Reconstructing Landscape Use Patterns Using Strontium Isotope Ratios

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RECONSTRUCTING LANDSCAPE USE PATTERNS USING STRONTIUM ISOTOPE RATIOS

by

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DISSERTATION

Submitted in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy
Anthropology

The University of New Mexico
Albuquerque, New Mexico

MAY 2018
DEDICATION

This dissertation is dedicated to my father, William Hamilton, the “original” Dr. Hamilton, for sharing his love of nature quietly, consistently, and brilliantly.
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RECONSTRUCTIONG LANDSCAPE USE PATTERNS USING STRONTIUM ISOTOPE RATIOS

By

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BA, HISTORY AND ANTHROPOLOGY (2004)
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ABSTRACT

Strontium isotope ratios derive from the age and composition of the bedrock underlying an area and are incorporated without detectable fractionation into calcium-bearing tissues (such as bone and tooth enamel) as animals eat. The isotopic composition of an animal’s tissues therefore derives from the location from which they derived the majority of their food. Strontium isotope ratios are useful for answering spatial questions about where an individual lived or moved throughout its lifetime. While researchers have frequently used this isotope system to address issue of archeological human mobility, it also holds potential to indicate dispersal and microhabitat preference in fauna. For example, because certain tissues like tooth enamel are metabolically inert after formation early in life, a comparison between the strontium isotope ratios in tooth enamel and the isotopic signature of where that animal lived as an adult should indicate the presence or absence of dispersal from their natal group at sexual maturity. Because strontium isotope ratios in riparian plant communities can be influenced by mobile surface water, animals with a preference for riparian or gallery forest microhabitat should have an isotopic signature unique from those with a preference for more xeric microhabitats in the same area.

This dissertation uses modern habitats and fauna to model the variability and predictive power of strontium isotope ratios in identifying dispersal patterns in primates and habitat preference in primate and non-primate fauna. It concludes that there are significant isotopic differences between gallery forest and xeric grassland habitats in the same area and that these differences are reflected in fauna with habitat preferences for one or the other. It also identifies the most reliable methodological approaches for identifying the philopatric and dispersing sex in primate communities. Finally, it applies this methodological recommendation to strontium isotope data from South African hominins, concluding that both *Australopithecus africanus* and *Australopithecus robustus* followed patterns of female dispersal and male philopatry while also suggesting a larger home range size for *A. africanus.*
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CHAPTER 1
INTRODUCTION

1.1 Introduction

Reconstructing the behavioral patterns of extinct hominins is an indirect science, and remains an open question in the study of human evolution. While the fossil record provides robust reconstructions of the evolution of diet, locomotion, and life history, empirical reconstructions of hominin social organization and relationships remain elusive. Certain patterns of mobility and landscape use, such as philopatric dispersal, home range size, and micro-habitat preferences, have direct consequences on the social behavior of primate species. For example, knowing the philopatric pattern of a hominid species could provide a proxy for more abstract social parameters such as rates of aggression and affiliation, social bonding, and patterns of coalition building. Micro-habitat preferences have profound implications on diet, predator avoidance strategies, group size, and range size. Previous work on behavioral reconstructions and aspects of hominin socio-ecology rely heavily on inferences from idealized behavioral models derived from chimpanzees and other primates, or assumptions based on patterns of sexual dimorphism - all highly indirect proxies.

Recently and rarely, researchers have begun to employ more direct methods of
assessment, including isotopic studies. Strontium isotope ratios vary by geological formation and have the potential to provide empirical insights into the way extinct species spatially utilized their landscapes, both how and where individuals ranged (philopatric dispersal, home range size assessment, migration routes) and in which parts, if any, of a given landscape were preferred and which were avoided.

Broadly, isotopes are different forms of the same element that differ only in the number of neutrons housed in their nucleus, and thus in their atomic weights. They are typically displayed as a ratio of the abundance of the heavier isotopic form in a substance of interest relative to the abundance of the lighter isotopic form (for example, carbon isotope ratios are $^{13}$C/$^{12}$C). Isotopic ratios of light, stable elements are common in many ecological studies (ex: carbon, oxygen, sulfur, hydrogen) and various geochemical and physiological processes alter the relative abundances in predictable ways.

Strontium isotopes ratios are the relative abundance of strontium-87 to strontium-86 ($^{87}$Sr/$^{86}$Sr) and are formed when radioactive rubidium-87 decays into radiogenic strontium-87 in bedrock. The strontium isotope ratios found within a given geologic area is therefore primarily a product of the age of the rock (how long has the rubidium had to decay into strontium?) and how much rubidium and strontium there is in that particular type of rock. Strontium isotope ratios do not fractionate as they move through food webs as the more commonly utilized lighter isotope systems do. Rather, they remain constant from plants through each level of consumer. Plants take up strontium in the same way as
they take up calcium due to their similar ionic radius, although the strontium isotope ratios between bulk bedrock, soil, and plants can vary because plants will only take up the labile, biologically available strontium within the substrate. Plants are therefore an excellent proxy for the biologically available strontium isotope ratios for animals living on a given geologic substrate.

In theory, therefore, strontium isotope ratios in faunal tissues should vary purely as a product of where they range during life. However, the literature suffers from a lack of modern studies to serve as models for this theory when applying it to fossil fauna. Modern studies are necessary to assess the reliability of strontium isotope ratios as a proxy for dispersal patterns or microhabitat preferences, and therefore proxies for social behavior. This work endeavors to fill this gap.

1.2 Strontium Isotope Geochemistry Background

Strontium is an alkaline earth metal with an ionic radius very similar to that of calcium. Therefore, it substitutes for calcium in many substances, from minerals in bedrock to bone and enamel apatite in skeletons. There are four major isotopes of strontium, three of which are non-radiogenic and one (\(^{87}\)Sr) which is stable and radiogenic. \(^{87}\)Sr forms as radioactive rubidium decays over time; ratios of radiogenic to common non-radiogenic \(^{86}\)Sr (\(^{87/86}\)Sr ratios) vary in accordance with the bedrock age.
Older rocks, having more time for rubidium to decay into \(^{87}\text{Sr}\), will have higher \(^{87}/^{86}\text{Sr}\) ratios, while younger bedrocks will have lower ratios (Capo et al 1998).

In addition to age, the original quantities of rubidium and strontium in bedrock will influence the observed \(^{87}/^{86}\text{Sr}\) ratio. Igneous basalt lavas, sedimentary limestones, and metamorphic marbles, generally have a higher concentration of \(^{86}\text{Sr}\) (500 ppm) and a lower Rb/Sr ratio (0.07) when compared to granites (100 ppm \(^{86}\text{Sr}\), Rb/Sr = 2) or shales (300 ppm \(^{86}\text{Sr}\), Rb/Sr = 0.05). Limestone, in particular, can have strontium concentrations up to 1000 ppm (Kulp et al 1952) and weathers easier than many other rock types, therefore contributing substantially to water and soil strontium isotope ratios. This lower original ratio of elements will lead to a lower \(^{87}/^{86}\text{Sr}\) ratio as the rubidium decays into \(^{87}\text{Sr}\) over time (Bentley 2006), and thus metamorphic rocks generally have lower \(^{87}/^{86}\text{Sr}\) ratios while sandstones, shales, and granites have higher ratios (Beard and Johnson 2000).

Due to these factors, radiogenic strontium isotope ratios are unique across different geologic bedrock zones, and can be used in spatial, sourcing, and mobility studies. Additionally, radiogenic strontium isotope ratios are consistent over long stretches of evolutionary time, as the half-life of rubidium is approximately 49 billion years. Ratios observed in bedrock today are therefore reflective of the ratios in existence for many millions of years into the past (Bentley 2006).

Bedrock weathering is the primary source of strontium in soils. The
radiogenic strontium isotope ratios of soil are reflective of the most easily eroded minerals in the bedrock on which the soil is found (Bentley 2006, Beard and Johnson 2000). Plants acquire the most easily accessible or “mobile” strontium from the soil on which they grow (Beard and Johnson 2000, Montgomery et al 2009). Numerous studies (Poszwa et al 2002, Sillen et al 1998, Hodell et al 2004) have found that a plant’s \(^{87}\text{Sr}/^{86}\text{Sr}\) ratio is not statistically different from that of its soil, but is simply a less variable, more consistent average of the bulk soil or bedrock ratio. This averaging effect is known as biopurification (Elias et al 1982). Other studies have found non-patterned and significant variation between plants and their associated soils (Hodell et al 2004), perhaps due to differential weathering of minerals with varying radiogenic strontium isotope ratios or groundwater effects. For studies concerning animals, these discrimination and averaging processes in plants are actually an advantage. Because of the averaging effect of biopurification and the fact that plants are representative of only the mobile strontium in soils, plants are considered a more accurate proxy than bulk soil or bedrock for the strontium that could potentially be consumed by animals living on that substrate (referred to as the biologically available strontium) (Bentley 2006, Capo et al 1998, Sillen et al 1998).

There is minimal to no fractionation as strontium flows through a food chain from plant to herbivore to carnivore. Because it is a very heavy element, there is a small relative difference in mass between the two strontium isotopes. In contrast, lighter isotope
systems have large relative mass differences. The relative difference between oxygen isotopes, $^{18}\text{O}$ and $^{16}\text{O}$, is 12%. The difference between the two isotopes of strontium ($^{87}\text{Sr}$ and $^{86}\text{Sr}$) is only 1% (Banner 2004). This relative similarity in atomic weights results in minimal fractionation in natural systems. The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of an animal’s tissues share the radiogenic strontium isotope ratios of the bedrock on which it - or its prey - fed over the time period of that tissue’s formation. This lack of fractionation holds true across multiple trophic levels; an herbivore’s tooth enamel reflects the average radiogenic strontium isotope ratio from all plant and water sources on which they subsisted during the enamel’s formation (Bentley 2006).

In addition to plant material, water constitutes another potential source of strontium, particularly for obligate drinking animals (Fenner and Wright 2014). Strontium is exclusively ionic $\text{Sr}^{2+}$ in aquatic systems, is non-volatile and therefore it is not taken up by evaporative processes; therefore, rainwater generally has little to no strontium, and has a minimal effect on the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of a substrate or body of water (Banner 2004, Frei and Frei 2013). Surface water reflects the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of the most easily dissolved minerals in the bedrock it flows over. Because some minerals dissolve more easily than others, the strontium isotope ratios of flowing water will not necessarily match those of the bulk soil on the same bedrock, and may in fact blend together the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios from all the bedrock zones over which it flows (Bentley 2006, Banner 2004, Aubert 2002). For obligate drinking species, the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in the water will be a
partial contributor to tissue strontium isotope ratios, and is an essential value to measure in ecosystem-level studies.

Many studies have found that river water $^{87}\text{Sr}/^{86}\text{Sr}$ ratios are strongly correlated with the ratios of the local soil or bedrock (Hoogewerff et al 2001, Rose and Fullagar 2005, Voerkelius et al 2010). Although models based solely on bedrock age can vary unpredictably between estimated and measured values (Hobson et al 2010, Hodell et al 2004), models which account for bedrock age, lithology, and strontium concentration were shown to be highly predictive of water $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (Chesson et al 2012, Bataille and Bowen 2012, Rose and Fullagar 2005). The accuracy of bedrock approximations may vary by topographic relief, with areas of low relief showing a higher correlation between bedrock and river $^{87}\text{Sr}/^{86}\text{Sr}$ ratios while areas of steep relief show a weaker correlation due to more extreme erosional and weathering processes (Montgomery et al 2009). Some studies (ex: Aubert et al 2002) have found that higher weathering rates and increased flow rates also increase $^{87}\text{Sr}/^{86}\text{Sr}$ ratios. Other research (Rose and Fullagar 2005) has found no correlation between increased precipitation or flow rates and changes in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios. Hegg and colleagues (2013) provide a predictive model for geological variation based on bedrock and lithology, specifically using the percentage of mafic and metamorphic rocks in the area of interest. They demonstrated, unsurprisingly, that increasing geologic heterogeneity increases the likelihood of high variability in radiogenic strontium isotope ratios (Hegg et al 2013).
Careful assessment of the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in local water sources and the effect of flowing surface waters on riparian vegetation is a critical contribution to any fauna provenance study. In South Africa, Sillen and colleagues (1998) found major influences of upstream erosional processes and differential mineral dissolution on downstream river water strontium isotope values, creating a significant difference in the strontium isotope values on the same bedrock substrate. The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in plants in the riparian zone of the Blaaubank stream more closely reflected the dissolved minerals of the local dolomite geology, while plants farther away from the water more closely approximated the bulk soil $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (Sillen et al 1998). This is in agreement with the conclusion in Montgomery et al (2009) that plants are reflective of the average $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in their entire catchment area. This illustrates that plants, acting as averaging agents for biologically available strontium, are the most accurate proxies for expected $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in animals foraging on a given substrate, and highlights the importance of thorough and strategic sampling procedures.

In animals, strontium can substitute for calcium and concentrates in skeletal elements (Beard and Johnson 2000). The expected $^{87}\text{Sr}/^{86}\text{Sr}$ ratios for any calcium-bearing tissue in an animal can be thought of as a concentration-dependent mixing model of all dietary and drinking water sources (Bentley 2006). The higher the concentration of calcium in a food source, the more that source will contribute to the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of an animal’s tissues (Fenner and Wright 2014, Burton and Wright 1995). Plant foods are
more likely to contribution to the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in a consumer than meat products, as plants have higher concentrations of strontium/calcium than the most commonly consumed muscle tissues of prey animals (Burton and Price 1999, Montgomery 2010, Haverkort et al 2008).

Radiogenic strontium isotope ratios can be assayed from any calcium-bearing substance in an organism’s body. Most commonly, bone apatite, tooth enamel, and dentine are sampled. Each has its own benefits and pitfalls. For fossil specimens, bone and dentine are particularly susceptible to diagenesis (Budd et al 2000), but if unaltered, can show an averaged signature over the last few years or decades of an animal’s life, as they stay constantly metabolically active (Lee-Thorp and Sponheimer 2003, Price et al 2002). Enamel is less susceptible to diagenesis due to its high density and low porosity (Lee-Thorp and Sponheimer 2003, Kohn et al 1999, Bocherens et al 1994). Enamel is entirely laid down before sexual maturity and does not remodel or exchange chemically with the body after formation (Montgomery 2010), which is completed prior to sexual maturity in primates (Smith et al 1994). Enamel thus provides a locational dietary signal of the individual as a juvenile which can provide a unique perspective on migration and movement over the course of a lifetime when compared with other samples from the same social group (Copeland et al 2011).

Hair, although less commonly sampled, can also be assayed for radiogenic strontium isotope ratios (Tipple 2013). Like tooth enamel, it is metabolically
inert. However, because it is continually growing and being lost, the $^{87}$Sr/$^{86}$Sr ratio in hair reflects the foraging behavior of the last few days (at the proximal point closest to the follicle) to the last few months or years (at the distal end of the hair). $^{87}$Sr/$^{86}$Sr ratios in bone and hair reflect the area on which an animal has been foraging much more recently than the $^{87}$Sr/$^{86}$Sr ratios in enamel. Unfortunately, hair is not available for most fossil species.

1.3 Research Goals

The overarching goal of this research is to provide a model for strontium isotope variation as it relates to philopatric dispersal and microhabitat preference in modern primate ecosystems in order to draw more informed conclusions about similar data in fossil contexts. This goal subdivides into four central aims:

1. This research will establish the most biologically meaningful method of quantifying strontium isotope variation in a landscape. These methods are particularly relevant in areas where the geology is unknown or where factors such as heavy erosion, windblown aeolian dust, heavy sea spray, and other environmental factors might make pure geologic boundaries unreliable indicators of isotopic clusters locations.

We will rely on statistical tools including cluster analysis and Bayesian modeling to
quantify isotopic variation across a landscape.

2. This research will use modern habitats to determine if strontium isotope ratios can be used reliably to differentiate between riparian and non-riparian habitat preferences. It will assess this at both the environmental level and at the faunal level, and then investigate whether patterns found in modern ecosystems can explain strontium isotope variance observed in fossil assemblages.

3. This research will identify the most accurate approach for using strontium isotope ratios to identify a taxa’s philopatric dispersal pattern. This is important because strontium isotope literature traditionally relies on one method only, in which individuals are classified as “migrants” or “locals” based on whether or not their tissue’s isotopic ratio falls within the ratios designated as “local” indicators. This research will compare the accuracy and robustness of this traditional proxy methods with three novel proxies, each relying on calculating an offset between an individual’s tooth strontium isotope ratio and either 1) their bone’s isotopic ratio, 2) their environment’s isotope ratio, or 3) the median isotope ratio of local fauna. These more quantitative approaches will allow for more extensive statistical comparisons between dispersing and philopatric groups.

4. This research will use the best-practice approaches identified in Kibale National Park to analyze strontium isotope ratios from South African hominid fauna, identify the most likely philopatric dispersal patterns for those taxa, and interpret
the behavioral implications of the identified landscape use patterns.

1.4 Background: Kibale National Park and Toro-Semliki Wildlife Refuge

Figure 1.1: Map of Toro-Semliki Wildlife Refuge (from Hunt and McGrew 2002)
<table>
<thead>
<tr>
<th>Species (Scientific Name)</th>
<th>Species (Common Name)</th>
<th>Specimen locations</th>
<th>Philopatric pattern</th>
<th>Home Range</th>
<th>Diet</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pan troglodytes</em></td>
<td>Common chimpanzee</td>
<td>KCP, SCP</td>
<td>Male philopatry, female dispersal (^{(1)})</td>
<td>Home range 5-27 km(^{12,3})</td>
<td>Frugivores (^{(9)})</td>
</tr>
<tr>
<td><em>Colobus guereza</em></td>
<td>Black and White colobus monkey</td>
<td>KCP</td>
<td>Female-biased philopatry, male-biased dispersal (^{(1)})</td>
<td>0.12 - 0.28 m(^{10})</td>
<td>Folivore (^{(8)})</td>
</tr>
<tr>
<td><em>Cercopithecus mitis</em></td>
<td>Blue monkey</td>
<td>KCP, SCP</td>
<td>Female philopatry, male dispersal (^{(1)})</td>
<td>~0.5 - 3.3 m(^{10})</td>
<td>Folivore (^{(11)})</td>
</tr>
<tr>
<td><em>Papio anubis</em></td>
<td>Olive baboon</td>
<td>KCP, SCP</td>
<td>Female philopatry, male dispersal (^{(1)})</td>
<td>~5 m(^{10})</td>
<td>Frugivore, omnivore (^{(14)})</td>
</tr>
<tr>
<td><em>Procolobus badius</em></td>
<td>Red colobus</td>
<td>KCP</td>
<td>Male philopatry, Female dispersal (^{(15)})</td>
<td>~0.65 m(^{10})</td>
<td>Folivore (^{(15)})</td>
</tr>
<tr>
<td><em>Cercopithecus ascanius</em></td>
<td>Redtail monkey</td>
<td>KCP, SCP</td>
<td>Female philopatry, male dispersal (^{(16)})</td>
<td>0.28 - 0.68 km(^{10})</td>
<td>Frugivore (^{(20)})</td>
</tr>
<tr>
<td><em>Tragelaphus scriptus</em></td>
<td>Bushbuck</td>
<td>KCP, MUBFS, SCP</td>
<td>Female philopatry, male dispersal (^{(21)})</td>
<td>0.3 m(^3) (m) and 0.13 m(^3) (f) (^{(22)})</td>
<td>Browser (^{(25)})</td>
</tr>
<tr>
<td><em>Cephalophus natalensis</em></td>
<td>Red duiker</td>
<td>KCP, MUBFS</td>
<td>Bisexual (^{(24)})</td>
<td>0.055 m(^3) - 0.24 m(^{10})</td>
<td>Browser, some fruit (^{(26)})</td>
</tr>
<tr>
<td><em>Kobus kob thomasi</em></td>
<td>Kob</td>
<td>SCP</td>
<td>Female philopatry, male dispersal (^{(27)})</td>
<td>Can travel 10-100 km to waterholes (^{(20)})</td>
<td>Grazer (^{(29)})</td>
</tr>
<tr>
<td><em>Tragelaphus spekii</em></td>
<td>Sitatunga</td>
<td>KCP, MUBFS</td>
<td>Bisexual dispersal (^{(28)})</td>
<td>Small, within wetlands and up to 100m away (^{(13,23)})</td>
<td>Aquatic browser (^{(30)})</td>
</tr>
<tr>
<td><em>Kobus ellipsiprymnus</em></td>
<td>Waterbuck</td>
<td>SCP</td>
<td>Female philopatry, male dispersal (^{(29)})</td>
<td>Up to 6 m(^3) female and 1.5 m(^3) for males (^{(30)})</td>
<td>Grazer (^{(34)})</td>
</tr>
<tr>
<td><em>Loxodonta spp</em></td>
<td>Elephant</td>
<td>KCP, MUBFS, SCP</td>
<td>Female philopatry, male dispersal (^{(31)})</td>
<td>Highly variable, over 100 km(^{20})</td>
<td>Fruits, leaves, bark; wide generalist (^{(39)})</td>
</tr>
<tr>
<td><em>Syncerus caffer</em></td>
<td>Forest buffalo</td>
<td>KCP, SCP</td>
<td>Bisexual; female-biased philopatry and male-biased dispersal (^{(32)})</td>
<td>126 - 1,075 km(^{10}) Up to 10 km(^{10})</td>
<td>Grazers (^{(32)})</td>
</tr>
<tr>
<td><em>Hylochoerus meinertzhageni</em></td>
<td>Giant forest hog</td>
<td>KCP</td>
<td>Bisexual (^{(33)})</td>
<td>3-10 km(^{10})</td>
<td>Foliage browse, &lt; 25% grass (^{(40)})</td>
</tr>
<tr>
<td>Species</td>
<td>Common Name</td>
<td>KCP</td>
<td>Female philopatry, male dispersal</td>
<td>Area (km²)</td>
<td>Diet</td>
</tr>
<tr>
<td>---------------------------------</td>
<td>----------------------</td>
<td>-----</td>
<td>-----------------------------------</td>
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<td>-----------------------</td>
</tr>
<tr>
<td><em>Potamochoerus porcus</em></td>
<td>Red river hog/bushpig</td>
<td>KCP</td>
<td></td>
<td>3 - 6</td>
<td>Omnivorous, generalist</td>
</tr>
<tr>
<td><em>Phacochoerus africanus</em></td>
<td>Warthog</td>
<td>KCP, SCP</td>
<td>Bisexual, some male biased dispersal</td>
<td>0.6 - 3.75</td>
<td>Grazers</td>
</tr>
<tr>
<td><em>Ichneumia albicauda</em></td>
<td>Mongoose</td>
<td>SCP</td>
<td>Bisexual dispersal, some female-biased philopatry</td>
<td>1 - 1.5</td>
<td>Carnivore, insectivore</td>
</tr>
<tr>
<td><em>Hippopotamus amphibius</em></td>
<td>Hippopotamus</td>
<td>MUBFS</td>
<td>Female philopatry and male dispersal</td>
<td>5</td>
<td>Grazer (terrestrial)</td>
</tr>
</tbody>
</table>

All samples were collected from the Toro-Semliki National Wildlife Refuge and the Kibale National Park, both located in southwestern Uganda, over two field seasons (July 2014 and July 2015). Both locations are protected habitats home to a wide variety of primate and non-primate species (see Table 1.1 for full species list and ecological details).
Toro-Semligi Wildlife Reserve is in the Albertine Rift, on the western edge of the Great Rift Valley. The Ruwenzori Mountains surround the reserve. Large escarpments reaching up to 1900 meters above sea level (most of the Reserve is around 800 meters above sea level) form the eastern borderer (Verner and Jenik, 1984) (see map in Figure 1.1).

Toro-Semligi is a mosaic habitat of forest, wooded grassland, and open grasslands (Langdale-Brown et al 1964). It has two major rivers, the Wasa and the Mugiri. The Wasa River flows north and feeds into Lake Albert; the Mugiri River ends in a swamp called the Jogo Jogo, perennially waterlogged and dominated by papyrus. Dozens of tributaries feed both rivers. To either side of the rivers and tributaries is dense gallery forest with canopies 30-50 meters tall, stretching between 50 and 200 meters from the edge of the water. These forests are dominated by Ugandan ironwood, *Millettia dura*, and *Kigelia africana* with abundant *Beilschmiedia ugandensis* dominating the understory (Allan et al. 1996, Hunt and McGrew 2002, Hunt personal communication). The wooded grassland is primarily *Acacia* and *Tamarindus indica*. The open grassland is dominated by *Themeda* and *Chloris* spp. grasses (Verner & Jenik 1984, Allan et al. 1996).

The Toro-Semligi Wildlife Reserve sits on top of undifferentiated Cenozoic sedimentary alluvium. The tops of the eastern escarpments transition to the Toro formation, comprising acid and basic gneiss and dating to the lower Paleoproterozoic. Many of the tributaries flowing into the Mugiri River originate on this older geologic
region, while the entirety of the Mugiri itself flows over the younger alluvium (Westerhoff et al 2014) (Figure 1.2).

Kibale National Park is located 10 kilometers due south of the Toro-Semliki Wildlife Refuge and is a 795-square kilometer protected tropical-climate rainforest. The vegetation is evergreen in the north shifting to moist deciduous forest in the south as the elevation decreases. Some areas of the forest are secondary growth recovering from logging efforts pre-dating the park’s protection. There are small open grassland patches in these areas, particularly in the northern portion of the park. There are four permanent
chimpanzee research sites within Kibale National Park: The Sebitole Chimpanzee Project in the far north, the Kanyawara Chimpanzee Project to the south of Sebitole, the Ngogo Chimpanzee Project, and the Kanyanchu Chimpanzee Project to the south. Ngogo and Kanyanchu Chimpanzee Project areas are within primary, unlogged forest areas (see map in Figure 1.3).

There are numerous small streams and some larger rivers within the park, the largest being the Dura River and the Kanyanchu River. Underlying Kibale National Park
are two major geologic zones: undifferentiated acid and basic gneisses as part of the Toro supergroup, dating to the early Paleoproterozoic (~2.5 GYA), and quartzites of the Buganda group, dating to the middle Paleoproterozoic (~2 GYA) (Westerhof et al 2014) (Figure 1.4).

1.5 Structure of the Dissertation

*Chapter 2* investigates whether strontium isotope ratios can be used to differentiate between riparian and non-riparian microhabitats by using the Toro-Semliki National Wildlife Refuge in southern Uganda. This area is primarily grassland-savanna with a few very large rivers hosting riparian rainforest habitat within a few hundred meters of its banks. This chapter explores the dietary and behavioral implications of riparian habitat preference in hominids, details the sampling technique used to assess environmental differences, and uses an opportunistically gathered skeletal collection of a wide variety of fauna to determine if differences in the environments are reflected in fauna with preferences for those habitats.

*Chapter 3* tests a series of hypotheses connecting strontium isotope ratios in faunal tissues to dispersal patterns using samples from an opportunistically gathered skeletal collection of fauna from Kibale National Park, Uganda. This chapter analyses how philopatric dispersal patterns relate to behavioral evolution in primates and a history of how behavioral reconstructions have been approached in the past. It outlines the sampling protocol necessary to compare Kibale National Park fauna to the local environment and then tests the correlation between known philopatric patterns of Kibale primates and four different strontium isotope proxies for dispersal: 1) the ‘traditional’
approach, determining migrant versus local individuals by comparing strontium isotope ratios in teeth and the boundaries of local plants; 2) comparing the offsets in males versus females between an individual’s tooth strontium isotope ratio and that of a high-turnover bone; 3) comparing the offset in males versus females between an individual’s tooth strontium isotope ratio and the local environment; and 4) comparing the offset in males versus females between an individual’s tooth strontium isotope ratio and the median isotopic ratio of that taxa. It explores the influence of range size on modeling efficacy and makes recommendations for applying these proxies to the fossil record.

Chapter 4 uses the recommendations from Chapter 3 as a model to analyze strontium isotope ratios from Sterkfontein and Swartkrans caves in the Cradle of Humankind, South Africa. This chapter first reviews the stratigraphic and geologic context of the fossils from this area and the implications for biologically available strontium isotope ratios during the roughly 2 million years ago time period that the included hominids lived on this landscape. It then uses environmental data from plants within the vicinity of the caves to draw new isotopic clusters on the landscape which more meaningfully capture the variation present in this highly active region, and finally hypotheses philopatric patterns for *Australopithecus robustus* and *A. africanus* based on the results.

Chapter 5 summarizes and concludes this work, makes recommendations for future studies, and assess the overall potential of strontium isotope ratios to explore
behavior of hominid behavior and landscape use.
CHAPTER 2
RIPARIAN HABITATS AND STRONTIUM ISOTOPES

2.1 Introduction

Climatic changes during the terminal Pliocene and into the early Pleistocene created more highly variable, colder, and drier environments. These changes led to the recession of vast swaths of rainforest that once covered central latitudes of the African continent, opening new woodland, grassy woodland, and grassland savanna habitats (Cerling et al 1988, Cerling 1992, Bobe and Behrensmeyer 2004, Levin et al 2004 and 2011, Wynn 2004, Fernandez and Vrba 2006, Quinn et al 2007, Bobe and Leakey 2009, deMenocal 2004). This division of habitats drove our ancestors apart from those of modern chimpanzees and bonobos; many point to evolution on the open grassland as a driving force behind making us uniquely human (Broom 1938, Dart 1925, Jolly 1978 and 1970, Brain 1981, Vrba 1995, Potts 1998, Teaford and Ungar 2000, Wheeler 1994, Richmond et al 2001, Pickering and Bunn 2007). However, subsisting in an open, drier environment as a large bodied, large brained hominin would not have been easy. Without tropical rainforests, hominins no longer had access to the plethora of fruiting trees and piths comprising the diets of modern chimpanzees. How would hominins, lacking in claws, large canines, or speed, defend themselves from savanna predators? One possibility is that rather than the open grasslands themselves, hominins favored riparian or gallery forests growing along rivers and streams. The purpose of this investigation is to determine the potential for strontium isotope ratios ($^{87}\text{Sr}/^{86}\text{Sr}$) to differentiate between
riparian and non-riparian habitat preference in a modern gallery forest environment, the Toro-Semliki National Wildlife Refuge in southwestern Uganda.

Many reconstructions of hominin paleoecology describe ancestral habitats as “mosaics” (Reynolds et al 2015). While this designation is a point of frustration for many, the “noisy” data pointing to multiple plausible habitat reconstructions could be a true signal of an extremely heterogeneous landscape. Some suggest that hominins utilized all microhabitats, and this habitat flexibility was critical to the survival and evolution of the human lineage (Wood and Strait 2004, Wells 2012, Potts 2012, Wynn 2004), while others argue that some species preferred certain microhabitats within the larger ecosystem. Specifically, researchers suggest that riverine forests (Behrensmeyer 1975, 1978, 1982), river deltas (Wrangham 2005), stream channel margins (Isaac 1966, 1978, Sept 1986), or gallery forests (Marean 1989, Blumenschine 1986, Blumenschine et al 1987, Cavallo and Blumenschine 1989) were particularly attractive to hominins.

Modern chimpanzees are generally regarded as being rainforest-adapted, but some populations live in areas that, if reconstructed by geologists millennia from now, would likely appear to be grassland-woodland-forest mosaics. These chimpanzees have a reputation as being “savanna chimpanzees,” living in such areas as in Fongoli and Mount Assirik, Senegal or Semliki, Uganda where temperatures are high (mean daily maxima at Mount Assirik is 35 degrees Celsius and 34 degrees Celsius at Semliki), rainfall is low (annual precipitation is 954 mm at Mount Assirik and 1204 mm at Semliki), and closed forested areas make up a very small percentage of the available habitat (Mount Assirik, 3 %; Fongoli 4 %) (McGrew et al 1981, Pruetz 2006, Bogart and Pruetz 2011, Hunt and McGrew 2002). However, the chimpanzees living in these open habits have a strong
preference for the gallery forest or riparian microhabitats, despite their small proportional abundance overall. For example, in Fongoli, gallery forest microhabitats contain the greatest density of chimpanzee feeding plants; chimpanzees unsurprisingly rely on them disproportionately for food and shelter (Pruetz 2006, Bogart and Pruetz 2008, Bogart and Pruetz 2011). Home ranges at these sites far exceed those in wetter rainforest chimpanzee habitats (50 km² at Semliki compared to a maximum of 14 km² at Mahale and 24 km² at Gombe (Hunt and McGrew 2002, Goodall 1983, Hasegawa & Hiraiwa-Hasegawa 1983)) in large part because the chimpanzees limit “most of their behavior to gallery forests” (Hunt and McGrew 2002, pg 47). The chimpanzees often get agitated and nervous when forced to move through open areas without tree cover; this is visibly not their preference (Hunt, personal communication).

In addition to food resources, gallery forests help chimpanzees with thermoregulation, as they have lower maximum temperatures than the surrounding savanna and are more heavily relied on in the hotter dry season than the more sheltered, cooler wet season (Baldwin et al 1982, McGrew et al 1981). They also provide access to water, occasionally in the form of dug wells near standing surface water (Hunt et al 1999, Nishida et al 1999, Galat-Luong and Galat 2000).

