RESEARCH ARTICLE

Environmental Variables Across *Pan troglodytes* Study Sites Correspond With the Carbon, but Not the Nitrogen, Stable Isotope Ratios of Chimpanzee Hair

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Diet influences the stable isotope ratios of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$ values) in animal tissue; but here we explore the influences of particular aspects of the local environment on those values in chimpanzees (*Pan troglodytes*). In this article we present new $\delta^{13}C$ and $\delta^{15}N$ values in Gombe chimpanzees using hairs collected from night nests in 1989. Then, we explore the influence of environmental factors by comparing our Gombe data to those from eight additional *Pan* study sites with previously published stable isotope data. We compare chimpanzee $\delta^{13}C_{hair}$ and $\delta^{15}N_{har}$ values to specific characteristics of local site ecology (biome and ecoregion) and to local Mean Annual Precipitation (MAP) to test hypotheses based on known effects of these variables on the $\delta^{13}C$ and $\delta^{15}N$ values in plant tissues. The comparison shows that hair from chimpanzees living in savanna sites with lower MAP have higher $\delta^{13}C_{hair}$ values than do chimpanzees living in woodland and forested sites with higher MAP. These results demonstrate the potential of using $\delta^{13}C$ values in primate tissue to indicate aspects of their local ecology in cases where the ecology is uncertain, such as samples collected early in the last century and in fossil hominins. In contrast to expectations, however, chimpanzee $\delta^{15}N_{hair}$ values from some savanna sites with lower MAP are lower, not higher, than those living in more forested areas with higher MAP. It is likely that diet selectivity by chimpanzees affects $\delta^{15}N_{hair}$ values to a greater extent than does the influence of precipitation on plants. Am. J. Primatol.　© 2015 Wiley Periodicals, Inc

Key words: **stable isotopes; carbon and nitrogen; chimpanzee diet and ecology**

INTRODUCTION

Chimpanzees (*Pan troglodytes*) often serve as referential models in human evolution studies or as parts of conceptual models describing species close to the last common ancestor of the human and ape lineages [see Moore, 1996]. Today, chimpanzees are found in a range of ecosystems, from closed canopy rainforests [e.g., Boesch & Boesch-Achermann, 2000] to closed woodlands [Goodall, 1986; Nishida & Uehara, 1983a] to more open "savanna" sites consisting of grasslands and variable amounts of closed and/or open woodland [McGrew et al., 1981; Moore, 1992; Ogawa et al., 2007]. Multiple lines of evidence suggest that the habitats of our early relatives, that is the australopithecines and early *Homo* sp. varied as well. For example, fossil fauna and the stable carbon isotope ratios ($\delta^{13}C$ values in per mil, ‰, notation) of fossil soil organics and pedogenic carbonates from several sites suggest that these early hominins inhabited woodland, bush savanna, and more open savanna sites, or mosaic ecological regions where plant communities varied over space within a single site [Cerling et al., 2011; Kingston, 2007; Reed, 1997; Wynn, 2000].

Observations of chimpanzee feeding behavior and the composition of their fecal material indicate that diets consist largely of fruit and leaves in all habitats [Basabose, 2002; Newton-Fisher, 1999; Nishida, et al., 1983; Nishida & Uehara, 1983b; Potts et al., 2011; Watts et al., 2012; Wrangham, 1977], and although ingested plant foods vary across seasons and habitats, the focus remains on fruit and leaves with little ingestion of high fiber foods [Macho & Lee-Thorp, 2014; Oelze et al., 2014; Tutin & Fernandez, 1993; Wrangham et al., 1998]. The sites with published feeding information on chimpanzee diets are few [Wrangham, 1977], and those with long-

term records [Boesch & Boesch-Achermann, 2000; Goodall, 1986] are biased towards woodland and forest regions [Collins & McGrew, 1988; McGrew et al., 1988]. However, published $\delta^{13}C$ values in chimpanzee tissues (hair, bone) from more open sites also show no indication of high fiber C_4/CAM foods such as grasses, sedges, and succulents [Schoeninger et al., 1999, 2006a]. In contrast, fossil hominin tooth enamel $\delta^{13}C$ data appear to indicate that the hominins ate some amounts of C_4/CAM foods [Cerling et al., 2013; Sponheimer & Lee-Thorp, 1999; Sponheimer et al., 2005, 2013; Wynn et al., 2013] with intra-annual dietary variation in some species [Sponheimer et al., 2006b]. Indeed, some researchers suggest that the ingestion of C_4 foods was fundamental to the separation of the ape and human lineages [Codron et al., 2008].

In interpreting $\delta^{13}C$ data in extant and fossil animals, however, commonly overlooked are the influences of the local ecology or ecosystem type (subsequently referred to more specifically as biome and ecoregion following The Nature Conservancy nomenclature) and Mean Annual Precipitation (MAP). These variables can affect the rate of local photosynthetic activity and the isotopic composition of the carbon dioxide available to plants [Farquhar et al., 1982, 1989; O'Leary, 1981], which consequently could affect the $\delta^{13}C$ values in primate plant foods. The resultant variation in plant food $\delta^{13}C$ values could affect the $\delta^{13}C$ values in the animals that feed on them. Most stable isotope studies on nonhuman primates and on fossil hominins focus on diet, which is estimated based on the animal's position along a straight mixing line drawn between the worldwide average $\delta^{13}C$ values for C_3 plants and C_4 plants [commonly taken from O'Leary, 1981, 1988]. Yet, small early studies on New World and Old World primates, including chimpanzees, showed a correlation between aspects of local ecology and the $\delta^{13}C$ values in primate tissues, which showed a range of almost 4‰ [Schoeninger et al., 1997, 1999]. Using the average $\delta^{13}C$ values for C_3 and C_4 plants to estimate the percent C_3 plants in the diets of the primates with the highest $\delta^{13}C$ values would have suggested that they fed on some amount of C_4 plants, which observational data disputes.

Studies of living and recent primates (including humans) also interpret tissue nitrogen stable isotope ratios ($\delta^{15}N$ values, ‰ notation) in terms of diet [for example: Fahy et al., 2013; Oelze et al., 2014; Richards et al., 2001, 2008; Schoeninger et al., 1999]. Yet, we have evidence in support of an early proposal [Heaton et al., 1986, 1987] that nitrogen stable isotope ratios in plants can be influenced by aridity. Analyses of multiple precipitation gradients from across the globe find that plant $\delta^{15}N$ values exhibit significant negative correlations with MAP [Amundson et al., 2003; Aranibar et al., 2004; Austin & Vitousek, 1998; Craine et al., 2009; Martinelli et al., 1999; Schulze et al., 1998]. Animals incorporate $\delta^{15}N$ values of consumed plants in their bodily tissues, and several studies have demonstrated significant correlations between bone collagen $\delta^{15}N$ values and MAP [Ambrose, 1991; Hartman, 2011; Johnson et al., 1998; Murphy & Bowman, 2009; Pate & Anson, 2008] and/or temperature [Stevens et al., 2006] in a variety of animals although not in primates. Such relationships do not manifest in all species. Studies on North American jackrabbits, for example, found no correlations between bone collagen $\delta^{15}N$ values and precipitation or temperature [Ugan & Coltrain, 2011].

