Hill are compared to bonebeds resulting from mass drownings at Masek Lake and Mara River, Tanzania (Dechant-Boaz, 1982; Capaldo and Peters, 1995). Float Group 1 includes those elements most likely to float (ribs, vertebrae, sacra, and sterna). Intermediate Group 1.5 includes only scapulae because phalanges were not reported for mass wildebeest drowning comparatives, Masek Lake and Mara River. Gradual Group 2 includes all long bones and Lag Group 3 includes crania and mandibles. MAU counts from Table 6.6 are used for Bovid Hill.

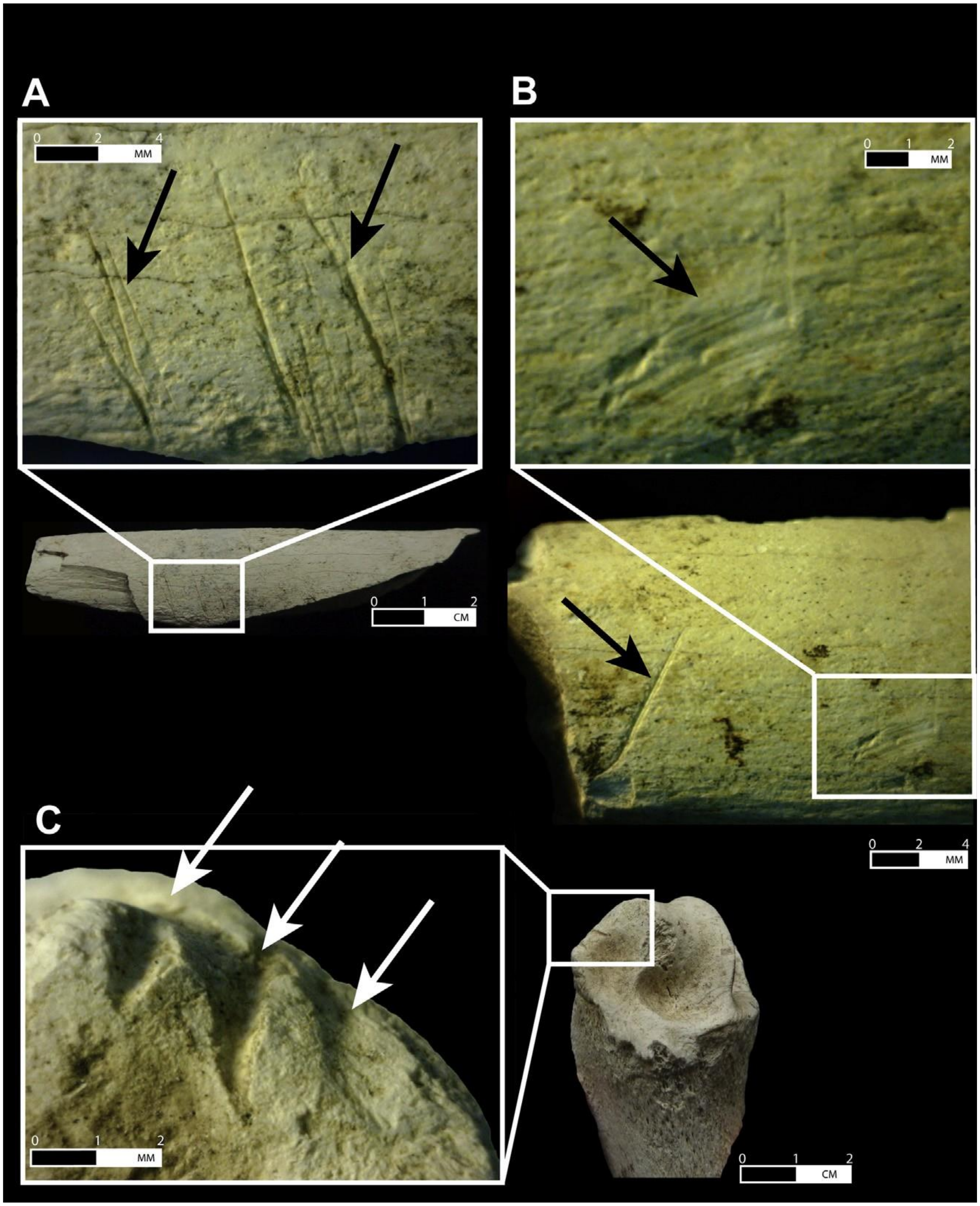

Figure 6.8: Bone surface modifications indicative of butchery: (A) Black arrows point to multiple parallel cut marks on a tibial shaft fragment, (B) Black arrows points to possible scrap mark (enlarged) and cut mark and on a radio-unlar shaft fragment, (C) White arrows point to V-shaped chop marks on the distal radius of the same specimen in B.