As most reconstructions of early hominin sites include some degree of forested cover, and many include a riverine or gallery forest component similar to those seen in modern chimpanzee habitats, many of these same benefits would be applicable. Access to water, shade and thermoregulation (Quinn et al 2013, Cerling et al 2011, Wheeler 1994), predator refuge, raw stone materials (Sikes 1996, Braun et al 2008), and high-quality food resources are all potential benefits to hominins with a preference for riparian
microhabitats. Woody C3 plants such as nuts, fruits, flowers, and beans are rare in savanna habitats but prolific in riparian or riverine systems, and they are both nutritionally dense and low in toxicity (Peters et al 1981, Peters et al 1984, Sept 1986, 1990). In modern chimpanzee gallery forest habitats, the gallery forest contains fruiting trees and other preferred foods while such items are absent from the surrounding savanna grassland (Hunt and McGrew 2002). Aquatic resources, including fish, would also be more abundant in riparian zones (Stewart 1994, Braun et al 2010), as would aquatic underground storage units (USOs) (Vincent 1985, Sept 1985). Modern baboons rely on dry-habitat USOs as fallback foods in areas where they are prevalent today (Wrangham 2005, Wrangham et al 2009). USOs are a commonly consumed food group for hunter-gatherer groups today (Marlowe and Berbesque 2009, Vincent 1985), and both isotopic and dental microwear studies show patterns consistent with USO consumption in many hominin taxa (Dominy et al 2008, Ungar and Sponheimer 2011, Grine et al 2012, Ungar 2012, Laden and Wrangham 2005, Yeakel et al 2007). They are low in fiber (Conklin-Britten et al 2002, Hardy et al 2015), have high nutritional value (Laden and Wrangham 2005), and because many are located underground and require extraction, there is less competition from other animals. Models of decision-making matrices incorporating characteristics of hominin dentition (such as enamel thickness and molar breadth) and resource abundance (clumped versus diffuseness of a resource, nutritional content, difficulty of processing, etc.) show that while in times of high energy reserve or highly productive environments, fruit and other high-risk, high-reward resources are optimal, in times of low energy reserves or in harsher environments, fitness is maximized when more reliable (if harder to process) resources are preferred, such as USOs (Yeakel et al 2007).
This effect becomes even more pronounced in species with megadont dentition, as many early hominins had, as individuals become older (wearing their enamel thinner), and for smaller-bodied individuals.

Riparian forests also provided a refuge from the intense competition encountered in more open habitats. Blumenschine (1986, Blumenschine et al 1987) explain the beginnings of meat incorporation into the hominin diet by suggesting a “woodland scavenging niche,” that would have helped them out-compete other predatory scavengers, such as jackals and hyenas. Blumenschine observes that these other scavengers are rarely spotted in riparian woodland and that carcasses remain in woodland areas for longer than they do in open plains. Dominguez-Rodrigo (2001) confirms this finding, observing fifty carcasses in both open and woodland localities and finding that woodland carcasses remained for up to one to two days, while savanna carcasses were depleted within hours. Riparian habitats therefore would have provided hominins with nutritionally dense and less dispersed food supplies, including potentially easier-to-scavenge meat resources, increased protection from predators, water resources, and shade as the rainforests began to recede.

2.2 Background: Microhabitat Reconstructions

Reconstructing microhabitats, as opposed to larger landscape environments, is a difficult task. Hominin sites all suffer from a bias in preservation such that fauna from dry environments will preferentially preserve over those from wet environments (Vrba 1995), and therefore some observed patterns, such as an abundance of hominin stone tool
depositions in an area reconstructed as being open and dry, might merely be an accident of preservation (Dominguez-Rodrigo 2001). Bovid assemblages have been used to identify microhabitats within a given locality (Shipman and Harris 1988, Spencer 1997), but these assemblages can be extensively time and space averaged, as well as biased from depositional or taphonomic issues (Shipman and Harris 1988). Ancient or modern hydraulic systems can rework and redeposit material great distances across a landscape, complicating interpretations from faunal assemblages (Feibel 2011, Quinn et al 2013, Behrensmeyer and Kidwell 1985, Kidwell and Behrensmeyer 1993).

Nevertheless, faunal assemblages, isotopic data, morphological interpretations, and climatic data have all been used to reconstruct hominin habitats, and with highly variable results. A wide survey of pedogenic carbonate carbon isotope ratios from across the last 6 million years in East Africa shows a more open, less woody cover habitat dominating the landscape in the late Miocene into the Pliocene, shifting to a more mesic and wooded environment around 3.6 million year ago, and growing increasingly open again through the Pleistocene, beginning in the Turkana basin and spreading to the Omo around 1.8 million year ago (Cerling et al 2011). Despite this increasing presence of grasslands, earlier paleosol carbon isotope work suggests that hominins did not preferentially inhabit these open grasslands because they make up less than half of the values observed in hominins until 1.5 million years ago (Cerling 1992). The presence of riparian forests along axial river systems could provide a mediating explanation for these seemingly conflicting conclusions (Cerling 2011, Levin et al 2011).

ramidus, one of the earliest hominins known from a substantial fossil evidence, as a woodland environment based on isotopic and faunal assemblage data (but see Cerling 2010). Comparisons between *A. ramidus* isotopic data and modern rainforest-dwelling primates from Kibale National Park support a woodland reconstruction, more open than modern rainforest (Nelson 2013).

Reconstructions of *Australopithecus afarensis* habitats generally agree that this was a eurytopic species (White et al 1993, Reed 1997). Reed (2008) tracks changes in ecological conditions in Hadar, Ethiopia from 3.8 to 2.35 million years ago. Habitats fluctuated from medium-density woodland/shrublands to more open wooded grasslands, with periodic floodplain and lake margin transgressions, mosaic gallery forests, and wetlands. *A. afarensis* persists through these fluctuating habitats, suggesting a lack of narrow habitat preference and substantial environmental flexibility (Reed 2008, Bonnefille et al 2004, Campisano and Feibel 2008). Bedaso et al (2013) also reconstruct the habitat of *A. afarensis* in Ethiopia as highly variable, with open grassland, wooded grassland, and grassy woodlands all persisting in different proportions throughout the duration of their study (from 3.8 and 3.2 million years ago). This suggests that *A. afarensis* was either tolerant of numerous habitat types or preferred one of the habitat types which persisted through the entire time interval, such as one of the grassland variants. Ecomorphological studies of bovids from along the paleo-Omo River from 3.4 to 1.9 million years ago also show varying heterogeneous habitats, with australopithecine remains more likely to be associated with closed-cover bovids than *Homo* (Plummer et al 2015), although the effectiveness of differentiating woodland and riparian forest habitats using bovid ecomorphology alone is not clear.
Moving south, Schoeninger et al (2003) analyzed stable isotope data from Allia Bay, Kenya and concluded it was an “overall mosaic of habitats” (Schoeninger et al 2003, pg 200). In Laetoli, Tanzania, researchers place *A. afarensis* in closed woodlands (Reed 1997), deciduous and riverine forest (Andrews and Bamford 2008), or mosaic ecotonal habitats including forest and open woodlands or grassland (Harrison 2005), although due to a lack of aquatic fauna, likely not a riverine forest. While highly disparate, these data most likely indicate *A. afarensis* was a successful environmental generalist, or that its preferred food resources were accessible across a range of habitat types. It is worth noting that open secondary grasslands do not feature in this array of potential reconstructions. Given the arboreal features of much of *A. afarensis* postcrania, it is not surprising that trees feature in all reliable habitat reconstructions.

Many lines of research place *Australopithecus boisei* in closed or mesic environments (Behrensmeyer 1978, Behrensmeyer and Cook 1985, Shipman and Harris 1988, Behrensmeyer 1985), but others argue that the robust East African species preferred open, drier habitats (Boaz 1977, Vrba 1975, Grine 1981). In the Turkana Basin, Quinn et al (2013) examine five hominin-bearing localities between 2.4 mya and 1.4 mya, a time period in which grasslands spread across the basin at large. However, areas with lithic deposits retain a stronger signal of woody cover when compared to the overall basin, suggesting that the hominins living there preferred closed habitat areas for tool production. If these toolmakers were members of *Homo*, the substantial proportion of C3 in their diet suggests that this was also a preferred feeding space. If the toolmakers were the more C4-dependent *A. boisei*, it suggests a differentiation in spatial use between tool production and foraging, or that *A. boisei* preferred the C4 resources within the wooded
areas over the C3 resources likely to have been found in that same locality (Quinn et al 2013).

Evidence initially placed South African *A. robustus* in open habitats (Shipman and Harris 1988, Coppens 1980, Vrba 1975). However, other work places them in a more ambiguous “mosaic” habitat (Avery 1995, Reed 1997), and the most recent work suggests that open habitats were *avoided* by *A. robustus* in favor of more wooded areas (de Ruiter et al 2012).

Marean (1998) and Behrensmeyer (1975) place *Homo habilis* in a riverine forest or lake margin and Marean (1998) places *H. erectus* in an open, xeric habitat, while Coppens (1980) and Bonnefille (1984) place both species in an open environment. Pedogenic carbonates from Olduvai around the appearance of *H. erectus* (1.85-1.78 million years ago) suggest a wet, wooded lake margin with between 40-60% C4 plant material (Sikes and Ashley 2007). Stable carbon isotopes from Bed II at Olduvai Gorge show ratios consistent with closed riparian forests ($\delta^{13}C = -19.5$ to -24 ‰) at 1.74 million years ago along the paleo-lake margin, suggesting that this may have been a preferred habitat for hominins at that time despite increasing habitat heterogeneity (Sikes 1994).

Riparian habitats hold great ecological potential in the evolution of the human lineage. Existing data are ambiguous and in some cases contradictory. We must therefore incorporate new lines of evidence to examine the issue. Strontium isotope ratios have the potential to differentiate between mesic riparian and xeric grassland environments in areas with gallery forest microhabitats.
2.3 Background: Strontium Isotopes in Aquatic Systems

Plants take up strontium through their roots from the exchangeable pool in soils. These soil strontium pools form from numerous inputs, including weathering bedrock, atmospheric aerosols and dust, and recycled organic matter. Different climate zones will fluctuate in the proportionate contributions from these different sources; for example, in the arid American southwest, aeolian dust makes a substantial contribution (Reynolds et al 2005). Along the South African coast, sea spray contributes so much to the soil strontium pool that expectations of isotopic ratios based on geology are very unreliable (Copeland et al 2016). Plants are a good approximation of the strontium that is biologically available to fauna living in an area, because most strontium in faunal tissues derives from dietary exposure (Glorennec et al 2016).

However, in riparian systems, river water could be an additional source of variation to the exchangeable strontium pool in soils, resulting in plants with a different strontium isotope composition in riparian versus non-riparian habitats. Strontium isotope ratios in water result from the dissolved soil and minerals that compose the ground over which they flow (Bentley 2006, Banner 2004, Aubert 2002). In an idealized system without inputs or outputs, the strontium isotope ratio of the water would mirror the dissolvable components of its underlying bedrock. More generally, the strontium isotope ratio of the water can be thought of as a three end-member mixing model between atmospheric inputs such as precipitation (or aeolian dust in xeric areas, see Gruastein and Armstrong 1983), carbonate mineral weathering, and alumino-silicate mineral weathering within the watershed (Bishop et al 1994, Douglass et al 2002, Krishnaswami et al 1992).
This means that the water will not necessarily mirror the isotopic ratios of the underlying bedrock, but rather an amalgamation of all inputs within the catchment area. Precipitation has very low strontium concentrations, around one microgram per liter; as strontium is a non-volitile element, it is not taken up readily through evaporation, and therefore precipitation does not exert a large influence on the isotopic composition of bodies of water except under specific circumstances (Banner 2004, Frei and Frei 2013). Its isotopic ratio is in equilibrium with marine sources (about 0.7092) with some fluctuation due to distance from the coast (Stewart et al 2001).

Silicates, such as basalts, feldspars, quartz, granites, or gneiss, are generally more resistant to weathering, have a lower strontium concentrations, and are more radiogenic than carbonates. Precambrian granites have isotopic ratios at or above 0.710, and silicate alluvium measured approximately 0.7165 (Beck et al 2013, Capo and Chadwick 1999). Both patterns are due to a higher Rb/Sr content (Palmer and Edmond 1992, Rose and Fullagar 2005). Carbonates, such as limestones and dolomite, are more easily weathered, have lower Rb/Sr ratios, and higher strontium concentrations, but lower strontium isotope ratios, averaging around 0.707-0.709 (Burke et al 1982). Due to these differences in both isotopic ratio and strontium concentration, it is possible to estimate the proportional contributions of different rock end-members (silicates vs carbonates) in a given hydraulic system (Bu et al 2016, Palmer and Edmond 1992). In general, shield areas (large areas of Precambrian basement rock exposures) have low overall concentrations of strontium due to a paucity of carbonate inputs, but overall higher ratios (Palmer and Edmond 1992).

Aside from these first-order determinants of aquatic strontium isotope ratios, mixed results exist regarding other influences. For example, Rose and Fullagar (2005),
Douglass et al (2002), and Bullen and Kendall (1998) all found no effects of precipitation seasonality, discharge flux, or (in one case, Douglass et al 2002) pollution on the strontium isotope composition of hydrological systems. Entirely conflicting results come from Aubert et al (2002), Tricca et al (1999), and Soler et al (2002), all of whom found pollutants and discharge fluctuations did alter the isotopic composition of rivers. Aubert et al (2002) focused specifically on discharge rates in the Vosges Mountains in France, and explained the shift resulting from increased or decreased discharge as a variable source effect. As discharge increased, there were more contributions from upstream systems, thus incorporating a wider variety of underlying geologic zones into the final river system. The importance of discharge rate and fluctuations therefore seems to be critical only in extremely heterogeneous hydraulic systems (Aubert et al 2002). Similarly, Rose and Fulligar (2005) found that larger watershed basins tended to have higher isotopic ratios, likely due to the increase in the quantity of high-rubidium potassium feldspars weathering and contributing to the larger catchment area. Water sourced from deeper base flow also increased in both strontium concentration and isotopic ratio simultaneously, likely also due to increased weathering of rubidium-rich basement rock, providing insight into the water source for flowing surface waters (Rose and Fulligar 2005). Interaction with other trace elements can also influence isotopic ratios, such as Hunt et al (1998) show in their study of iron in manmade wetlands. Areas with large quantities of peat, which is rich in iron, had increased strontium isotope ratios, likely because the high quantities of iron in some way reduce the solubility of minerals containing high proportions of non-radiogenic $^{86}\text{Sr}$.

Many studies find that river water $^{87}\text{Sr}/^{86}\text{Sr}$ ratios correlated strongly with the
ratios of the local soil or bedrock (Hoogewerff et al 2001, Rose and Fullagar 2005, Voerkelius et al 2010). Soil and plant strontium in turn can be traced to a mixture between bedrock and precipitation (Miller et al 1993). Although models based solely on bedrock age can vary unpredictably between estimated and measured values (Hobson et al 2010, Hodell et al 2004), models which account for bedrock age, lithology, and strontium concentration were shown to be more predictive of water $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (Chesson et al 2012, Bataille et al 2012, Rose and Fullagar 2005). The accuracy of bedrock approximations may vary by topographic relief, with areas of low relief showing a higher correlation between bedrock and river $^{87}\text{Sr}/^{86}\text{Sr}$ while areas of steep relief show a weaker correlation due to more extreme erosional and weathering processes (Montgomery et al 2009). Hegg and colleagues (2013) provide a predictive model for geological variation based on bedrock and lithology, specifically using the percentage of major rock types in the area of interest. They demonstrated, unsurprisingly, that increasing geologic heterogeneity increases the likelihood of high variability in radiogenic strontium isotope ratios (Hegg et al 2013).

The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in local water sources can affect the isotopic composition of riparian vegetation. While water has very low strontium concentration compared to plant material, it can still directly influence the isotope ratios of obligate drinking animals (Fenner and Wright 2014). More importantly, by influencing the isotopic ratios of riparian plants, flowing surface water with unique isotopic signatures can introduce new sources of variation into an ecosystem and potentially act as an indicator of riparian habitat preference. In South Africa, Sillen and colleagues (1998) found major influences of upstream erosional processes and differential mineral dissolution on downstream river
water strontium isotope values, creating a significant difference in the strontium isotope values between riparian (mean $^{87}\text{Sr}/^{86}\text{Sr} = .72237$) and non-riparian (mean $^{87}\text{Sr}/^{86}\text{Sr} = .73390$) plants growing on the same bedrock substrate with the riparian plants mirroring the water values at the transect point (water $^{87}\text{Sr}/^{86}\text{Sr} = .72117$). The $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in plants in the riparian zone of the Blaubank stream more closely reflected the dissolved minerals of the local dolomite geology, while plants farther away from the water more closely approximated the bulk soil $^{87}\text{Sr}/^{86}\text{Sr}$ ratios (Sillen et al 1998). This agrees with the conclusion in Montgomery et al (2009) that plants are reflective of the average $^{87}\text{Sr}/^{86}\text{Sr}$ ratios in their entire catchment area; plants growing in proximity of an isotopically unique water source will reflect this averaged catchment value. It is also in keeping with the conclusions from Maurer et al (2012), stating that water and vegetation are the clearest indicators of bioavailable strontium in an environment. Together, these data suggest that strontium isotopes are an underused potential indicator of riparian microhabitat preference.

This research will assess this claim by testing the following hypotheses: first, do the strontium isotope ratios of forest (riparian) and savanna (non-riparian) habitats differ in a gallery forest/grassland savanna habitat? Second, if so, how far laterally from the water’s edge does this ‘riparian effect’ extend? Finally, if this difference is present in vegetation, can we use it to differentiate forest-versus-savanna habitat preference in fauna?
2.4 Methods

2.4.1 Plant sample collection

We collected non-riparian plant samples at approximately 0.5 km intervals in transects covering all accessible geologic zones within Kibale National Park (Figure 1.1 and 1.2) and Toro-Semliki Wildlife Refuge (Figure 1.3 and 1.4), as identified by geologic maps from the Ugandan Society for Geology and Mines. As we are interested in mapping faunal habitat preference and mobility onto the landscape, a direct measurement of the strontium isotope ratios of the underlying bedrock or soils was not the most relevant metric due to the presence of non-biologically mobile strontium within the bedrock. Glorennec et al (2016) showed that strontium exposure through dietary inputs accounted for 95% of total strontium exposure in children. Therefore, non-riparian plants are a reliably proxy for the mobile, dietary soil strontium available within each landscape (Maurer et al 2012, Glorennec et al 2016). These non-riparian plant samples are referred to as “bedrock-associated plant samples” for this study. Each sample comprised three to five leaves from ground-covering plants, weighing approximately one gram when dried. All samples were marked with GPS coordinates and dried between 50-60 degrees Celsius on a food dehydrator within 24 hours of collection. They were manually crushed and stored in air-tight plastic bags.

Water samples of approximately 24 ml were collected at each water source encountered on the transects and marked with GPS coordinates. We collected an
accompanying riparian plant sample with each water sample, comprising three to five leaves from the plant growing in closest proximity to the location of the water sample (never greater than 1 meter). When possible, we collected plants in a localized transect from the water’s edge extending approximately ten meters (Kibale National Park) or 100 meters (Toro-Semliki Wildlife Refuge) to assess the lateral extent of any riparian signal in the plant community. Also, when possible, we collected water and riparian plants samples from multiple locations along the length of rivers to investigate changes in aquatic strontium isotope ratios.

2.4.2 Faunal sample collection

Strontium isotope ratios can be assayed from any calcium-bearing substance in an organism’s body. In modern, unaltered conditions, bone shows an averaged strontium isotope signature over the last few years or decades of an animal’s life (Lee-Thorp and Sponheimer 2003, Price et al 2002). Enamel is less susceptible to diagenesis due to its high density and low porosity, and is laid down entirely before sexual maturity after which it is metabolically inert (Bocherens et al 1994, Montgomery 2010, Smith et al 1994). We collected bone and tooth enamel samples from existing opportunistically-gathered skeletal collections from the Kibale Chimpanzee Project, Ngogo Chimpanzee Project, and Makerere Biological Research Station in Kibale National Park, Uganda and the Semliki Chimpanzee Project and Semliki Wildlife Lodge in the Toro-Semliki National Wildlife Refuge (see Table 1 for species list). We removed approximately 5 mg of tooth enamel and 5 mg of bone from each specimen using an electric Dremel drill with
a diamond-tipped bit. When possible, bones with rapid turnover times, such as ribs and mandibles, were preferentially sampled to ensure the most recent signal before death (Frost 1969, Parfitt 2002). To assess intra-individual variation, we collected samples from multiple teeth within the same individual when present.

2.4.3 Laboratory Analysis

I performed all sample preparation and analysis in a clean lab at the University of Utah, Salt Lake City, USA in the Department of Geology and Geophysics. Plant and apatite (bone and tooth enamel) samples had to first be digested with nitric acid. For plants, I prepared 50 mg of each sample for digestion in 6 mL polytetrafluoroethylene (PTFE) digestion micro-vessel using 2 ml of nitric acid (trace metal grade) and 285 microliters of hydrogen peroxide. Plant samples were digested in a microwave digester (Ethos EZ® microwave digestion system, Milestone, Inc., Shelton, CT, USA) at 200 degrees Celsius for 20 minutes to break down the sample matrix and transfer the elements of interest into a solution. For bone and enamel samples, I used a cold digestion method to minimize the inclusion of dirt or metallic contaminants. Contamination from metal tools or detrital dirt were monitored by measuring aluminum, iron, titanium, and cerium concentrations within each sample. I included at minimum 5 mg of powdered sample with 2 ml of 1M acetic acid under a laminar flow hood for three hours. Water samples were filtered and acidified in the lab after cleaning thoroughly the bottles used in the field.

After digestion, I spiked each sample with ten nanograms of indium per milliliter
as internal reference standard. We measured the concentration of strontium in each sample using an Agilent 7500ce quadrupole ICPMS. After this measurement, I assembled a solution of each sample containing concentrated nitric acid and 200 nanograms of strontium to run through the PrepFAST purification system (ESI, Omaha, Nebraska), in which a column containing Sr-Spec resin (Eichrom, Lisle, Illinois) captures the strontium from the sample and separates it from the remainder of the material. This purified sample is dried down on a PTFE-covered hot plate at 250 degrees under a laminar flow hood for approximately 2 hours, concentrating all present solids and eliminating the 6 M nitric acid. Solids are rehydrated using 2 ml of 2.4% clean nitric acid. Strontium isotope measurements are made on a Neptune Plus multi-collector ICP-MS (ThermoFisher Scientific, Bremen, Germany). We included a blank following each sample or standard to avoid any internal contamination sample and a standard (NIST SRM 987) after every three samples.

2.4.4 Statistical analysis

I completed all data analysis using R Studio version 0.99.902. All statistical comparisons used Wilcoxon Mann-Whitney rank sum tests for nonparametric data. Wilcoxon Mann-Whitney tests do not require that the data fit assumptions of normality or equivalent sample sizes, only that the data have similarly shaped distributions. I assessed this qualitatively though box and whisker plots or kernel density graphs for each dataset.

Simple linear mixing models use one isotope system to calculate the proportionate contribution of two different sources to a mixture of interest through the following
equations:

\[ \%\text{Source1} = \frac{(S_{\text{mix}} - S_{\text{Source2}})}{(S_{\text{Source1}} - S_{\text{Source2}})} \]

\[ \%\text{Source2} = 1 - \%\text{Source1} \]

Where \( S_{\text{mix}} \) is the strontium isotope ratio of the mixture of interest (usually a faunal tissue measurement), and \( S_{\text{Source1}} \) and \( S_{\text{Source2}} \) are the mean strontium isotope ratios of the potential dietary sources (this could be locational, such as plants in a certain environmental zone of interest, or typological, such as plant species). To be an effective tool, the two sources must be differentiated in isotopic space (Phillips 2012). If a mixture measurement exceeds the mean of potential sources, percentage contribution can be rounded to 100% for the source most closely aligned with the mixture’s measurement. Alternatively, there are mixing model methods which account for uncertainty within definitions rather than relying strictly on the mean measurement. Bayesian mixing models (Phillips 2012, Moore and Semmens 2008, Parnell et al 2010) use the mean and standard deviation of potential sources and the mean and standard deviation of the mixtures of interest and can be run through the R package SIAR (Parnell et al 2010). A series of 200,000 Markov Chain Monte Carlo simulations with 50,000 burn ins estimate the probability of each source contributing to the mixture. These models account for the probability distributions of all variables, including the sources and mixtures, and allow a calculation of the probability distribution of each estimated proportionate contribution. In other words, not only can you calculate the estimated mean probability of each source’s contribution (by averaging the simulation results), but you can assess how likely that
estimated contribution is to the actual contribution from the source by examining the standard deviation of the simulations. The smaller the standard deviation, the more confidence can be vested in the estimated mean proportionate contribution.

This more complex method is appropriate when there is uncertainty in the source definitions, either from a wide range of possible values within each source or due to measurement error (Phillips 2012). For example, when estimating proportionate contributions from forest and savanna habitats within Toro-Semliki Wildlife Refuge, the Bayesian methods are preferable to simple linear models because of the wide range of values present within each of the potential sources.

2.5 Results

2.5.1 Water and Plants

Longitudinal sampling of rivers in Kibale National Park shows that water gradually becomes more similar to the underlying bedrock the longer that it flows along a uniform substrate, and the strontium isotope ratios of riparian plants are a mixture of those from the water and the surrounding non-riparian bedrock (Table 2.1, Figure 2.1). Therefore, the farther downstream along a uniform bedrock a sampling is taken, the smaller the isotopic differences between riparian and non-riparian plants. However, it is important to note that at no point along any sampled river is the percentage contribution
of the water to the riparian plant community null; the mean contribution from water to the riparian plant isotopic signature is 71% and the median contribution is 90%. Thus, even in areas far downstream along a uniform bedrock zone, it is reasonable to expect the riparian plant community to differ from the surrounding non-riparian community due to the influence of water.

The Toro-Semliki Wildlife Refuge bedrock is uniform Cenozoic alluvium throughout the park; despite this underlying homogeneity, there is significant patterned variation between different ecological zones. The strontium isotope ratios of the plants collected in the forest paralleling the Kyankara tributary, the forest paralleling the Mugiri River, and in the savanna grasslands are significantly different from one another (Kyankara forest plants, \( N = 7 \), mean \( ^{87}\text{Sr} / ^{86}\text{Sr} = 0.70913 \); Mugiri forest plants, \( N = 16 \), mean \( ^{87}\text{Sr} / ^{86}\text{Sr} = 0.71056 \); savanna forest plants, \( N = 10 \), mean \( ^{87}\text{Sr} / ^{86}\text{Sr} = 0.71206 \); Kruskal Wallace ANOVA, chi squared = 40.82, \( p < 0.001 \); Tukey’s Honest Significant Difference for all pairwise comparisons \( p < 0.001 \) (Figure 2.2). When pooled together, forest plants ratios remain significantly lower than savanna plant ratios (forest plants \( N = 32 \), mean \( ^{87}\text{Sr} / ^{86}\text{Sr} = 0.71005 \); savanna plants \( N = 13 \), mean \( ^{87}\text{Sr} / ^{86}\text{Sr} = 0.71177 \); Wilcoxon Mann-Whitney rank sum test, \( U = 19.5 \), \( p < .001 \) (Figure 2.3). The strontium concentrations in these plants do not differ by location (mean dry plant strontium concentrations: forest (riparian) plant mean concentration = 272.6167 mg / kg, savanna (non-riparian) plants = 357.1154 mg / kg, Wilcoxon Mann-Whitney rank sum test \( p > 0.1 \).
Table 2.1: Linear mixing models of water/bedrock contributions to Kibale riparian plants

<table>
<thead>
<tr>
<th>River Name and Sample Locality (see Figure 5)</th>
<th>*^{87}Sr/^{86}Sr of riparian plant</th>
<th>*^{87}Sr/^{86}Sr of water</th>
<th>*^{87}Sr/^{86}Sr of nearest bedrock-associated plant</th>
<th>% contribution of water *^{87}Sr/^{86}Sr to riparian plant *^{87}Sr/^{86}Sr</th>
<th>% contribution of bedrock *^{87}Sr/^{86}Sr to riparian plant *^{87}Sr/^{86}Sr</th>
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</thead>
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<tr>
<td>Dura River A</td>
<td>0.7109691</td>
<td>0.7121268</td>
<td>0.7089630</td>
<td>63%</td>
<td>37%</td>
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<tr>
<td>Dura River B</td>
<td>0.7096841</td>
<td>0.7091786</td>
<td>0.7142086</td>
<td>90%</td>
<td>10%</td>
</tr>
<tr>
<td>Dura River C</td>
<td>0.7142745</td>
<td>0.7116801</td>
<td>0.7168784</td>
<td>50%</td>
<td>50%</td>
</tr>
<tr>
<td>Nyakagera A</td>
<td>0.7175561</td>
<td>0.7170554</td>
<td>0.7092595</td>
<td>100%</td>
<td>0%</td>
</tr>
<tr>
<td>Nyakagera B</td>
<td>0.7116400</td>
<td>0.7145900</td>
<td>0.7077956</td>
<td>57%</td>
<td>43%</td>
</tr>
<tr>
<td>Nyakagera C</td>
<td>0.7122245</td>
<td>0.7198588</td>
<td>0.7097023</td>
<td>25%</td>
<td>75%</td>
</tr>
<tr>
<td>Nyakagera D</td>
<td>0.7101600</td>
<td>0.7145900</td>
<td>0.7097240</td>
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<td>91%</td>
</tr>
<tr>
<td>Nyakagera E</td>
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<td>0.7105197</td>
<td>0.7084941</td>
<td>45%</td>
<td>65%</td>
</tr>
<tr>
<td>Mikana A</td>
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<td>0.7164600</td>
<td>0.7087570</td>
<td>100%</td>
<td>0%</td>
</tr>
<tr>
<td>Mikana B</td>
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<td>0.7204190</td>
<td>0.7088400</td>
<td>90%</td>
<td>10%</td>
</tr>
<tr>
<td>Mikana C</td>
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<td>0.7202200</td>
<td>0.7093800</td>
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<td>1%</td>
</tr>
<tr>
<td>Kanyanchu A</td>
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<td>0.7174044</td>
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<td>0%</td>
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<tr>
<td>Kanyanchu B</td>
<td>0.7248100</td>
<td>0.7245500</td>
<td>0.7234300</td>
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<td>0%</td>
</tr>
<tr>
<td>Kanyanchu C</td>
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<td>0.7194400</td>
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<td>55%</td>
</tr>
<tr>
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<td>1%</td>
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<td>71%</td>
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</tr>
<tr>
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<td></td>
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</tr>
</tbody>
</table>
Figure 2.1: River maps from Kibale. (A) Locations of each river sampled within the park; (B) Mikana River isotopic ratios; (C) Dura River isotopic ratios; (D) Nyakagera River isotopic ratios; (E) Kanyanchu River isotopic ratios. (B)-(E) show heat maps (left) illustrating the underlying bedrock as estimated from local non-riparian plant samples for each location (labeled A-E on each map), triangles show strontium isotope ratios of water samples for each location, circles show strontium isotope ratios for riparian plants for each location. Gray line and arrows show direction and flow of the river. Line graph (right) show strontium isotope ratios of the nearest bedrock measurement (as estimated from non-riparian plant samples) in red, water sample in blue, and riparian plant sample in green for each location (labeled A-E on each map).
Figure 2.2: Map of plant samples collected in Toro-Semliki Wildlife Refuge. Boxplots show plant (red) and water (blue) values from three areas: the savanna (mean = 0.71206), the gallery forest along the Mugiri River (mean = 0.71056), and the gallery forest along the Kyankara tributary (mean = 0.70913). Plants in all three areas are significantly different from one another (Kruskal-Wallis ANOVA, chi squared = 40.802, p < 0.001). Water in the Kyankara tributary is not distinct from plants growing in its gallery forest; water in the Mugiri River is not distinct from the underlying Cenozoic alluvium (Wilcoxon Mann Whitney rank sum test U = 35, p = 0.6354). Plans in the Mugiri River gallery forest show a mixed effect of the water from the Mugiri and Kyankara tributary (see text for mixing model details).
This variation in plant strontium isotope ratios by habitat type relates to variation in the isotopic ratios of the water supply for plants in the forests versus on the savanna. The water in the Kyankara tributary has lower isotopic ratios than the plants in the savanna (Kyankara tributary water N = 4, mean $^{87}\text{Sr}/^{86}\text{Sr} = 0.7091$) (Figure 2.2); however the isotopic ratio of the Kyankara tributary water is indistinguishable from the Kayankara forest plants (Wilcoxon Mann Whitney rank sum test, $U=16 \ p > 0.1$). Water and sediment originating from Toro formation Paleoproterozoic gneiss capping the escarpments and flowing into the park via numerous tributaries like the Kyankara likely cause these lower ratios. Groundwater recharge from these same geologic areas is another probable factor. Although not directly measured in this area, non-riparian plants growing
on the Toro formation in Kibale National Park had lower isotopic ratios than non-riparian plants growing on the Cenozoic alluvium in Semliki (Kibale non-riparian plants on Toro formation, N = 27, mean \(^{87}\text{Sr}/^{86}\text{Sr} = 0.70944\); non-riparian Cenozoic alluvium plants, N = 10, mean \(^{87}\text{Sr}/^{86}\text{Sr} = 0.71206\); Wilcoxon Mann-Whitney rank sum test, U = 5, p < 0.001). These Toro formation plants in Kibale have similar \(^{87}\text{Sr}/^{86}\text{Sr}\) ratios to those influenced by the Kyankara tributary water (Kyankara forest plants, N = 7, mean \(^{87}\text{Sr}/^{86}\text{Sr} = 0.70913\); Kibale non-riparian plants on Toro formation, N = 27, mean \(^{87}\text{Sr}/^{86}\text{Sr} = 0.70944\); Wilcoxon Mann-Whitney rank sum test, U = 103, p > 0.1). It is reasonable to conclude that these relatively low ratios seen in the Kyankara water (mean \(^{87}\text{Sr}/^{86}\text{Sr} = 0.7091\) and the plants growing in the gallery forest surrounding this tributary (mean \(^{87}\text{Sr}/^{86}\text{Sr} = 0.70913\) are due to the water’s origins in the Toro gneiss capping the escarpment.