In the present study, we investigate whether there is a correlation between several environmental indicators, on the one hand, and the $\delta^{13}C$ values and $\delta^{15}N$ values in chimpanzee hair on the other. More specifically, we test the hypothesis that chimpanzee hair stable isotope ratios correlate with ecoregion, plant biome and precipitation. To do this, we analyze samples from one site (i.e., Gombe, Tanzania) for which there were no published stable isotope data, and compare the results with published data from other chimpanzee research sites across Africa. A negative correlation between the $\delta^{13}C$ values in chimpanzees and their local MAP would support previous arguments against using single $\delta^{13}C$ values as the end member of C_3 plants in diet estimates for extant primates and in fossil hominins. Instead, as presented most clearly by Murphy & Bowman [2009] the full range of $\delta^{13}C$ values of C_3 plants must be considered. If there is a negative correlation between MAP and chimpanzee $\delta^{15}N$ values, then some measure of aridity must be considered when interpreting the $\delta^{15}N$ values in living and recent primates (including humans). Also, if supported, these broader comparisons should improve future modeling of chimpanzee habitats from animal samples that were collected without specific ecological information. For earlier material such as fossil hominins, such results of the comparison would indicate that tooth enamel $\delta^{13}C$ values should be interpreted with attention to habitat ecology in addition to diet.

Over the past several decades, analyses of carbon and nitrogen stable isotope ratios have become routine in studies of animal diet [Koch, 2007; Sandberg et al., 2012]. The approach is based on the premise that animal stable isotope ratios vary in direct relation with the stable isotope ratios in the animal's diet [DeNiro & Epstein 1978, 1981], which in the case of primates is largely plant based. In those cases where we lack the ideal of baseline data [Crowley, 2012; Warinner et al., 2013], we base expectations on well-established principles of stable isotope biogeochemistry [Fry, 2006; Hoefs, 2009; Lajtha & Marshall, 1994; Rundel et al., 1989]. This latter approach is the one employed in the present study.

The primary source of variation in $\delta^{13}C_{plant}$ values is the plant's method of photosynthesis [Smith & Epstein, 1971], but we now know that several variables other than the photosynthetic pathway affect the final $\delta^{13}C_{plant}$ value [Marshall et al., 2007]. The following discussion focuses largely on C_3 plants because these variables affect C_3 plants to a far greater extent than they do C_4 plants [Marino & McElroy, 1991] and, as discussed below, living primates largely feed on C_3 plants. The most commonly cited average for C_3 plants worldwide is $-27‰$; but the values show a range from $-37‰$ to $-20‰$ [O'Leary, 1988]. Specific values result from a balance between the photosynthetic rate and the $\delta^{13}C$ value of the carbon dioxide (CO_2) available to the plant [Farquhar et al., 1989] both of which are affected by available water, altitude, temperature, plant phylogeny, canopy cover, and leaf type [Farquhar et al., 1982; Marshall et al., 2007]. Global distributions of $\delta^{13}C_{plant}$ values, however, demonstrate that of all these variables MAP has the strongest influence on C_3 plants [Diefendorf et al., 2010; Kohn, 2010]. A compilation of over 1,300 C_3 plant samples from 570 individual sites that span a large range of MAP, Mean Annual Temperature (MAT), altitude, and latitude show a monotonic decrease between $\delta^{13}C_{plant}$ values and increasing MAP with far lower effects of MAT, altitude, latitude, and other variables than expected [Kohn, 2010]. The highest $\delta^{13}C_{plant}$ values come from scrub bushlands like those in Israel [$-22‰$ see Hartman & Danin, 2010] and extremely arid environments (e.g., the Atacama Desert) [up to $-20‰$ see Kohn, 2010] while those below $-31.5‰$ come from tropical closed canopy forests that result from the uptake of recycled ^{13}C-depleted CO_2 released from soil respiration as well as lower light levels [Bonafini et al., 2013; van der Merwe & Medina, 1991; Vogel, 1978; Yakir & Israeli, 1995]. In addition to the distribution of $\delta^{13}C_{plant}$ values, overall plant biomass varies linearly with precipitation globally [Kohn, 2010]. Usually there is a greater amount of canopy cover with lower $\delta^{13}C_{plant}$ values in regions with higher MAP although there are regions where local temperature and specific soil types can affect these relationships [Michaletz et al., 2014] .

In contrast to C_3 plants the range in C_4 plants (arid adapted grasses and a few species within the sedge family) is much smaller, approximately $4‰$, with a range from $-15‰$ to $-11‰$ and a mean $\delta^{13}C_{plant}$ value of $-13‰$ (O'Leary, 1988). Crassulacean Acid Metabolism plants (CAM), which are also arid adapted plants [Ehleringer, 1978; Stowe & Teeri, 1978; Tieszen et al., 1979] include cacti and succulents with $\delta^{13}C$ values that can overlap with C_4 plants [Smith & Epstein, 1971].

The habitats of most primates are characterized as having predominantly C_3 plant species [Cerling et al., 2004] and their diets reflect this bias. Thus far, there is little evidence that either C_4 or CAM plants are significant foods for living nonhuman primates [Crowley et al., 2010; Sandberg et al., 2012; Schoeninger, 2014]. While macaques observed raiding maize fields on a seasonal basis had somewhat elevated $\delta^{13}C_{hair}$ values, their bone collagen indicated a pure C_3 diet [O'Regan et al., 2008]. Although baboon fecal samples recovered beneath a succulent plant (i.e., CAM) in a marginal environment had $\delta^{13}C$ values in the C_4 range, baboon tooth samples from the same area indicated a complete C_3 diet [Codron et al., 2006]. Even geladas, which feed extensively on grass live in regions of high altitude that are relatively cool with relatively high rainfall where most plant species, including grasses, are C_3 [Fashing et al., 2014].

Because primates feed so extensively on C_3 plants, it was unsurprising that primate $\delta^{13}C$ values varied with canopy cover (which, in turn, varies with MAP) rather than dietary specifics [Schoeninger et al., 1999]. Still, recent work demonstrates that some C_3 plant foods can have strikingly different $\delta^{13}C$ values than other foods within the same ecoregion [representative examples included in: Cerling et al., 2004; Codron et al., 2005; Oelze et al., 2014]. For example, some fruits within the Ituri Forest had carbon stable isotope ratios that were much higher (e.g., $-30‰$ to $-31‰$) than those in leaves taken from the canopy floor ($-37‰$) [Cerling et al., 2003]. Yet, within the canopy (i.e., the main area of feeding for primates) both leaves and fruits had values that were $5‰$ higher than leaves and fruits from the subcanopy. Significantly, there was no association between primate $\delta^{13}C$ values and the differential mix of fruit and leaves among sympatric folivorous, frugivorous, and omnivorous primate species; all species had $\delta^{13}C$ values within $1‰$ of each other [Cerling et al., 2004].