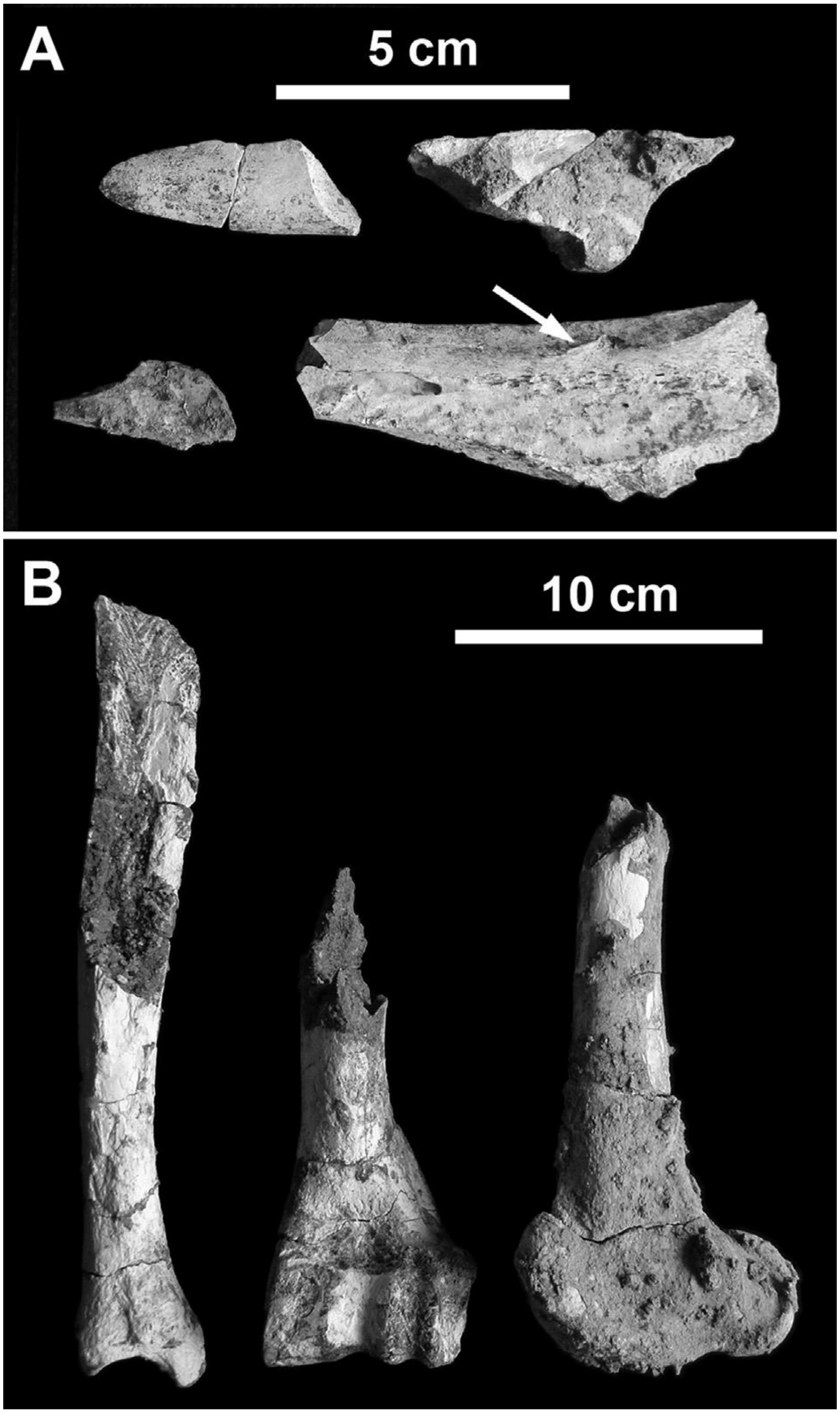

Figure 6.9: Examples of fresh breaks: A. Long bone shaft fragments with V-shaped and curved outlines and high-angled fractures; white arrow indicates notch. B. Long bone shafts with sharp V-shaped and curved outlines.