The plants in the gallery forest surrounding the Mugiri River also have lower ratios than the surrounding savanna (Mugiri forest plants N = 16, mean \(^{87}\text{Sr}/^{86}\text{Sr} = 0.71056\); non-riparian Cenozoic alluvium plants N = 10, mean \(^{87}\text{Sr}/^{86}\text{Sr} = 0.71206\); Wilcoxon Mann Whitney rank sum test U = 0, p < .001), even though the Mugiri River itself flows exclusively along the Cenozoic alluvium sedimentary complex and has ratios that match (Mugiri water N = 6, mean \(^{87}\text{Sr}/^{86}\text{Sr} = 0.71193\); non-riparian Cenozoic alluvium plants N = 10, mean \(^{87}\text{Sr}/^{86}\text{Sr} = 0.71206\); Wilcoxon Mann Whitney rank sum test U = 35, p > 0.1) (Figure 2.2). This shows a mixed effect of the low-ratio Kyankara tributary water and the higher-ratio Mugiri water on the plants growing at the confluence of the two sources. Simple two-end member mixing models show a 49% contribution from the Toro formation-derived depleted water in the Kyankara tributary and a 51% contribution from the Cenozoic alluvium-derived enriched water of the Mugiri River on
the plants in the Mugiri gallery forest plants (mean \( ^{87}\text{Sr}/^{86}\text{Sr} \) of Kyankara water = 0.7091; mean \( ^{87}\text{Sr}/^{86}\text{Sr} \) of Mugiri water = 0.711938; mean \( ^{87}\text{Sr}/^{86}\text{Sr} \) of Mugiri plants = 0.71056).

In addition to surface water flow from tributaries like the Kyankara originating on the Toro formation of the escarpment, a shallow groundwater recharge likely contributes to the gallery forest signal. The plants growing on the north side of the river, closer to the escarpment, trend towards lower ratios than those growing on the south side (farther from the escarpment), although the effect is not significant (north side plants \( N = 6 \), mean \( ^{87}\text{Sr}/^{86}\text{Sr} = 0.7107 \); south side plants \( N = 8 \), mean \( ^{87}\text{Sr}/^{86}\text{Sr} = 0.71046 \); Wilcoxon Mann-Whitney rank sum test, \( U = 9 \), \( p = 0.06 \) (Figure 2.4). However, this trend is consistent with a groundwater recharge in addition to contribution from the surface water tributaries to the Mugiri River forest plants. These data emphasize the robustness of a riparian gallery forest signal; even a small contribution of water with a distinct isotopic signature into the riparian system can generate a clear distinction between riparian and non-riparian zones.
Transects taken perpendicular to rivers show that the riparian plant signal extends laterally from the water’s edge through the entire riparian forest zone in Toro-Semliki Wildlife Refuge (approximately 100 meters - Figure 2.5). Plants in transects have $^{87}\text{Sr}/^{86}\text{Sr}$ ratios consistent with forest plant ratios (transect plants $N = 15$, mean $^{87}\text{Sr}/^{86}\text{Sr} = 0.7101$; forest plants $N = 32$, mean $^{87}\text{Sr}/^{86}\text{Sr} = 0.71005$; Wilcoxon Mann-Whitney rank sum test $U = 227.5$, $p > 0.1$) and distinct from savanna plant ratios (savanna plants $N = 13$, mean $^{87}\text{Sr}/^{86}\text{Sr} = 0.71177$; Wilcoxon Mann-Whitney rank sum test $U = 9$, $p < 0.001$). Unique gallery forest isotopic signatures are therefore not confined to plants directly along the edge of the water, but rather can be expected throughout the extent of the forest habitat zone. We observed a similar effect anecdotally at Kibale National Park, but need to collect more data with longer transects before conclusions regarding lateral extent of
riparian signals in rainforest ecosystems can be quantified. Existing qualitative data include transects up to ten meters from the surface water source and show plant $^{87}\text{Sr}/^{86}\text{Sr}$ remain more consistent with riparian plants at the surface water source than plants associated only with bedrock at distances up to 5 or potentially beyond 10 meters, depending on the sampling locality (Figure 2.6).
Figure 2.5: Lines show strontium isotope ratios of plants in transects sampled through gallery forests beginning at the surface water source (left, 0 meters) through the entire gallery forest to the savanna (right). Blue point at 0 meters shows isotopic measurement of water at the transect location. Purple band shows mean of savanna plants +/- 2 SDs; green band shows gallery forest mean (A: for Kyankara tributary, B and C: for Mugiri forest). Isotopic ratios in the transect remain consistent with forest ratios through the entire gallery forest emphasizing the robustness of the gallery forest signature.
Figure 2.6: Lateral extent of the “Riparian Isotopic Zone” for rivers in Kibale National Park: (A) Dura River; (B) Mikana River; (C) Kanyanchu River. Blue square indicates the strontium isotope ratio of the water at the transect location. Red circle indicates the strontium isotope ratio of the nearest non-riparian plant, used as a proxy for the local bedrock. Green triangles indicate riparian plant samples taken incrementally for up to ten meters from the water source. Arrows indicate the direction of the transect. While some sampling localities retained a unique riparian signal for the full ten meter transect (Dura river west, Mikana river northeast), others dropped to mirror the local bedrock by 5 meters from the water’s edge (Kanyanchu River west, Dura River east).
These results suggest that there is a clear riparian signal in the plants growing in the gallery forests of the Mugiri and its tributaries, driven by the influx of water derived from older bedrock with lower strontium isotope ratios at the tops of the escarpments surrounding the Semliki Wildlife Refuge. This signal extends through the entirety of the forest (up to 200 meters on either side of the Mugiri river). There is a reasonable expectation that animals preferring to live and eat within the forest habitat will show a different isotopic signature than animals preferring to live and eat on the surrounding savanna.

2.5.2 Fauna

Fauna samples from the Toro-Semliki Wildlife Refuge isotopically match their preferred habitats (gallery forest versus savanna) based on strontium isotope ratios of tooth and bone (Figure 2.7). Fauna who spend the majority of their time in forested microhabitats included bushbucks, waterbucks, blue monkeys, redtail monkeys, and chimpanzees (MacLeod et al 1996, Ben-Shahar and Skinner 1988, Hunt and McGrew 2002). These fauna’s bone and tooth ratios are more depleted than those in savanna-dwelling fauna. Fauna with a clear preference for the open grasslands include buffalo, kob, warthog, and mongoose (Ryan et al 2006, Deutsch 1994, Waltert 2009, Admasu 2004), all of which have elevated ratios compared to forest fauna (savanna-dwelling fauna N = 12, mean $^{87}\text{Sr}/^{86}\text{Sr} = 0.7111$; forest fauna N = 24, mean $^{87}\text{Sr}/^{86}\text{Sr} = 0.70947$; Wilcoxon Mann-Whitney rank sum test, $U = 22.5$, $p < 0.001$) (Figure 2.8). This pattern of elevated ratios from the savanna and depleted ratios from the forest is consistent with
the plant and water ratios from each locality. Bayesian mixing model show heavily skewed proportionate contributions of forest plants to forest-preferring fauna and savanna plants to savanna-preferring fauna (see Table 2.2 for mixing model results).

Figure 2.7: Strontium isotope ratios from all tissues (bone and tooth enamel) from fauna at Toro-Semliki National Wildlife Refuge. Purple band shows minimum and maximum values for forest plants. Pink band shows minimum and maximum values for savanna plants. All tissues from species plot within their preferred habitat (forest fauna on the left and savanna fauna on the right), with elephants showing the most mixed signal from both habitats, consistent with their large home range. See Table 3 for mixing models showing proportionate contributions from each habitat to the isotopic ratios of the animals.
Figure 2.8: Fauna with a habitat preference for the forest vs the savanna, Toro-Semliki Wildlife Refuge. Savanna-dwelling fauna N = 12, mean $^{87}\text{Sr}/^{86}\text{Sr} = 0.7111017$; forest fauna N = 24, mean $^{87}\text{Sr}/^{86}\text{Sr} = 0.7094796$; Wilcoxon Mann-Whitney rank sum test, $U = 22.5$, $p < 0.001$
Table 2.2: Bayesian mixing models of contributions from forest/savanna resources to Semliki fauna

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat preference</th>
<th>Mean $^{87}\text{Sr}/^{86}\text{Sr}$</th>
<th>% contribution of forest plants</th>
<th>% contribution of savanna plants</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bushbuck</td>
<td>Forest</td>
<td>0.70859</td>
<td>60%</td>
<td>40%</td>
<td>24%</td>
</tr>
<tr>
<td>Chimpanzee</td>
<td>Forest</td>
<td>0.70938</td>
<td>95%</td>
<td>5%</td>
<td>5%</td>
</tr>
<tr>
<td>Blue monkey</td>
<td>Forest</td>
<td>0.70955</td>
<td>70%</td>
<td>30%</td>
<td>23%</td>
</tr>
<tr>
<td>Waterbuck</td>
<td>Forest</td>
<td>0.70957</td>
<td>78%</td>
<td>22%</td>
<td>18%</td>
</tr>
<tr>
<td>Redtail monkey</td>
<td>Forest</td>
<td>0.70959</td>
<td>70%</td>
<td>30%</td>
<td>23%</td>
</tr>
<tr>
<td>Olive baboon</td>
<td>Forest</td>
<td>0.70976</td>
<td>67%</td>
<td>33%</td>
<td>23%</td>
</tr>
<tr>
<td>Elephant</td>
<td>Mixed</td>
<td>0.71009</td>
<td>53%</td>
<td>47%</td>
<td>20%</td>
</tr>
<tr>
<td>Water buffalo</td>
<td>Savanna</td>
<td>0.71155</td>
<td>39%</td>
<td>61%</td>
<td>23%</td>
</tr>
<tr>
<td>Kob</td>
<td>Savanna</td>
<td>0.71186</td>
<td>41%</td>
<td>59%</td>
<td>24%</td>
</tr>
<tr>
<td>Warthog</td>
<td>Savanna</td>
<td>0.71218</td>
<td>41%</td>
<td>59%</td>
<td>24%</td>
</tr>
<tr>
<td>Mongoose</td>
<td>Savanna</td>
<td>0.71617</td>
<td>*</td>
<td>*</td>
<td></td>
</tr>
</tbody>
</table>

Table 2.2: Results of Bayesian mixing models (modeling using SIAR package in R) showing proportionate contributions of the savanna and forest habitats to the strontium isotope composition of all tissues from each faunal group.

*Mongoose omitted from modeling because all values fell outside of the ranges of all potential source measurements.

We found the white-tailed mongoose included in the sample set along the roadway cutting through the park; this sample was an outlier in our dataset, with ratios significantly higher than any source measured within our sampling range (Figure 2.7). As both the bone and tooth ratios from the same individual share abnormally high values, contamination from the road surface or other non-biological source is not likely. Rather, it is plausible that we missed a more radiogenic area of the park in our sampling protocols. Alternatively, the mongoose is the only species in our sample who burrows,
and it is possible that differential mineral weathering of rocks below the surface of the alluvium contributed more radiogenic strontium into the body pool of the mongoose.

Data from the olive baboons and elephants are also notable. Locals report that olive baboons primarily spend time in the open grasslands; however, data from one olive baboon presented here place it clearly in the forest (olive baboon SML 5, mean $^{87}\text{Sr}/^{86}\text{Sr} = 0.70976$; mean forest plant $^{87}\text{Sr}/^{86}\text{Sr} = 0.71005$). These data suggest that even if the baboons spend time in the grasslands, most their food comes from the forest. This agrees with carbon isotope data from modern and fossil baboons (Papio hamadryas ursinus and Papio hamadryas robinsoni) which demonstrate a significant C3 component to the diet of these grassland-dwelling species (Sponheimer 2006, Codron 2003, Codron et al 2005).

The three elephants included in this data set have isotopic ratios that are intermediate between forest and grassland ratios, particularly in the two bone samples collected (reflecting adult behavior) (Figure 2.7; elephant SML 6, bone $^{87}\text{Sr}/^{86}\text{Sr} = 0.71090$, linear mixing models 51% forest plant contribution 49% savanna plant contribution; elephant SML 7 bone $^{87}\text{Sr}/^{86}\text{Sr} = 0.71051$, linear mixing models 73% forest contribution 26% savanna contribution). This is consistent with the large home range of elephants as well as their slow bone turnover time, increasing the geographic range averaged into the isotopic ratios of the bone tissues.

2.6 Discussion

These data show that in areas with clear differentiation between riparian and non-riparian microhabitats, strontium isotope ratios can be used to identify the microhabitat.
preference of local fauna. Small contributions of water originating on unique geologic substrates, even at appreciable distances from the gallery forest in question, can exert an influence on riparian plants that is significant and identifiable isotopically. However, applying this work to the fossil record will require establishing where these riparian zones may have been, and what isotopic ratios we could expect to find there that would differentiate them from neighboring non-riparian zones. While difficult, this is not an impossible task, and applications of strontium to the fossil record to identify microhabitat preference are viable.

First, in areas where the ancient fluvial systems are well reconstructed, we could estimate inputs from flowing water sources by measuring modern plants in their areas of origin. For example, even without being able to measure the water of the Kyankara tributaries in Toro-Semliki, if we know that water flowed from the tops of the escarpments into the Mugiri, measurements from plants on the escarpments would allow us to estimate the ratios of the inputs from such tributaries, and the expected effect on the riparian forest. The same modeling could function in well-reconstructed ancient fluvial systems. If we know from where tributaries or side channels originated, measurements of modern plants from those areas will allow us to estimate the values of the inputs and the effects on the ancient riparian forest.

Second, paleoenvironmental indicators such as paleosols and pedogenic carbonates could be used to reconstruct the isotopic ratios of past riparian zones. Pedogenic carbonates are formed from the re-precipitation of soil inorganic carbon in various morphologies, including carbonate nodules, which capture a widely time-averaged picture of the soil carbonate pool at the time of its formation. Calcium, and
therefore strontium, gets incorporated into pedogenic carbonates through the weathering of limestones and dolomites, as well as any non-carbonate calcium-bearing mineral, and through atmospheric deposition (Zamanian et al 2016). These are the same inputs that determine the strontium isotope ratios within water sources. Although we did not measure any bulk soils or soil carbonate nodules in this study, it is reasonable to expect that these pedogenic carbonates would incorporate the mobile strontium, and therefore share the strontium isotope ratio, of water sources and plants growing in their riparian zones. This is an area that warrants further investigation.

Finally, using fossil fauna from hominin bearing localities with known microhabitat preferences, such as monkeys and aquatic fauna for riparian-zone indicators and grassland bovids for non-riparian zone indicators, could help us place hominins in their habitat of choice or, as indicated by the elephants in the current study, see if they subsisted equally among multiple microhabitats. These data demonstrate that animals such as monkeys and grassland bovids (kob, buffalo) are strong indicators of riparian versus non-riparian isotopic signatures, and are likely to be the most viable test going forward with fossil communities.

Examining hominin site geology and paleolandscape reconstructions can allow us to predict areas in which riparian habitat signals may be detectable. Olduvai Gorge was the site of a major paleo lake fed by ephemeral streams and rivers during the Pleistocene (1.75mya) (Liutkus et al 2005). Hay (1976) reconstructs the rivers on the western alluvial plain and along the main drainage way as the most robust, likely including riparian gallery forests along their banks. These easterly flowing rivers have potential origination points or water recharge coming from the Precambrian granites located 60 km west of the
Gorge; more locally, Proterozoic tectonic and metamorphic belts could also contribute to the isotopic composition of these river waters (Figure 2.9). In contrast to these very old formations, Olduvai Gorge sits on Pliocene-era volcanics. Older formations have more time for rubidium to decay into the radiogenic strontium isotope ($^{87}$Sr) leading to higher strontium isotope ratios; in addition, felsic rocks such as granites have naturally higher rubidium concentrations, also leading to higher predicted ratios. On the other hand, younger metamorphic rocks have lower rubidium concentrations and less time for radioactive decay to take place. We can therefore predict, even before sampling, that the Precambrian and Proterozoic formations would contribute more radiogenic strontium isotope ratios to the paleorivers flowing into the more isotopically depleted Olduvai Gorge during the Pleistocene, potentially leading to a unique signal for fauna with a habitat preference for the riparian gallery forests.
Figure 2.9: Map (right) from Liutkuuset et al 2005; geology map (left) from OneGeology.org. Geology of Olduvai Gorge region and reconstruction of paleolandscape. Rivers on the western alluvial plain could have water originating from older bedrock formations to the west of the Gorge creating a unique riparian isotopic signature in the surrounding gallery forests.
Researchers have measured a few strontium isotope ratios from fauna in the Olduvai Gorge area (Figure 2.10). As predicted from the geology, modern animals from near the gorge have lower ratios that those on the Precambrian bedrock to the west (Copeland et al 2012). Measurements of rodents from owl pellets nearest the gorge (Barafu site) yielded ratios around 0.7045; measurements approximating the Precambrian granites on which paleo-rivers may have originated (Western corridor, Serengeti) yielded measurements around 0.708. The fossils from the western gorge - the most probable site of gallery forests fed from Precambrian sources - included three unknown bovids, two crocodiles, and two potential Reduncini antelopes (such as a waterbuck). These are all
fauna likely to be found in a riparian/gallery forest area. Their strontium isotope ratios averaged around 0.7054, higher than the modern rodents collected at the Barafu site near the gorge, with no overlap in values. One explanation is the water from a paleo-river flowing through this area, as indicated by Hay (1976), carried a more enriched isotopic signature from the Precambrian granites and drove the strontium isotope ratios of plants and fauna living along the riparian zone higher than animals living on the same geological substrate but in the non-riparian areas. This would match the trend seen at Toro-Semliki today.

Additionally, fossil fauna from the Western gorge site are also significantly enriched in strontium isotopes compared to fossils collected at the HWKE site on the eastern side of the gorge (Final Report to Leakey Foundation, *Using strontium isotopes to investigate land use at Olduvai Gorge*). The HWKE fossils included undetermined bovids/mammals, Antilopini/Alcelephini antelopes, a porcupine, a suid, and a hippo. All but the latter are more indicative of open habitats, not riparian or gallery forests. We would not expect to see the influence of enriched water derived from Precambrian areas in this site.

The Western gorge fossil fauna are not significantly different in their isotopic ratios from fossil collected from the VEK site, also on the eastern side of the gorge and near the HWKE site. The VEK and HWKE fossil fauna collections are significantly different from one another (Final Report to Leakey Foundation, ‘*Using strontium isotopes to investigate land use at Olduvai Gorge*’). The VEK site is the only other site to contain crocodiles as well as another potential Reduncini antelope. Potentially the VEK site could be another riparian or gallery forest locality, particularly during periods of
increased precipitation and surface water flow, despite its location on the eastern side of the gorge.

2.7 Conclusion

Vegetative and faunal samples from Toro-Semliki National Wildlife Refuge, a modern gallery forest habitat, show clearly that strontium isotope ratios can be used to distinguish forest versus savanna microhabitat preferences. They are effective in areas of even moderate geologic heterogeneity, as seen at Toro-Semliki. In order to successfully test for isotopic indicators of microhabitat preference in fossil localities, first one must identify paleohabitats with the potential for riparian forest microhabitats. This could include identifying major rivers or other waterways that could support a gallery forest, or identifying such habitats through carbon isotope analysis or faunal assemblage data. Second, it is important to have a thorough understanding of the geology of the area, both in the immediate vicinity of the fossil locality of interest and in the area from which the paleorivers originated. As illustrated by the Olduvai Gorge example, knowing the expected strontium isotope ratio for a river’s area of origin can help predict the influence such a river will exert on the riparian forest surrounding it. Third, one must select and measure samples to directly test for the presence of a riparian signal in strontium isotope ratios. These sample could include paleosol nodules from ancient riverbeds or enamel samples from fauna known to prefer riparian / non-riparian habitats from the same locality. As demonstrated by the Toro-Semliki faunal assemblage, guenons and forest-
dwelling bovids (such as waterbuck and bushbucks) are clear indicators of riparian habitat preferences. Large ungulates, such as buffalo and kob, or savanna-dwelling suids such as warthogs have ratios indicative of savanna-grassland habitat preferences.

It is important to establish a reasonable expectation of a distinction between riparian forest and non-riparian habitats before proceeding. This reasonable expectation can be grounded in faunal samples, paleosol nodules, or (in the event that neither are available) distinctive geologic and isotopic areas at the river’s point of origin. Regardless of method, it is critical to define and demonstrate a significant difference between the expected riparian and savanna strontium isotope ratios before proceeding.

Finally, measurements of hominin tooth enamel from the same locality can be collected and compared to the expected ratios for each microhabitat. Bayesian mixing models, like those used on fauna from Toro-Semliki in this research, are a robust and appropriate tool to assess contributions from each isotopically distinctive microhabitat. When possible, large-ranging fauna, such as elephants, should also be included in this analysis in order to determine what a habitat generalist (in other words, one without a clear habitat preference) would look like isotopically.

Strontium isotopes hold great potential for identifying microhabitat preference of hominins and associated fauna. This study highlights their ability to differentiate between riparian / gallery forest habitats and open grassland / savanna habitats in areas with modern geologic heterogeneity. This study also outlines the importance of thorough sampling to identify expected signals from each of these habitats, either through paleosol nodules or habitat-specific fauna, as well as the expected isotopic signal from wide-ranging habitat generalists before interpreting results from hominins. Future work should
empirically test the use of paleosol nodules as proxies for riparian habitat signals in ancient river systems and test the robustness of this method in other modern gallery forest habitats.
3.1 Introduction

Reconstructing the behavioral patterns of extinct hominins is an indirect science, and important puzzles are unresolved. While the fossil record enables robust reconstructions of the evolution of diet, locomotion, and life history, empirical evidence for hominin social organization and relationships remains elusive. Certain patterns of mobility and landscape use, such as philopatric dispersal, have direct consequences on the social behavior of primate species. If we were able to accurately reconstruct dispersal patterns, they could provide a proxy for estimating more abstract social parameters, such as patterns of aggression and affiliation, social bonding, and coalition formation. The purpose of this investigation is to assess the reliability and accuracy of strontium isotope ratios as proxies for dispersal patterns in a modern primate habitat, and to identify the most accurate methods for analyzing strontium isotope ratios to identify the philopatric versus dispersing sex within a species.

Previous work reconstructing hominin mating systems, group composition, and dispersal patterns have relied heavily on inferences from behavioral models based on observations of chimpanzees and other primates, or assumptions based on patterns of sexual dimorphism (ex: Lovejoy 2009; Gordon 2008). Recently, researchers have tried
employing other proxies including hormonal measurements (Nelson and Shultz 2010) and geochemical data like strontium isotope ratios (Copeland et al 2011). Strontium isotope ratios vary by geological formation and have the potential to act as a mobility tracer, providing empirical insights into the way extinct species spatially utilized their landscapes. In geologic formations, the ratio of a heavier isotope of strontium ($^{87}$Sr) to the lighter isotope ($^{86}$Sr) varies in accordance with bedrock age and type. The strontium isotope ratio ($^{87}$Sr/$^{86}$Sr) of underlying bedrock is incorporated into soil and plants, and then into calcium-bearing tissues of animals eating those plants without fractionation effects. Therefore, the $^{87}$Sr/$^{86}$Sr ratio within calcium-bearing tissues of animals, including bones and tooth enamel that frequently fossilize, should reflect the isotopic fingerprint of the area that animal lived on during the time of that tissue’s formation. Some of these tissues, like tooth enamel, form early in life and then are metabolically inert, capturing the isotopic fingerprint of the location the animal lived during early life. Comparison of tissues reflecting this juvenile signature, like tooth enamel, to other adult-age proxies (such as bone or the local environment at the place of fossil deposition) can be used to track animal movement and dispersal across geologically heterogeneous landscapes.

To date, no $^{87}$Sr/$^{86}$Sr ratio studies have been conducted on modern primate communities, and therefore there are no extant models assessing their reliability as a proxy for behavior. The following research addresses this gap in the literature by sampling environmental and faunal strontium isotope ratios in Kibale National Park, a protected rainforest in southwestern Uganda home to multiple communities of wild chimpanzees (Pan troglodytes schweinfurthii) as well as numerous species of primates, bovids, suids, and others. The project begins with extensive environmental sampling
across Kibale National Park to identify meaningful isotopic clusters across the landscape, both in riparian and non-riparian habitat zones. It then tests the efficacy of different methods for determining the dispersal patterns of five primate species: male philopatric chimpanzees and red colobus monkeys, and female philopatric black and white colobus monkeys, olive baboons, and guenons (blue monkeys and redtail monkeys).

Kibale National Park is an ideal study location for this project because there is sufficient geologic variability to imply meaningful isotopic variation between different areas of the park. Additionally, the species available in skeletal collections represent both male and female philopatric dispersal patterns and a variety of ranging behaviors. We predict the efficacy of certain methods will be contingent on the relative size of a species’ home range relative to the geographic spread of isotopic variation across the landscape; species with larger home ranges will assimilate a wider range of isotopic ratios into their tissues as they form, an averaging effect that could obscure dispersal signals in between-tissue comparisons (see Hypothesis C, below) but accenting them in tissue-environment comparisons (see Hypothesis D, below). We expect taxa with small home ranges relative to the isotopic variability on the landscape will show the opposite bias.

We will test the following hypotheses:

(A) $^{87}\text{Sr}/^{86}\text{Sr}$ ratios within the plants of Kibale National Park vary in accordance with the age and composition of the underlying bedrock, resulting in isotopically distinct and geographically isolated clusters across the landscape.

(B) A greater proportion of dispersing sex individuals will have tooth strontium isotope
ratios that fall outside of the range of local environmental values compared to the proportion of philopatric sex individuals in all species with sex-biased dispersal patterns.

(C) The difference between the $^{87}$Sr/$^{86}$Sr ratio in tooth enamel and the $^{87}$Sr/$^{86}$Sr ratio in bone will be greater in the dispersing sex than the philopatric sex, particularly in species with range sizes smaller than the landscape’s isotopic clusters (tooth/bone offset). A greater proportion of members of the dispersing sex will fall above the taxa’s mean tooth/bone offset than the proportion of members of the philopatric sex.

(D) The difference between the $^{87}$Sr/$^{86}$Sr ratio in tooth enamel and the $^{87}$Sr/$^{86}$Sr ratio in local environment will be greater in the dispersing sex than the philopatric sex, particularly in species with range sizes as large or larger than the isotopic clusters on the landscape (tooth/environment offset). A greater proportion of members of the dispersing sex will fall above the taxa’s mean tooth/environment offset than the proportion of members of the philopatric sex.

(E) The difference between the $^{87}$Sr/$^{86}$Sr ratio in tooth enamel and the median tooth enamel $^{87}$Sr/$^{86}$Sr for other local fauna will be greater in the dispersing sex than the philopatric sex (tooth/local fauna offset). A greater proportion of members of the dispersing sex will fall above the taxa’s mean tooth/local fauna offset than the proportion of members of the philopatric sex.

3.2 Why is philopatry relevant to behavioral evolution?

By understanding the dispersal patterns of hominin groups, we can infer downstream behavioral effects such as patterns of affiliation and aggression, coalition
formation, and the nature of intra- versus inter- group competition. Dispersal patterns establish the foundation for social bonds by determining which sex - male or female - gains the benefit of lifelong bonds with kin. Social bonds yield fitness benefits in primates. They reduce stress (Crockford et al 2008; Wittig et al 2008; Silk 2002; Taylor et al 2000), facilitate alliances during aggressive encounters (Goodall et al 1979), and provide allies to defend territory and mates (Watts 1998), all of which increase an individual’s fitness (Silk 2007; Silk et al 2004). Kin selection theory (Hamilton 1963) predicts bonds between kin to be preferred to bonds between non-kin because of the potential increases in inclusive fitness. That is, when socially bonded with kin, one enjoys the individual fitness benefits of social bonding in addition to the inclusive fitness benefits through their kin, all of whom are also reaping the rewards from mutual social bonds. Observations of philopatric females across the animal kingdom support these predictions (Archie et al 2008; Gero et al 2008; Holekamp et al 2007; Silk, 2006; Widdig et al 2001 and 2002; Bastani 2009; Dunbar and Spoors 1995; Moore 1990).

The benefits of being the philopatric sex are clear and numerous. This begs the question, why would females ever disperse? One theory on the development of philopatric patterns suggests that the sex which benefits more from social interactions will remain philopatric while the other sex disperses to avoid inbreeding (Le Galliard et al 2006; Perrin and Goudet 2001; Perrin and Lehmann 2001). Frequently, basic ecology and resource distribution predict which sex will incur the greatest benefit. For example, Wrangham (1980) explains that clumped resources lead to female defense of those resources, and subsequent female kin bonding, female philopatry, and male dispersal. This is based on the premise that females distribute across the landscape based on
available food, as food resources are the limiting factor for female reproductive output (Trivers 1972). Males, on the other hand, are limited in their reproductive capacity by access to females (Kappeler 2000) and will distribute themselves based on those females. Clumped food resources benefit group living, resulting in female nepotistic relationships, bonding of female kin, coalitions, and female philopatry. Males must then disperse to avoid inbreeding (Wrangham 1980). When resources are more diffuse, there is less pressure for females to bond and form resource-defending coalitions. In this case, females spreading out may be preferred to decrease resources competition. This eliminates the pressure for female philopatry and either sex may disperse; if males gain a fitness benefit from forming coalitions, males remain philopatric (van Hoof 2000, Ostner and Schülke 2014, Silk 2017).

Great apes do not follow the predictions of this socioecological model, and explanations of which sex benefits most from social bonding require going beyond resource distribution. Chimpanzees live in areas with clumped resources, yet follow a pattern of female dispersal and male philopatry (Mitani et al 2002). Bonobos are also male philopatric (Doran et al 2002, Stumpf 2011). One theory is that this is due to oversized “outbreeding pressure” brought on by alpha male tenures which are significantly longer than in monkeys or other mammals (Clutton-Brock et al 1976, Isbell 2004). Another idea is that the nature of intra- versus inter- group competition tilts the scales for which sex benefits more from social bonding. In chimpanzees, territory patrol and defense is a predominantly male activity with heavy fitness repercussions (Williams et al, 2004; Wrangham et al 2006; Watts and Mitani 2001). Strong social bonds are an important predictor for which males join boundary patrols with one another (Watts and
Mitani 2001). Affiliative bonds with numerous group members across the community is beneficial when this type of between-group competition is particularly important, and these types of wide-spread affiliative bonds are more easily achieved by and within the philopatric sex (Langergraber et al 2009).

In mountain gorillas (Gorilla beringei), a high proportion of groups are multi-male, with males showing philopatric tendencies and females often dispersing numerous times before reproducing (Robbins et al 2009; Yamagiwa et al 2003), although this may be an evolutionarily recent development. Western lowland gorillas (Gorilla gorilla), however, live in predominantly single-male groups, likely due to patchier distribution of food resources (Robbins 2007). Limited data suggests that individuals of both sexes leave their natal group (Robbins et al 2004), but potentially there are patrilocal patterns to neighboring silverbacks (Bradley et al 2004, but see Inoue et al 2014). In orangutans (Pongo pygmeus), genetic studies suggest that both sexes disperse equally from their natal areas (Utami et al 2002; Goossens et al 2006), although some studies suggest that females do not disperse as far as males and maintain relationships with neighboring related females (Singleton et al 2002; Knott et al 2008).

Our two closest living relatives (chimpanzees and bonobos) both exhibit male philopatric tendencies. While the pattern is not as marked in gorillas, the argument can be made that male philopatry forms the basis for their dispersal structures. The most parsimonious reconstruction for human ancestors is thus also one of male philopatry and female dispersal. However, the ancestral dispersal pattern for modern humans remains a debated topic; since the rise of agriculture, male philopatry and female ‘dispersal’ to the village or home of her husband appears typical. According to Hill et al (2011), a
A worldwide survey of 32 hunter-gatherer societies revealed a bisexual dispersal pattern that often include co-residence of brothers and sisters, but with individual groups consisting of a high proportion of entirely unrelated individuals. Genetic studies suggest that the shift to patrilocality and female dispersal was a consequence of wealth accumulation and inheritance (Wilkins and Marlowe 2006, Marlowe 2000), and that previous to pastoralism humans may have followed a pattern of male-biased dispersal (Melnick and Hoelzer 1993). Therefore, whether female dispersal is an ancestral biological trait or an artifact of cultural practices that came along with the agricultural revolution is still under debate (Wilkins and Marlowe 2006; Hill et al 2011; Burton et al 1996; Murdock 1981).