Some, although not all, fruits eaten by both chimpanzees and gorillas at Loango, Gabon had $\delta^{13}C$ values that are about $1‰$ higher, on average, than leaves, and the chimpanzees there had higher $\delta^{13}C_{hair}$ values than did the gorillas [Oelze et al., 2014]. Because approximately 60–75% of the carbon used in synthesizing tissue proteins comes from dietary protein [Fernandez in press; Froehle et al., 2010] Oelze et al. [2014] concluded that the higher $\delta^{13}C$ values in chimpanzees reflected their higher fruit intake relative to gorilla, and that fruit provided significant amounts of protein to the chimpanzees. However, fruits normally consist of carbohydrates with little to no protein [Fleagle, 2013; Murray et al., 2001] and the C:N ratios in fruits at Loango [Oelze et al., 2014] are extremely high, which is consistent with general expectations for fruit. To be certain of the situation with regards to protein at Loango, nutritional analyses must be done on the various plant foods before it can be concluded whether or not the fruits provide chimpanzee dietary protein. On the other hand, 25–40‰ of the carbon in collagen (and hair) comes from nutritional sources other

than protein, and fruit carbohydrate (simple sugar and nonstructural carbohydrate) is the most likely source. Therefore, the higher $\delta^{13}C_{hair}$ values in chimpanzees versus gorillas could still be a result of fruit intake even though it is not the protein fraction of the diet that is the source. Alternatively, perhaps the situation at Loango is similar to that at Taï where chimpanzees have a similar focus on fruit. Researchers there concluded that the fruit diet at Taï provided overall protein intake lower than recommended by the National Research Council resulting in diets that could be protein deficient [N'guessan et al., 2009].

The variation in nitrogen stable isotope ratios ($^{15}N/^{14}N$ represented by $\delta^{15}N$ values) within the biosphere differs from that of carbon stable isotope values. The variation in plant $\delta^{15}N$ values is determined by the $\delta^{15}N$ value of the nitrogen used by plants, which can be atmospheric (N_2) via bacterial nodules on plant roots or, more commonly, soil nitrogen [Shearer & Kohl, 1994]. Animal $\delta^{15}N$ values are determined by $\delta^{15}N$ values in their foods [DeNiro & Epstein, 1981], which as mentioned previously are mostly plant based. In general, herbivores overall have $\delta^{15}N$ values in their tissues that are approximately 3‰ higher than the plants on which they feed, and carnivores are approximately 3‰ higher than the animals on which they feed [Minagawa & Wada, 1984; Schoeninger & DeNiro, 1984; Schoeninger, 1985] although there can be quite a bit of variation around these values [Koch, 2007]. Individual chimpanzees observed eating animal material had higher $\delta^{15}N_{hair}$ values than did their more herbivorous companions [Fahy et al., 2013], the results of a similar study on bonobos were less clear [Oelze et al., 2011] and in both cases, the overall effect was quite small.

Global soil $\delta^{15}N$ values vary between -2.0‰ and 10.3‰ [Amundson et al., 2003] depending on the amount of biomass degradation, the parent material, precipitation, salinity, and various processes such as leaching, ammonia volatilization, and denitrification [Heaton, 1987; Shearer & Kohl, 1994]. But, based on the available data thus far African soil $\delta^{15}N$ values vary by less than 3‰, on average, and within the region where the chimpanzee sites are located, the soil $\delta^{15}N$ values vary by less than 2‰ (9–10.3‰) [Amundson et al., 2003]. In sum, the range of baseline $\delta^{15}N$ values across the chimpanzee sites is, on average, much lower than global distributions and nitrogen cycling processes would suggest.

Plant $\delta^{15}N$ values are normally lower than soil and across Africa they can be 2–5‰ lower [Amundson et al., 2003], which increases the expected range of $\delta^{15}N$ values within plants. Several studies, based on work begun in the early part of the last century, demonstrate that the greatest effects on plant $\delta^{15}N$ values are MAP and MAT [Amundson et al., 2003; Austin & Vitousek, 1998; Handley et al., 1999; Martinelli et al., 1999]. In general, systems that are

wet and cool have lower $\delta^{15}N$ values [Evans, 2001] compared to those systems that are open, warm and dry [Amundson et al., 2003; Austin & Vitousek, 1998; Shearer & Kohl, 1986]. Some studies suggest that in temperate latitudes with marked seasonal variation in MAT, the animals most affected are ones that must drink water [Cormie & Schwarcz, 1994, 1996]. Water independent species, such as jackrabbits in North America and northern Mexico, can show no correlation between the $\delta^{15}N$ values of bone collagen and MAP [Ugan & Coltrain, 2011], or show significant positive correlation with MAT rather than with MAP (Somerville, in preparation). MAT is expected to have the smaller effect across the chimpanzee sites because of the relatively narrow range of MAT across within the tropical latitudes inhabited by chimpanzees. Additionally, although altitude can vary within sites, the magnitude is small relative to that observed affecting soil $\delta^{15}N$ values [Amundson et al., 2003] and chimpanzees feeding is not limited to a single altitude.

Analyses from precipitation gradients across Australia, Africa, and in Israel find that $\delta^{15}N$ values in plants and animals consistently show higher $\delta^{15}N$ values in environments with lower water availability indices or with lower MAP, than in wetter zones [Ambrose, 1991; Grocke et al., 1997; Hartman, 2011; Heaton et al., 1986; Murphy & Bowman, 2006, 2009; Pate & Anson, 2008; Sealy et al., 1987]. This pattern occurs because water is a limiting nutrient in dryer systems resulting in a relative excess of soil nitrogen, which "... leaves the system more readily through fractionating pathways" [Murphy & Bowman, 2009:1046] that enrich the remaining soil nitrogen in ^{15}N. The relationship, however, is not linear in either plants or in animals. Studies on Australian macropods [Murphy & Bowman, 2006; Pate & Anson, 2008] and eutherian mammals in Africa [Heaton et al., 1986] found the largest increases in bone $\delta^{15}N$ values in regions with less than 400 MAP with smaller increases in regions with >400 and <1,000 MAP and little to no effect above 1,000 MAP. There is a marked range of MAP across the chimpanzee sites that could affect chimpanzee hair $\delta^{15}N$ values.

METHODS

Our study analyzed samples from Gombe National Park in western Tanzania, which has been the location of Jane Goodall and colleagues' ongoing research since 1960 [see Goodall, 1986; Wilson, 2012 for overviews]. It covers an area of about $35.4\,km^2$, and is a mosaic of evergreen forest, open woodland, and grassland [Clutton-Brock & Gillett, 1979; Goodall, 1986; Wilson, 2012]. The dry season lasts from May to October [Wallis, 1995], average yearly rainfall has been variously reported from 750 to 1250 mm [Teleki et al.,

1976] to 1546 [Clutton-Brock & Gillett, 1979]. Our study included samples from the Kasekela community [Goodall, 1986], which is located centrally in the park.

Stable isotope analysis was performed on hair from 13 known individuals (see Table I) collected in 1989 from night nests by J.J.M. and collaborators as part of another project. The hair collection involved no invasive techniques nor did it involve any animals directly; that is these were naturally shed hairs. The project received approval from IACUC and followed the American Society of Primatologists' principles for the ethical treatment of nonhuman primates. The Tanzanian Commission on Science and Technology (COSTECH) permitted data collection on the Gombe chimpanzee community.