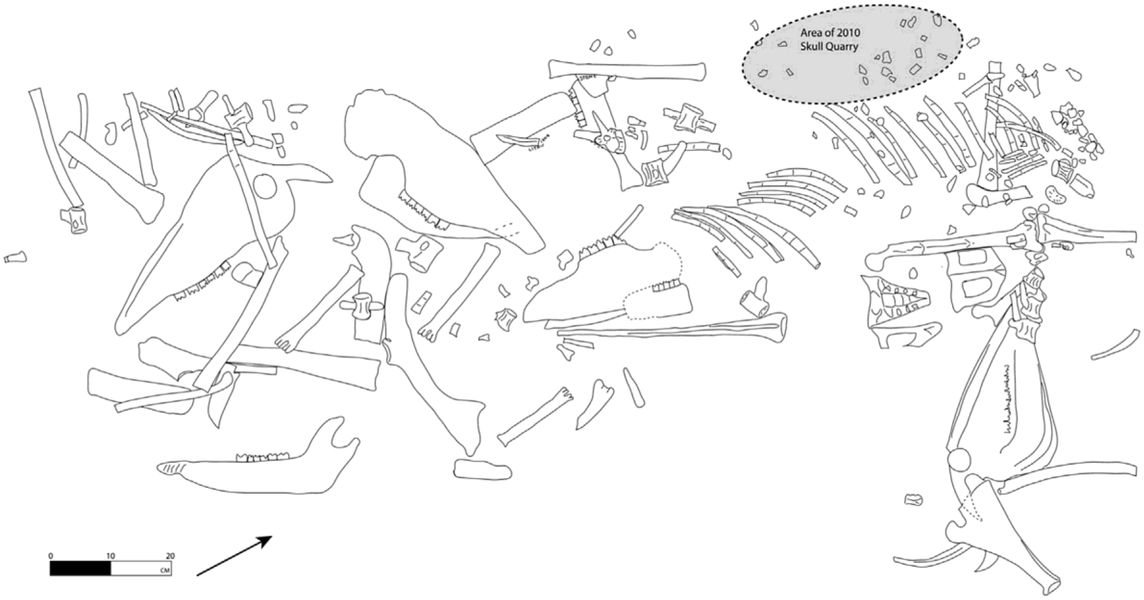

Figure 6.10: Sketch map from Grid 3. A partially articulated juvenile was recovered from the northern part of the grid. Grayed area shows rescue excavations from 2010. Black arrow indicates North.