A direct, empirical reconstruction of the philopatric patterns of australopithecines would help determine the ancestral state for the African great ape clade and differentiate between the derived and ancestral conditions for the chimpanzee/bonobo/human last common ancestor. Understanding this basal social structure is important because it provides an evolutionary root for the trajectory of unique Homo sapiens traits, such as extended life histories, pair-bonding, cooperative hunting, multi-family social structures, and female-female bonding. For example, in strictly male philopatric chimpanzees, males form coalitions with kin for border patrols and territory protection (Manson et al 1991; Wilson and Wrangham 2003). If male philopatry and strong male kin bonds are the ancestral condition on the human lineage, this could form the basis for the cooperative hunting and territory defense seen in our own species (Chapais 2009). Male philopatric patterns in human ancestors would also carry implications for life history reconstructions, including the Grandmother Hypothesis explanation of menopause in human females.
Hawkes and colleagues propose that the human female post-reproductive period be selected for under conditions in which older females were key food providers to younger, reproductively aged female kin (Hawkes et al 1998). Under a pattern of strict male philopatry, in which females disperse from natal groups and reproduce among non-kin, such a system would not be sufficient to explain human extended life history traits, including menopause (but see models by Cant and Johnstone 2008; Hawkes and Coxworth 2013). Finally, very limited data on female chimpanzee social behavior suggests that females form social dyads with unrelated females beyond that which cannot be explained by kinship/kin-biased dispersal or selective ranging (Langergraber et al 2009, Foerster et al 2015). In humans, young girls are less gregarious than their male counterparts (Benenson et al 2015, Barbu et al 2011), and older females rely more heavily on verbal communication and support to their peers (Benenson 2014). Other studies suggest a stress response of “tend and befriend” more closely aligns with observations of female behavior than the traditional “fight or flight” (Taylor et al 2000). Together, data suggest that female social strategies are centered on their survival and the survival of their offspring, creating a balancing act of needing bonds with others to support them in times of need while also avoiding same-sex, same-age competitors for resources (Krems et al 2016, Beneson 2014). Evidence supporting a shared ancestral dispersal pattern for humans and chimpanzees might suggest that these patterns of female bonding are an ancestral, rather than derived, trait in modern humans and justify a more complex framework for investigating female-female bonds.
3.3 Previous research on reconstructing behavioral systems

Reconstruction of the realized socio-ecological niche of an extinct species poses many challenges. While progress has been made in areas such as diet and climate, the behavioral aspects of socioecological niche space are elusive and can often only be indirectly determined. Even in extant populations, researchers can only observe correlations between ecological, phylogenetic, and environmental factors and the behavioral repertoire of a species and use them to infer the ultimate drivers of social organization. Correlations between feeding ecology and social organization (Trivers 1972; Kappeler 2000; Wrangham 1980) hold for many species of Old World monkeys (ex: Mitchell et al 1991; Barton et al 1996; Sterck and Steenbeek 1997; Koening et al 1997), but not great apes (Clutton-Brock et al 1976; Doran et al 2002; Bradley et al 2004). Predation pressure is another possibility. High predation risk leads to high group cohesion and intra-group competition. This selects for female coalitions to protect resources and female philopatry. If predation risk and competition are low, females disperse (van Schaik 1983; 1989). The number of cycling females within a group causes the number of males to increase (Mitani et al 1996; Nunn 1999), but high predation risk can also result in similar increases in the number of males relative to females (Hill and Lee 1998). This shifts intra-group dynamics and increases male-male competition. Infanticide avoidance may contribute to social organization also, particularly the development of long-term male-female associations (van Schaik and Kappeler 1997) and pair bonding (Opie et al 2013). Researchers have also long ignored phylogenetic constraints as potential drivers of social systems, as they were thought to be exceedingly
fluid, but some recent studies (ex: Schultz et al 2011) have amassed evidence that social systems are highly predicted by phylogenetic relationships. Food abundance (Isbell 2004), operational sex ratios (Jack and Isbell 2009), and cognitive abilities (Shultz and Dunbar 2012) are also hypothesized social system drivers.

If we cannot fully understand the drivers of social organization in modern primates, what can we use to infer it in fossil species? Patterns of philopatry in australopithecines are often discussed in tandem with levels of sexual dimorphism within the genus, as both are commonly used metrics for reconstructing social systems and, in particular, mating patterns. Estimates of sexual dimorphism are based primarily on *Australopithecus africanus* and *Australopithecus afarensis* due to sample sizes. In *A. afarensis*, there appears to be relatively high body mass dimorphism (similar to that seen in modern gorillas or orangutans) (Gordon et al 2008; McHenry 1991; but see Reno et al 2010) and greater single-element post-cranial dimorphism than that observed in any living hominoids (Harmon 2006; Richmond and Jungers 1995). In *A. africanus*, body size dimorphism is generally lower than in *A. afarensis*, but is still at or above levels observed in modern human populations (McHenry and Berger 1998; Harmon 2009).

Increased body size dimorphism in primates is linked to increased male-male competition for mates. In species in which the operational sex ratio is such that males can monopolize receptive females, selection favors males with larger body size (Mitani et al 1996; Plavcan 2012). In the fossil record, high degrees of sexual dimorphism are assumed to indicate high levels of male aggression and competition. However, when we include other types of sexual dimorphism in australopithecines (such as cranio-facial and canine size), the picture becomes more complex. Contrary to the high degree of body size
dimorphism, there is a clear pattern of *decreasing* relative and absolute canine size through time in the hominin lineage, as well as decreased canine size dimorphism between the sexes. Although there is not a strong correlation between canine size dimorphism and specific mating systems in primates, some researchers conclude there was *less* male-male competition and a less promiscuous, and perhaps even monogamous, mating system in this genus (ex: Plavcan and Van Schaik 1997; Lovejoy 2009; Reno et al 2003). Chapais (2009) proposes more complex trajectories involving a one-male multi-female harem intermediary between chimpanzee-like multi-male multi-female mating and human-like pair-bonding.

Like the ultimate mechanisms for social structure, the social and ecological drivers of cranio-facial dimorphism are not well understood. Ecological variables, such as resource scarcity or diffuseness, may play a role in total body size dimorphism under certain conditions (Leigh and Shay 1996; Gordan 2013), while canine size is thought to be less influenced by resource stress. Alternatively, canine size could be influenced by aspects completely independent of sociality, including selection for maximum gape (Hylander 2013). However, a reduction in canine size may merely represent a shift in the “weapon of choice” among hominin males rather than a decrease in competition. A direct reconstruction of the philopatric pattern in this species could help resolve some of the questions arising from this combination of dimorphic and non-dimorphic traits, and help elucidate the evolutionary trajectories of mating patterns in modern humans.

A few studies have attempted to use other lines of evidence to reconstruct social systems, including foetal testosterone exposure based on second-to-fourth digit ratios (Nelson and Shultz 2010) and demographic estimations based on death assemblages.
Strontium isotopes could be a powerful contribution, but only one study has used them in examining Neanderthals (Richards et al 2008), and two for australopithecines (Sillen et al 1998; Copeland et al 2011). All of these studies suffer from a lack of a comparative extant model through which to interpret isotopic results, as well as issues with quantifying the strontium isotope variation of their study sites. This study aims to provide such a model.

3.4 Strontium isotope ratios as proxies for philopatric dispersal

Strontium isotopes incorporate into animals’ calcium-bearing tissues. These ratios derive from the bedrock on which their food grows (for herbivores), or the bedrock on which the food of their prey grew (for carnivores). The higher the concentration of calcium in a food source, the more that source will contribute to the ${}^{87}\text{Sr}/{}^{86}\text{Sr}$ ratios of an animal’s tissues (Fenner and Wright 2014; Burton and Wright 1995). Plants, with higher concentrations of strontium than other food sources, contribute more to the ${}^{87}\text{Sr}/{}^{86}\text{Sr}$ ratios of consumers than meat products or water sources (Burton and Price 2000; Montgomery 2010; Haverkort et al 2008).

Strontium isotope ratios can theoretically be used to identify patterns of philopatric dispersal by comparing proxies for an individual’s juvenile period and that of their adult life. Tooth enamel (for the juvenile period) and bone (for the adult period) are useful because of their differing turnover times. Enamel mineralizes early in life into calcium hydroxyapatite $[\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2]$ with some carbonate impurities (Simmer and Hu 2001). Strontium has a similar ionic radius to calcium, and therefore gets incorporated
into the enamel in the same way that calcium does (Capo et al 1998). After this
mineralization process, enamel is metabolically inert for the remainder of an animal’s life
(Hillson 1997). Permanent tooth eruption ages in primates range widely, but all enamel
eruption is complete by age at dispersal (Smith et al 1994). As eruption times are an over-
estimation for enamel formation times (enamel is fully formed before a tooth erupts from
the gum line), it is safe to say that enamel is a reliable proxy for isotopic ratios
incorporated when the individual was young, before any potential dispersal.

Additionally, enamel is built by tightly packed, highly organized, elongated
crystallites which contain more than one thousand times the number of crystals as
corresponding structures in bones or dentin. While these other structures contain
approximately 20% organic material, enamel contains less than 1%. Together, these
properties make enamel the hardest structure in the vertebrate body (Simmer and Hu
2001). This means that enamel is far less likely to be subject to diagenetic alteration than
other fossilized tissues, such as dentin or bone, and is not likely to absorb environmental
strontium during deposition (Lee-Thorp and Sponheimer 2003; Kohn et al 1999;
Bocherens et al 1994). In either extant or fossil populations, enamel is therefore a reliable
proxy for the strontium isotope ratios an individual accumulated in their very young pre-
dispersal life.

Bone and dentin, conversely, remain metabolically active during life (Manolagas
2000; Price et al 2002; Jowsey 1971; Bentley 2006; Grupe 1997). In healthy bones,
reabsorption and replacement are linked processes in which osteoclasts remove old bone
and osteoblasts replace it with new tissue. Together, the osteoclasts and osteoblasts form
the basic multicellular unit, or BMU (Parfitt 1994). The remodeling of bone takes place
in four phases: activation, resorption, reversal, and formation. The processes is essentially the same in both trabecular and cortical bone; however, the latter is more dense and less metabolically active, resulting in faster turnover rates in areas of trabecular or cancellous bone (Clarke 2008). In humans, approximately 5-10 % of the skeleton is replaced annually, with the entire skeleton being replaced over ten years (Sims and Martin 2014).

In addition to the type of bone, strain and mechanical stress during life also effect the turnover time of bone tissues. Flexure stress triggers remodeling, in particular in the form of dynamic and cycling loads (rather than static load bearing) (Frost 1973), and so bones on which loads are more often exerted will have faster turnover times. An experiment on a beagle found that cancellous bone turnover was significantly lower near yellow bone marrow (found in long bones) than near red bone marrow (found in flat bones, such as the pelvis, cranial bones, or ribs) (Wronski et al 1980). Even within a single bone, bone tissue near the surface will remodel faster than the interstitial bone beneath (Parfitt et al 1987). Putting all of these factors together, bones such as the ribs have a rapid turnover time when compared to other bones in mammalian bodies: they are under constant dynamic stress with respiration, they are flat, and they are made primarily of cancellous bone (Frost 1969; Parfitt 2002). For similar reasons, the cancellus bone of the iliac blade has a very high turnover rate (nearly 20% each year (Balena et al 1992)). Strontium isotope ratios from bone therefore reflect activity during the last year or years (< 10) before death and can be used as an estimate of an individuals’ strontium isotope landscape during adulthood.

When working with the fossil record, many doubt the integrity of isotopic data from fossilized bone due to diagenetic alterations. While some studies suggest that with
proper treatment, bone can retain a biological signal (Sillen et al 1989; Sillen 1992), it is often not a safe assumption, especially when working with paleontological rather than archeological specimens (Budd et al 2000; Sponheimer and Lee-Thorpe 2006). An alternative to using bone to represent adult strontium isotope ratios is to define the available adult signal using a proxy from the local environment. There are many different methods to do this. Geologic maps showing the age and composition of bedrock can be used to estimate local strontium isotope ratios (Bataille and Bowen 2012), but this only serves as the roughest of proxies. Whole-rock strontium is not necessarily reflective of the labile, biologically available strontium in a system (Bentley 2006), which is the relevant metric for research involving fauna. While bedrock age and composition do predict strontium isotope ratios, they explain a very small proportion of the variance across space and often vary in an unpredictable way when compared to biologically available strontium isotope ratios (Chesson et al 2012; Hodell et al 2004). Bedrock maps should be used to estimate local strontium isotopes ratios only in the absence of any other options (Beard and Johnson 2000).

Rather than bedrock, a more appropriate method is to use a biological proxy, such as local vegetation or small mammals. This eliminates the issue of differentiating total $^{87}\text{Sr}/^{86}\text{Sr}$ ratios from the biologically available $^{87}\text{Sr}/^{86}\text{Sr}$ ratios because the biopurification process has already occurred. Bones or teeth from local small mammals can provide an estimate of locally available strontium (Bentley 2004). Mobility patterns and dietary biases could result in a skew in the strontium isotope ratios; however, these same factors may help approximate the most average local signal as well. With these variables in mind, the isotopic mean or median of local fauna can be used as a proxy for a local
isotopic signal.

Potentially the most accurate measurement of biologically available strontium in a local area comes from plants (ex: Evans et al 2009; Hodell et al 2004). Plants incorporate strontium in the same manner as calcium, and reflect labile, biologically available strontium isotope ratios (Sillen et al 1998) with the added benefit of no mobility and increased ease of collection. Plants have already undergone biopurification and only take up labile strontium, and because of the low mass difference between the heavy and light isotopes of strontium, there is no additional fractionation between plants and animals which consume them.

Most commonly in the existing literature, researchers use the adult proxy of choice (usually plants) to define a “local” area. Price et al (2002) suggest using the mean of the adult proxy mean ± 2σ while others (ex: Montgomery 2010) advocate using the true minimum and maximum measurements of the local/adult proxy. Sjogren and Price 2013 recommend integrating multiple definitions of a local value based on the geographic scale of interest. With any of these cases, researchers then classify individuals with a juvenile measurement falling within the local boundaries as “locals”, or philopatric individuals, and those falling outside of it as “migrants”, or dispersing individuals.

Less commonly, researchers calculate an offset value between the juvenile and adult proxies (tooth enamel/bone apatite, tooth enamel/local fauna median, or tooth enamel/plants from the local environment) with the expectation that the offset for dispersing individuals will be greater than the offset for local individuals. These predictions are complicated by the effect of different range sizes on the accumulation of strontium in tissues; animals who range over a larger geographic area during the
formation of their tissues, be it bone or enamel, will incorporate more variable strontium isotope ratios than animals who range over a tightly constricted area during tissue formation. Both large home range and slow life history, which increases the time it takes for tissues to be entirely formed, would increase the variability in strontium an animal might encounter during tissue formation. All the strontium ingested over the time it takes a tissue to form is averaged into the bulk strontium isotope ratio of that tissue. This averaging effect means that species with large home ranges could show muted offsets between different tissues (for example, tooth and bone), even when they do disperse, while comparisons between teeth and the averaged local environment during adulthood will highlight offsets in members of the dispersing sex. Conversely, species with small home ranges incorporating less varied strontium in each tissue will show more accentuated offsets between tissues, while offsets with the local environment might encapsulate too large an area to differentiate between dispersing and philopatric individuals.

These methods have been applied sparsely to mapping the migration patterns of non-humans, for example in mapping the migratory strategies of caribou (Britton et al 2009), tracking changes in landscape use by elephants (Koch et al 1995; Vogel et al 1990) and large South African herbivores (Radloff et al 2010), and identifying the natal origins of fish (Kennedy et al 1997, Barnett-Johnson et al 2008, Martin et al 2013). For paleontological applications, strontium isotope ratios have been used to reconstruct mammoth and mastodon migrations in North America (Hoppe et al 1999 and 2004), sharks habitat use in the Late Carboniferous (Fischer et al 2013), domestic animal mobility in western Sweden (Sjogren and Price 2013), and Holocene fauna range size in
Yellowstone National Park (Ferenac et al 2007).

Applications into the hominin fossil record are even more rare. A team of researchers in southern Greece used strontium isotopes to assess Neanderthal mobility (Richards et al 2008) with disputed results (Nowell and Horstwood 2009). In South Africa, strontium isotope data were used to hypothesize a system of philopatry and landscape use for *Australopithecus robustus* and *Australopithecus africanus* (Copeland et al 2011; Sillen et al 1998). Sterkfontein and Swartkrans caves, where the fossils were discovered, are surrounded by a variety of thin geologic bands. The band on which the fossils were recovered, the Malmani dolomite, is a thin ribbon-shaped zone, stretching over 30 km from east to west but only ten kilometers from north to south. The results of this study are intriguing, and highlight the number of issues that we do not yet understand regarding strontium isotopes as a signal of dispersal. For example, how does home range size affect the isotopic signature of different taxa? Both *A. africanus* and *A. robustus* were bipedal, a highly efficient form of locomotion for covering large distances. Modern chimpanzees have home ranges that range from 15 km² in Kibale National Forest (Chapman and Wrangham 1993) to 27.4 km² in Mahale (Nakamura et al 2013), both forested habitats, and over 85 km² in the open habitat of Fongoli, Senegal (Pruetz and Lindshield 2013). Bipedal hominins in a more open habitat likely inhabited home ranges at least as large, and probably much larger, than knuckle-walking, forest-dwelling chimpanzees. The researchers used the same methodologies to identify local/migrant hominins and local/migrant rodents, despite the complicating effects of extremely different ranging behaviors. If the neighboring substrate is included in the definition of ‘local,’ none of the *A. africanus* teeth and only two of the *A. robustus* teeth are left
designated as migrants. There are not currently any methodologies developed or tested to address these issues, nor any data on which methodological approaches are best employed when asking questions about wide-ranging versus small-ranging fauna. Additional variables such as the rate and timing of tooth enamel development, the dispersal distance of the migrating sex, microhabitat preference, the incorporation of underground storage organs in the diet, and the impact of obligate drinking are also confounding factors that require exploration. This research will address some of these gaps, including exploring the impact of isotopic variability and home range size.

3.5 Methods

3.5.1 Plant and Water Sample Collection

Over two field seasons in Kibale National Park (Summer 2014 and 2015), we collected 262 GPS-referenced plant samples at approximately one km intervals in transects covering multiple geologic zones (as identified by geologic maps from the Ugandan Society for Geology and Mines (Westerhoff et al 2014)). Each sample comprises three to five leaves from ground-covering plants, weighing approximately one gram when dried. We dried each sample between 50-60 degrees Celsius on a food dehydrator within 24 hours of collection. They were manually crushed and stored in airtight plastic bags. We collected and geo-referenced 54 water samples (approximately 24 ml each) at each water source encountered on the transects. We collected an accompanying riparian plant sample with each water sample, comprising three to five
leaves from the plant growing in closest proximity to the location of the water sample (never greater than one meter). We prepared riparian plant sample in the same way as the non-riparian plant samples mentioned above.

3.5.2 Faunal Material Collection

Strontium isotope ratios can be assayed from any calcium-bearing substance in an organism’s body. For fossil specimens, bone and dentin are particularly susceptible to diagenesis (Budd et al 2000), but if in modern samples or if unaltered in the fossil record, can show an averaged signature over the last few years or decades of an animal’s life (Lee-Thorp and Sponheimer 2003, Price et al 2002). Enamel is less susceptible to diagenesis due to its high density and low porosity, and is laid down entirely before sexual maturity after which it is metabolically inert (Bocherens et al 1994, Montgomery 2010, Smith et al 1994).

We collected bone and tooth enamel samples from existing opportunistically gathered skeletal collections housed at the Makerere Biological Research Station in Kibale National Park, Uganda with assistance from the Kibale Chimpanzee Project and the Ngogo Chimpanzee Project as well as fauna from the Toro-Semliki National Wildlife Refuge with help from the Semliki Chimpanzee Project. Samples from Toro-Semliki were not related to dispersal methods. For both tooth enamel and bone samples, we removed five milligrams of tissue using an electric Dremel drill. When present, we sampled bones with rapid turnover times, such as ribs (Parfitt 2002), to ensure the most recent signal before death.
The collection sampled included 97 bone samples from Kibale National Park and Toro-Semliki Wildlife Refuge. Of the samples from Kibale National Park, 57 adult primates had both bones and teeth available for sampling, including six female-philopatric black and white colobus monkeys (four males and two females), seven female-philopatric guenons (three male redtail monkeys, three female redtail monkeys and one female blue monkey), nine female-philopatric olive baboons (five males and four females), 17 male-philopatric chimpanzees (eleven males and six females), and 18 male-philopatric red colobus monkeys (eight males and ten females) (see Table 1.1 for ecological information about sampled species). We did not pool male-philopatric or female-philopatric species due to the differences in home range sizes, which could alter the absolute value of the offset and could obscure patterns.

Two individuals from the Kibale Chimpanzee Project collection were not included in calculations in which place of origin was essential because of ambiguity in their provenience information (KFB 59, a male red colobus; KFB 182/56, a female redtail monkey). This lack of provenience is critically important in the tooth/environment calculation; because of relatively small sample sizes, results could be heavily skewed based on single incorrect provenience issues, undermining the more important methodological conclusions of this study. To ensure that results were not biased based on provenience issues, these skeletons were omitted from analysis. Additionally, one female chimpanzee from Kibale National Park ("Rosa," KCP 6) was classified as a local, philopatric individual despite her sex because she was known to be natal to the Kanyawara community and did not disperse before her death. We did not want to introduce any known biases into the data set, particularly given the small sample sizes.
3.5.3 Laboratory Methods

We performed all sample preparation and analysis in a clean lab at the University of Utah, Salt Lake City, USA in the Department of Geology and Geophysics. We prepared 50 mg of each plant sample and about 5 mg of powdered tooth or bone for digestion in PTFE digestion micro-vessels using 2 ml of clean nitric acid. A microwave digester (Ethos EZ microwave digestion system, Milestone, Inc., Shelton, CT, USA) digested the samples at 200 degrees Celsius for 20 minutes to break down the sample matrix and transfer the elements of interest into a solution. Tooth and bone samples were digested in two milliliters of acetic acid under a laminar flow hood. This “cold” digestion decreased the dissolution of any soil or heavy contaminants that may have been mixed in with the enamel or bone powder (D. Fernandez, personal communication).

Once cooled, we spiked each digest an internal indium standard and used an Agilent 7500ce quadrupole ICPMS to measure the concentration of strontium in each sample. Using this measurement, we prepared a one- or three- milliliter solution of each sample containing 30 ppb strontium and purified it using the PrepFAST purification system (ESI, Omaha, Nebraska. We then dried down purified samples on a PTFE-covered hot plate at 250 degrees under a laminar flow hood for approximately two hours, concentrating all present solids. We rehydrated the solids using two milliliters of 2.4% clean nitric acid. Finally, a Neptune Plus multi-collector ICP-MS (Thermo Finnigan, Bremen, Germany) took the strontium isotope measurements. Each sample was followed by a blank. Every three samples, we ran one standard reference material sample (NIST
SRM 987). Our mean for reference standards was 0.710287 +/- 0.000011. Each sample or standard was followed by a blank.

3.5.4 Statistical Methods

Because the geology underlying Kibale National Park is not reliably categorized, we could not use it to estimate the strontium isotope ratios encountered by different animals within the park. In addition, inputs beyond bedrock age and composition, such as precipitation and wind-blown dust, can influence strontium isotope ratios. Therefore, we directly used isotopic data to identify zones of similar isotopic composition on the landscape and used these as the meaningful spatial units over which Kibale fauna could range. To define isotopic clusters, I included all non-riparian plant samples from Kibale (N=64) in a hierarchical cluster analysis using an average linkage distance, which groups the most similar data points together by grouping together clusters with the shortest mean distance between all of their constituent data points. Using a dendrogram based on these clusters (Manning and Schütze 1999), I assigned each non-riparian plant to a cluster group. To determine if these groups were isotopically distinct from one another, I used Kruskal-Wallace rank sum tests. I qualitatively assessed whether the clusters were geographically distant from one another based on map generated using the ‘ggmap’ package in R Studio (version 0.99.902).

For fauna, first we assessed the reliability of $^{87}\text{Sr}/^{86}\text{Sr}$ ratios to accurately source individuals to their area of collection. To do this, we assessed whether bone ratios (indicative of adult strontium isotope ratios) for individuals collected at each research
facility (Kanyawara/Sebitole, Ngogo/Kanyanchu, and Toro-Semliki) fell within the
minimum/maximum values of non-riparian plant ratios measured for the isotopic clusters
including that research facility. We calculated the percentage of individuals correctly
sourced to their known area of provenance. Given that this collection has been assembled
over the last 40 years with variable degrees of accuracy in provenience records, we set an
80% success rate of sourcing as the minimum required to move forward with the study.

Next, we assessed the efficacy of four proxies for determining patterns of
philopatry with our sample of known primates from Kibale National Park. First, we
plotted the strontium isotope ratios of the earliest forming tooth (preferably M1 as
available) over local environmental strontium isotope ratios. The local environmental
ratios were defined in two ways: first, as the minimum and maximum values measured
for non-riparian plants within the cluster on which the samples were collected
(Montgomery 2010), and second, falling within two standard deviations of the mean of
that local cluster (Price et al 2002). This study represents the first comparison of these
two definitions. Individuals with tooth strontium isotope ratios falling outside of the local
area were considered non-local, or members of the dispersing sex, while individual with
tooth strontium isotope ratios falling within the local cluster were considered local
individuals, or members of the philopatric sex. We then calculate the number of errors
(individuals of the philopatric sex classified as dispersing, and individuals of the
dispersing sex classified as philopatric). This was the methodology, utilized by Copeland
et al (2011), is important to test for accuracy.

The other three proxies all included the calculation of an offset value between
juvenile and adult strontium isotope proxies. First, we calculated the difference between
the strontium isotope ratio of an individual’s earliest forming tooth and that of their bones (tooth/bone offset). We predict that because bone forms during adulthood and teeth form before sexual maturity, the offset for members of the dispersing sex (who change location) will be greater than the members of the philopatric sex (who remain in one place throughout life), particularly in species with small home ranges for which each tissue incorporated limited strontium variability. Second, we calculated the offset between an individual’s earliest forming tooth and the mean of the local environment (tooth/environment offset). This is important because bone ratios will not typically be present in paleontological contexts and, when they are present, the biological strontium signal is not likely to be preserved due to diagenetic alteration. Having an alternative metric to compare tooth ratios to is imperative to translating these methods to the fossil record. Like the tooth/bone offset, we predict that members of the dispersing sex will have a larger tooth/environment offset than members of the philopatric sex, although this will be more pronounced in species with larger home ranges because tissues will have a greater strontium variability averaged into their bulk ratio. Finally, we calculated the offset of an individual’s earliest forming tooth’s strontium isotope ratio with the median tooth enamel ratio for the fauna in that locality (tooth/local fauna offset). Like the other offsets, we predict that members of the dispersing sex will have larger offsets with the group median than members of the philopatric sex, and like the tooth/bone offset, this will be more successful for species with smaller home ranges.

For the three offset calculations, we used Wilcoxon Mann-Whitney U-tests to determine if there was a statistically significant difference between the sexes. Given the small sample sizes by sex for many species, we used parametric bootstrapping to
investigate the implications of non-significant trends in the data. Parametric bootstrapping estimates parameters of interest based on sampled data and draws a normal distribution based on those parameters. Using the mean and standard deviation of the collected data for each sex in each taxa, we generated these bootstrapping distributions. From them, we randomly sampled 100 data points and used Student’s t-tests to compare the means of the bootstrapped distributions. We repeated this simulation 10,000 times and determined the percentage of times that the p-value was significant (p < 0.05). Parametric bootstrapping is particularly useful for very small sample sizes. Although it requires an assumption of an underlying normal distribution, it guards against under-estimations of true population variance and spurious fine structures that nonparametric methods, which sample only from the data points gathered, could propagate. Moreover, by iterating the bootstrap 10,000 times, we could go beyond a frequentist interpretation (significant or non-significant difference in means) and assess the probability of retrieving a significant p-value under multiple iterations of the simulation.

Finally, we determined the proportion of members of each sex that had high offsets relative to the other members of their species, defined as any offset that fell above the species’ mean offset. We predict that a higher proportion of members of the dispersing sex will fall above the mean offset for their species than to the proportion of members of the philopatric sex. We did this for all three offset calculations (tooth/bone, tooth/environment, tooth/fauna median) This categorical classification method is useful in that it would allow researchers working with fossil collections to look at the distribution of offset values within their sample and, provided that the sex of each individual could be estimated, determine which sex is more likely to be philopatric.
without other data from the study site.

3.6 Results

3.6.1 Landscape Isotopic Variation

Hierarchical cluster analysis identified three main isotopic clusters across the surveyed area of Kibale National Park: a northern cluster (mean strontium isotope ratio 0.7094426 +/- 0.001), a southern cluster (0.7169347 +/- 0.0026), and an anomalously high cluster centered around the research area for the Ngogo Chimpanzee Project (0.7273086 +/- 0.004). These clusters are all significantly different from one another isotopically (Figure 3.1, Kruskal-Wallace rank sum test, chi-squared = 51.712, df = 2, p < 0.001) and sufficiently separated geographically (Figure 3.2). The greatest path length within each of the unique clusters is approximately 10 km. There is substantial variation within each cluster, although it does not group together into smaller geographically isolated units. The largest distance that an individual could travel within Kibale and remain in a homogenous isotopic area is approximately 3 km; this value is important because it helps us define ‘large’ and ‘small’ home ranges relative to the isotopic variation on this specific landscape. We can define fauna with home ranges/dispersal distances greater than or equal to 3 km as ‘large home ranges’ in this context (this includes chimpanzees and olive baboons, for primates) and those below 3km as having ‘small home ranges’ (including both species of colobus monkey and guenons).
Figure 3.1: Isotopic clusters in Kibale National Park, non-riparian plant samples. Northern cluster values 0.7078 - 0.712, mean = 0.7094426 +/- 0.001; Southern cluster values 0.71289 - 0.72193, mean = 0.7169347 +/- 0.0026; Ngogo cluster values 0.72343 - 0.73392, mean = 0.7273086 +/- 0.0043. Kruskal Wallace rank sum test chi squared = 51.712, df = 2, p < 0.001
When we include riparian plants in the analysis along with the non-riparian plants, the three clusters remain isotopically distinct from one another (Figure 3.3, Kruskal Wallace rank sum test, chi-squared = 66.576, df = 2, p < 0.001) although the overlap increases substantially and the geographic isolation of each cluster becomes more obscure (Figure 3.4). This is important for two reasons. First, it emphasizes the role that feeding on riparian plants could play in increasing variation within an individual independent of increased mobility. Second, this shows that even with this increased variation, the Kibale National Park system is sufficiently isotopically unique to retain distinctive isotopic clusters despite this increase in within-cluster variation. Riparian vegetation has the potential to derive a unique strontium isotope signal from its nearby
surface water, although the lateral extent of this in a rainforest environment, such as Kibale, has yet to be definitively determined (see Chapter 2).

Figure 3.3: Isotopic clusters in Kibale National Park, all plant samples. Northern cluster values 0.7062 - 0.7201, mean = 0.7106739 +/- 0.0026; Southern cluster values 0.70968 - 0.72391, mean = 0.7170059 +/- 0.0032; Ngogo cluster values 0.71899 - 0.73392, mean = 0.7262458 +/- 0.0047. Kruskal-Wallis rank sum test chi squared = 66.576, df = 2, p < 0.001.
We took multiple samples of plants in the same area, both varying the species and over the course of two field seasons, in order to assess the consistency of the strontium isotope signal. We collected four pairs of plants in the same area (within 100 meters of the same collection location) in 2014 and 2015. The mean difference between plants was 0.0003 with plants sampled away from riparian areas being the lowest values (riparian plant resample 1, difference = 0.00038; riparian plant resample 2, difference = 0.00074; non-riparian plant resample 1, difference = 0.00012; non-riparian plant resample 2, difference = 0.00008). We also collected four pairs of plants of different species within ten meters of each other and compared their values. Strontium isotopes should not vary based on the species of plant, and we found the mean difference between collected pairs...
to be 0.00023. While both of these differences are greater than instrument error, they are also at least one order of magnitude less than the differences seen between sexes and species, as well as between park areas, and so any variation arising from inter-year or inter-species variability should not have an effect on conclusions.

3.6.2 Faunal Sourcing by Bone Strontium Isotope Ratios

Because bone tissue forms during adulthood, one test for the accuracy of strontium isotope ratios to place fauna accurately on a landscape is to assess the difference between a known point of collection and the ratio of faunal bones. Table 3.1 shows the percentages of Kibale (Kanyawara and Ngogo) and Toro-Semliki Wildlife Reserve fauna with bone ratios that accurately place them in their reported area of collection (Figure 3.5). An average of 83% of specimens across all sampling locations was accurately sourced based on bone strontium isotope ratios. It is important to note that all but one of the misclassified individuals lacked strong provenience data, and their area of origination was assumed based on the skeletal collection they were found in (for example, skeletons in the Kibale Chimpanzee Project collection, housed at the Kanyawara field station, were assigned “Kanyawara” as their area of origination). Therefore, these error rates may be misleadingly high and the actual percentage of correct assignment as high as 97%. Only one individual with definitive provenience had an inaccurate sourcing based on strontium isotope ratios (KFB 228, a blue monkey). KFB 228 was collected in 2015 from Ngogo and had isotopic ratios lower than any measured in the area. This is likely because it ranged in life in the northern range of the Ngogo
community where isotopic ratios are likely to be more similar to the Kanyawara community, but from which we did not obtain plant samples. Given this success rate even in light of provenience questions, we can conclude that strontium isotope ratios are sufficiently variable and reliable to continue with this study at this location.