In addition to the new data in our study, we compiled published data from eight other study sites to evaluate the association between habitat characteristics and rainfall levels (MAP, an indirect proxy for vegetation) with carbon and nitrogen stable isotope ratios across regions and researchers (Table II). These sites include Ishasha, Zaire and Ugalla, Tanzania [Schoeninger et al., 1999]; Fongoli, Senegal [Sponheimer et al., 2006a]; Kibale, Uganda [Carter, 2001]; a restricted area within central Cameroon [Macho & Lee-Thorp, 2014]; Taï, Cote d'Ivoire [Fahy et al., 2013]; Ganta, Liberia [Smith et al., 2010]; and Loango, Gabon [Oelze et al., 2014] (Fig. 1).

When the original data were derived from bone collagen samples [e.g., Smith et al., 2010 from Ganta], we converted the values to $\delta^{13}C_{hair}$ values. In doing so, we chose not to follow Fahy et al. [2013] in using the value of 2‰ because the source they cite is a paper on nitrogen stable isotopes [DeNiro & Epstein, 1981], and the earlier paper on carbon [DeNiro & Epstein, 1978] reported on chitin and bone collagen, but not keratin. Instead, we applied the conversion (-1.4‰

for $\delta^{13}C$ values and -0.86‰ for $\delta^{15}N$ values) following O'Connell et al. [2001] even though the data are limited to modern British people and the $\Delta^{13}C$ values show a large amount of variation (i.e., S.D. = 0.45 for $\delta^{13}C$ values and 0.17 for $\delta^{15}N$ values). We chose not to follow Crowley et al. [2010] in using apparent enrichment values (ε^*) because while they are necessary when comparing materials with vastly different $^{13}C/^{12}C$ ratios relative to the PDB or SMOW standards (e.g., geochemical versus biological materials) [Hoefs, 2009] we compare only biological materials (e.g., hair versus bone collagen) that are relatively similar to one another. In addition, the majority of ecological and biological papers use delta values. The reader can convert the $\delta^{13}C_{hair}$ values to apparent enrichment values using the following equations: (1) $\varepsilon^* = (\alpha - 1)$ and (2) $\alpha collagen\text{-}keratin = (1,000 + \delta^{13}C_{collagen})/(1,000 + \delta^{13}C_{hair})$ where ε^* is the apparent enrichment value and α is the apparent fractionation factor [see Crowley et al., 2010 for apparent enrichment and alpha values]. In any case, within this study any errors resulting from these choices will be constants (with the exception of the Ganta data) and will not affect the assessments of relationships between the variables.

In addition, museum samples (Ganta and Cameroon) collected in the last century had to be corrected as adjustment for the lower $\delta^{13}C$ values in today's atmospheric CO_2. We chose not to follow [Kohn, 2010] who applied a correction of 0.023‰/ year to plant samples collected within the last 10–15 years because the museum samples were collected in the early 1940's. The massive changes in the $\delta^{13}C$ values of atmospheric carbon dioxide (Keeling Curve at Scripps Institution of Oceanography, https://scripps.ucsd.edu) have occurred since 1960 so atmospheric $\delta^{13}C$ values in the years of museum collecting would be virtually identical to 1960. For the Ganta and Cameroon specimens, we subtracted an additional 1.1‰ from the bone collagen $\delta^{13}C$ values [following Smith et al., 2010] who relied on Hoppe's estimate from prehistoric bison tooth enamel samples standardized against ice core data [Hoppe et al., 2006]. This figure is almost identical to the 1.2‰ used by Crowley [Crowley et al., 2011a] who relied on Chamberlain's estimate from prehistoric condors that was also standardized against ice core data [Chamberlain et al., 2005].

The different Pan sites were characterized using The Nature Conservancy's (TNC) online spatial dataset for the terrestrial ecoregions and biomes of the world (see http://maps.tnc.org/). Categories of the TNC system were designated through collaborations with the World Wildlife Fund and over 1,000 scholars from diverse fields, including ecologists, biogeographers, taxonomists, and conservationists. The categories provide highly accurate spatial categorization of different

TABLE I. Isotope Results From Gombe Chimpanzee (*P. troglodytes*) Hair

Spec #	Name	Sex	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N
MS-6174	Evered	M	-23.6	3.2	3.7
MS-6175	Fifi	F	-23.1	3.1	3.7
MS-6177	Faustino	M	-22.7	3.4	3.7
MS-6179	Frodo	M	-22.7	3.8	3.4
MS-6181	Gimble	M	-23.1	4.0	3.5
MS-6182	Goblin	M	-23.5	3.6	3.5
MS-6186	Prof	M	-22.8	3.0	3.6
MS-6190	Pax	M	-23.0	3.9	3.5
MS-6191	Sandi	F	-23.7	3.1	3.6
MS-6192	Spindle	M	-23.2	3.6	3.7
MS-6193	Sparrow	F	-23.2	3.8	3.5
MS-6194	Tubi	M	-22.7	3.4	3.6
MS-6197	Wilkie	M	-23.0	3.4	3.7

TABLE II. Summary Statistics of Stable Isotope Values From Chimpanzee Sites

Site	Biome[a]	Ecoregion	MAP (mm)	$\delta^{13}C$ (‰)			$\delta^{15}N$ (‰)		
				n	Mean	SD	n	Mean	SD
Ishasha[b]	TSGSS	Sahelian Acacia Savanna	750	8	−23.1	0.2	7	5.9	0.8
Fongoli[c]	TSGSS	West Sudanian Savanna	950	36	−22.2	0.4	36	2.9	0.3
Ugalla[b]	TSGSS	Central Zambezian Miombo Woodlands	1050	12	−22.0	0.3	8	2.3	0.8
Gombe[d]	TSGSS	Central Zambezian Miombo Woodlands	1250	13	−23.1	0.3	13	3.5	0.3
Kibale[e]	TSMBF	Albertine Rift Montane Forest	1500	15	−23.5	0.5	15	7.0	0.8
Cameroon[f]	TSMBF	Northwestern Congolian Lowland Forests	1700	39	−24.9	0.9	39	9.1	1.7
Taï[g]	TSMBF	Western Guinean Lowland Forest	1800	52	−24.9	0.5	52	7.4	0.9
Ganta[h]	TSMBF	Western Guinean Lowland Forest	1956	37	−24.6	0.5	21	6.2	0.7
Loango[i]	TSMBF	Atlantic Equatorial Coastal Forest	2215	14	−24.6	0.5	14	4.8	0.4

[a]Biome types. TSGSS, Tropical and subtropical savannas, grasslands, and shrublands; TSMBF, Tropical and subtropical moist broadleaf forests. Both designations follow the nature conservancy nomenclature.
[b]Schoeninger et al. [1999].
[c]Sponheimer et al. [2006].
[d]This study.
[e]Carter [2001].
[f]Macho and Lee-Thorp [2014].
[g]Fahy et al. [2013].
[h]Smith et al. [2010] with MAP data from Harley [1939].
[i]Oelze et al. [2014].

environmental regions [Olson et al., 2001]. The freely available georeferenced maps provide a standard reference for scholars around the globe. All chimpanzee sites included in the present meta-study fall within two broad biomes: Tropical and Subtropical Moist Broadleaf Forests (TSMBF) and Tropical and Subtropical Savannas, Grasslands, and Shrublands (TSGSS). Within these categories, seven separate terrestrial ecoregions are represented and are identified in Table II.