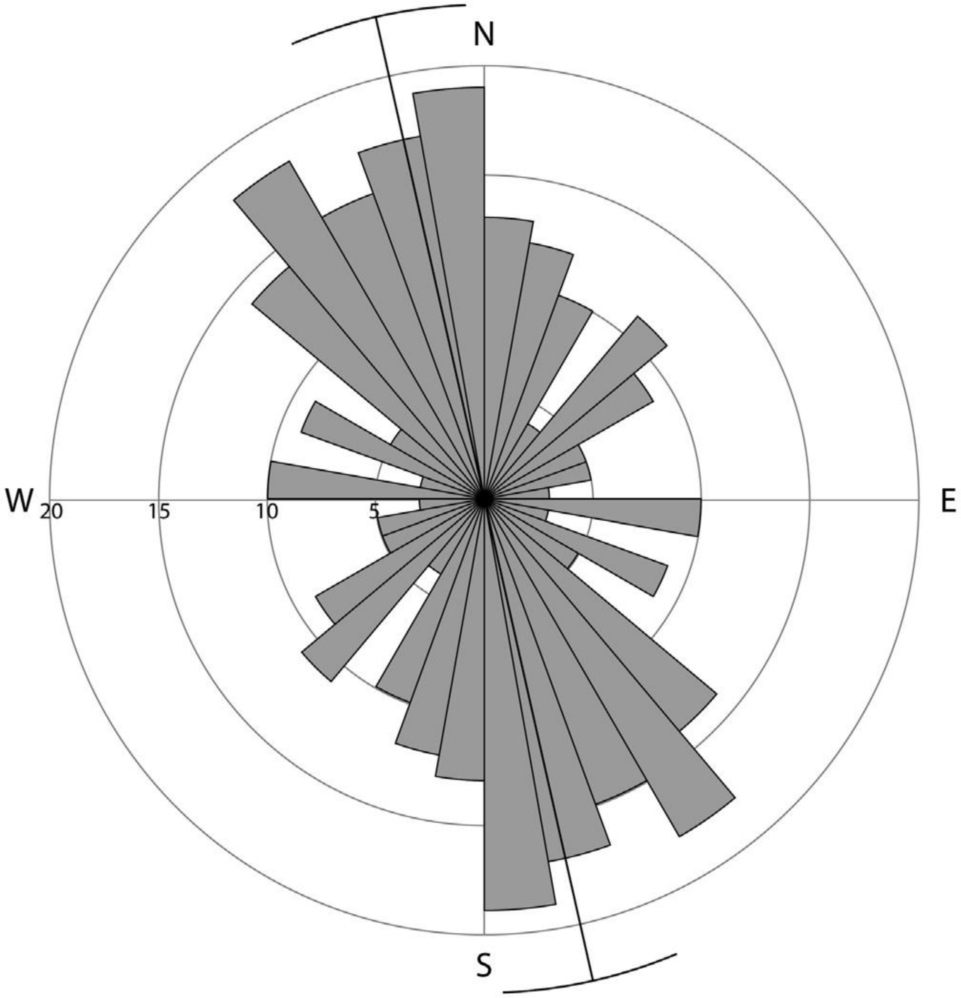

Figure 6.11: Mirror image rose diagram showing anisotropic preferred bone orientations from Grids 1 and 3: NNE/SSW (Rayleigh's R = 0.28, $p < 0.05$; Rao's U = 158.2, $p < 0.05$; Watson's U2 = 2.39, $p < 0.05$).