**Table 3.1**: Correctly sourced specimens based on bone strontium isotope ratios by collection

<table>
<thead>
<tr>
<th>Collection</th>
<th>Specimens with bone sample</th>
<th># correctly sourced by bone ratio</th>
<th>% correctly sourced by bone ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kanyawara fauna</td>
<td>56</td>
<td>41</td>
<td>73.2%</td>
</tr>
<tr>
<td>Ngogo fauna</td>
<td>25</td>
<td>22</td>
<td>88.0%</td>
</tr>
<tr>
<td>Toro-Semliki fauna</td>
<td>16</td>
<td>14</td>
<td>87.5%</td>
</tr>
<tr>
<td><strong>AVERAGE</strong></td>
<td></td>
<td></td>
<td><strong>82.9%</strong></td>
</tr>
</tbody>
</table>

Figure 3.5: Strontium isotope ratios of bones of (A) Kanyawara fauna, (B) Ngogo fauna, and (C) Toro-Semliki fauna with colored bands showing minimum and maximum strontium isotope values of local non-riparian plants. For Kanyawara fauna, vegetation bands include the Northern Cluster (0.7062 - 0.7201) (A). For Ngogo fauna, vegetation bands include the Southern Cluster (0.71289 - 0.72193) and the Ngogo Cluster (0.72343 - 0.73392) (B). For Toro-Semliki fauna, local vegetation values fall between 0.70871-0.71257) (C).
Figure 3.5: Strontium isotope ratios of bones of (A) Kanyawara fauna, (B) Ngogo fauna, and (C) Toro-Semliki fauna with colored bands showing minimum and maximum strontium isotope values of local non-riparian plants. For Kanyawara fauna, vegetation bands include the Northern Cluster (0.7062 - 0.7201) (A). For Ngogo fauna, vegetation bands include the Southern Cluster (0.71289 - 0.72193) and the Ngogo Cluster (0.72343 - 0.73392) (B). For Toro-Semliki fauna, local vegetation values fall between 0.70871-0.71257) (C).
3.6.3 Proxy 1: Proportions falling within/outside of local cluster boundaries

First, we qualitatively determined the number of non-locals versus locals by plotting tooth strontium isotope ratios (a juvenile signature) on top of the range of plant strontium isotope ratios (an adult signature) for the local cluster. The expectation is that members of the dispersing sex (“non-local”) will have strontium isotope ratios of their tooth enamel that fall outside of the local range at a greater frequency that members of the philopatric sex (“locals”). This is a commonly utilized method in strontium isotope literature (ex: Copeland et al 2011, Hodell et al 2004) and so assessing its accuracy is of great methodological importance. To calculate the success rate of this method, we designated all individuals with tooth enamel strontium isotope ratios falling outside off the minimum/maximum values of the cluster as “non-local” and those falling within the local cluster “locals.” We then calculated the percentage of true locals (members of the philopatric sex) who were correctly and incorrectly categorized, and the number of true non-locals (members of the dispersing sex) who were correctly and incorrectly categorized.

There are two definitions of “local” which commonly appear in the literature when using this method. First, “local” values can be those which fall two standard deviations above and below the local plant mean (Price et al 2002) and second, they can be everything falling within the minimum and maximum values of plants measured in the local area (Montgomery 2010). Using minimum and maximum values resulted in a smaller range of local values, while using +/- 2 σ from the mean resulted in larger local definitions. However, neither the number of individuals properly classified based on bone
ratios nor the number of individuals classified as local/migrant based on tooth ratios changed between methods, and therefore only the results from the minimum/maximum definitions are reported in detail here.

60% of Kibale primates were correctly identified as migrant or local based on falling within the local bedrock bands or outside the local bedrock bands based on the area of the park from which they were collected (Table 3.2, Figure 3.6). There is a strong bias towards correctly identifying local individuals and misidentifying migrants (82% of local individuals were correctly identified, 35% of migrants were correctly identified). Because of the wide range of possible values measured in and around the Ngogo park area, we failed to identify any Ngogo migrant individuals correctly. Success rates for identifying migrants/dispersing sex individuals correctly were never above 50%.

If this were an unknown fossil assemblage, based on the proportion of each sex falling outside of the local area, we would have correctly identified chimpanzee females, olive baboon males, and red colobus monkey females as the dispersing sex (Figure 3.6E). Black and white colobus monkey females would have been incorrectly inferred to be the dispersing sex (100% of females fell outside of the local range while only 66% of males fell outside of the local range) as would have female guenons (25% of females fell outside of the local range while no males did). We can conclude that at best, this method I can identify the philopatric sex in species with large home ranges relative to the variation on the landscape (chimpanzees and potentially olive baboons). Overall, the method severely handicaps the identification of migrants, particularly in areas with higher environmental variability (such as Ngogo). It is no appropriate for use with species with
small home ranges relative to the isotopic variation on the landscape.

<table>
<thead>
<tr>
<th>Species</th>
<th># of samples</th>
<th>True # of locals / philopatric sex</th>
<th>% locals correctly identified</th>
<th>True # of non-locals / dispersing sex</th>
<th>% correctly identified</th>
<th>% of total samples correctly categorized</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chimpanzees</td>
<td>17</td>
<td>11</td>
<td>82%</td>
<td>6</td>
<td>50%</td>
<td>71%</td>
</tr>
<tr>
<td>Red colobus monkey</td>
<td>18</td>
<td>10</td>
<td>100%</td>
<td>8</td>
<td>25%</td>
<td>56%</td>
</tr>
<tr>
<td>Black and white colobus monkeys</td>
<td>6</td>
<td>2</td>
<td>0%</td>
<td>4</td>
<td>50%</td>
<td>33%</td>
</tr>
<tr>
<td>Olive baboons</td>
<td>9</td>
<td>4</td>
<td>100%</td>
<td>5</td>
<td>40%</td>
<td>67%</td>
</tr>
<tr>
<td>Guenons</td>
<td>7</td>
<td>4</td>
<td>75%</td>
<td>3</td>
<td>0%</td>
<td>43%</td>
</tr>
<tr>
<td>TOTAL</td>
<td>57</td>
<td>31</td>
<td>82%</td>
<td>26</td>
<td>35%</td>
<td>60%</td>
</tr>
</tbody>
</table>
A  Strontium Isotope Ratios of Teeth by Species and Sex: Kanyawara Primates

![Graph showing strontium isotope ratios for Kanyawara primates.]

Figure 3.6: Strontium isotope ratios of teeth of (A,B) Kanyawara primates, (C) Ngogo primate, (D) Kanyawara non-primates, and (E) Ngogo non-primates. Red band shows the minimum and maximum isotopic range of non-riparian plants in the local area (Kanyawara: 0.7062 - 0.7201 (A,C); Ngogo: 0.71289 - 0.73392 (B,D)). Red circles are members of the philopatric sex ("locals") who are expected to fall within the local bedrock bands; blue triangles are members of the dispersing sex ("migrants") who are expected to fall outside of the local bedrock bands. Green squares indicate individuals of unknown sex.

B  Strontium Isotope Ratios of Teeth by Species and Sex: Ngogo Primates

![Graph showing strontium isotope ratios for Ngogo primates.]

Status
- Red: Philopatric sex / "local"
- Blue: Dispersing sex / "migrant"
Figure 3.6: Strontium isotope ratios of teeth of (A, B) Kanyawara primates, (C) Ngogo primate, (D) Kanyawara non-primates, and (E) Ngogo non-primates. Red band shows the minimum and maximum isotopic range of non-riparian plants in the local area (Kanyawara: 0.7062 - 0.7201 (A,C), Ngogo 0.71289 - 0.73392 (B,D)). Red circles are members of the philopatric sex ("locals") who are expected to fall within the local bedrock bands; blue triangles are members of the dispersing sex ("migrants") who are expected to fall outside of the local bedrock bands. Green squares indicate individuals of unknown sex.
3.6.4 Proxy 2: Tooth/bone offset

None of the intra-taxon comparisons by sex yielded significant differences in tooth/bone offsets (Figure 3.7a). However, all species except for chimpanzees trended towards higher offset for the dispersing sex. To determine the robustness of these trends, we used parametric bootstrapping (Figure 3.7b). The male philopatric primates (guenons, olive baboons, and black and white colobus monkeys) returned significant p-values ($p < 0.05$) in 100% (olive baboons), 100% (guenons), and 92% (black and white colobus monkeys) of bootstrap simulations. Female philopatric red colobus monkeys returned significant p-values in 99% of simulations. Chimpanzees, however, which are
also female-philopatric, returned significant p-values in only 5% of bootstrap simulations. This means that for most of bootstrapped samples, the difference between chimpanzee male and female offsets were indistinguishable from one another. These data suggest that tooth/bone offsets have the potential to discriminate between members of the philopatric and non-philopatric sex for many primate species, but not for chimpanzees (Table 3.3). This is in keeping with our predictions regarding methodologies and range size; chimpanzees have large home ranges relative to the variation on the landscape in Kibale, and therefore while both their tooth enamel and bones form, they are incorporating a wide variety of strontium sources into those tissues. Due to this averaging effect, the difference between tissues even for dispersing individuals becomes muted. However, for species with small home ranges, each tissue incorporates only a very small, specific strontium source during formation. The differences between the specific sources incorporated into bone for dispersing versus philopatric individuals is accentuated.
Table 3.3: % significant bootstrap simulations, tooth/bone isotopic ratio offset

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Sample mean tooth/bone offset - philopatric sex</th>
<th>Sample mean tooth/bone offset - dispersing sex</th>
<th>% of significant p-values (10,000 simulations)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chimpanzees (N=15)</td>
<td>0.001206 (males)</td>
<td>0.001247 (females)</td>
<td>5%</td>
</tr>
<tr>
<td>Red colobus monkeys (N=19)</td>
<td>0.000669 (males)</td>
<td>0.001669 (females)</td>
<td>99%</td>
</tr>
<tr>
<td>Black and white colobus monkeys (N=6)</td>
<td>0.001735 (females)</td>
<td>0.002748 (males)</td>
<td>92%</td>
</tr>
<tr>
<td>Olive baboons (N=9)</td>
<td>0.000848 (females)</td>
<td>0.002615 (males)</td>
<td>100%</td>
</tr>
<tr>
<td>Guenons (N=7)</td>
<td>0.00072 (females)</td>
<td>0.001153 (males)</td>
<td>100%</td>
</tr>
</tbody>
</table>
We then calculated the proportion of each sex with high offsets (offset values falling above the mean tooth/bone offset for each species) (Table 3.4, Figure 3.8). We expect that a higher proportion of individuals of the dispersing sex will have high offsets than the proportion of the philopatric sex. Red colobus monkeys, olive baboons, and guenons all had a higher proportion of the dispersing sex with high offsets compared to the proportion of the philopatric sex with high offsets (red colobus: 40% of dispersing sex individuals versus 10% of philopatric sex; olive baboons: 40% of dispersing sex individuals versus 0 philopatric sex individuals; guenons: 100% of dispersing sex individuals versus 0 philopatric sex individuals). Chimpanzees and black and white colobus monkeys had approximately equal proportions of each sex fall above the group mean (chimpanzees 33% of dispersing sex individuals versus 27% of philopatric sex individuals; back and white colobus 50% of members of both sexes had high offsets). While not perfectly, reliable, this method is most effective for small home range fauna. It is not at all reliable for fauna with chimpanzees, which have the largest home ranges in the sample.
**Table 3.4**: % out of local bedrock boundaries / with high offsets by dispersal type

<table>
<thead>
<tr>
<th>Method:</th>
<th>Falling outside local bedrock area</th>
<th>Tooth/bone offset</th>
<th>Offset from environmental mean</th>
<th>Offset from local fauna median</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Philopatric sex</td>
<td>Dispersing sex</td>
<td>Philopatric sex</td>
<td>Dispersing sex</td>
</tr>
<tr>
<td>Chimpanzees</td>
<td>18%</td>
<td>50%</td>
<td>27%</td>
<td>33%</td>
</tr>
<tr>
<td></td>
<td>18%</td>
<td>50%</td>
<td>18%</td>
<td>50%</td>
</tr>
<tr>
<td>Red colobus</td>
<td>0%</td>
<td>25%</td>
<td>10%</td>
<td>40%</td>
</tr>
<tr>
<td></td>
<td>0%</td>
<td>25%</td>
<td>25%</td>
<td>30%</td>
</tr>
<tr>
<td>Black and White colobus</td>
<td>100%</td>
<td>50%</td>
<td>50%</td>
<td>75%</td>
</tr>
<tr>
<td></td>
<td>100%</td>
<td>50%</td>
<td>50%</td>
<td>75%</td>
</tr>
<tr>
<td>Baboons</td>
<td>0%</td>
<td>40%</td>
<td>0%</td>
<td>40%</td>
</tr>
<tr>
<td></td>
<td>0%</td>
<td>40%</td>
<td>25%</td>
<td>80%</td>
</tr>
<tr>
<td>Guenons</td>
<td>25%</td>
<td>0%</td>
<td>0%</td>
<td>100%</td>
</tr>
<tr>
<td></td>
<td>25%</td>
<td>0%</td>
<td>0%</td>
<td>33%</td>
</tr>
</tbody>
</table>
Figure 3.8: Offsets between tooth and bone strontium isotope ratios for (A) chimpanzees, (B) red colobus monkeys, (C) black and white colobus monkeys, (D) olive baboons, and (E) guenons. Females (red circles) are the dispersing sex in chimpanzees and red colobus monkeys while males (blue triangles) are the dispersing sex in black and white colobus, olive baboons, and guenons. Horizontal black line indicates the mean offset between tooth and bone ratios for the species.
Figure 3.8: Offsets between tooth and bone strontium isotope ratios for (A) chimpanzees, (B) red colobus monkeys, (C) black and white colobus monkeys, (D) olive baboons, and (E) guenons. Females (red circles) are the dispersing sex in chimpanzees and red colobus monkeys while males (blue triangles) are the dispersing sex in black and white colobus, olive baboons, and guenons. Horizontal black line indicates the mean offset between tooth and bone ratios for the species.
Figure 3.8: Offsets between tooth and bone strontium isotope ratios for (A) chimpanzees, (B) red colobus monkeys, (C) black and white colobus monkeys, (D) olive baboons, and (E) guenons. Females (red circles) are the dispersing sex in chimpanzees and red colobus monkeys while males (blue triangles) are the dispersing sex in black and white colobus, olive baboons, and guenons. Horizontal black line indicates the mean offset between tooth and bone ratios for the species. (F) provides a summary of individuals by sex falling above their species' mean offset.
3.6.5 Proxy 3: Tooth/local environment offset

Next, we assessed the offset between individual tooth ratios, again using M1 as it was available, and the local environment. We used the mean non-riparian plant strontium isotope ratio for the cluster on which the animal was collected, based on provenience records from the time of collection. This proxy would be applicable to the fossil record, where often teeth are not found in conjunction with bone and, even in cases where they are, bones are often subject to extreme diagenetic altering making the isotopic ratios retrieved from them invalid. In addition, it is common practice in archeological studies to determine the “local” or “non-local” nature of a specimen by comparing tooth ratios to local environmental proxies, so assessing the validity of this proxy on a known population is of extreme methodological relevance.

We defined the local environment’s strontium isotope signature on the geochemical cluster underlying each research area. Kanyawara and Sebitole are indistinguishable geochemically, both falling on the northern cluster (0.7094426 +/- 0.001). Kanyanchu Chimpanzee Project sits entirely within the southern cluster (0.7169347 +/- 0.0026). The Ngogo Chimpanzee Project is located on top of the anomalously high cluster (0.7273086 +/- 0.004) and extends into the southern cluster, and so was defined as the average of both clusters together (0.7188973 +/- 0.005).

Similar to the tooth/bone offset calculations, no comparisons yielded significant results (Figure 3.9a). There are some notable differences in the results between these two proxies, however. For example, female-philopatric black and white colobus monkeys had greater mean offsets for females, the opposite of the ecologically expected trend
contrary to the pattern of the bone/tooth offsets; the proportion of significant bootstrapped results for chimpanzees increased substantially, but the same proportion decreased steeply for smaller-range red colobus monkeys.

![Offset between tooth and environment strontium isotope ratios: Kibale primates](image)

*Figure 3.9: Offsets between tooth and environment strontium isotope ratios within individuals of each species of Kibale primate by sex, raw data (A) and bootstrapped data (B). For raw data sets (A), Wilcoxon Mann-Whitney rank sum tests $p > 0.05$ for all species. In plot (B), bars show median offset for each sex, diamonds show mean offset, Wilcoxon Mann-Whitney rank sum test $p < 0.05$ in 39% (black and white colobus), 98% (chimpanzees), 100% (olive baboons), 5% (red colobus monkeys), and 100% (guenons) of 10,000 bootstrapped simulations of difference in mean.*

Parametric bootstrapping methods (*Figure 3.9b*) show that 98% of 10,000 simulations yield significant $p$-values ($p < 0.05$) for male-philopatric chimpanzees and 100% of simulations yield significant $p$-values for female-philopatric baboons and guenons. In male-philopatric red colobus monkeys, only 5% of simulations yield significant $p$-values. In female-philopatric black and white colobus monkeys, only 39% of $p$-values are significant, and the trend in the means is the opposite of what is expected based on known philopatric patterns (*Table 3.5*). Taken together, these results show that for small home range primates overall (with the notable exception of the guenons),
comparing the mean of a large geographic area to the tooth strontium isotope ratio cannot
distinguish between philopatric and non-philopatric members. However, for species such
as chimpanzees and baboons with larger home ranges, comparing tooth ratios to the local
environment is an effective metric for distinguishing philopatric and non-philopatric
members. Chimpanzees and baboons both have ranging patterns that are wide enough
given the distribution of strontium variation in Kibale to move dispersing members into
significantly different geochemical areas. Conversely, even dispersing members of
smaller range primates, such as the two species of colobus monkeys, do not move far
enough to significantly differentiate their juvenile tooth signature from the underlying
geochemical cluster; even those that disperse may not move far enough to encounter
isotopic heterogeneity in the environment (recall that the maximum distance for
isotopically homogenous areas in Kibale was 3 kilometers, potentially much farther than
even a dispersing colobus monkey would travel).

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Sample mean tooth/mean environment offset - philopatric sex</th>
<th>Sample mean tooth/mean environment offset - dispersing sex</th>
<th>% of significant p-values (10,000 simulations)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chimpanzees (N=15)</td>
<td>0.001813 (males)</td>
<td>0.003132 (females)</td>
<td>98%</td>
</tr>
<tr>
<td>Red colobus monkeys (N=18)</td>
<td>0.001796 (males)</td>
<td>0.001802 (females)</td>
<td>5%</td>
</tr>
<tr>
<td>Black and white colobus monkeys (N=6)</td>
<td>0.004413 (females)</td>
<td>0.003853 (males)</td>
<td>39%</td>
</tr>
<tr>
<td>Olive baboons (N=9)</td>
<td>0.003626 (females)</td>
<td>0.0081289 (males)</td>
<td>100%</td>
</tr>
<tr>
<td>Guenons (N=7)</td>
<td>0.001234 (females)</td>
<td>0.002458 (males)</td>
<td>100%</td>
</tr>
</tbody>
</table>
We then calculated the proportion of each sex with high offsets (those falling above the mean tooth/environment offset for each species) (Figure 3.10, Table 3.4). Here, all taxa all had a higher proportion of the dispersing sex fall above the group mean offset compared to the proportion of the philopatric sex falling above the group mean offset (chimpanzees: 50% of dispersing sex individuals versus 18% of philopatric sex individuals; red colobus: 30% of dispersing sex individuals versus 25% of philopatric sex individuals; black and white colobus: 75% of dispersing sex individuals versus 50% of philopatric sex individuals; olive baboons: 80% of dispersing sex individuals versus 25% of philopatric sex individuals; guenons: 33% of dispersing sex individuals versus 0 philopatric sex individuals).

Comparing the proportion of each sex above the group mean successfully identified the philopatric sex for all taxa. Even in small-ranging species for which the mean offsets between the sexes were insignificant, this categorical classification method correctly assigns philopatric/dispersal status to the ecologically accurate sex. This suggests that the issue with the comparison of means is a product of small sample size, and proportionately calculated how many individuals of each sex have high offsets relative to the rest of the species is a more robust way to handle data of this sort when sample sizes are low, as they often are in fossil assemblages. This conclusion must be taken with caution and should be verified on larger sample size collections. This proxy should be relied upon only in conjunction with other methods for verification, and is most reliable for species with large home ranges relative to the isotopic variation on the landscape.
Figure 3.10: Offsets between tooth and environment strontium isotope ratios for (A) chimpanzees, (B) red colobus monkeys, (C) black and white colobus monkeys, (D) olive baboons, and (E) guenons. Females (red circles) are the dispersing sex in chimpanzees and red colobus monkeys while males (blue triangles) are the dispersing sex in black and white colobus, olive baboons, and guenons. Horizontal black line indicates the mean offset between tooth and environment ratios for the species. (F) provides a summary of individuals by sex falling above their species’ mean offset.
Figure 3.10: Offsets between tooth and environment strontium isotope ratios for (A) chimpanzees, (B) red colobus monkeys, (C) black and white colobus monkeys, (D) olive baboons, and (E) guenons. Females (red circles) are the dispersing sex in chimpanzees and red colobus monkeys while males (blue triangles) are the dispersing sex in black and white colobus, olive baboons, and guenons. Horizontal black line indicates the mean offset between tooth and environment ratios for the species. (F) provides a summary of individuals by sex falling above their species' mean offset.
Figure 3.10: Offsets between tooth and environment strontium isotope ratios for (A) chimpanzees, (B) red colobus monkeys, (C) black and white colobus monkeys, (D) olive baboons, and (E) guenons. Females (red circles) are the dispersing sex in chimpanzees and red colobus monkeys while males (blue triangles) are the dispersing sex in black and white colobus, olive baboons, and guenons. Horizontal black line indicates the mean offset between tooth and environment ratios for the species. (F) provides a summary of individuals by sex falling above their species’ mean offset.
3.6.6 Proxy 4: Tooth/local fauna median offset

Finally, we assessed whether individuals of the philopatric sex had a smaller offset from the median strontium isotope ratio of local fauna (those collected from the same locality). We used the median tooth ratio for local fauna as opposed to the mean as the reference proxy in order to be more robust against single extreme values biasing the estimation of central tendency.

Similar to the previous two proxies, no species yielded significant p-values in a direct comparison of the means for each sex; only red colobus monkeys and olive baboons had means that trended in the direction that would be predicted by ecological parameters (Table 3.6, Figure 3.11). In bootstrap simulations, 100% of trials yielded significant p-values for red colobus monkeys, and olive baboons. Only 22% of p-values were significant for guenons with the trend in the opposite direction as expected based on behavioral data, although the omission of KFB 228 (the only adult primate in our sample with definitive provenience yielding a mismatched signal between known location and bone isotope ratios) reverses the trend in the data to match expected patterns and yields 100% significant p-values. Chimpanzees and black and white colobus monkeys both show a trend in the opposite direction as expected based on behavioral data with 16% of simulations yielding significant p-values in this “reversed” pattern for chimpanzees and 10% for black and white colobus monkeys (Table 3.6). These results suggest that comparing mean offsets from the local fauna’s median is not a reliable indicator of philopatric patterns.
**Table 3.6:** % significant bootstrap simulations, tooth/local fauna median isotopic ratio offset

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Mean offset from species median - philopatric sex</th>
<th>Mean offset from species median - dispersing sex</th>
<th>% of significant p-values (10,000 simulations)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chimpanzees</td>
<td>0.002209 (males)</td>
<td>0.002077 (females)</td>
<td>16%</td>
</tr>
<tr>
<td>Red colobus monkeys</td>
<td>0.000703 (males)</td>
<td>0.001481 (females)</td>
<td>100%</td>
</tr>
<tr>
<td>Black and white colobus monkeys</td>
<td>0.003413 (females)</td>
<td>0.003213 (males)</td>
<td>10%</td>
</tr>
<tr>
<td>Olive baboons</td>
<td>0.001006 (females)</td>
<td>0.005374 (males)</td>
<td>100%</td>
</tr>
<tr>
<td>Guenons*</td>
<td>0.002709 (females)</td>
<td>0.002023 (males)</td>
<td>22%</td>
</tr>
</tbody>
</table>

*omitting KFB 228 decreases the philopatric sex / female mean offset to 0.000165 with 100% significant simulations
We then calculated the proportion of each sex with high tooth/local fauna offsets (Figure 3.12, Table 3.4). Despite the failure of the comparison of means, like the tooth/environment offset all taxa all had a higher proportion of the dispersing sex with high offsets compared to the philopatric sex (chimpanzees: 50% of dispersing sex individuals versus 45% of philopatric sex individuals; red colobus: 40% of dispersing sex individuals versus 12% of philopatric sex individuals; black and white colobus: 75% of dispersing sex individuals versus 50% of philopatric sex individuals; olive baboons: 80% of dispersing sex individuals versus 25% of philopatric sex individuals; guenons: 33% of dispersing sex individuals versus 25% of philopatric sex individuals).

Overall, the proportion of the dispersing sex with high offsets was the same or
higher for all species using the tooth/local fauna offset proxy as using the tooth/environmental offset proxy, even though the environmental offset was more reliable when comparing means via parametric bootstrapping than the local fauna offset, particularly for fauna with large home ranges relative to the isotopic variation on the landscape. This is potentially an artifact of sample size, and should be further investigated using a larger data set when one become available. Until such a time, the categorical classification approach using either the tooth/environment or tooth/local fauna proxy shows promise.
Figure 3.12: Offsets between an individual's tooth and the local fauna's median strontium isotope ratios for (A) chimpanzees, (B) red colobus monkeys, (C) black and white colobus monkeys, (D) olive baboons, and (E) guenons. Females (red circles) are the dispersing sex in chimpanzees and red colobus monkeys while males (blue triangles) are the dispersing sex in black and white colobus, olive baboons, and guenons. Horizontal black line indicates the species' mean offset between tooth and local fauna's median ratio. (F) provides a summary of individuals by sex falling above their species' mean offset.
Figure 3.12: Offsets between an individual’s tooth and the local fauna’s median strontium isotope ratios for (A) chimpanzees, (B) red colobus monkeys, (C) black and white colobus monkeys, (D) olive baboons, and (E) guenons. Females (red circles) are the dispersing sex in chimpanzees and red colobus monkeys while males (blue triangles) are the dispersing sex in black and white colobus, olive baboons, and guenons. Horizontal black line indicates the species’ mean offset between tooth and local fauna’s median ratio. (F) provides a summary of individuals by sex falling above their species’ mean offset.
Proportion of each sex falling above their species’ mean offset: tooth/local fauna median offset calculation

Figure 3.12: Offsets between an individual’s tooth and the local fauna’s median strontium isotope ratios for (A) chimpanzees, (B) red colobus monkeys, (C) black and white colobus monkeys, (D) olive baboons, and (E) guenons. Females (red circles) are the dispersing sex in chimpanzees and red colobus monkeys while males (blue triangles) are the dispersing sex in black and white colobus, olive baboons, and guenons. Horizontal black line indicates the species’ mean offset between tooth and local fauna’s median ratio. (F) provides a summary of individuals by sex falling above their species’ mean offset.
Table 3.7: Summary of Effectiveness of Proxies

<table>
<thead>
<tr>
<th></th>
<th>Local / Non-local</th>
<th>Tooth/Bone offset</th>
<th>Tooth/Environment offset</th>
<th>Tooth/Local fauna median offset</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chimpanzees</td>
<td>&lt;80% correct</td>
<td>Categorical classification</td>
<td>Means</td>
<td>Categorical classification</td>
</tr>
<tr>
<td></td>
<td>No</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Red colobus monkeys</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Black and white colobus monkeys</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Olive baboons</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Guenons</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
</tbody>
</table>

The categorical classification approach was considered ‘effective’ when a higher proportion of the dispersing sex had ‘high offsets’ (offsets above the species’ mean offset) than the philopatric sex.

A comparison of means was considered effective when 90% or more simulations yielded significant p-values with the dispersing sex having the greater mean offset.

The local/non-local designation proxy was effective if over 80% of individuals was correctly identified as philopatric or dispersing.

“Highly effective” proxies are indicated in bold, when both approaches were effective for a given species.

3.7 Discussion

Results were mixed for all four proxies used to assess philopatric versus dispersing individuals within Kibale National Park primates (Table 3.7). However, there were trends to the successes and failures for each method based on the home range size for each species. Determining the philopatric sex based on a difference in mean tooth/bone offsets between the sexes was successful for the primates with the smallest
home ranges compared to the isotopic variation on the landscape (both species of colobus money and guenons) and also for olive baboons, which have home ranges approximately as large as the meaningful units of isotopic variation across Kibale (5 square kilometers according to Rowell 1966, making dispersal distances of approximately 3 kilometers highly likely for all dispersing individuals based on the correlation between home range and dispersal distance illustrated in Bowman et al 2002). However, it was not successful for identifying the philopatric sex in chimpanzees, who have a home range much larger than the landscape’s isotopic variation. We observed a similar pattern when using the offset from an individual’s tooth and the local fauna median.

In addition to larger home ranges, chimpanzees have a slower life history than monkeys, meaning their enamel takes a longer time to form, during which time they are ranging over a larger area. This leads to a greater averaging effect in both enamel and bone ratios and a broader, more encompassing, and less precise signal. We see this effect illustrated in the teeth of elephants from Kanyawara and Ngogo (Figure 3.6). Elephants have enormously large home ranges, and very slow enamel formation times. Their teeth strontium isotope ratios incorporate ratios from both Ngogo and Kanyawara, leading to overall bulk tissue measurements falling more often in the middle of the two isotopic zones rather than staunchly in one or the other. In addition, while male chimpanzees do live in their natal home ranges for their entire lives, these ranges are quite large and males can inhabit different sub-areas with the home range as a sub-adult with their mother than as an independent adult fighting for a place in the group’s hierarchy. These factors compound to mitigate differences between tooth and bone tissues within the philopatric sex, distorting the expected difference with the dispersing females. Smaller primates have
a faster life history, meaning their enamel and bones are formed over a shorter time span during which they are ranging over a smaller and thus less variable isotopic landscape. The tissue signal is therefore more specific. Because there is sufficient variation within each of the isotopic clusters, the dispersing sex incorporates a different narrow signal in their bones as adults. As there is less time and space incorporated into each tissue, the differences between dispersing and philopatric individuals are more easily distinguished.

Comparing mean offsets between tooth ratios and the local environment successfully identified philopatric patterns in chimpanzees, olive baboons, and guenons, but not in the colobus species, who have the smallest home ranges. This result hinges on having isotopic clusters on the landscape that are commensurate with home range of a given species. In Kibale, the isotopic cluster groups are on the order of tens of kilometers with the greatest distance to encounter isotopic variability being about three kilometers; a small colobus monkey that disperses at most 1-2 kilometers from its natal group, and ranges only a few square kilometers as a home range, will not show a different offset from that large environmental cluster when compared to an individual that did not disperse at all. The mean ratio of the isotopic cluster encompasses too large of an area to be spatially meaningful to an animal with a home range and dispersal distance that much smaller. Chimpanzees, on the other hand, have home ranges that more closely approximate the size of the isotopic clusters. Therefore, it is reasonable to assume that individuals which move will show a difference from the averaged environment versus those whom have always lived on it. This tooth/environment method is therefore appropriate for species with ranging behaviors similar in scale to the isotopic clusters on the landscape.
Tooth/bone and tooth/local fauna median offsets also did not lead to conclusive results for chimpanzees when examining the proportion of each sex with high offsets, although it worked moderately well for most monkeys. This difference in conclusions for the chimpanzees can be explained by the nature of the tooth/local fauna offsets; while fewer philopatric males had above-average offsets than dispersing females, those males which did have large offsets had much larger ones than the females did. This drives the means to be indistinguishable, while the number of individuals does separate out by philopatric pattern. Nonetheless, the differences between the sexes were still very small, and we can conservatively conclude that offsets between tooth and bone and between tooth and local faunal median ratios work well for small-ranging primates, but not for wider ranging primates, particularly when coupled with slow life histories. In conjunction with other methods, however, the proportion of each sex falling above the mean for tooth/local fauna median offsets is worth examining.

We also evaluated a categorical classification approach to identifying which sex was philopatric and which dispersed based on the proportion of each sex with high offsets - that is, the proportion of each sex falling above the mean offset for the species. For tooth/bone offsets, this approach was only marginally successful in chimpanzees and not at all for black and white colobus monkeys, despite the significant difference in means between male and female black and white colobus. This is likely because black and white colobus moneys overall had very high offsets between tooth and bone tissues, and because the sample size for this species was small, the proportionate differences were unclear. Because the small sample issue is one that we expect to encounter when working with fossil material, this is not a recommended method for assessing which sex disperse
and which does not for any taxa, regardless of range size, based on these data.

Comparing the proportion of each sex with a tooth/environment high offset was reliable for all species, even for small-range monkey species for whom the comparison of means was not significant, and was the most reliable method for identifying the philopatric versus dispersing sex in chimpanzees. For fossil species with ranges that approximate the size of the landscape’s isotopic clusters, this should be the method of choice for identifying dispersal patterns.