Rainfall figures (MAP) in the literature can vary greatly as a function of sampling period and methodological issues (as noted above for Gombe). We use the values reported for individual sites by the authors of the papers reporting the stable isotope data. In the case of Gombe, we chose the high end of the range reported by Teleki and colleagues [750–1250 mm; Teleki et al., 1976], which covered a 10-year period, because the value presented by Clutton-Brock & Gillett [1979;
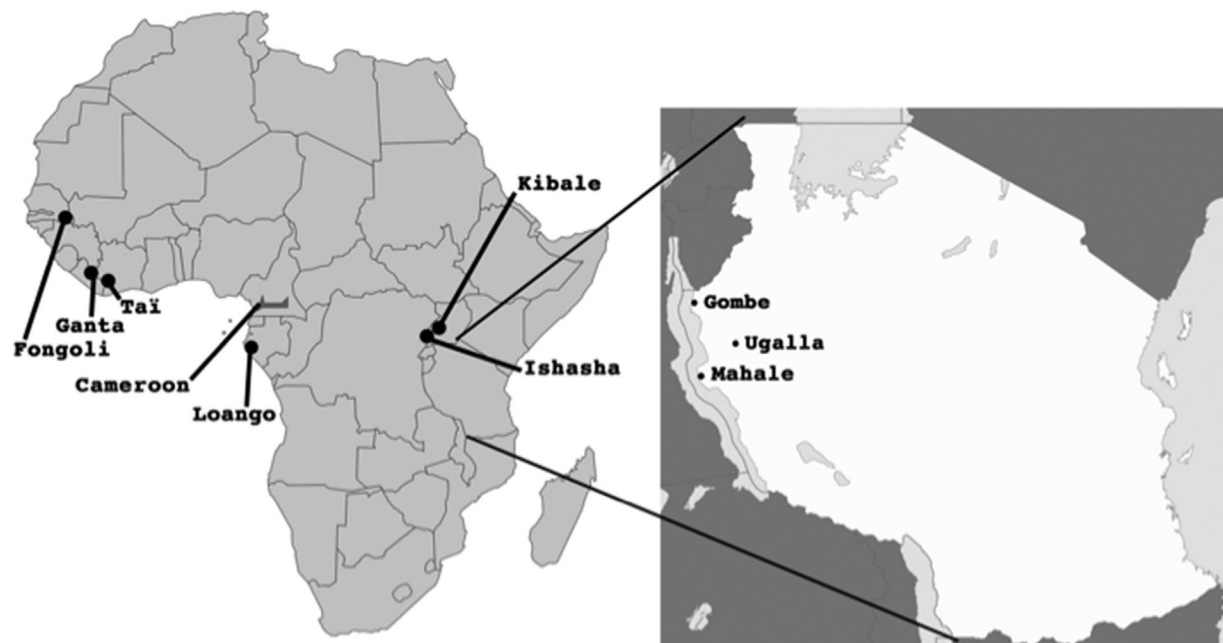

Fig. 1. Map of sites used in the present study.

1546 mm] fell so far outside the 10-year report. For Ganta, we follow Smith et al. [2010] who base their estimate on a 6 year average of values recorded between 1927 and 1936 [Harley, 1939].

To test for differences between males and females at Gombe, we used the non-parametric Mann–Whitney U test. Comparisons of chimpanzee $\delta^{13}C$ and $\delta^{15}N$ hair values between the two biomes were made with independent samples *t*-tests. Simple linear regressions determined the relationship between MAP and stable isotope ratios. A one-way analysis of variance (ANOVA) and Tukey's post hoc tests of significance assessed the differences in stable isotope ratios between the individual sites. All statistical analyses were conducted with SPSS v. 22.

All hair samples were washed in sequential ultra-sonic baths of double-distilled de-ionized water and acetone to remove environmental contaminants and extraneous body oils. Hairs were dried at 50°C overnight in a laboratory oven. To homogenize bulk samples, hairs were finely cut with a stainless steel scalpel into small (∼1 mm) pieces and mixed. Between 0.5 and 1.0 mg were added directly to tin capsules for combustion. Samples were analyzed in an automated fashion on a Thermo-Finnigan Delta XP Plus, Conflow and Costect EA in the Analytical Laboratory at Scripps Institute for Oceanography (SIO). Data are expressed using the standard formula $\delta = ((R_{sample}/R_{standard}) - 1) \times 1,000$ where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The carbon sample was standardized relative to relative to the Pee Dee Belemnite standard (PDB) while the nitrogen sample was standardized relative to the ambient inhalable reservoir (AIR). Repeated analysis of an internal laboratory standard over the last 5 years indicates a precision of 0.12‰ and 0.15‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. All hair samples had C:N ratios falling within the acceptable range of 2.9–3.8 [O'Connell et al., 2001].

RESULTS

There are no statistically significant differences in hair stable isotope values between males and females within the Kasekela community at Gombe ($\delta^{13}C_{hair}$ females = −23.2‰ and males = −23.0‰; $P = 0.573$, $\delta^{15}N_{hair}$ females = 3.3‰ and males; = 3.6‰ $P = 0.371$). We note that the sample size for females is small ($N = 3$ versus 10 males), and more samples are needed to be sure of the apparent lack of difference. Based on the lack of significant differences, however, we combined the samples when comparing with the published data from other sites.

When the Gombe isotope data are combined with data from the other *Pan* sites (Fig. 2), some patterns emerge. Highly significant differences exist between the individual chimpanzee sites in both carbon ($P < 0.001$; Table III) and nitrogen ($P < 0.001$; Table IV) stable isotope values. There is a statistically significant negative regression equation ($r^2 = 0.5579$, df = 285.3, $P < 0.001$) between MAP and $\delta^{13}C_{hair}$ values at the various study sites (Fig. 2a) although two sites fall off the line. Ishasha, which has the lowest MAP value, falls below the line and Ugalla with 250 mm more MAP per year than Ishasha falls above the line. In addition, most of the Cameroon samples fall below the line and there are two outliers. The simple
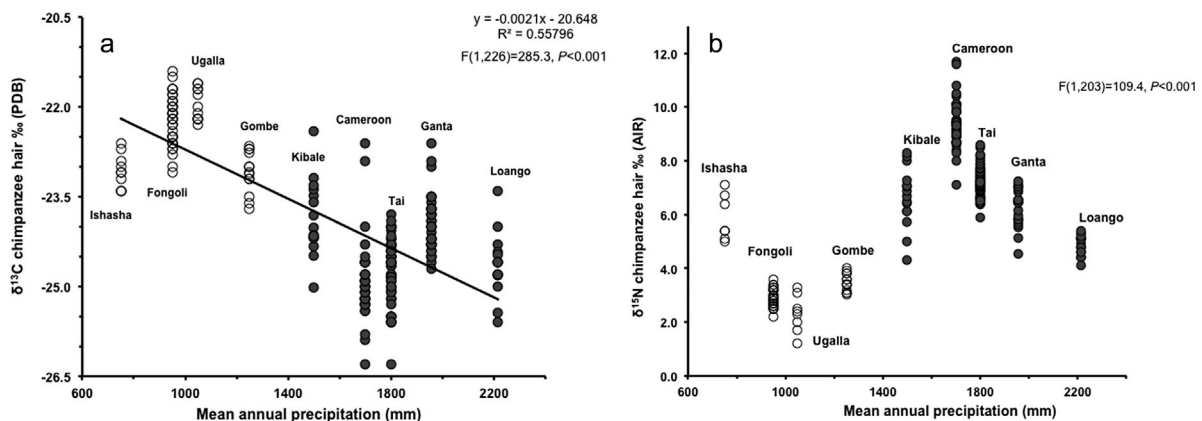