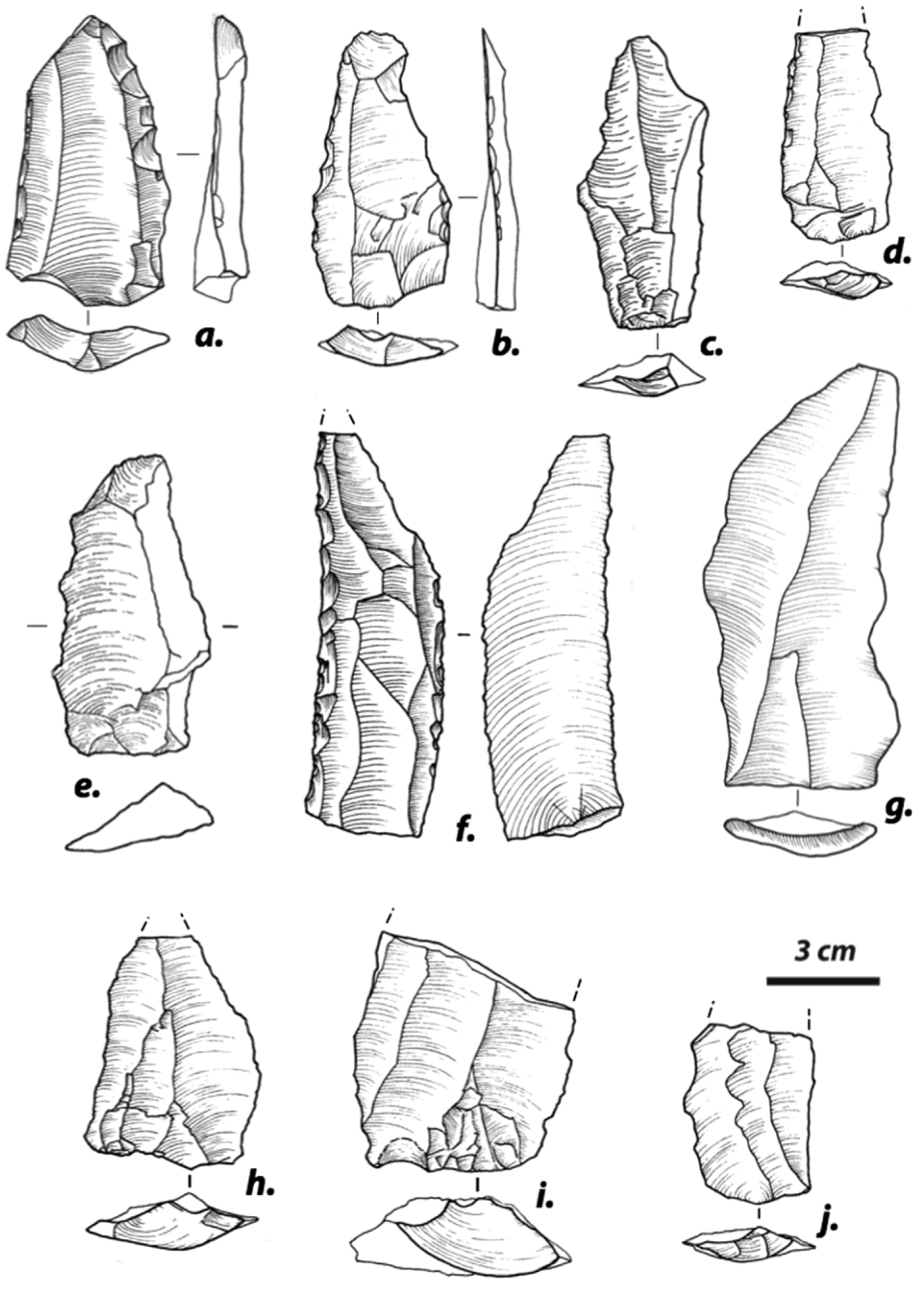

Figure 6.12: Retouched and modified lava blades and blade fragments from the Bovid Hill assemblage. Artifacts a, b, d, e, f, h, j were recovered in situ. Artifacts c, g, and i were recovered during surface surveys.

CHAPTER 7 CONCLUSIONS

This dissertation examines paleoanthropological research questions across Miocene and Pleistocene of Rusinga Island using the application of taphonomic methods with detailed and precise field collection. Research in Chapter 2 provide context for paleoenvironment, paleohabitat, and paleo-community reconstructions at arguably Rusinga's most important Miocene site despite a long history of unprovenienced surface collections and discordant paleoenvironmental reconstructions. Chapter 4 shows the utility of examining taphonomic trends from a single taxon across sites, rather than a site based approach to assess predation trends. Chapter 6 reports on a Pleistocene bonebed that yields evidence of sophisticated hunting behaviors during a time period of critical behavioral evolution in our species.