Using the proportion of each sex with a high offset within the tooth/local fauna approach was also successful for all species, although less powerful than the tooth/environment offset method for chimpanzees. For baboons and black and white colobus, it was equally as successful as the tooth/environment offset, and was marginally more successful for guenons and red colobus monkeys. Based on these results, we would recommend using tooth/environment offsets to establish the philopatric sex for species with home ranges approximating the size of the isotopic clusters on the landscape and tooth/local fauna median offsets for species with smaller home ranges. Additionally, we recommend that alternative approaches, particularly this categorical classification method, always be used as a secondary evaluation of the data for all species in question.

The most commonly used method in human archeology of determining “non-locals” (here, members of the dispersing sex) versus “locals” (here, members of the philopatric sex) is qualitatively assessing who falls within the boundaries of local bedrock and who does not. This method’s highest success rate was 71%, for chimpanzees, and substantially lower for all other species. It was not successful for any taxa at the Ngogo field site, which had a much wider spread of isotopic values within the local area, nor was
it particularly successful at identifying migrants. In fact, the proportion of migrants successfully identified through this method was never higher than 50%. This method suffers from the same spatial scale issues as the tooth/environment offset method; the philopatric pattern of species with dispersal distances that do not take them off the local isotopic cluster, even as they disperse, will be undetectable. Partially because of this bias, this method consistently overestimates the number of “locals” within a population while failing to identify non-local / dispersing individuals. Any conclusions drawn using this method must bear this bias in mind; the number of philopatric/local individuals is likely to be overestimated, and the number of dispersers/non-local is likely to be underestimated. This method should generally be regarded as unreliable for identifying philopatric patterns, particularly when species have home ranges small relative to the isotopic variation on the landscape.

The proxy chosen to identify the philopatric versus dispersing sex in each species must depend on the relative sizes of the species’ home ranges and the isotopic clusters on the landscape. If the ranging and dispersal distances of your species of interest approach the size of the distance between isotopically homogeneous areas, calculating individual offsets from the local environmental mean is the most reliable method to determine which sex is philopatric and which disperses, with offsets from the local faunal median as a good secondary verification, particularly when we categorically classify the data. If your species of interest has a home range and dispersal distances that are very much smaller than the identified isotopic clusters on the landscape, then offsets from the local faunal median is the most reliable proxy, tentatively with offsets between tooth and bone ratios of the same individual (if available) as a secondary approach.
3.8 Conclusions and Future Work

Strontium isotope ratios hold great potential for uncovering aspects of social behavior and landscape use for fossil species. However, standard methodologies in which researches look only at whether an individual’s tooth strontium isotope ratios fall with the local bedrock ratios are not sufficient or effective metrics for all taxa. First, it is critical to establish meaningful geochemical clusters on the landscape which may or may not align with bedrock types; in some areas, such as South Africa, it may be that multiple bedrock types have overlapping or similar enough ratios such that they are not geochemically distinct zones. In other areas such as Kibale, the geologic mapping of the region may not align with isotopic measurement, either due to poorly mapped areas or due to other isotopic inputs, such as dust or precipitation. In any of these cases, if the question revolves around the geochemical measurements of faunal tissues, clear mapping of the landscape’s meaningful geochemical clusters in the region is a necessary first step.

The size of these clusters and the distance between isotopically homogenous areas must be regarded in relationship to the ranging behavior of the species of interest. For fauna with meaningful ranges and dispersal distances that are much smaller than the geochemically homogenous areas on the landscape, it is the variation within each cluster that holds potential for identifying movement patterns; the variation between clusters will not be relevant. For these kinds of species, measurements such as the offset between the individual’s tooth and bone, when available, or the offset between the individual’s tooth and the median tooth ratio for the local fauna, is more likely to clearly illustrate those
individuals who changed localities during life (the dispersing sex). That is because these measurements do not require offsets from the greater environmental geochemical cluster; rather, they provide relative metrics of how different the individual is from either itself at another point in time (tooth/bone offset), or how different the individual is from the median of the group (tooth/local fauna offset). As long as there is variation within the isotopic cluster, these measurements will both be higher for members of the dispersing sex.

For species for which the geochemical clusters on the landscape are nearer the size of a meaningful geospatial cluster for the species (such as chimpanzees or potentially olive baboons in Kibale, who have a home range approximately the same size as the distance between isotopically uniform landscape areas), these offset proxies are not effective ways to measure mobility patterns. Instead, larger range sizes cause a greater range of strontium isotope ratios from the landscape to incorporate into tissues, creating averaging effects that blur differences from philopatric dispersal versus other mobility patterns (such as preferring different parts of the home range at different life stages, as male chimpanzees). Instead, because ranging and dispersal distances are great enough to cross geochemical clusters, the differences between clusters become informative comparisons for deciphering philopatric mobility, specifically. In the case of these species, comparing the offset between individual teeth and the local environment is the most accurate method for identifying the philopatric versus dispersing sex.

This study has improved on previous work by incorporating the size of general home range into the calculation of philopatric patterns, potential variation from riparian versus non-riparian areas, and the role of life history and enamel development times. We
have tested multiple proxies and developed methods for the most accurate prediction of philopatric patterns taking these variables into consideration. This work can be expanded through broader identification of the sex of more non-primate remains from Kibale National Park. While many specimens of suids and bovids are included here, very few of them have clear sex identification. Therefore, the methods developed here using the primate dataset cannot yet be tested on non-primate fauna.
Chapter 4:
RE-EXAMINING DISPERsal SYSTEMS IN SOUTH AFRICAN HOMININS USING STRONTIUM ISOTOPES

4.1 Introduction

This reconstruction of our ancestral dispersal patterns has major implications for the evolution of modern human behavior. Dispersal patterns determine which sex remains with kin and reaps the benefits of that inclusive fitness. The sex who remains with their kin is more likely to form strong affiliative bonds with their siblings and cousins of that same sex; in chimpanzees, this forms the foundation for male coalitions that influence everything from territory patrols to mating. In most monkeys, females are philopatric, and female coalitions defend resources, and protect infants from potentially infanticidal males (van Schaik, 1989, Hrdy 1999).

Strontium isotope ratios are incorporated into enamel based on the location of the food eaten during that enamel’s formation. Therefore, a comparison between tooth enamel strontium isotope ratios and the strontium isotope ratio from the plants growing in the area surrounding the area where the fossils were excavated (and presumably near where the hominins lived near the end of their lives) could identify those hominins which were local, presumably members of the philopatric sex, and which were migrants, or members of the dispersing sex.

While this paradigm is very clear in theory, there have never been any studies in modern primate ecosystems examining the reliability of strontium isotopes as markers of
dispersal. Many areas surrounding fossils deposits are extremely geologically complex, and the simple “local” versus “non-local” distinctions for strontium isotope ratios may not be the most accurate way to capture the variation incorporated into tooth enamel in a slow-growing, wide-ranging taxa such as the australopithecines. One study, published in Nature in 2011 by Copeland and colleagues, collected and compared strontium isotope ratios from *Australopithecus africanus* and *Australopithecus (Paranthropus) robustus* from Swartkrans/Sterkfontein caves in South Africa. The authors use techniques common to strontium isotope analysis in archeological literature which generally do not take into account the numerous variables making modern human mobility different from faunal dispersal patterns. The purpose of the following study is to apply best-practices identified through modern strontium isotope ratio modeling studies for dispersal markers (see Chapters 1 and 2) to strontium isotope ratios of hominin tooth enamel and reconstruct the most likely dispersal patterns for South African hominins.

4.2 History of Sterkfontein and Swartkrans Excavations

In August of 1936, Dr. Robert Broom discovered the first adult *Australopithecus africanus* (TM 1511) at Sterkfontein Cave, an old limestone quarry located about 50 kilometers northwest of Johannesburg, South Africa. In 1948, barely a kilometer away, the discovery of *Australopithecus (Paranthropus) robustus* specimens opened excavations at Swartkrans Cave. Together, along with over dozen other caves in the vicinity, these fossil rich deposits are a protected UNESCO World Heritage site referred to as the “Cradle of Humankind” and are one of the most prolific paleontological fossil
deposits in the world, yielding remains of several hundred hominins (Tobias 2000). Some of the most notable finds from these cave systems include “Mrs. Ples” (Sts 5), a complete skull of *A. africanus* (Thackeray 2000), “Little Foot” (StW 573), a nearly complete skeleton (including eponymous small foot) just recently removed from the cement-like breccia of the cave (Clarke 2008), and the type specimen of *A. robustus* from the associated Kromdraai cave (Brain 1983). The cave systems also contain some of the earliest evidence of fire (although disputed as to origin) (Sillen and Brain 1990), tools used for digging (Brain and Shipman 1993), and sympatric species of hominins (*Homo* and *A. robustus*). More recent discoveries such as *A. sediba* at the Malapa site and *H. naledi* in the nearby Rising Star cave system (Berger et al 2015) hint at how much material is certainly left to discover within these deposits.

Swartkrans and Sterkfontein caves are part of a system formed by the Blaaubank River and today are located on either side of the small waterway, approximately 30 meters above the modern river (Avery 2001). Formation processes within the Plio-Pleistocene sediments of the cave are inactive today, although younger deposits below the hominin bearing layers are still active (Herries and Shaw 2011). The original area of excavation at Sterkfontein, today referred to as the Type Site, is located on the eastern side of Sterkfontein Cave (“Sts” specimens). To the west is the Extension locality (Sw specimens). At Swartkrans, specimen labels differentiate between the primary breccia (SKa) and those from the secondary breccia (SKb). The nearby Kromdraai cave, part of the same vast cave system and home to the type specimen of *A. robustus*, also yields significant faunal and *Australopithecus* fossils from similar time periods (KA and KB specimens) (Vrba 1974). Today, fossils from the caves are primarily housed at the
4.3 Geologic Setting for the Cradle of Humanity

The Cradle of Humankind sits on the western edge of an Archean basement gneiss formation referred to as the “Johannesburg Dome,” a 3.1 billion year old basement complex (Anhausser 2006, Robb et al 2006). The Dome is surrounded by sedimentary and volcanic deposits including the Malmani dolomites, on which we find the famous cave deposits (Eriksson et al 2006). The Malmani dolomites are part of the Malmani subgroup of the Chuniesporrt Group and Transvaal Supergroup. This supergroup is between 2.2 and 2.6 billion years old (Eriksson and Reczko 1995, Eriksson et al 2001). The Malmani subgroup is characterized by stromatolithic dolomite with chert inbeds; the dolomite itself is rich in iron and manganese (Matini et al 2003, Sutton 2013). The subgroup is composed of five formations: the Oaktress, the Monte Cristo, the Lyttleton, the Eccles, and the Frisco formations (S.A.C.S. 1980). Swartkrans and Kromdraai cave sit entirely on the Monte Cristo formation white Sterkfontein sits at the contact between the Oaktree and Monte Christo formation. The Oaktree formation sits on top of Black Reef quartzite, which is primarily quartzite and conglomerate. Oaktree is characterized by chert-poor dolomite deposits and thick horizons of shale. In contrast, the Monte Christo formation is rich in chert within the shale horizons (Dirks and Berger 2013, Sutton 2013).

Today, Swartkrans and Sterkfontein sit on a strip of exposed dolomite approximately 10 km wide (Figure 4.1). To the immediate northwest, quartzite and shale
of the Pretoria group outcrop, dating to approximately 2.2 billion years old. Beyond these outcrops are the Daspoort quartzite formation and alternating bands of diabase and undifferentiated quaternary sedimentary deposits. To the southeast of the caves is the Witswatersrand Supergroup (3-2.7 gya), underlain by 3 billion year old Archean granites which outcrop to the east of the caves. Much farther to the southeast of the cave systems are outcrops of the Karoo Supergroup (2.8-1.8 mya), which would have been part of the African erosional surface during the time of *A. robustus* and *A. africanus* as well as some of early *Homo* (Dirks and Berger 2013).

Figure 4.1: Geologic context for Swartkrans and Sterkfontein caves, from Copeland et al (2011) (left) and Dirks and Berger (2013) (right). Black outline on right map shows the boundaries of the Cradle of Humanity. Black square shows relative position of Copeland et al (2011) map.
It is important to explore how this landscape geology may have differed from present 2-4 million years ago. First, the Timeball Hill shale formation would have covered a more extensive area than today. The downcutting of the Scheerpoort River has progressively removed large areas of the Timeball shale over the past few million years. This rapid removal of the shale relative to the slow erosion of the dolomite results today in an elevational drop between the two formations, and increased dolomite surface area exposure concurrent with a decrease in the area covered by the shale (Dirks et al 2010, Dirks and Berger 2013). Second, the African erosional surface of 2-4 million years ago was formed in part by the Karoo Supergroup. Today this can be found as outcrops to the southeast of the cave system, but would have covered larger sections of the Cradle before eroding away (Dirks and Berger 2013, see Fig 10). This means that depending on how sound models of geologic dynamics in the Cradle of Humanity are, the underlying geology around Swartkrans and Sterkfontein caves may have been quite different in the past.

4.4 Overview of cave stratigraphy and dating

The stratigraphy and dating of the Sterkfontein Formation is complex due to both natural and anthropogenic factors. In the late 1800s, both Swartkrans and Sterkfontein caves were active limestone quarries, and copious amounts of dynamite and explosives were used to expose and break apart the breccia. Removal of material during this mining, infilling processes, and heavy sedimentary reworking have all cause unnatural and unintuitive shifts in the stratigraphy of the cave (Granger et al 2015). Even without
humans’ help, the system includes numerous overlapping stratigraphic layers with few exposed sections and suffers from both heavy erosion and natural cave collapses, all of which complicate dating methods (Granger et al 2015, Herries and Shaw 2011, Avery et al 2010). Nevertheless, decades of dedicated work have brought with them order and understanding of the caves’ complex deposits.

Brain (1983) describes the formation of the Sterkfontein and Swartkrans cave systems occurring in six stages. First, below the water table, eroding or dissolving dolomite created cavern spaces, a process is called karst process which occurs when rainwater is in equilibrium with both atmospheric carbon dioxide and the soil, forming a weak carbonic acid that can dissolve calcite (Leyland 2008). In the second stage, the water table drops below the cavern space, leaving it filled with only air. Third, vertical shafts called avens form in the dolomite reaching from the cavern to the open air above; fourth, these avens pierce through to the surface leaving openings on the ground through which bones and detritus can fall. Once open to the surface, bones and detritus begin to gather in a talus cone within the cavern. This calcifies as lime solution drips downwards. The resulting calcified mass is called cave breccia. In stage five, as the openings into the cave from the avens grow larger, so does the breccia, slowly filling the cavern space. In the final stage the surface is entirely worn away, exposing the breccia layer and all the calcified and fossilized bones within (Brain 1983, Sutton 2013).

Partridge (1978) divided the breccia Sterkfontein Cave stratigraphy into 6 main members. Members 4-6 are exposed on the surface while earlier members are accessible only within the cave system itself (Granger et al 2015). Partridge believed that the members were chronological (Patridge and Watt 1991), but later worked showed that
Sterkfontein Cave actually has an “inverted age stratigraphy” with flowing water depositing new material beneath the now-inactive Plio-Pleistocene cave deposits (Herries and Shaw 2011).

Relative dating attempts of Sterkfontein lead to a wide variety of age estimates (Vrba 1985, McKee et al 1995, Delson 1984, Berger et al 2002, Kuman and Clarke 2000) as did early attempts to absolutely date deposits with electron spin resonance (ESR) (Shwarcz et al 1994, Curnoe 1999), cosmogenic nuclide dating (Partridge et al 2003), uranium/lead dating (Walker et al 2006), and paleomagnetic on brecciate and clastic deposits (Adams et al 2007, Herries and Shaw 2011). Finally, a consensus combining paleomagnetic dates from more reliable speleothem deposits (Partridge et al 1999), ESR, and relative dating techniques landed the bulk of Member 4 deposits around 2.2-2.6 mya, Member 5A around 1.8-1.5 mya, 5B 1.4-1.2 mya, and 5C from 1.2 - 1.07 mya (Herries and Shaw 2011). These new consensus dates are important because they place the *A. africanus* fossils in Member 4 and below, including Mrs. Ples and Little Foot, slightly older than the 1.95 mya *A. sediba* fossils from Malapa (1.95 mya, Dirks et al 2010) and also slightly older than the concurrent early *Homo* and *A. robustus* fossils in Member 1 of Swartkrans (2 mya, Herries et al 2006).

Originally Swartkrans was divided into two members, the six meter thick Member 1 including three sub-divisions and 10 meter thick Member 2 (Butzer 1976). Later excavations by CK Brain (1981, 1993) further divided Swartkrans into five members, potentially filled during interglacial periods in the Plio-Pleistocene (Brain 1995, Avery 2001). Member 1 consists of the Hanging Deposit and the Lower Bank, both of which have yielded specimens of *A. robustus* and early *Homo*. Member 2 likewise has record of
both species; in Member 3, excavators only find *A. robustus*. Member 4 does not have any definitive hominin skeletal material but does have a plethora of Middle Stone Age stone tools. Member 5 also has both *Homo* and *A. robustus* material (de Ruiter 2003).

Similar to Sterkfontein, early attempts to date the deposits at Swartkrans lead to a wide array of conclusions (de Ruiter 2003, Blackwell 1994, Curnoe et al 2001, Balter et al 2008, Sutton 2013, Vrba 1995). Based on fauna alone, there is very little to distinguish Member 1 from either Member 2 or 3. Herries et al (2009) summarized results from multiple dating methods (faunal analysis, archeology, paleomagnetism, ESR, and uranium series techniques) to settle on a date of approximately 2 mya for Member 1, and wide ranges of 1.7 - 1.1 mya for Member 2 and 1.0 - 0.6 mya for Member 3.

4.5 Paleoecological reconstructions

Swartkrans and Sterkfontein cave sit along the banks of the Bluubank River, which today is approximately 4 meters across at its widest point. However, 2-4 mya this waterway would have been much more substantial, carving the valley that currently separates the two cave localities (Watson 1993). Vrba’s hypothesis of increasing aridity through the last 3 million years in Africa is consistent with data from these South African sites (Vrba 1975, Rowan and Reed 2015) and isotopic studies (Lee-Thorpe et al 2007). Broadly speaking, paleoecological reconstructions of the Cradle of Humankind are mosaic environments, consisting of gallery forests along the edges of the larger rivers extending into more open grasslands or grassy woodlands with a mixture of C3 and C4 vegetation (Dirks and Berger 2013). For example, the presence of bovids in the
Antilopini and Alcelephini tribes in all three members of Swartkrans cave suggest available grassland ecotones, while hippopotamus fossils mandate permanent sources of water, and larger fauna such as elephants and giraffes suggest some extensive open woodland habitat in the area as well (de Ruiter 2003).

Very little work has been done on the earliest Sterkfontein members. Pickering et al (2004) examined the faunal composition of the Member 2 deposit, concurrent with Stw 573, possibly up to four million years old. The authors note that most fauna is either primate or felid, biasing towards taxa more likely to be climbers. With this caveat, they nonetheless conclude that the valley must have had some standing permanent water source due to the presence of monkey fossils and Alcelephini bovids. Caracals were the most common felid in the deposits. The presence of this “rock cat” coupled with an abundance of “goat-like” bovids (*Makapania broomi*) suggest that the terrain was rocky brush and scrubland.

More recent members receive more thorough attention. Beginning with Sterkfontein Member 4 (roughly 2.2-2.6 mya), we can see changes in habitat through time more concretely. Reed (1997) employs a whole-community paleoecological approach to habitat reconstruction based on patterns between modern African ecosystem death assemblages and habitat vegetation structure. She notes the absence of arboreal mammals in the Member 4 deposits but a high percentage of frugivores, and she designates it an open woodland with nearby brush and thicket (Reed 1997). This is similar to the description in Vrba (1975) of a “medium density woodland” based on bovid composition and more open than McKee (1991)’s “forest.” Avery (2001) looked at micro mammals specifically, and notes a high proportion of riparian grassland species but a low
minimum number of individuals for each of these species. The author interprets this as a
decrease in grasslands during this time due to an increase in riparian forest habitat.

At Member 5, accumulated roughly 2 mya, small mammal assemblages suggest
more extensive riverine grasslands with the convergence of savanna and grassland
ecotones not far away (Avery 2001). This is consistent with Reed (1997)’s
reconstruction. She notes that there are no longer any arboreal species present nor any
frugivores; meanwhile, the number of grazing species increases dramatically from
Member 4. She describes it as an open-to-wooded grassland, or moderately open savanna
ecosystem with a mesic closed woodland microhabitat. Neither interpretation are in
conflict with Vrba’s assessment of an open savanna ecosystem based on the bovid
composition (Vrba 1975). Likewise, McKee (1991) concludes that Member 5 represents
a more open habitat than that present during Member 4’s accumulation, but also holds
that there must have been nearby riparian forest.

Swartkrans members roughly concurrent with Sterkfontein Member 5 show a
higher proportion of riverine grassland micro mammal taxa, suggesting that Swartkrans
were closer to the paleo-Bluubank River than neighboring Sterkfontein (Avery 2001,
Kuman and Clarke 2001). Reed (1997) reconstructs Swartkrans Member 1 as an open
habitat with a medium-density woodland and/or edaphic grasslands near the river. The
presence of aquatic fauna mandates a standing water source, and a high percentage of
frugivores indicates that a riverine or riparian forest was present surrounding it. Watson
(1993) also suggests that Member 1 is a riparian woodland habitat. Isotope ratios from
small mammals likewise point towards a permanent water source surrounded by open, C4
grasslands. *Otomys* spp., a wetland specialist rat species, is robustly present. These
individuals have low carbon isotope ratios consistent with waterlogged food sources. Meanwhile, other small mammals in the same deposit have much more enriched carbon isotope ratios more consistent with a hefty C4 component to their diets (Leichlitter et al 2017).

Despite the suggestion that Member 2 and 3 at Swartkrans might be relatively contemporaneous with Member 1 (Brain 1993), there is a marked decrease in frugivores in Member 2 compared to Member 1 and an increase in fresh grass eaters and grazers (Reed 1997). Together these shifts suggest a more open habitat, agreeing with Vrba (1975) that it was a moderately open savanna. This trend continues through Member 3, as frugivores continue to decrease but fresh grass eaters and grazers continue to increase, suggesting that the riparian forest continued to give way to increasing grasslands (Reed 1997).

4.6 Summary And Evaluation of Copeland et al (2011)

In 2011, Dr. Sandi Copeland and colleagues made news headlines across the popular and professional scientific press with a letter in the journal Nature. This short article described their research using laser ablation to measure the strontium isotope ratios of tooth enamel from *Australopithecus africanus* and *Australopithecus (Paranthropus) robustus* from Swartkrans/Sterkfontein caves in South Africa. They concluded that more of the small molars had “non-local” strontium isotope signals compared to the large molars. Australopithecines have high levels of sexual dimorphism, so researchers assumed that the small teeth represented the females of each species and
the large teeth represented the males. Therefore, Copeland et al (2011) concluded that, similar to chimpanzees today, males remained in their natal communities through life while females dispersed to other communities to reproduce.

Copeland et al (2011) focused their research on 11 *A. robustus* specimens from Swartkrans cave Member 1 and 8 *A. africanus* specimens from Sterkfontein cave Member 4. The *A. robustus* specimens are therefore about 2 million years old, and the *A. africanus* specimens slightly older at around 2.2 - 2.6 million years old (Herries 2009, Herries and Shaw 2011). Ecologically, Sterkfontein was most likely an open-to-medium-density woodland with nearby areas of brush and thicket with a riparian forest along the banks of the Bluubank (Reed 1997, Vrba 1975, Avery 2001). Swartkrans around the time of Member 1’s accumulation was likewise in or near a riparian forest and/or edaphic grassland (Watson 1993, Reed 1997), but with C4 food sources nearby (Leichliter et al 2017).

Based on occlusal surface size (buccolingual distance multiplied by mesiodistal distance, in mm²), Copeland’s team designated individuals as either ‘male’ or ‘female,’ with the former falling above the species’ mean for that particular tooth and the later falling below the species mean for that particular tooth. Those falling more than one standard deviation either above or below the mean were treated with extra certainty. Species means were determined through measurements of all available teeth housed at the Ditsong National Museum of Natural History in Pretoria, South Africa. In addition to hominins, Copeland et al (2011) included 7 fossil cercopithecines, 11 rodents in the family *Procaviidae* (similar to modern hyraxes), and 19 ungulates from the family *Bovidae*, all also from the same time period in Swartkrans and Sterkfontein caves.
Using a collection of 170+ plants from across the multiple geologic outcrops within 50 km of the caves, the researchers created a map of possible strontium isotope ratios considered “local” to each geologic formation (see Figure 4.1). These geologic sections are often quite thin, and according to the authors there is very little vegetative or geographic distinctions that would hinder travel across the boundaries. The measured strontium isotope ratios on each geologic area overlapped extensively, meaning that a given isotopic value could be considered “local” to multiple geologic areas (Figure 4.2). They used a relatively new and much less destructive method called laser ablation multi-collector inductively coupled plasma mass spectrometry (MC-ICP-MS) to measure the strontium isotope ratios from hominin and non-hominin tooth crowns. They found that a much higher proportion of small hominin teeth (50%) fell outside of the “local” range of the dolomite underlying the cave systems than large hominin teeth (11%) or any of the other fauna (15% or less). When only the largest and smallest teeth were included, thus making the sex assignments more certain, 75% of small teeth and only 17% of large teeth fell outside of the possible local range. From these data, Copeland and colleagues concluded that the small-tooth females were dispersing at sexual maturity while the large-tooth males remained philopatric.
While their conclusion is consistent with the most parsimonious model of hominin philopatry, there are some methodological concerns to this study. The laser ablation method with which they obtained the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios has been called into question (see Balter et al 2012). Briefly, when using laser ablation on curved surfaces, such as the outside of teeth as in Copeland and colleagues’ work, some measured areas are out of the focus depth of the laser. This can produce differences in the size of the particles being ablated and isotopic fractionation during the ionization process. This can lead to increased variance and widely variably intra-tooth isotopic ratios. Balter et al (2012) claim this non-biological process explains why the smallest teeth in Copeland et al’s dataset, which also happen to be those that are the most different from the local dolomite isotopically, have the highest intra-tooth variance. This observation causes
Balter et al (2012) to dismiss the findings from the 2011 paper despite the fact that their own measurements (taken with more traditional methods) of different hominin teeth show high strontium isotope variability, particularly in *A. robustus*, including measurements that fall outside of the range off the local dolomite based on Copeland et al (2011)’s plant data. Balter and colleagues do not test differences in isotopic ratios by tooth size as in the original paper, so a comparison of the results between the studies is not possible to do directly.

In addition to methodological concerns, the scenario in which male hominins confined their range to the very small Malmani dolomite is highly unlikely. Both *A. africanus* and *A. robustus* were bipedal, a highly efficient form of locomotion for covering large distances. Modern chimpanzees have home ranges that range from 15 km² in Kibale National Forest (Chapman and Wrangham 1993) to 27.4 km² in Mahale (Nakamura et al 2013), both forested habitats, and over 85 km² in the open habitat of Fongoli, Senegal (Pruetz 2006). The mean estimated local group range for Old World non-equestrian hunter-gathers such as the Hadza is 471 km² (with hunting behavior driving a large portion of this range size) (Marlowe 2005). Bipedal australopithecines in an open habitat are likely to have home ranges intermediary between knuckle-walking chimpanzees and hunting modern humans. The authors do not consider the impacts of a larger range, likely one that would have encompassed numerous geologic zones. There is no discussion of an “averaging” effect or attempts to use methods that take range size into consideration. It is also possible that food from certain substrates contribute disproportionately to the isotopic makeup of an animal’s tissues. For example, dolomite generally has high calcium concentrations, while gneiss (the neighboring rock formation
to the Malmani dolomite) is more variable in its elemental concentrations (Rowe et al 2012). While the concentration of an element in a given formation will not have an effect on the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio itself, the ratio that is incorporated into animal tissues could be disproportionately affected by formations with higher elemental concentrations, even if plants on all formations are consumed equally.

The “local” isotopic ranges on each of the geologic substrates surrounding the fossil sites overlap extensively (Figure 4.2). If the geologic substrate immediately adjacent to the Malmani dolomite is included in the local range - very possible, considering the likely daily ranging patterns of bipedal hominins - then none of the $A. \text{africanus}$ teeth and only two of the $A. \text{robustus}$ teeth become non-local. Given the small sample size, large error bars on some of the tooth measurement, and likely ecological conditions, it is imperative to discuss this variability when drawing any conclusions. Methods that rely on independently-derived geochemical clusters rather than geologic boundaries could incorporate all this variation into the model and draw more geospatial informed conclusions.

As described in Dirks and Berger (2013), while strontium isotope ratios in a given geologic context are the same today as they would have been 4 million years ago due to the very long half-like of rubidium-87 (Bentley 2006), the assumption that the geology of an area as active as South Africa would remain stable may not be valid. Today, the Malmali dolomite stretches in a thin 10 km ribbon across the Cradle of Humankind; however, two and four million years ago, the Timeball Hill shale deposits to the north of the cave systems would have been far less eroded and covered a greater geographic area. Large portions of the area’s surface would have been covered by the Karoo mud and
sandstone, today just outcrop deposits far to the west of the cave system and not included in the sampling area by Copeland et al. The Bluubank River would have been much wider (Watson 1993), also diminishing the exposed land area underlain by dolomite. Given these geologic dynamics, it is worth exploring methods that do not rely on modern strontium isotope mapping to determine local versus non-local individuals when possible. These types of methods have not been fully developed until the present work.

There are also alternative explanations worth exploring for the more radiogenic $^{87}\text{Sr}/^{86}\text{Sr}$ ratios observed in small hominin teeth. For example, strontium from water sources may shift ratios due to erosion processes upstream. The authors do not discuss the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of the water, although they do mention that the dolomite has abundant water resources. Sillen et al (1998) measure the strontium isotope composition of many of the nearby water sources and find that most fall on the low end of the ratios measured within the dolomite. Sillen and colleagues find evidence for a strong riparian effect near the Bluubank River, which we can extrapolate would have existed in the riparian forest present there two million years ago (see Chapter 2 for more discussion on riparian forests). Aquatic and riparian plants acquire the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of the water they grow in rather than the bedrock, as we demonstrate in our work at Semliki Wildlife refuge. Many dietary reconstructions for particular $A.\ robustus$ show a generalized mixed C3/C4 diet (Lee-Thorpe et al 1994), of which riverine resources such as wetland sedges could have been an important component.

Finally, the effects of vertical position within an ecosystem on $^{87}\text{Sr}/^{86}\text{Sr}$ ratios are not well understood. Poszwa et al (2002) demonstrate that $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of roots generally increase with depth in an Amazon ecosystem up to 50 centimeters below the
surface. If this is the case, the $^{87}\text{Sr}/^{86}\text{Sr}$ ratios of small individuals could be driven up if their diet included a larger proportion of underground storage organs than the larger individuals. Conversely, the effects of canopy height on $^{87}\text{Sr}/^{86}\text{Sr}$ ratios have not been established. This is essential information to test whether or not the difference in $^{87}\text{Sr}/^{86}\text{Sr}$ ratios by size could be driven by other factors unrelated to philopatry and dispersal.

Even if the findings by Copeland et al (2011) are taken to be robust, Koenig and Borries (2012) raise the possibility that a Pan-like philopatric pattern is not the only model that fits such results. A gorilla-like pattern, for example, which includes bisexual dispersal but patrilocality of males would also generate the same predicted pattern of radiogenic strontium isotope ratios. Lockwood et al (2007) also suggest that $A. \text{robustus}$ may have been gorilla-like in their social structure. In other words, dispersal distance of each sex is also an important factor to consider. Therefore, estimates of range size are critical for the interpretation of philopatric signals. Although much less work has been done on the topic, populations of local ranging fauna (those that do not leave one geological area) have less variance in their strontium levels, while animals that range over a wide area will have much higher ranges of variance (Bentley 2004, Feranec et al 2007). The best way to differentiate between the two patterns of philopatry is a comparison with modern datasets, such as chimpanzees or gorillas, with known philopatric patterns.

4.7 Methods

4.7.1 Plant samples
For this study, we used strontium isotope ratios from 154 plant samples collected in a 50 km area around Swartkrans and Sterkfontein caves (Copeland et al, unpublished data). Replicating methods that were successful at identifying primate dispersal patterns in Kibale National Park, Uganda (see Chapter 1), we used hierarchal cluster analysis with an average linkage distance to identify isotopic clusters across the South African landscape rather than relying on geologic boundaries, as in the original study. We mapped these clusters using the GG-Map package in R Studio.

4.7.2 Faunal samples

For faunal data, we used strontium isotope ratios from hominins and associated fauna published in Copeland et al (2011) and Balter et al (2012). Copeland et al (2011) divided their hominin teeth into ‘large’ and ‘small’ specimens, working under the assumption that, due to the high degree of sexual dimorphism in australopithecines, the small teeth were from females and the large teeth were from males. Large teeth were any falling above the mean occlusion surface tooth size for the species while small teeth were any that fell below. Balter et al (2012) did not publish size measurements or sex estimations for their sampled hominin teeth. Where possible, we found measurements from the literature for the samples included in Balter et al’s study and designated these teeth (N=6) as ‘small/female’ or ‘large/male’ based on comparison to published species’ means (see Table 4.1). For those that were confirmed to be fragments of enamel (N=6), and therefore not measurable, and for which no information could be found (N=1),
strontium ratios are shown but the teeth are not included in any further analyses.