Fig. 2. Carbon ($\delta^{13}C_{hair}$ values) and nitrogen ($\delta^{15}N_{hair}$ values) stable isotope ratios in chimpanzee hair plotted against Mean Annual Precipitation (MAP). The data come from Gombe (this study) and from eight other, previously published chimpanzee sites. The open symbols indicate Tropical and Subtropical Savanna, Grassland, and Shrubland Biome (TSGSS) sites; the closed symbols indicate Tropical and Subtropical Moist Broadleaf Forest (TSMBF) Biome sites. (**a**) The $\delta^{13}C_{hair}$ values show a statistically significant negative correlation with MAP as expected based on the worldwide distribution of C_3 plant $\delta^{13}C$ values. The higher $\delta^{13}C_{hair}$ values come from sites within TSGSS Biome sites, and within this Biome the Savanna Ecoregion sites have higher MAP values than those from Woodland Ecoregions. The lower $\delta^{13}C_{hair}$ values come from TSMBF Biome sites and within this Biome those with higher $\delta^{13}C_{hair}$ values come from Forest Ecoregions with lower MAP than those with higher precipitation levels. (**b**) The $\delta^{15}N_{hair}$ values show no clear pattern in the plot against MAP although there is a statistically significant positive relationship, which is opposite to expectations based solely on the ecological variation in soil, plant, and faunal $\delta^{15}N$ values from across the globe. The values probably reflect an as yet unidentified differential in diet selectivity between the two types of Biomes (see text for discussion).

TABLE III. Pairwise Comparisons of $\delta^{13}C_{hair}$ Values Between Chimpanzee Site Locations

	Fongoli		Ugalla		Gombe		Kibale		Cameroon		Taï		Ganta		Loango	
Ishasha	**0.00**	**	**0.00**	**	1.00		0.01	*	**0.00**	**	**0.00**	**	**0.00**	**	**0.00**	**
Fongoli			**0.00**	**	0.86		**0.00**	**	**0.00**	**	**0.00**	**	**0.00**	**	**0.00**	**
Ugalla					**0.00**	**	**0.00**	**	**0.00**	**	**0.00**	**	**0.00**	**	**0.00**	**
Gombe							0.01	*	**0.00**	**	**0.00**	**	**0.00**	**	**0.00**	**
Kibale									**0.00**	**	**0.00**	**	0.99		**0.00**	**
Cameroon											0.63		**0.00**	**	0.63	
Taï													**0.00**	**	1.00	
Ganta															**0.00**	**

Bold values indicate statistical significance between the sites compared.
**$P < 0.05$.
*$P < 0.001$.

linear regression assessing the relationship between $\delta^{15}N_{hair}$ and MAP found a significant positive regression equation ($r^2 = 0.35012$, df $= 109$, $P < 0.001$). But the relationship is not entirely clear because MAP explains only 35% of the variation in $\delta^{15}N_{hair}$ values. For that reason, we have plotted the data without a regression line (Fig. 2b).

As seen in the plot of $\delta^{15}N_{hair}$ against $\delta^{13}C_{hair}$ values (Fig. 3), most of the samples from the Tropical and Subtropical Moist Broadleaf Forests (TSMBF) biomes (Kibale, Cameroon, Taï, Ganta, and Loango) exhibit $\delta^{13}C_{hair}$ values between $-24.0‰$ and $-26‰$ whether they are from Montane or Lowland Forest Ecoregions. In contrast, most of the samples from the Tropical and Subtropical Savannas, Grasslands, and Shrublands (TSGSS) biomes (Ishasha, Fongoli, Ugalla, and Gombe) have $\delta^{13}C_{hair}$ values between $-23.0‰$ and $-21.5‰$ whether they are Savanna or Miombo Woodland ecoregions. There is some overlap of samples from Gombe, Fongoli, and Ishasha (TSGSS biomes) with those from Ganta and Kibale (TSMBF biomes). Independent sample t-tests found a highly significant difference in $\delta^{13}C_{hair}$ hair values between TSGSS ($N = 71$, Mean $= -22.5‰$, SD $= 0.57$) and TSMBF ($N = 157$, Mean $= -24.6‰$, SD $= 0.7$) biomes; $t(226) = 21.6$, $P < 0.001$. The majority of the $\delta^{15}N_{hair}$ values from the TSMBF biomes fall between 5‰ and 10‰, and those from TSGSS biomes fall between 2‰ and 4‰. Ishasha is an exception: its $\delta^{15}N_{hair}$ values fall well within the values for the TSMBF biomes even though it is located within a Savanna ecoregion of the TSGSS Biome. Even so, independent sample t-tests found a highly significant difference in $\delta^{15}N_{hair}$ values between TSGSS ($N = 64$, Mean $= 3.3‰$, SD $= 1.1$) and TSMBF ($N = 141$, Mean $= 7.5‰$, SD $= 1.6$) biomes; $t(173.75) = -18.73$, $P < 0.01$.

DISCUSSION

The correlation between MAP and $\delta^{13}C_{hair}$ values follows the predicted pattern of higher $\delta^{13}C$ values in animal tissues from drier regions with some exceptions although the chimpanzee $\delta^{13}C_{hair}$ values at Ishasha are, on average, almost 1‰ lower than expected. These chimpanzees live in the gallery forest that lines a perennially flowing river with their night nests situated within the gallery forest and most feeding takes places within this more humid region [Sept, 1992]. In contrast, the chimpanzees from Ugalla have $\delta^{13}C_{hair}$ values that are higher than expected based on reported MAP (Fig. 2a) although they are well within expected values for eating a complete C_3 diet. Ugalla has leguminous trees that form a continuous but thin

TABLE IV. Pairwise Comparisons of $\delta^{15}N_{hair}$ Values Between Chimpanzee Site Locations

	Fongoli		Ugalla		Gombe		Kibale		Cameroon		Taï		Ganta		Loango	
Ishasha	**0.00**	**	**0.00**	**	**0.00**	**	0.233		**0.00**	**	**0.00**	**	0.92		0.03	*
Fongoli			0.41		0.14		**0.00**	**	**0.00**	**	**0.00**	**	**0.00**	**	**0.00**	**
Ugalla					**0.00**	**	**0.00**	**	**0.00**	**	**0.00**	**	**0.00**	**	**0.00**	**
Gombe							**0.00**	**	**0.00**	**	**0.00**	**	**0.00**	**	**0.00**	**
Kibale									**0.00**	**	0.09		0.76		**0.00**	**
Cameroon											**0.00**	**	**0.00**	**	**0.00**	**
Taï													**0.00**	**	**0.00**	**
Ganta															**0.00**	**