A sometimes-unpopular view (see Lucas, 2001; Roosevelt et al., 2015) is that excavation and fossil collection is the destruction of a site (Wheeler, 1954). Unlike testing in most sciences, paleontological and archaeological collection cannot be repeated at the same site. During my field collections, my aim was to collect as much contextual and taphonomic data as possible, even if the application of that data was not immediately clear; such data may be important in the future for research questions yet unknown. While detailed work is more time consuming, expensive, and (to some) even dull, thorough documentation is the scientifically and ethically responsible thing to do at paleontological and archaeological sites alike.

In the same vein, taphonomy as a discipline within paleoanthropology is often met with pessimism—taphonomists must readily acknowledge equifinality in their interpretations and need to address collection and preservation biases in their work. However, informed taxonomy, ecomorphology, and behavioral and paleoenvironmental reconstructions rest on taphonomic reconstructions grounded in actualistic studies and many types of fossil data. Taphonomy is a step that is often skipped. Similarly, reconstructing fossil site formation is sometimes lumped in the domain of geologists. However, this approach assumes that fossils accumulate as sediments did (a hypothesis that requires independent testing) and ignores the biogenic processes of fossil organisms. Fossils assemblages can and do accumulate independently of sedimentation processes and may not reflect the time scales evident from sedimentation. The strongest taphonomic interpretations are those that employ a multitude of analyses from data collected in the field and in the laboratory; examinations of skeletal part frequencies, surface modifications, breakage patterns, mortality profiles, spatial patterns, and geologic association. For these reasons, taphonomy and field collection go hand in hand.

In each of these three projects, conditions for assessing site formation processes were sub-ideal. Deposits at R5-Kaswanga have a history of collection “baggage”. Some collections were done very diligently and lend themselves to taphonomic assessment quite nicely, while older collections lacked any detailed provenience and little is known about collection biases. Yet, fossils discovered during those older collections are those that paleoanthropologists are in fact interested in. To combat the shortcomings of these data, I approached the site as if it were newly discovered--sampling strata for *in situ* remains with archaeological-style excavations, proveniencing surface collections with limited sampling bias, and digging new geologic sections. When this new assessment of the site was put together using taphonomic data collected from new excavations and surface collections, older work is more readily put into a broader site context. With this approach, I am able to show that R5-Kaswanga may have been a longstanding riparian environment and that faunal differences across strata may be more taphonomically-influenced than ecologically. The results of this new work urge caution against a long held view that R5-Kaswanga records faunal community and paleoenvironmental changes over time (Andrews and Van Couvering, 1975).

Ideally, if one were to assess trends in predation, associated assemblages would be best for identifying predatory agents. An assemblage level analysis allows for comparisons of skeletal part frequencies, breakage patterns, mortality profiles, and faunal size classes. However, in the Chapter 4, much of the surveyed primate material from Rusinga lacks both an associated provenience and associated specimens. Recent advances in the analysis of surface modification (i.e. more actualistic samples and detailed descriptions of the mark interiors, including this paper) make this key piece of taphonomic data extremely valuable for reconstructing biogenic agents in site formation processes. Using surface modifications alone, I was able to examine trends in predation across the different primate taxa around Rusinga, regardless of site. Despite the lack of contextual information about much of the historic primate collections, surface modifications on the specimens themselves reveal new insights on the Rusinga's Miocene predatory guild. Using actualistic material of raptor predated monkeys, I was able to identify avian raptor damage and carnivore/creodont damage on Rusinga's Miocene primate specimens. Carnivore/creodont damage was found *on E. heseloni*, *E. nyanzae*, and *D. macinnesi.* Unexpectedly, raptor damage was found on the larger *E. nyanzae*, as well as *E. heseloni* and *D. macinnesi.* It is possible that this difference in presumed predatory agents reflects varied preferred substrates, activity budgets, or sociality between the two primate genera. The survey of predation damage on the primate material on Rusinga is the first of it's kind for a fossil primate assemblage.