**Table 4.1: Tooth dimensions from available Balter et al (2012) samples**

<table>
<thead>
<tr>
<th>Specimen ID</th>
<th>Species</th>
<th>Tooth sampled</th>
<th>Occlusal surface in ( \text{mm}^2 ) (BL * MD)</th>
<th>Species mean occlusal surface (( \text{mm}^2 ))</th>
<th>Male/female (?)</th>
</tr>
</thead>
<tbody>
<tr>
<td>STS 72</td>
<td><em>A. africanus</em></td>
<td>M3</td>
<td>182(^1)</td>
<td>150.6 ± 17.4(^4)</td>
<td>Male</td>
</tr>
<tr>
<td>TM 1517</td>
<td><em>A. robustus</em></td>
<td>M3</td>
<td>190(^2)</td>
<td>250 +/- 28(^5)</td>
<td>Female</td>
</tr>
<tr>
<td>SKx 21841</td>
<td><em>A. robustus</em></td>
<td>M3</td>
<td>257(^3)</td>
<td>250 +/- 28(^5)</td>
<td>Male?</td>
</tr>
<tr>
<td>TMPAL 99</td>
<td><em>A. robustus</em></td>
<td>M2</td>
<td>182(^1)</td>
<td>250 +/- 28(^5)</td>
<td>Female</td>
</tr>
<tr>
<td>KB 5223</td>
<td>early <em>Homo</em></td>
<td>M1</td>
<td>178(^2)</td>
<td>151 +/- 20 ((H. erectus) 168 +/- 18.7 ((H. habilis)))</td>
<td>Male?</td>
</tr>
<tr>
<td>SKw 268</td>
<td>early <em>Homo</em></td>
<td>M1</td>
<td>170(^3)</td>
<td>151 +/- 20 ((H. erectus) 168 +/- 18.7 ((H. habilis)))</td>
<td>Male?</td>
</tr>
</tbody>
</table>

1 - de Ruiter 2004  
2 - Grine 1982  
3 - Grine 1989  
4 - Quam et al 2009  
5 - Grine and Strait 1994  
6 - Grine 2005

4.7.3 *Determination of Appropriate Proxy*

   Earlier work (see Chapter 3) assessed the accuracy of four proxies for determining philopatric dispersal patterns in chimpanzees and various monkey species in Kibale National Park, Uganda. We explored the viability of each method as it applies to fossil
data (summarized in Table 4.2).

<table>
<thead>
<tr>
<th></th>
<th>Local / Non-local</th>
<th>Tooth/Bone offset</th>
<th>Tooth/Environment offset</th>
<th>Tooth/Local fauna median offset</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chimpanzees</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Red colobus monkeys</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Black and white colobus monkeys</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Olive baboons</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Guenons</td>
<td>No</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
</tbody>
</table>

The semi-quantitative approach was considered ‘effective’ when a higher proportion of the dispersing sex had ‘high offsets’ (offsets above the species’ mean offset) than the philopatric sex.

A comparison of means was considered effective when 90% or more simulations yielded significant p-values with the dispersing sex having the greater mean offset.

The local/non-local designation method was effective if over 80% of individuals was correctly identified as philopatric or dispersing.

“Highly effective” methods are indicated in bold, when both approaches were effective for a given species.

4.7.3.1 Proportions falling within/outside of local cluster boundaries:

The first proxy was based on the proportion of small (female) versus large (male)

individuals designated as “local” or “non-local” based on minimum and maximum
strontium isotope ratios from the local environment. This proxy is the one used most commonly in strontium isotope literature, including Copeland et al (2011). We found it was successful only for those species with large home ranges relative to the isotopic variation on the landscape, and only in areas of Kibale National Park that had a relatively small range of local environmental isotopic values. In the Ngogo area of the park, which has a wide range of local environmental values, it was not successful at identifying the dispersing sex for any taxa. In South Africa, there is also a very wide range of strontium isotope ratios within each local cluster (Figure 4.3). Therefore, this proxy is not the most reliable based on extant models.
Figure 4.3a: Strontium isotope ratios from plants collected within 50 km of Swartkrans and Sterkfontein caves (Copeland et al, unpublished data) clustered through hierarchical cluster analysis with an average linkage distance. Kruskal-Wallace rank sum test, p < 0.001

Figure 4.3b: Strontium isotope ratios from plants collected within 50 km of Swartkrans and Sterkfontein caves (Copeland et al, unpublished data) clustered through hierarchical cluster analysis with an average linkage distance. Kruskal-Wallace rank sum test, p < 2.2e-16
4.7.3.2 Offset Proxies:

Each of the next three proxies involves first calculating an ‘offset’ value between an individual’s tooth enamel strontium isotope ratio and one of three proxies for a local measurement:

· The individual’s bone (this is not discussed here because bone does not preserve well in the fossil record; for more information, see Chapter 1);
· the environmental mean isotopic ratio;
· the median isotopic ratio of the local fauna overall (based on tooth enamel measurements).

For each, we used three methodologies to determine the proxy’s viability:

• **Wilcoxon Mann-Whitney U-tests** determined if male and female mean offsets were significantly different from one another;

• Due to small samples sizes, we used **parametric bootstrapping** to explore trends that may not have been statistically significant but still may be of biological interest. To do this, we used the mean and standard deviation of the collected data for each sex in each species to generate a bootstrapping distribution. From each sex’s distribution, we randomly sampled 100 data points and used Student’s t-tests to compare the means of the bootstrapped distributions. We repeated this simulation 10,000 times and determined the percentage of times that the p-value was significant (p < 0.05).

• **Categorical classification** allows us to compare of the proportion of males versus females considered to have a “high offset” or a “low offset.” We defined high and low offsets relative to the species’ central tendency, specifically the mean of the offset of
interest (tooth/individual bone, tooth/environmental mean, or tooth/local fauna median, each explained in detail below). “High offsets” fell above the taxa mean offset while “low offsets” fell below it. We expect that the sex with a higher proportion falling into the “high offset” category will be the dispersing sex.

4.7.3.3 Tooth/environment offset

The first offset proxy we tested was comparing offsets between tooth enamel and the local environment, using the mean isotopic ratio from local plants as a local environmental proxy (tooth/environment method). In the comparison of means and parametric bootstrapping, this method worked well for species with large enough home ranges such that they would encounter isotopic variation on their landscape, but not those with home ranges too small to take them out of isotopically homogeneous areas. This makes a good candidate for hominin data analysis. This proxy is of particular interest because using categorical classification methods, all modern species had a higher proportion of dispersing sex individuals with high offsets compared to the proportion of philopatric sex individuals with high offsets, regardless of home range size.

4.7.3.4 Tooth/local fauna offset

Finally, we pooled local fauna ratios together, calculated their median tooth enamel strontium isotope ratio, and calculated the difference between each individual and this value (tooth/local fauna method). We used the local fauna median instead of mean
because median is more robust against outlier values. This proxy worked well in bootstrap simulations for small-ranging taxa, but not for wide-ranging taxa such as chimpanzees. When we categorically classify the data, however, similar to the tooth/environment proxy, all modern species had a higher proportion of the dispersing sex with high offsets than the proportion of the philopatric sex with high offsets, regardless of range size.

4.7.4 Recommendations for hominin fossil data

Given the outcomes of each of these proxies on extant fauna in Kibale (see Table 4.2 for a summary) and the constraints imposed through the South African hominin dataset, we will primarily rely on two approaches to assess likely australopithecine dispersal patterns: tooth/environment and tooth/local fauna. The tooth/environment proxy was the most effective proxy for fauna with larger home ranges; in Kibale, this included chimpanzees and olive baboons. It is reasonable, given the home range sizes of dry-habitat chimpanzees and modern hunter-gatherers, to assume that hominins in South Africa would have had large home ranges covering extensive isotopic variation on the South African landscape. This proxy is therefore the most promising.

Secondarily, we will use the offset between tooth and the local fauna’s median tooth enamel ratio, with particular focus on categorical classification (the proportion of each sex with high offset versus low offsets) because this proxy’s categorical classification approach was effective for all extant taxa in Kibale National Park. Additionally, the isotopic clusters in South Africa are much larger than those in Kibale
with larger areas of isotopic homogeneity. Although we can make educated estimates of hominin home ranges, we do not know them with any certainty; if home ranges are smaller than we expect, this proxy will help highlight those differences.

4.8 Results

4.8.1 Landscape Isotopic Variation

We used data from 154 plant samples collected around the region and georeferenced (Copeland et al, unpublished data). Grouping plants by geologic boundaries leads to extensive overlap in isotopic boundaries, complicating definitions of “local” and “non-local.” For example, the minimum and maximum isotopic ratios from the Malmani dolomite, where the fossiliferous caves are located, overlap with ratios from six other geologic areas (Figure 4.2). Rather than relying on these geologic boundaries, we used hierarchical cluster analysis to identify natural isotopic clusters that are isotopically unique and geographically distinct across the landscape. There are three isotopic clusters in the study area around Swartkrans and Sterkfontein: Cluster A has a mean strontium isotope ratio of 0.713083, Cluster B has a mean of 0.7306824, and Cluster C has a mean of 0.7511364 (Kruskal-Wallace rank sum test, chi-squared = 98.019, df = 2, p-value < 0.001, Figure 4.3a). Each cluster has substantial variation within it, although it is not geographically patterned to allow the formation of smaller, meaningful sub-clusters. The longest distance an individual must travel to move off of an isotopically homogenous area is approximately 10 km; in Kibale National Park, this maximum distance is about 3
km.

The overall size of the isotopic clusters in South Africa are also much larger than those in Kibale: the B cluster stretches approximately 50 km at its longest point (Figure 4.3b). The C cluster is much smaller, stretching at most 30 km at its longest point, and the A cluster is the most constrained, found in only one sampling locality far from the fossil deposits. For the most part, the clusters were distinct in the geologic substrates represented in each. The A cluster consists exclusively of the Bushveld Gabbro formation. The B cluster contains Archean granite granite/gneiss, the Black Reef quartzite, Daspoort quartzite, the Hospital Hill formation, the Magaleisberg quartzite, the Malmani dolomite (on which the fossil localities are located), and Orange Grove quartzite. The C cluster contains a single sample from the Black Reef quartzite (primarily grouped with the B cluster) and a single sample from the Magaleisberg quartzite (also primarily grouped with the B cluster), as well as Hekpoort andersonite/basalts, Timeball Hill shale, and the Witwatersrand quartzite.

The fauna were all found at Swartkrans and Sterkfontein fossil localities, both located within the B cluster on the Malmani dolomite. It is worth noting that the Timeball Hill shale deposits, which fall into Cluster C, are the geologic substrate projected to have possibly covered much of the area currently occupied by that Malmani dolomite, which could have broad implications for the strontium values available to local hominins at the site millions of years ago.

4.8.2 Local versus Non-local: Comparison with Kibale National Park data
Copeland et al’s original analysis determined philopatry through examining the proportions of local (philopatric) and non-local (dispersing) individuals based on whether or not an individual’s tooth strontium isotope ratios fell within the local range for the Malmani dolomite. The results they reach are similar to results obtained for chimpanzees through comparable methods in the Kanyawara area of Kibale National Park, Uganda (see Chapter 3). In South Africa, Copeland et al (2011) identified 50% of small-tooth hominins (presumed female) as non-local/dispersing; in Kanyawara, I identified 60% of female chimpanzees as non-local/dispersing (3 out of 5 samples). 11% of large-tooth hominins were identified as non-local/dispersing in South Africa while 25% of male chimpanzees in Kanyawara were identified as non-local/dispersing (2 out of 8 samples). South African cercopithecines had just over 10% identified as non-local/dispersing; here, small monkeys were designated as non-local/dispersing 24% of the time (6 out of 25 total colobus and guenon samples). Of these 6 non-local small monkeys, 4 were actually members of the dispersing sex and only 2 (8%) were of the philopatric sex for their species. Copeland and colleagues also found that 16% of contemporaneous bovids were non-local/dispersing; in our sample it was 42% (5 of 12 Kanyawara bovids), substantially more than in the South African sample, although we cannot rule out that this is due to incorrectly recorded provenience data for older non-primate specimens in the Kanyawara collection. However, as discussed above, this method of assessing philopatric patterns is not the most reliable based on known dispersal patterns among Kanyawara primates. Therefore, in the following sections, we will re-analyze data from the Sterkfontein Valley (Copeland et al 2011, Balter et al 2012) using the best practices identified through results from Kibale National Park.
4.8.3 Tooth/environment offset

Fauna, including hominins, from the South African localities have widely variable strontium isotope ratios, as would be expected from the wide array of values represented in the plants and geology. Partially due to the large geographic area covered and partially to the high isotopic variability within each cluster, the traditional method of classifying ‘local’ versus ‘non-local’ (sensu Copeland et al 2011) based on these isotopic clusters, not geology, leaves only two specimens of *A. robustus* and two bovids designated as non-local (Figure 4.4). This emphasizes the need to use other proxies, such as the offset calculations, in order to draw more robust conclusions about dispersal patterns.

![Figure 4.4: South African fossil fauna strontium isotope ratios. Red band indicates the minimum and maximum values for the local cluster (Cluster B in Fig 3). Based on the variability in these clusters, only two bovids and one small *A. robustus* specimen are “non-local.”](image)

We estimated the mean of the local environment for the hominins in South Africa
by using the mean of Cluster B (Figure 4.3, mean = 0.7306824) As with the chimpanzees at Kibale, a statistical comparison of the tooth/environment offset between large-toothed (presumed male) and small-toothed (presumed female) hominins from Copeland et al (2011) and Balter et al (2012) did not yield significant results for either A. robustus (N = 7 large/male hominins, mean offset = 0.004225919; N = 5 small/female hominins, mean offset = 0.009301622) or A. africanus (N = 4 large/male hominins, mean offset = 0.00213791; N = 6 small/female hominins, mean offset = 0.004512271) (Figure 4.5a).

This sample suffers from the same small sample size issues at the primates in Kibale; because the trend in the means is as compelling as the Kibale data, we applied the same parametric bootstrapping methodology as we did there. Briefly, this involved drawing 100 random samples from within the distribution defined by the mean and standard deviation of each hominin sample, and then comparing the means of the
sampled distribution. This is repeated 10,000 times after which we calculate the percentage of significant p-values from those simulations. For *A. robustus*, 100% of simulations were significant with the small/female hominin having a greater mean offset than the large/male hominins; for *A. africanus*, 99% of simulation were significant with the small/female hominin having a greater mean offset than the large/male hominins (Figure 4.5b).

Classifying the data categorically, two out of five (40%) small-toothed *A. africanus* specimens had high offsets (falling above the species’ mean offset) and one out of four (25%) large-toothed hominins had high offsets. For *A. robustus*, five out of seven (71%) small-toothed hominins were high-offset while 38% (three out of eight) of large-toothed were high-offset (Figure 4.6). The difference between the two species is strikingly similar to the difference between chimpanzees (similar to *A. africanus* data) and olive baboons (similar to *A. robustus* data) from Kibale National Park, both of which exhibit sex-biased dispersal patterns. Tooth/environment data therefore supports a small-tooth/female-dispersal pattern for both species of hominins in South Africa.
Of the unidentified *A. africanus* specimens, one is low-offset while the other two are high-offset. One of these, STS 1881, has nearly the highest offset of any *A. africanus* specimen. Of the unidentified *A. robustus* specimens, all four are high-offset. Data from *Homo* spp are available from Balter et al (2012), however there are only 3 individuals in the sample. As best as we can estimate, two of these molars are likely
males and represent both the largest and smallest of the three offset values. Due to this very small samples size, we cannot draw any conclusions regarding the possible dispersal patterns in early *Homo* from these data (Figure 4.4).

4.8.4 Tooth/local fauna median offset

Using the offset from the local fauna median was a reliable proxy in Kibale for primates with smaller home ranges and dispersal distances. Because the clusters are much larger in South Africa, it is worthwhile to apply this proxy on the hominin data here. In addition, although this proxy was not successful at identifying the philopatric versus dispersing sex in chimpanzees through a comparison of means, it was successful at identifying the philopatric versus dispersing sex for all species using categorical classification, based on proportion of each sex with high offsets.

The mean tooth/local fauna offset for all *A. africanus* specimens was 0.002825833, much smaller than the mean for all *A. robustus* specimens, 0.004663684. When split into large and small individuals, large/male *A. africanus* specimens (N=4) had a mean offset of 0.00243 while small/female specimens (N=5) had a slightly higher mean of 0.002768. For *A. robustus*, large specimens (N=8) had a mean offset of 0.00297125 while small specimens (N=7) had a much higher mean offset of 0.007432857. While there is greater difference between large/male and small/female specimens in *A. robustus* than in *A. africanus*, neither of these are statistically significant (Figure 4.7a).

Using parametric bootstrapping, only 18% of bootstrapped p-values were significant for *A. africanus*. For *A. robustus*, 100% of bootstrapped p-values were
significant (Figure 4.7b). Using categorical classification, for *A. africanus* two out of five (40%) of small/female specimens had high offsets while two out of four (50%) of large/male specimens did. Four out of seven (71%) small/female *A. robustus* had high offsets and only two out of eight (25%) large/male specimens did (Figure 4.8).

Figure 4.7: Offsets between tooth and local fauna median strontium isotope ratios within individuals of each South African taxa, raw data (A) and bootstrapped data for hominids by tooth size/sex (B). For raw data sets (A), Wilcoxon Mann-Whitney rank sum tests *p* > 0.05 for both species of hominids by tooth size/sex. In plot (B), bars show median offset for each sex, diamonds show mean offset. Wilcoxon Mann-Whitney rank sum test for bootstrapped data showed *p* < 0.05 in 100% (*A. robustus*) and 18% of (*A. africanus*) of 10,000 bootstrapped simulations of difference in mean.
These tooth/local fauna results support a female-biased dispersal pattern for *A. robustus*, in agreement with the tooth/environment offset results, but do not support the same for *A. africanus*, in which more of the large/male hominins had high offsets than the small/female hominins. This is in conflict with the conclusions from the tooth/environment method for *A. africanus*. The pattern seen in *A. africanus*, in which the
two proxies led to two different conclusions (female dispersal, based on the
tooth/environment offset, and male dispersal, based on the tooth/local fauna offset)
indicates the either the home range of *A. africanus* was too small for the
tooth/environment method to be effective, or too large for the tooth/local fauna proxy to be effective. Based on modern plant sampling, within 10 km or less of any given sample point around Swartkrans/Sterkfontein one would encounter isotopic heterogeneity; it is highly unlikely that *A. africanus* ranges would be smaller than this. Of the two explanations, it is therefore most realistic to conclude that the home ranges of *A. africanus* was too large for the tooth/local fauna offset proxy to work properly, as seen with modern chimpanzees in Kibale National Park, and the reconstruction of female dispersal and male philopatry for this species is the more reliable conclusion.

**4.9 Discussion**

**4.9.1 Influence of Home Range Size**

Based on modeling using extant primates in Kibale National Park, the most effective proxy for determining the dispersal system of a primate with large home ranges is comparing males’ and females’ offsets between individual tooth enamel and local environmental strontium isotope ratios (*tooth/environment offset*). Quantitatively, these differences in offsets can be illustrated through parametric bootstrapping; the sex with the greater offset is the dispersing sex. Using categorical classification, we can see these differences between the sexes based on the proportion of each sex with high offsets
(offset values falling above the taxa’s mean offset). Based on both of these approaches using the tooth/environment offset, both A. africanus and A. robustus appear to have male philopatric / female dispersal system.

Using another proxy, the offset between an individual’s tooth strontium isotope ratio and the median ratio for the local fauna (tooth/local fauna), was effective for all extant species in Kibale when classify data into high and low offset categories, and for those with smaller home ranges through parametric bootstrapping. Given that we do not know the size of hominin home ranges in South Africa and because the landscape there is more isotopically homogeneous than that in Kibale, we applied this for the hominin data as well. Based on this method, A. robustus is still reconstructed as male philopatric, but the results from A. africanus are more equivocal and, if anything, contradictory to the tooth/environment conclusions for this species.

The variation in effectiveness of these proxies centers on the connected concepts of home range size and dispersal distance (Bowman et al 2002), with the important note that “large” and “small” home ranges are entirely relative to the amount of isotopic variability on a given landscape. The tooth/environment proxy works for species with larger home ranges because as these animals navigate their geochemically diverse landscape, they incorporate a variety of different strontium isotope ratios into their bulk tissues. This creates an averaged effect such that the bulk tissue is reflective of the average environmental signature in their home range area. Individuals who are philopatric and do not leave this area will therefore not have a large difference between their bulk tissues and the environmental mean. Because home range size and natal dispersal distances are correlated (Bowman et al 2002), individuals who do leave this
natal area must travel a greater distance than dispersing individuals of species with smaller home ranges. Therefore, they will establish a new adult home range in an area that is isotopically distinct; their juvenile bulk tissue measurement will show a greater difference when compared to the mean of their natal area. This proxy is not effective for species with small home ranges relative to the geochemical variability in their habitat. If home ranges are smaller than the isotopically homogeneous areas on a landscape, dispersing individuals are unlikely to move far enough to establish adult ranges on area that are geochemically distinct from the environmental average of their natal regions. The averaged isotopic signature of the environment will be *equally as* similar to the small area inhabited by dispersers as it is to the small area inhabited by non-dispersers. There will not be a detectable difference between disperser and non-disperser offsets from the environmental average.

The tooth/local fauna median proxy, on the other hand, does not use variation in the environment in its offset calculations. Rather, the median strontium isotope ratio of the taxa itself defined the expected central tendency. This offset proxy works well to identify dispersers in fauna with smaller home ranges, but does not work as well for the fauna with very large home ranges. This is because of the same averaging effect in bulk tissue ratios that made the tooth/environment offset method so effective for wide-ranging species. For fauna with larger home ranges, the larger amount of variation incorporated into tissues will create an averaging effect which will draw all individuals, including dispersers, closer to a homogeneous mean value. Therefore, the distinction between dispersing and philopatric individuals will not be as dramatic for this proxy.

In Kibale, olive baboons have a large enough home range relative to the variation
on the landscape that the tooth/environment proxy accurately identifies the dispersing sex, but also small enough that the tooth/local fauna proxy remains effective as well. The patterns in olive baboon data from Kibale are remarkably similar to those seen in *A. robustus*. The differing conclusions from the tooth/environment and tooth/local fauna proxies, as seen with *A. africanus*, is similar to the pattern seen in modern chimpanzees. This difference in effectiveness between *A. robustus* and *A. africanus* and their extant analogs suggests that the gracile australopithecine had a larger range size than its robust counterpart, similar to how chimpanzees today have a larger range size than olive baboons (olive baboons have an average range size of about 5 square kilometers while chimpanzees have a home range of about 15 square kilometers in Kibale National Park (Rowell 1966, Chapman and Wrangham 1993). Because of the difference in geospatial distribution of isotopic variation on the two landscapes, we cannot say anything about *absolute* range sizes, only relative to the range sizes of the other species.

Some dietary reconstructions of these South African hominins depict *A. africanus* as occupying a more generalized niche compared to *A. robustus* (Vrba 1998, van der Merwe et al 2003). If this is true then this relative range size reconstruction would be consistent with other studies of sympatric generalist/specialist mammals. For example, the specialized Canadian lynx has a maximum home range estimate of 94 square miles, while the more generalized bobcat has ranges up to 126 square miles (Hunter 2015, Mech 1980, Nowell and Jackson 1996, Whitaker and Hamilton 1998). Similar studies of small mammals show that the oak specialist *N. macrotis* has a home range size half that of the sympatric *N. lepida* and *N. albigula*, both of which have more diverse, generalized diets (Skopec et al 2008, Bleich and Schwartz 1975). However, others argue that the
masticatory apparatus that makes the robust australopithecines so unique in appearance was actually an adaptation to expand dietary breadth, and that both *A. robustus* and *A. africanus* had similar, flexible diets (Scott et al 2005, Sponheimer et al 2006) and even suggest that baboons might be a good ecological analogue to *A. robustus* diets (Spomheimer et al 2006, Jolly 2001).

4.9.2 Influence of Riparian Microhabitats

Sillen et al (1998) discuss potential riparian habitat signals along the greenbelt surrounding the Blaaubank stream, which meanders through the center of the Malmani dolomite formation. The Malmani dolomite ranges from 0.721-0.734 based on plants collected by Copeland et al (2011); Sillen et al (1998) have plants ranging from 0.723 - 0.748 on the same substrate. However, Sillen et al divide their plant samples into those collected from the more xeric veld and those in the riparian “greenbelt” near the Bluubank stream. A transect perpendicular to the stream showed strontium isotope ratios around 0.722 within 50 meters on either side of the water, contrasting strongly with the ratios around 0.733 on the non-riparian areas of the dolomite. Based on paleoecological reconstructions, there would have been a substantial riparian forest surrounding the water sources around Swartkrans at this time (Reed 1997, Watson 1993). Fossil *Theropithecus* and bovids from Swartkrans Member 1, both fauna who presumably preferred the open veld habitat, have strontium isotope ratios that match that habitat (mean ratio = 0.72926, N = 5). Contemporary riparian-preferring white-tailed rats, meanwhile, have average bone strontium isotope ratios around 0.71982 (N = 3). This suggests that a riparian signal
would be identifiable, if present in other fossil species.

Our Semliki study confirmed that riparian areas do leave a clear habitat preference signal in the fauna that preferentially feed in those microhabitats, under proper geochemical and environmental conditions (see Chapter 2), but this does not appear to be the case with the Swartkrans/Sterkfontein hominins. With the exception of a one large *A. robustus* specimen (SK 876) and one small *A. robustus* (TMPAL 99), none of the hominins fall at or below the most radiogenic measurement within the greenbelt riparian area (maximum strontium isotope ratio in the riparian zone was 0.723). These hominins therefore do not have any clear signal for riparian habitat preference (Figure 4.9).

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**Figure 4.9:** Riparian habitat strontium isotope ratios (blue rectangle) and veld/non-riparian strontium isotope ratios (green rectangle) around modern Swartkrans/Sterkfontein caves (data from Sillen et al 1998). There are not strong riparian signals in any South African faunal group (faunal data from Copeland et al 2011, Balter et al 2012).
4.9.3 Influence of Extended Timeball Hill Shale Outcropping

Dirks and Berger (2013) introduce an intriguing possibility regarding shifts in available geologic substrates in South Africa millions of years ago. Different geological substrates erode at different rates; the Timeball Hill Shale, which today lies to the northwest of the dolomite formation and the fossil-bearing caves, erodes much more quickly than the dolomite. Based on the authors’ reconstruction, the dolomite band would have been, “narrower by up to several kilometers as shale of the Timeball Hill formation was still covering large parts of the now exposed dip slopes of Rooihoogte formation” (Dirks and Berger 2013: pg 127). The African erosional surface would have also still covered large swaths of the Cradle of Humanity. Additionally, the wider Bluubank stream (Watson 1993) would have decreased the land area available to the dolomite formation.

The Timeball Hill Shale formation today is a thin ribbon stretching no more than 5 km at its widest point. Isotopically, it is completely distinct from the Malmani dolomite, falling into a separate cluster in the hierarchical cluster analysis (see Methods section), ranging from 0.748 - 0.758 (Copeland et al 2011). None of the fauna reported in Copeland et al (2011), Balter et al (2012), or Sillen et al (1998) have values radiogenic enough to be categorized as ‘local’ on this geological formation, making it unlikely that it formed a central part of the Swartkrans/Sterkfontein hominin home range even given erosion rates 2 million years ago. However, a wider Bluubank stream and a more extensive Timeball shale would have decreased the available dolomite area substantially,
so averaging the shale and the dolomite together may be a better estimate for the local values encountered by hominins. The isotopic mean for the Timeball Hill shale is 0.7524767; averaged with the far less radiogenic values from the dolomite (0.7274937) puts a Timeball/dolomite conglomerate at a mean isotopic value of 0.7325578.

Shifting this definition of the local environment for tooth/environment offset calculations radically changes the conclusions for *A. robustus*, although only partially changes those reached for *A. africanus*. For *A. robustus*, the difference in mean offset between large and small hominins is still not statistically significant using Wilcoxon Mann-Whitney U-tests. However, the trend is such that small hominins (females) trend towards lower offsets, a sign of philopatry, from the combined Timeball-dolomite “local” environment and the large hominins (males) trend towards higher offsets, a sign of dispersal. This is substantiated through parametric bootstrapping, in which 99% of simulations yield significant p-values (*Figure 4.10b*). Six of eight large hominins (75%) have high offsets while only two of seven (29%) of small hominins have high offsets (*Figure 4.11b*). This would suggest that it was the large/male individuals that were the dispersers while the smaller/female individuals were philopatric, the exact opposite of the conclusion reached with using the larger local geochemical cluster which excludes the Timeball shale. However, because no individuals fall within the local boundaries under this definition, this interpretation is unrealistic.

For *A. africanus*, there is no significant difference in means based on Wilcoxon Mann-Whitney U-tests, and parametric bootstrapping yields only 5% of simulations with a significant p-value (*Figures 4.10a, 4.10c*). Three of five (60%) small hominins fall into the high-offset category and three of four (75%) of large hominins do (*Figures 4.11a,
4.11c). There is no consistent evidence for differences in the dispersal patterns of *A. africanus* based on these offsets. This is the same conclusion reached through tooth/local fauna median offsets, although contrasts with the results from the tooth/environmental offsets when using the values from the local Malmani dolomite cluster.

Figure 4.10: Offsets between tooth and environmental strontium isotope ratios from the Timeball Hill Shale/Malmani dolomite combined areas within individuals of each South African taxa, raw data (A) and bootstrapped data for hominids by tooth size/sex (B). For raw data sets (A), Wilcoxon Mann-Whitney rank sum tests *p* > 0.05 for both species of hominids by tooth size/sex. In plot (B), bars show median offset for each sex, diamonds show mean offset. Wilcoxon Mann-Whitney rank sum test for bootstrapped data showed *p* < 0.05 in 100% (*A. robustus*) and 5% of (*A. africanus*) of 10,000 bootstrapped simulations of difference in mean.
Figure 4.11: Offsets between tooth and environmental strontium isotope ratios on the Timeball Hill Shale/Malmani dolomite combined areas for (A) *A. africanaus* and (B) *A. robustus*. Small-tooth hominids are presumed females, shown by red circles; large-tooth hominids are presumed males, shown by blue circles. Those of unknown size/sex are shown by green circles. Horizontal black line indicates the mean offset between tooth and taxa median ratios for the taxa. (C) provides a summary of individuals by sex falling above their species’ mean offset (high offset individuals).
Given the lack of ‘local’ signals from any of the fossil species samples cited across the literature, any conclusion reached using the Timeball Hill shale as a local environmental proxy is unrealistic. However, this comparison highlights the importance of selecting an accurate ‘local’ proxy. It also highlights the more extreme difference in small versus large individuals in *A. robustus* compared to *A. africanus*. This could derive from larger dispersal distances and/or smaller home ranges for *A. robustus* compared to *A. africanus*, which would exaggerate differences between philopatric and dispersing individuals in the former compared to the latter, or could be a product of methodological issues, as mentioned in Balter et al (2012).

Another possible interpretation is that *A. africanus* relied more on riparian habitats for food sources, therefore diminishing the influence of more radiogenic xeric habitats despite wide home ranges and dispersal distances. If this were true, we would expect that the large *A. africanus* samples (presumably local males) would have a less radiogenic mean strontium isotope ratio than the large *A. robustus*, consistent with greater intake of riparian resources. This is not the case. As noted in Copeland et al (2011), there is no significant different when comparing means with Wilcoxon Mann-Whitney U-tests for the species overall, although *A. africanus* specimens trend towards less radiogenic values (more consistent with riparian habitats) than *A. robustus*. When we compare only the large (more likely to be local) specimens, parametric bootstrapping yields only 37% significant p-values. There is therefore no convincing evidence of a difference in microhabitat preference between the taxa based on strontium isotope ratios. A fascinating test of this application would be in East African deposits, where *A. boisei* high-carbon and low-oxygen isotopic values are indicative of potential reliance on riparian habitat
resources, such as grasses and sedges (Cerling et al 2011).

4.10 Conclusions and Future Work

Results from Kibale National Park, Uganda suggests that the most appropriate metrics or proxies for determining philopatric patterns in primates with home ranges large enough to encounter isotopic heterogeneity on the landscape, as with the hominins in South Africa, are:

1. The offset values from an individual’s tooth and the surrounding environmental average;
2. The offset values from an individual’s tooth to the local taxa’s median isotope value, when classified into high and low offset categories.

Parametric bootstrapping of means when using the tooth/environment offset accurately indicates the philopatric sex for large home range taxa, but is inaccurate for small range faunal, with range size defined as relative to the isotopic heterogeneity on the landscape. Parametric bootstrapping using the tooth/local fauna median offset, however, accurately indicates the philopatric sex for smaller range fauna, although not for large-range fauna when applied quantitatively. Categorical classification identifies more members of the dispersing sex as having high offsets (offsets above the species’ mean offset value) than members of the philopatric sex for both tooth/environment and tooth/local fauna offsets, although the results are more pronounced when using the tooth/environment metric. Because of this, both methods were worth applying to the fossil dataset.
When we apply these proxies to South African hominin data gathered from Copeland et al (2011) and Balter et al (2012), the tooth/environment proxy indicates a greater offset for small/female hominins compared to large/male hominins for both species (*A. africanus* and *A. robustus*). A greater proportion of small/female hominins have high offsets compared to than the proportion of large/male hominins placed in that group (40% versus 25% for *A. africanus*, 71% versus 38% for *A. robustus*). These findings strongly indicate that the small/female hominins are the dispersing sex and the large/male hominins are philopatric.