Bold values indicate statistical significance between the sites compared.
**$P < 0.05$.
*$P < 0.001$.
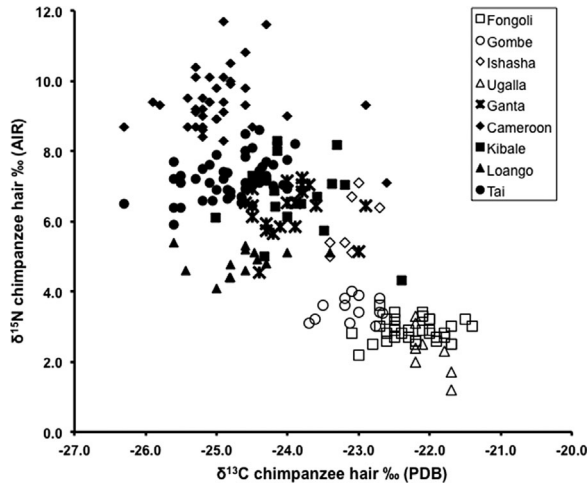
Fig. 3. Plot of the $\delta^{13}C_{hair}$ and $\delta^{15}N_{hair}$ values from Tropical and Subtropical Savanna, Grassland, and Shrubland Biome (TSGSS represented by the open symbols) and Tropical and Subtropical Moist Broadleaf Forest (TSMBF represented by the closed symbols) Biomes. The TSGSS Biome sites are significantly higher in $\delta^{13}C_{hair}$ values and lower in $\delta^{15}N_{hair}$ values. Ishasha, in contrast to the other TSGSS Biome sites, has $\delta^{15}N_{hair}$ values that fall within the distribution of TSMBF sites. These chimpanzees feed in the gallery forest that lines the ever-flowing river and may have access to different foods than those living in the other TSGSS Biome sites.

canopy, which allows enough light for C_4 grasses in the understory (the botanical identifier for a TSGSS biome). It is possible that Ugalla is a case where the MAP in an unreliable indicator of canopy cover or that the lacey leaves of leguminous trees have relatively high $\delta^{13}C$ values. A large project is collecting vegetation samples at present, and the stable isotope analyses of the samples should further our understanding of this site [Piel et al. unpublished data].

The average values for the rest of the sites fall on or close to the regression line, although there is a lot of scatter in individual $\delta^{13}C_{hair}$ values around the line. Some of this scatter is probably the result of chimpanzee dietary selectivity. For example, although the average $\delta^{13}C_{hair}$ value at Loango falls on the regression line, many individuals fall above the line, which may reflect the elevated $\delta^{13}C$ values in some fruits eaten by chimpanzees as discussed by Oelze et al. [2014]. To evaluate the possibility that the $\delta^{13}C_{hair}$ values reflect fruit-eating rather than MAP, we compiled published data on percent of feeding time spent on fruit, leaves, flowers, bark, stem/pith, seeds, and other (Table V). Such data are not available for the majority of the sites included in the present study and we decided that there was not a way to compare feeding information taken from fecal material directly with percent of feeding time so we list those sites as not having available feeding data and report only on sites with observations of feeding. Semliki, Uganda [Hunt & McGrew, 2002], in a TSGSS biome with a permanently flowing

river, shows the lowest amount of feeding time spent on fruit (39%) of all the sites for which we have data. Fongoli, Senegal [Pruetz, 2006] another TSGSS biome site reports 62.5% feeding time devoted to fruit based on a limited sample size. We include three different dietary estimates for Gombe, Tanzania (also a TSGSS biome), all of which cite Wrangham [1977]. Two of these report amounts of feeding time spent on fruit (59.4% and 63%) that are relatively similar to each other [Newton-Fisher, 1999; Watts et al., 2012] and to Fongoli; but the third [Morgan & Sanz, 2006] reports a much lower amount of time (43%). Based on personal observations, JMM thinks that the lower value is unlikely; but we include it because it is often cited.

For the TSMBF biome sites, Kanyawara [Wrangham et al., 1996] and Ngogo [Watts et al., 2012] at Kibale, Uganda (a TSMBF biome) are similar to each other (>70% of feeding time spent on fruit), and also Taï, Cote d'Ivoire (77%) [based on Doran, 1997; Watts et al., 2012]. But, Budongo, Uganda, another TSMBF biome reports 64.5% of feeding time spent on fruit [Newton-Fisher, 1999], which is similar to that reported for Fongoli and Gombe (TSGSS biome sites). Overall the wetter sites (Kibale and Taï; but not Budongo) report greater percent feeding time focused on fruit and have lower $\delta^{13}C_{hair}$ values than do the dryer sites (Fongoli and Gombe) suggesting a negative correlation between fruit eating and $\delta^{13}C_{hair}$ value whereas the higher $\delta^{13}C$ values in some fruits at Loango suggest that a higher fruit intake would associate with higher, not lower, $\delta^{13}C_{hair}$ values [Oelze et al., 2014]. In other words, the relationship (if there is one) is the opposite of that expected based on assumptions that fruit $\delta^{13}C$ values would be higher than leaf $\delta^{13}C$ values. Our results, however, compare individuals from multiple populations over a large geographic scale, and do not necessarily negate isotopic patterning across different foods within single sites where data are available on the $\delta^{13}C$ values of individual foods. But, they serve to underscore the possibility of error if using high $\delta^{13}C$ values in primate tissues to indicate fruit-eating.

Therefore at this time, we can say only that the $\delta^{13}C_{hair}$ values correlate with MAP as expected based on a worldwide survey of C_3 plants [Kohn, 2010], and not with fruit-eating. The average $\delta^{13}C_{hair}$ values demonstrate a range in $\delta^{13}C_{hair}$ values over 4‰ where all of the animals eat C_3 foods. Therefore, the general pattern strongly supports the need to take aspects of habitat ecology (biome and ecoregion) into consideration when interpreting the $\delta^{13}C$ values in tissues from extant primates and also fossil primates, including hominins.