While surface modifications are often the "smoking gun" of biogenic taphonomic agents, they are also the most fragile of taphonomic data. At Wakondo, surface modifications were exceedingly rare due to extensive concretions and sediments cemented to bone surfaces. A fluvial context at Bovid Hill seemed further damning to taphonomic reconstructions as streams and rivers are known to winnow away important smaller or less dense artifacts and bone from a site and to hinder the identification of surface modifications by eroding their unique morphologies. However, these taphonomic data disasters helped illustrate the important context of the stream itself. At Bovid Hill, skeletal part frequencies suggest a density mediated (or winnowed) site suggesting that the bones were deposited in an active fluvial environment. Bone orientation patterns showed anisotropic directionality, likely due to fluvial reorientation. The cemented sediments obscuring bone surfaces are evidence of algae mats, also forming in water, likely after carcasses were skeletonized. Independent evidence of the fluvial context from sedimentology, bone orientation patterns, and winnowing further help to temper expectations about surface modifications—they may be few and they may not exhibit usual microscope features that may be more easily eroded. Indeed, only a handful of cutmarked specimens are known from Bovid Hill. The stream is a crucial physical agent in Bovid Hill's taphonomic history, but it is also the setting for what was likely a dramatic scene. A monospecific and prime-aged death assemblage of *Rusingoryx* with associated MSA stone tools in a river likely means one of two things: (1) a scavenged mass drowning or (2) a planned tactical hunt of a herd deliberately driven into drainage where they could be more easily dispatched. Taphonomic evidence alone from Bovid Hill alone is not enough to confidently reject either of these hypotheses. However, geologic evidence that the stream was likely ephemeral and higher elevation, unlike the geographic contexts of most wildebeest drownings today, coupled with the knowledge that MSA humans employed tactical hunting elsewhere in Africa, suggest that hunting is the more reasonable hypothesis. At Bovid Hill a battery of taphonomic analyses make up for the lack of visible and fresh bone surfaces and help tell a compelling story of planned hunting by MSA humans.

When applied rigorously, taphonomy is a powerful tool that allows researchers to disband and address unsupported assumptions and produce faithful paleoenvironmental and behavioral reconstructions. In the face of sub-ideal assemblages, important information can still be wrung from sites and specimens as illustrated from work in this dissertation. Biases from previously collected sites can be rectified with additional field collection to inform site level paleoenvironmental reconstructions. Predation trends can be identified from surface modifications alone to assess potential selection pressures across taxa. When surface modifications are not preserved, additional taphonomic data can reconstruct a site and the biogenic processes that formed it. Taphonomy may be slow, laborious, and fraught with equfinality, but it is worthwhile and an important foundation for paleoenvironmental studies, behavioral reconstructions, and taxonomy.

Future work

Perhaps the only drawback to detailed taphonomic analyses is that it requires similar levels of investment to have comparable samples for regional analysis. The work presented in this dissertation is small with respect to questions about the early Miocene faunal communities and continental diversity in MSA foraging behaviors. Fortunately, taphonomic samples for other Hiwegi (R106, R1, and R3), Kulu (R4), and Wayondo (R74) sites have been collected and are under study. Preliminary analysis of R106 and R1 suggest that these sites may also have attritional fluvial contexts and be taphonomically comparable to R5. Kulu fossils at R4 appear to consist of specimens that “bloated and floated” as well as organisms caught in a catastrophic landslide (Jenkins, 2013; 2014). Furthermore, I have identified additional predation damage on other Miocene catarrhines from R.E.A.C.H.E. (Research on East African Catarrhine and Hominoid Evolution) project materials. A regional analysis of predation has the potential to examine more types of predators and assess hypotheses of competition between immigrating carnivores from Eurasia and indigenous creodonts. However, these assemblages require additional analysis before these interpretations are well supported and used in boarder regional faunal comparisons.

At Wakondo, much of the *Rusingoryx* bone bed remains. Bone with additional surface modifications and tools are likely still *in situ*. Surface distributions of material suggest the deposit is quite large and may be work further exploring.

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