We reach the same conclusion for *A. robustus* with the tooth/local fauna median offset proxy using both bootstrapped means and categorical classification methods. However, with *A. africanus*, there is no significant difference in means and only 27% of p-values are significant in bootstrapped simulations. 40% of small/female *A. africanus* and 50% of large/male *A. africanus* have high offsets. Data from Kibale National Park showed that the tooth/local fauna offset was not as accurate for taxa with home ranges as large or larger than the isotopic clusters on the landscape; therefore, one possible interpretation is that *A. africanus* had a larger home range than *A. robustus*, with the former being analogous to chimpanzees in Kibale National Park and the latter being analogous to Kibale’s olive baboons, who today have a ranges that fall intermediate between the small-range arboreal monkeys and the large-range chimpanzees.

Another possible philopatric pattern not yet evaluated is one of bisexual dispersal, as in gorillas or hamadryas baboons, in which males form harems of females from which both sexes are likely to disperse at maturity. Koenig and Borries (2012) argue that the original findings from Copeland et al (2011) are entirely parsimonious with a gorilla-like
system of dispersal. In an equally bisexually dispersing species, we would not expect a difference in the offsets between the sexes; rather, we would expect both sexes would have relatively similar, high offsets indicating dispersal. The most rigorous way to address expected patterns for patrilocal or matrilocal species (those with bisexual dispersal, but with one sex moving farther from the natal group that the other) would be to sample environmental and faunal strontium isotope ratios from extant gorillas and compare the observed patterns to those in South Africa; this is work that remains to be done. Given the data available at present, there are striking similarities in the patterns observed between *A. africanus* and modern chimpanzees (43% of chimpanzee females and 40% of small/female *A. africanus* individuals have high tooth/environment offsets, versus 25% of chimpanzee males and 25% of large/male *A. africanus* individuals). The most parsimonious conclusions for these data is a system of female dispersal and male philopatry for *A. africanus* similar to that seen in modern chimpanzees. The differences between the sexes for *A. robustus* are more dramatic than those in its gracile conspecific with values similar to the olive baboons in the modern Kibale habitat (38% of philopatric large/male *A. robustus* and 25% of philopatric female baboons had high offsets, versus 71% of dispersing small/female *A. robustus* 80% of dispersing male baboons). This greater difference in baboons may be because of multiple dispersal events for males rather than one dispersal at sexual maturity, or due to smaller home range sizes coupled with greater dispersal distances (compared to the larger home ranges of larger primates, like chimpanzees). More data on range size and dispersal distances for male baboons is necessary to address these hypotheses. Nonetheless, the similarities in data between hominins and specific modern primates suggests that a pattern of sex-biased (in the case
of the hominins, female-biased) dispersal is the most parsimonious conclusion given present data.

The conclusion that males were philopatric while females dispersed is not contrary to that reached by Copeland et al (2011). However, these results solidify those conclusions by basing them in tested methodological metrics and protocols. This also allows us to expand on this work by hypothesizing a larger home range size for *A. africanus* and providing evidence against a preference for riparian habitats in both South African species, despite strong evidence that such habitats existed during these time periods.

These results on philopatric tendencies are not surprising in light of the pattern of our closest living relatives, chimpanzees, who also follow a pattern of male philopatry and female dispersal; however, elucidating this pattern in a fossil hominin population allows us to make evidence-based hypotheses about the socio-biological roots of behavior in our fossil ancestors. For example, these data lend credence to the hypothesis that male philopatry/female dispersal represents the ancestral condition along the hominin lineage, and emergent patterns in humans that buck this trend with the advent of agriculture (Wilkins and Marlowe 2006) are derived conditions. Male coalitionary violence, displayed in both human and chimpanzee societies, likely also has roots within this dispersal pattern. These male-kin based coalitions made possible by male philopatric patterns likely form the basis for the cooperative hunting and territory defense seen in modern *Homo sapiens* and our closest relatives (Chapais 2009).

These findings have life history implications as well. For example, the Grandmother Hypothesis suggests the reason for long post-menopausal lifespan in female *H. sapiens* is
related to the inclusive fitness benefit grandmothers can provide for their grandchildren. This data suggests that such mechanisms must be placed squarely in later hominins and the genus *Homo* and could not have been present in earlier taxa, for if females leave their home groups to reproduce, grandmothers could only provide benefits to their son’s offspring. This would necessitate that australopithecine species have paternal kin recognition and paternity certainty, which is intimately tied to monogamous mating patterns. While some argue that monogamy is a hallmark of humanity (Lovejoy 2009), large body size sexual dimorphism persists through until the rise of the genus *Homo*. Coupled with this strong evidence for female dispersal, grandmother and paternal kin investment in offspring, monogamous pair-bonding, and associated life history traits such as the energetic ability to stack offspring and the markedly slower pace at which human babies grow up are increasingly unlikely for pre-*Homo* taxa. Reconstructing dispersal patterns in early *Homo* could provide a fascinating insight into the presence of these life history traits with the rise of our own genus.

Finally, modern psychological studies show that modern *Homo sapiens* women form fewer, more dyadic bonds with other women and with significant others while men are more likely to form larger and more diffuse social circles (David-Barrett et al 2015, Benenson et al 2012). This bonding pattern in modern humans makes sense with a biological root in female dispersal and male philopatry; for chimpanzees, when making inroads into new groups, one of the most secure points of entry for a dispersing female is in bonding with males in the group for protection (Kahlenberg et al 2008). In bonobos today, non-related females form dyadic and coalitionary bonds for protection against aggressive males and defense of food, leading to earlier ages of first reproduction and
therefore greater lifetime reproductive success (Parish 1996).

Based on methodological protocols and metrics tested on primates in Kibale National Park, data from *A. africanus* and *A. robustus* in South Africa point strongly towards patterns of female dispersal and male philopatry. Potentially, these data also point towards a larger home range for *A. africanus* when compared to *A. robustus*. Neither hominin shows evidence for strong riparian habitat preference, despite ample evidence that contemporaneous riparian forests were plentiful. These data are not contradictory to earlier claims made by Copeland et al (2011), but do provide more thorough evidence for the philopatric reconstructions and allow for comparisons between living primate communities and our australopithecine ancestors.
5.1 Summary of findings

Researchers across disciplines rely on strontium isotopes as indicators of provenance, from identifying the natal origins of fish to the migration patterns of archeological humans, from sourcing archeological building timbers to sourcing wine. Although it is firmly established that strontium isotope ratios vary based on geologic formation age and composition, the nuances of exactly what mobility and landscape use conclusions are valid to draw from isotopic comparisons are often left unexplored. This work addressed three of these more nuanced methodological questions:

1) Given that flowing surface water can dissolve and transport soil and debris from one geologic area to another, can strontium isotope ratios differentiate riparian near-water habitats from non-riparian habitats?

2) Given that tooth enamel forms during the juvenile period and bone re-forms continuously throughout adult life, can a comparison in the strontium isotope ratios between tooth enamel and bone identify individuals who lived in different areas as a juvenile and as an adult?

3) Given that associated teeth and bones are often not available for fossil individuals, and the increased risk of diagenesis in bone, can we compare tooth enamel to other
proxies (local vegetation, other individuals from the same area) to show mobility patterns through the lifetime?

Based on the results of these methodological studies, this work then applied the recommendations and best practices to a set of fossil data from the Cradle of Humankind in South Africa.

5.2 Methodological Findings

*Question 1: Can strontium isotope ratios differentiate between riparian and non-riparian habitats?*

Yes, under the proper geologic conditions. In Toro-Semliki Wildlife Refuge, mobile surface water in the Mugiri River flowed from the older Toro deposits on tops of tall escarpments surrounding the reserve, carrying with it less radiogenic strontium isotope ratios compared to those derived from local Cenozoic alluvium underlying the refuge. These less radiogenic values in water strongly influenced vegetation within the Semliki gallery forest, which grows up to 200 meters on either side of the Mugiri River. In addition to vegetation in the gallery forest showing less radiogenic values compared to those in the surrounding grassland, fauna with a habitat preference for the forest also had less radiogenic values in their tooth enamel and bone compared to fauna with a habitat preference for the open grassland.
Given that gallery forests are a strong contender for the preferred habitats of many hominins, this methodology could be critical to future hypothesis testing. However, it is important to carefully examine the geologic conditions of the fossil site to determine if there is a reasonable expectation of variation. In order for this to be so, it must adhere to the following criteria:

1. The paleo-river is large enough and permanent enough to have supported a gallery forest or riparian area distinct from the surrounding area.

2. The paleo-river must originate (or flow past) a different geologic formation than the one on which the fossil species are presumably living.

3. The water in the paleo-river originating (or flowing over) this unique geologic substrate must be the primary source of water input for the river.

Some of these criteria are easier to assess than others. For example, if the tract of the paleo-river can be reasonably reconstructed, local vegetation at the site of the paleo-gallery forest and at the origin point (or flow-through point) of the water can be collected and compared to determine if they are geologically distinct from one other. Determining if there were other major source of input to the water may be more difficult.

In the absence of sampling actual gallery forest habitat versus surrounding grassland, as is possible in extant habitats, there are two potential proxies for a riparian signal in a fossil context: the paleosol along the paleo-riverbed and other fossil fauna with known habitat preferences. For example, in areas reconstructed as gallery forests in which colobine monkeys and open-habitat bovids coexist, the strontium isotope ratios of colobine monkeys would be a reasonably proxy for a riparian habitat signal while the
bovid would be a proxy for the open habitat signal. These data from Toro-Semliki validate the use of fauna with known habitat preferences as proxies for those signals.

**Question 2:** *Can a comparison in the strontium isotope ratios between tooth enamel and bone identify individuals who lived in different areas as a juvenile and as an adult?*

For species with home range sizes small relative to the isotopic variation on the landscape, generally yes. For species with large home ranges size relative to the variation on the landscape, generally no. The isotopic clusters in Kibale National Park stretched approximately 10 km at their largest points with 3 km being the largest distance between unique isotopic samples. Therefore, animals that travel distances exceeding 3 km in Kibale can be classified as having “large” home ranges. Those with home ranges that will not take them close to 3 km traveling distance, such as colobus monkeys or red-tailed monkeys, both of whom have home ranges less than a single square kilometer, have small home ranges relative to the isotopic variation found here. Olive baboons are an interesting case in Kibale because they have home ranges of approximately 5 square kilometers and day ranges of over 2 km (Rowell 1966, Mitani and Rodman 1979). This places the olive baboons right in the middle between small and large home range definitions in Kibale based on the landscape’s isotopic variation.

In our sample of primates from the Kanyawara, Ngogo, and Kanyanchu areas of Kibale National Park, the offset between tooth and bone strontium isotope ratios for monkeys with home range sizes equivalently sized or smaller than the isotopic variability
(colobus monkeys and guenons, as well as the intermediary olive baboons) was reliably
greater in the dispersing sex compared to the philopatric sex. However, for chimpanzees,
which can range farther than 10 km within their home ranges, there was no clear
distinction in the offset value between the sexes.

All fauna incorporate the variation present in their home range area into their
tissues as they form. The more geochemical variation there is within a home range, the
more variation will be averaged into an individual's bulk tissue value. Because
chimpanzee home ranges are large enough to cover an area with a lot of variation during
the formation of both tooth enamel and bone, they incorporate a wide variety of strontium
sources into those tissues. Due to this averaging effect, the difference between tissues
even for dispersing individuals becomes muted. However, for fauna with small home
ranges (like colobus monkeys in our sample), each tissue incorporates only a very small,
specific strontium source during formation. The differences between the specific source
incorporated into tooth enamel and that incorporated later in life into bone for dispersing
individuals is accentuated, while the similarity is maintained for philopatric individuals.

It is important to reiterate the concept of “small” versus “large” home range is
relative to the variation present in the landscape. In areas that are more geologically
heterogeneous than our study area, isotopic clusters might only extend a kilometer, which
would then adjust the definition of “small” home ranges to those less than a kilometer,
while anything greater than a kilometer would become a “large” home range. This
highlights the importance of thorough environmental sampling in an area before drawing
conclusions.
**Question 3:** Can we compare tooth enamel to other proxies (local vegetation, other individuals from the same area) to show mobility patterns through the lifetime?

Under certain conditions, yes. The local environment can be estimated by calculating the average strontium isotope ratio of local plants within that isotopic cluster. The offset between this environmental average and an individual’s tooth enamel is reliably greater in species with home ranges approaching the size of the isotopic clusters on the landscape or larger, such as chimpanzees and olive baboons. It is not reliable for fauna with relatively small home ranges, such as both black and white and red colobus monkeys in Kibale National Park. Species with larger home ranges necessarily must disperse greater distances in order to leave their natal range; therefore, dispersing individuals of species with home range sizes approaching the size of the landscape’s isotopic clusters must move into geochemical distinct areas when they migrate. Conversely, even dispersing members of smaller range primates do not move far enough to reach a geochemically distinct area in their adult home range compared to where they were as juveniles. By using the environmental average of an area, this method also accounts for the averaging effect that occurs during tissue formation that muddled tooth/bone offset dispersal signals in primates with large home ranges. By comparing an isotopic clusters’ average ratio to the ratio of an individual’s bulk tissue, we are assuming that an ideal local signal accounts for all variation within the isotopic cluster area. This assumption is violated for small home range taxa that do not range over the entire isotopic cluster, but is upheld for taxa with larger home ranges. Therefore, this proxy is
applicable only to taxa with home ranges that would allow an individual to cover most of the area in an isotopic cluster during tissue formation.

The other potential proxy, the offset value between an individual’s tooth and the median tooth isotopic ratio for the local fauna, had very similar outcomes to the tooth/bone offset proxy discussed above. It correctly identified the philopatric sex for species with small or equivalent home ranges relative to the isotopic variation on the landscape (colobus monkeys, olive baboons) but not for the chimpanzees, which have large home ranges relative to the landscape’s variation. Similar to the tooth/bone offset, the proxy in this method for the local signal (the median ratio of the teeth of local fauna) comprises values that capture mostly a small spatial snapshot. Over half of the fauna in the sample are small-range monkeys (55% of the sample are small-range monkeys, 15% are medium range monkeys, and 30% are large-range apes), and so the median is primarily representative of the small home ranges captured in those enamel formations. Therefore, the outcomes of this proxy are strikingly similar to the outcomes for the tooth/bone proxy, which likewise relies on a local signal that captures a primarily small spatial scale (bone ratios). Like the tooth/bone proxy, therefore, this approach was primarily successful with small-range fauna and not large-range fauna, although categorically it did assign the correct philopatric sex to all species, making it slightly more successful than the tooth/bone proxy overall.

5.3 Why did some proxies work and others do not?
The key to unraveling why some methods work for certain species while others do not lies with the relative geographic sizes of that species’ home range and the isotopic variation on the landscape. In Kibale, the largest isotopic clusters on the landscape are about 40 square kilometers with their widest points being about 10 km apart from one another. There is a significant amount of non-geographically patterned isotopic variation within each of these clusters, however; the upper range distance that an animal could travel and still remain in an area that is isotopically indistinguishable is about 3 km, and usually less. Therefore, animals that travel distances exceeding 3 km in Kibale can be classified as having “large” home ranges. Those with home ranges that will not take them close to 3 km traveling distance, such as colobus monkeys or red-tailed monkeys, both of whom have home ranges less than a single square kilometer, have small home ranges relative to the isotopic variation found here. Olive baboons, with home ranges of approximately 5 square kilometers and day ranges of over 2 km (Rowell 1966, Mitani and Rodman 1979), fall intermediate between small and large home range definitions in Kibale based on the landscape’s isotopic variation. It is not a coincidence that they are the species for which all proxies and methodologies successfully identify the philopatric sex as male - they have a small enough home range that tooth/bone distinctions are not lost, but a large enough one that comparisons to the environmental mean are still significant.

Animals with small home ranges relative to landscape isotopic variation will encounter and incorporate less variable isotopic values into their tissues as they grow. The result is an isotopic signature in a tissue that is highly precise and specific to the area the animal lived in as their tissue formed. Because they will not move far enough to encounter variation in the landscape, there is no averaging effect on the bulk tissue
(because there is not a wide array of values incorporated to average together). This means that any slight change in the underlying area on which an animal is foraging will stand out as markedly different; an individual need not leave the isotopic cluster entirely.

Smaller changes in the strontium isotopes available in the landscape will show up as significant changes when comparing tissues. This is why comparisons between teeth and bones of small ranging primates are more likely to highlight dispersing individuals versus philopatric individuals; each bulk tissue (the tooth and the bone) formed when the individual was eating only a highly specific, non-variable food source (at least as far as strontium isotopes are concerned). Those that disperse even a short distance will incorporate a different highly specific isotopic signature; those that do not will continue to feed on the same highly specific area their whole lives. The overall variation in strontium isotope ratios within small-ranging species will be lower than the variation in species with a larger home range, but the differences between the two highly specific tissue values in a disperser will be dramatically greater than their non-dispersing conspecifics. In other words, proxies in which the ‘local’ area captured in the tissue measurement is small relative to the variation on the landscape are more likely to work with small home range species.

Meanwhile, individuals from species with larger home ranges will encounter more variation in the landscape as they form their tissues. This means that rather than being a snapshot of a highlight specific, localized value, each tissue represents the average of many the different isotopic ratios which exist the wide area that individual traveled over during the tissue’s formation. This averaging effect on tissues formed both
pre- and post-dispersal means that differences between the two tissues are more likely to be muted and non-significant.

We can show this through a modeling experiment. Using the isotopic variation within the northern cluster of Kibale and the home range sizes of chimpanzees, representing a large home range, and red colobus monkeys, representing a small home range, we can simulate the effects of home range and dispersal on the expected isotopic values within each tissue. To do this, we randomly select an area within Kibale National Park the size of each species’ home range and sample the isotopic values present within that area. This represents the formation of a tooth during the juvenile period. Then, we shift the home range area to simulate a dispersal event and re-sample the isotopic values present within the new area, simulating the formation of bone during adulthood. After 10,000 iterations, the mean offset between the simulated tooth and bone ratios for small-range colobus monkeys is 0.0024. The mean offset for large-range chimpanzees is 0.0012, half the size of the colobus monkey offset. The small home range size exacerbates the differences between the tissues while the averaging effect created by a large home range size mutes it, even in dispersing individuals.

The opposite effect occurs when using a proxy that does not compare two tissues from the same animal, such as the tooth/environment offset proxy. Again, it is home range relative to landscape isotopic variation that is the key variable. For species with small home ranges, like the red colobus, the highly specific value incorporated into their teeth during the juvenile period is no longer compared to another highly specific value from a different location; rather, the comparison value to calculate the offset is an averaged value from the entire isotopic cluster, which is much larger than their home
range. This means that the tooth value of philopatric red colobus males and the tooth values of their dispersing sisters, presumably highly similar values from their shared juvenile periods, will both be compared to the same environmental mean, with the very rare exception of dispersers who live close enough to cluster boundaries to cross them when they leave home. Dispersers and philopatric individuals are not differentiable when the ‘local’ metric captures an area that is larger than the home range of a species.

Meanwhile, individuals with large home ranges are significantly more likely to disperse into or off of the isotopic clusters we use to determine the mean local environment. Even if they have not left the cluster completely, their home ranges are large enough for them to have encountered enough variability outside of the local area during tissue formation to produce noticeable differences. We can see this problem when we compare the inter-quartile ranges of tooth values from a small home range species (red colobus) to that of a large home-range species (chimpanzee). The mean tooth isotopic ratio for the two species are not different but the inter-quartile range (a good measure for the spread of data) for chimpanzee teeth is 0.005555, while for red colobus teeth it is a much smaller 0.0016375. Because of their small home ranges (and correspondingly small dispersal distances), there is much less offset from the environment for any red colobus monkeys, regardless of dispersal patterns. For chimpanzees, larger range sizes generate greater offset from the environment value which can elucidate dispersal patterns.

The tooth/local fauna proxy is an interesting intermediary between these two extremes. The local fauna median strontium isotope ratio is a metric for local variation that encompasses a larger geographic area than a single individual’s bone isotopic ratio,
but not nearly as large an area as the entire isotopic cluster assayed through vegetation (unless the local fauna used are all very wide-ranging species, like elephants or chimpanzees). When the local faunal median can be calculated using an array of species of various range sizes, this proxy is a reliable compromise utility for only small-range species and only large-range species.

5.4 Application to hominin research

When we apply the proxy and methodological recommendations from Kibale National Forest to hominins from South Africa, we reconstruct both *Australopithecus robustus* and *Australopithecus africanus* as male philopatric, female dispersing based on the tooth/environment offset proxy. When we apply the tooth/local fauna proxy, *A. robustus* remains firmly male philopatric, but the data for *A. africanus* becomes much more ambiguous; only 18% of parametric bootstrapped means were significantly different between males and females, and the categorical designations were nearly even (40% and 50% for male and female individuals, respectively).

This is a pattern that we have seen before. In the Kibale data, both olive baboons and chimpanzees had the philopatric sex clearly indicated using the tooth/environment offset proxy; both had home ranges large enough relative to the isotopic variation on the landscape such that dispersing individuals were significantly more offset from the local environmental mean than those than remained in their natal groups, even with the local environment being defined as the mean for a large, isotopically variable cluster area. However, the tooth/local fauna offset could not currently identify the philopatric sex for
chimpanzees, which have a larger home range than olive baboons in Kibale. This is because the local fauna median as a proxy for a ‘local’ measurement does not encompass as wide a geographic range as the menu of all the plants within the isotopic cluster; rather, because the majority of the fauna from the locality are small-range monkeys, the median value is more reflective of highly localized “snapshot” values. The wide-ranging chimpanzees and the averaging effect in their teeth were equally offset from this hyper-local signal whether or not they dispersed.

These parallels in methodologies are informative. For both chimpanzees and \textit{A. africanus}, the tooth/environment proxy had 98-100\% significant p-values when bootstrapped, and a much higher percentage of the dispersing sex with a high offset compared to the philopatric sex (40\% verse 25\% for \textit{A. africanus} and 50\% versus 18\% for chimpanzees). Also for both, the tooth/local fauna offsets yielded very few significant p-values when bootstrapped (16\% for chimpanzees and 18\% for \textit{A. africanus}) and nearly even proportions of each sex falling into the high offset category (40\% and 50\% for \textit{A. africanus}, 45\% and 50\% for chimpanzees). These ambiguous data do not represent a challenge to the conclusions of the tooth/environment offset proxy; rather, their lack of significant differences between the sexes suggest that this approach is not capturing meaningful differences between the sexes at all. Because the local fauna median is a local proxy that captures a small geographic area, this failure is most likely because the home range size of these species were large enough that both sexes averaged plentiful variation into their teeth during formation, making them distinct from the small-range snapshots of the local fauna median regardless of dispersal patterns.
On the other hand, both *A. robustus* and olive baboons showed significant differences between the sexes for both approaches. The tooth/environment proxy led to 100% significant p-values during bootstrapped simulations and a far high proportion of the dispersing sex with high offsets than the philopatric sex (71% versus 38% for *A. robustus* and 80% versus 25% for olive baboons). The same pattern held for the tooth/local fauna proxy; 100% significant p-values with bootstrapping and a far high proportion of the dispersing sex with high offsets than the philopatric sex (71% versus 25% for *A. robustus* and 80% versus 25% for olive baboons). In Kibale, olive baboons have home ranges that very closely approximate the greatest distance between isotopically uniform areas of the park - approximately 3 kilometers. This positions them in a “sweet spot” to have a large enough home range so that the whole-cluster environmental average is a meaningful local signal that differs in its offset between philopatric and dispersing individuals, but not so large such than local signals that capture smaller geographic variation, such as the local faunal median, are overwhelmed by the averaging effect of their range. The parallels in the data between the two species suggest that *A. robustus* might have a similar relationship between their home range size and the size of the isotopic clusters on its South African landscape; here, the distance between isotopically unique areas was larger (about 5-10 kilometers). The home range size of *A. robustus* may have scaled accordingly.

Altogether, this paints a picture of a late-Pliocene South Africa in which *A. africanus* ranged farther than *A. robustus*. It again highlights the importance of understanding the size of the isotopic clusters on the landscape as well as the distances between areas of variation within each of those clusters, rather than just focusing on the
variation between them. In applications where we do not know the home range size of a species, these proxies could be used to indicate larger or smaller ranges relative to the landscape variation (or to other fauna in that ecosystem).

Methodologically, the tooth/local fauna application, while not the most accurate for large-range species (presumably a category that will include most hominins), holds the most potential. Especially when used to categorize data as high-offset or low-offset, it reliably predicts the philopatric sex in Kibale primates; used in this way, it is functional for both large-range and small-range species. Perhaps most importantly, it does not rely on secondary sources for ‘local’ proxies – teeth need not be coupled with bone from the same individual, concerns about diagenesis for bone in particular are not in consideration, and in areas where local vegetation is not available to build an isoscape or in area where the underlying geology has changed substantially from the time when hominins inhabited the area, the local fauna will still be a reliable proxy. When possible, this proxy should be used in conjunction with a tooth/environment offset proxy because the latter are more reliable for large-range fauna and because comparisons between the two proxies are informative on relative range size, as demonstrated with the South African hominin data.

5.5 Promising areas for future application of strontium isotope research

With the exception of the work that Copeland and colleagues have done in South Africa (Copeland et al 2011, 2016), no other hominin sites have significant strontium isotope datasets available. This is unsurprising, as the data are expensive and pilot studies investigating the viability of less invasive, less expensive methodologies were
unsuccessful (Sponheimer and Lee Thorpe, *Final Report to Leakey Foundation, ‘Using strontium isotopes to investigate land use at Olduvai Gorge’*). However, we now have significant foundational data and tested models through which to interpret hominin strontium isotope ratios.

What would make a viable hominin field site? First, there would need to be ample fossils from the field site, preferably of a variety of identifiable species, in order to have sufficient local fauna to use as a local proxy. Second, we must be able to take modern plant samples from around the site in order to quantify the variation present on the landscape. This would include both the identification of isotopic clusters and also the extent and nature of variation within those clusters, both critical components of determining which methodology is most appropriate. Finally, the isotopic clusters and the variation within them would need to be at geographic scales relevant to the species of interest; in other words, if the clusters on the landscape are beyond the scope of possible hominin range sizes, then strontium isotopes are not an appropriate tool to use at that locality. This was the issue identified at Chaco Canyon, a paleo-Native American site in New Mexico where the question at hand was the importation of timbers to build large houses. The hypothesis was that the timbers came from up to 60 km away (English et al 2001, Reynolds et al 2005); however, the isotopic clusters on the landscape were uniform for up to 160 km, making any conclusions drawn from strontium isotopes no better than guesses (Drake et al 2014).

While researchers have raised issues of potential diagenetic alterations of fossil enamel at Olduvai Gorge, this is the only other hominin locality with any strontium isotopes ratios sampled in the surrounding environment, and from a geochemical
perspective is very promising as a field site for future development (Copeland et al 2012). The gorge sits on young volcanic rocks approximately 30 km away from Precambrian granites to the west and south, with outcrops of quartzite and gneiss to the north and southeast. Modern samples from owl roosts show extremely variable strontium isotope ratios, the majority falling between 0.704 and 0.708 but with some reaching as high at 0.718 (Copeland et al 2012). This variation is spread out over a wide geographic area, and careful sampling of plant material is necessary to ensure that the variation is patterned enough to create smaller isotopically distinct clusters. Paleo-rivers also flowed through the gorge and the few isotopic values from fossil fauna hint at isotopically unique riparian environments as well (see Chapter 2).

The East African rift valley is a difficult area to predict strontium isotope ratios due to volcanism. Hadar, Ethiopia sits on top of Pleistocene limestone and tuft, which extends far to the north and south of the site. Approximately 10 miles to the west are Oligocene-Miocene basalts, and approximately 10 miles to the east are Miocene-Pliocene aged basalts. The Pleistocene limestone underlying the site and Oligocene-Miocene basalts to the west each extend north/south 100+ miles, but to the east the Miocene-Pliocene basalts are intermixed with other Pleistocene limestone outcrops as well as differentiated Pleistocene basalt flows. Although most of this area is volcanic, deposits from the geologically recent past, it may be sufficiently variable to warrant survey and pilot data.

This area brings up a critical point that is consistently relevant in East Africa -- recent volcanic eruptions and sedimentary layers that post-date the hominins of interest will make strontium isotope surveys of modern plants non-reflective of the isotopic
variation present during the terminal Pliocene/early Pleistocene. These more recent geologic events deposit new geologic layers that would not have existed on the landscapes of our hominin ancestors; the plants growing on them today reflect the strontium isotope ratios present within these more recent rocks, rather than those that would have been present before their deposition. There are a few ways to handle this. First, careful geologic survey can determine contact points with the underlying basement layer that would have been present previous to the more recent geologic deposition. If other areas of the landscape still have these older rocks outcropping, estimates from them can be extrapolated to the covered areas. This is of course imperfect given the myriad factors that can contribute the strontium isotope ratios available in a specific location, but it is more accurate than relying on plants growing on rocks younger than the australopithecines. Secondarily, geologic cores from these areas can show the layers beneath the recent volcanic or sedimentary deposits. In the event that no other areas in the vicinity have outcrops of these older deposits to sample, strontium leaches from the rocks themselves (Sillen 1998) can provide an (again imperfect) estimate of the biologically available strontium for plants growing on this substrate before it was covered.

In Kenya, both sides of Lake Turkana and the numerous fossil localities surrounding it are underlain again primarily by Pleistocene volcanics, although there are variations within these layers. To the east underlying the Ileret and Allia Bay sites, is a thin band of alluvium ranging from 1 to 8 km wide. After is an equally thin band of recent sedimentary deposits, and within approximately 12 km of the lake margin the geology shifts to Pliocene volcanics with a thin band of Precambrian gneiss extending from the north. Likewise, the western side of the lake has a < 12 km band of alluvium on
the lake margin transitioning to Pliocene volcanics, including with both mafic basalts and felsic rhyolites. While there is potential for variation within these volcanic sediments, particularly given the abundance of paleo-rivers cutting through the area, it cannot be assessed accurately from the geologic maps alone. Pilot sampling studies would reveal quickly whether the exposures of different volcanic outcrops and their underlying areas differ enough isotopically to be meaningful for a wandering hominin, although similar to the issue in the Afar region, this sampling would have to be done with a very careful eye to avoid any primary deposits that are younger than the hominins of interest.

Based purely on geologic maps, which, as discussed above, are only the roughest way to approximate isotopic variability in an area, the most promising places geologically to conduct strontium isotope studies would be continued work in South Africa, where we know the geologic variation is sufficiently patterned at spatial intervals meaningful to hominin range sizes, and potentially expanding to include Olduvai Gorge. This is both because we have preliminary data from the site that is encouraging as far as the isotopic variability present there, but also because it has a sufficiently variably underlying geology such that, even without the pilot data, it would be promising. The sites in the Afar region of Ethiopia, including Hadar and Dikika, as well as those along the banks of Lake Turkana have more uniform underlying substrates, although with sufficient potential variation within the region to warrant pilot surveys. They also suffer from the unfortunate reality that much of what is bedrock presently has been deposited since the hominin lived on the land, meaning researchers would need to rely more exclusively on comparisons with local fauna from the same time period rather than tooth/environment offsets.
Outside of Africa, there is abundant geologic variation underlying some of the most informative hominin sites to date. For example, the areas around Shkul and Qafzeh caves in Israel include Late Cretaceous sediments of Mount Carmel, in which we find the Shkul cave, stretching approximately 10 km in both north-south and east-west directions. This area is surrounded by lower Eocene and Paleocene deposits surrounding it to the east and south. These surrounding deposits are intermixed with quaternary alluvium and more recent Quaternary volcanics (Gvirtzman et al 2011, Segev et al 2014). The presence of these relatively new deposits nearby again highlights the importance of the tooth/local flora method, but the immense variability in rock ages and types underlying the greater area strongly indicates sufficient variation to detect differences in mobility and dispersal patterns in the hominins found here.

Researchers interested in later, modern Homo sapiens archeological populations in Europe have already completed strontium isotope surveys in numerous localities with extremely high strontium isotope variability. For example, the modern Romanian/Serbian boarder (Borić and Price 2013), southwestern Germany (Bentley et al 2002), southern England in the Glouchester area (Chenery et al 2010), central-western France (Britton et al 2011) have all been surveyed to address questions linked to archeological modern human population mobility. These surveys all reveal highly variable geology and strontium isotope ratios. These areas are likewise near fossil hominin deposits, including La Chapelle aux Saintes and Saint Cesaire in France, Mauer in Germany, Peştera cu Oase in Romania, all localities with Neanderthal and/or early modern human fossil remains.

The possibilities to apply strontium isotope ratios to hominin remains and uncover philopatric patterns are numerous and varied across geography and time. In all of these
localities, comparisons between tooth enamel and the local environment as assayed through vegetation samples have the strongest potential to elucidate sex differences in philopatric dispersal; however, all localities also have the option of comparisons between hominin teeth and other local fauna as well. This secondary reliable method increases the flexibility of strontium isotope ratio applicability beyond areas with vegetation that can be sampled and areas in which the underlying bedrock is unchanged in the past few million years. In either case, care must be taken to properly measure and quantify the size of the isotopic clusters on the landscape, determine the relative size of estimated home ranges for the fauna of interest, and always bear in mind that spatial measurements are relative. With these frameworks in mind, strontium isotope ratios have powerful potential to reveal novel aspects of hominin behavior, socio-ecology, and landscape use which have previously remained invisible.
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