In a simple example, an early paper on $\delta^{13}C_{hair}$ values in tooth enamel of *Australopithecus africanus*

TABLE V. Percent of Time Feeding

Site	Fruit (%)	Leaves (%)	Flowers (%)	Bark (%)	Other (%)	Stem/pith (%)	Seeds (%)	Total
Fongoli[a]	62.5	16	11	2.5		3		95
Gombe[b]	43	27	10	0	7	8	7	102
Gombe[c]	63	19						82
Gombe[d]	59.4	21.2			19.4			100
Kibale- Kanyawara[e]	79	2.6			16.9			98.5
Kibale-Ngogo[f]	70.7	19.6	2.5			2.2	4	99
Taï[g]	77	17.5			1		4	99.5
Semliki[h]	39	30	3	12				84
Budongo[i]	64.5	19.7	8.8			3.2		96.2
Not available								
Cameroon[j]								
Ganta[j]								
Loango[k]								
Ugalla[j]								
Ishasha[j]								

[a]Pruetz [2006].
[b]Morgan and Sanz [2006] citing Wrangham [1977].
[c]Newton-Fisher [1999] citing Wrangham [1977].
[d]Watts [2012] citing Wrangham [1977].
[e]Wrangham et al. [1996].
[f]Watts [2012].
[g]Based on Doran [1997] and Watts [2012].
[h]Hunt and McGrew [2002].
[i]Newton-Fisher [1999].
[j]No collection or no systematic collection.
[k]Fecal prevalence, Oelze et al [2014].

reports an average value of $-8.2‰$, concluding "this early hominid...ate large quantities of carbon-13 enriched foods..." [Sponheimer & Lee-Thorp, 1999:368]. Corrected for differences in atmospheric carbon dioxide $\delta^{13}C$ values ($-1.5‰$) and the offset between diet and tooth enamel $\delta^{13}C$ values (approximately $10‰$ for a species with a simple gastrointestinal tract) yields a diet value of $-19.7‰$. This value is approximately $2‰$ higher than that expected for C_3 plants in an open, but not desert, environment [Hartman & Danin, 2010]. Diagenetic alteration of approximately $1‰$ [following Lee-Thorp, 2000] is expected to enrich the tooth enamel in ^{13}C for a C_3 feeder [see Schoeninger et al., 2003]. Subtracting the diagenetic alteration of $1‰$, lowers the estimated diet $\delta^{13}C$ value to $-20.7‰$ or approximately $1‰$ higher than that expected for a C_3-feeding early hominin feeding in the dryer portion of a Tropical and Subtropical Savanna, Grassland, and Shrubland biome and indicates a diet around 5% C_4 foods. Using the lowest *Australopithecus africanus* value reported by Sponheimer & Lee-Thorp [1999], that is $-11.3‰$, the estimated diet value ($-22.8‰$) falls within the range for C_3 plants in this biome. Using the highest value $-5.6‰$ corrected in the same manner as presented above, gives a diet estimate of $-17.1‰$, which would include upwards to 25% C_4 foods. If, on the other hand, *Australopithecus africanus* had a more complex gastrointestinal tract as suggested by the Expensive Tissue Hypothesis [Aiello & Wheeler, 1995]. A diet to enamel offset of

$14‰$ as reported for modern hindgut and foregut fermenters [Passey et al., 2005] results in a diet estimate of $-21.1‰$ or 5% C_4 plants in the diet. We do not purport to know the specifics of the digestive tract in *Australopithecus africanus*; but this simple exercise suggests that the overall calculation of diet in fossil species is more complicated than is often presented.

In contrast, the $\delta^{15}N_{hair}$ values do not follow the predicted pattern of higher values in regions of lower rainfall. In fact, our regression analysis found a weak, but significant, correlation of increasing $\delta^{15}N_{hair}$ values with higher levels of MAP, which is the exact opposite of the expected relationship. The overall scatter indicates that although the relationship between $\delta^{15}N_{hair}$ values and MAP is statistically significant, it is probably meaningless biologically. More likely, chimpanzee $\delta^{15}N_{hair}$ values reflect diet selectivity within individual sites as suggested previously [Fahy et al., 2013; Oelze et al., 2014; Schoeninger et al., 1999] rather than any direct effect of MAP. Some unexpected and interesting relationships appear in the data, however. With one exception (Ishasha), the chimpanzees from the TSGSS biomes have $\delta^{15}N_{hair}$ values are significantly lower than those from the TSMBF biomes. Again, we considered the possibility that the explanation might be different amounts of fruit eating in TSGSS and TSMBF biomes; but we lack a clear pattern of association of fruit-eating with specific biomes. Another possibility is that the chimpanzees in savanna and woodland ecoregions

may be eating more flowers, pods, and leaves of leguminous trees that are engaged in N_2-fixation. Such a relationship was shown for mantled howler monkeys (*Alouatta palliata*) in a similar environment [Schoeninger et al., 1997] and in sportive lemurs (*Lepilemur leucopus*) [Schoeninger et al., 1998]. The consumption of leguminous species by chimpanzees is suggested by fecal data from Ugalla [see Schoeninger et al., 1999 for original references] and by species lists noting that leguminous plants are eaten throughout the year at Fongoli [Pruetz, 2006]. We look forward to more detailed publications including dietary information at TSGSS sites [e.g., Bogart & Pruetz, 2011; Hernandez-Aguilar et al., 2007; Stewart & Piel, 2014; Webster et al., 2014] and also truly comparative data from TSMBF sites.

It is unlikely that the variation in $\delta^{15}N_{hair}$ values is due to differences in soil baseline $\delta^{15}N$ values. The difference between the average of the four sites within TSGSS biomes (3.3‰) and the five sites within the TSMBF biomes (7.5‰) is 4.2‰. If Ishasha is dropped because it is a riverine environment (2.9‰ average of Fongoli, Ugalla, and Gombe) the average difference between biome types is 4.6‰. In contrast, the anticipated variations in soil values in this region of Africa are on the order of 2‰ [Amundson et al., 2003]. We look forward to additional studies on $\delta^{15}N$ values in plants and soils from across Africa since the expected relationship between MAP and $\delta^{15}N_{hair}$ values is unsupported in our study. The data thus far do not support the use of nitrogen stable isotope data in habitat reconstructions; but could be extremely useful in identifying specific aspects of diet choice in chimpanzees from different sites.

In summation, we show that the carbon stable isotope data in chimpanzees correlate with environmental variation in ecology (forest vs savanna) and with Mean Annual Precipitation (MAP) across most of the nine chimpanzee habitats for which we have stable isotope data, and can serve as indirect estimators of those habitats. The only exception is the chimpanzee habitat within a riverine gallery forest that lies within a larger region of low rainfall. Where similar regions occur within the fossil record (e.g., the Turkana basin in northern Kenya at 3.9 my with sites along a perennially flowing Omo River), regional habitat reconstructions [Cerling et al., 2011] may not capture the local areas in which fossil hominins lived and fed. For example, if the $\delta^{13}C$ values in tooth enamel of fossil hominin material collected along a perennial river are at the lower end of the expected range for eating C_3 foods, it would suggest that they are feeding and sleeping in a forest even though the overall ecoregion might look to be a grassland or savanna based on associated faunal species or soil $\delta^{13}C$ values. Those with values that are high for eating C_3 foods such as *Australopithecus anamensis* [Cerling et al., 2013] could be feeding away from the forest on C_3 foods rather than including small amounts of C_4 foods in their diet as is often suggested [Codron et al., 2008; Sponheimer & Lee-Thorp, 1999].

Most importantly, researchers can use stable isotope data to address scales of space and time that are impractical by direct observation over the course of long periods of time and between distant ecological regions. The stable isotope values can, in turn, provide the basis for modeling aspects of the habitats of animals whose behavior is unobservable such as mouse lemurs [e.g., Crowley et al., 2011b] or chimpanzees where the specimens were collected without habitat information. Indeed, we demonstrate that we must consider that the carbon stable isotope values of extinct hominins and other nonhuman primate species contain more information than a diet positioned somewhere along a C_3 to C_4 continuum.

ACKNOWLEDGMENTS

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