

## Do “savanna” chimpanzees consume C<sub>4</sub> resources?

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### Abstract

Several stable carbon isotopic studies have shown that South African australopiths consumed significant quantities of C<sub>4</sub> resources (tropical grasses, sedges, or animals that eat those foods), but relatively little is known about the consumption of such resources by chimpanzees. Here, we present stable carbon isotopic data for 36 chimpanzee hair samples from Fongoli, one of the driest and most open areas inhabited by chimpanzees. These data suggest that the Fongoli chimpanzees consume little in the way of C<sub>4</sub> vegetation or animals that eat such vegetation, even though these resources are locally abundant and preferred fruits are more widely scattered than at most chimpanzee study sites. The homogeneity of the Fongoli results is especially striking and recalls the narrow isotopic distribution of stenotopic savanna mammals. This is in stark contrast to what has been observed for australopiths, which had highly variable diets and consumed about 35% C<sub>4</sub> vegetation on average. Carbon isotope data for modern and fossil *Papio* depict a dietarily variable genus with a tendency to consume C<sub>4</sub> vegetation. This trophic flexibility, or willingness to consume C<sub>4</sub> savanna resources, may make *Papio* a more profitable ecological analog for australopiths than chimpanzees. © 2006 Elsevier Ltd. All rights reserved.

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### Introduction

Several studies of carbon isotopes suggest that australopiths, unlike chimpanzees (*Pan troglodytes*), consumed C<sub>4</sub> foods such as tropical grasses, sedges, or animals that ate these foods (Lee-Thorp et al., 1994, 2000; Sponheimer and Lee-Thorp, 1999; van der Merwe et al., 2003; Sponheimer et al., 2005; see partial review in Peters and Vogel, 2005). These studies indicate that a series of anatomical and behavioral changes that abetted utilization of these resources may have been fundamental hominin adaptations (Lee-Thorp et al., 2003; Sponheimer et al., 2005). However, the reality of this

australopith/chimpanzee dietary dichotomy might be questioned on two counts. First, chimpanzees have been observed to consume C<sub>4</sub> foods, such as the grass *Brachiaria brizantha* (Suzuki, 1969), although such behavior is far from typical (Goodall, 1986). Second, there are relatively few stable isotope data for chimpanzees. In fact, about twice as many carbon isotope data have been published for australopiths than for chimpanzees. Thus, our understanding of C<sub>4</sub> resource consumption by chimpanzees based on stable isotopic data remains embryonic.

Unpublished data on chimpanzees from Kibale reveal no evidence for the consumption of C<sub>4</sub> foods (Carter, 2001), which is hardly surprising considering the dearth of such resources and the abundance of preferred C<sub>3</sub> fruits available in that forested environment (Wrangham et al., 1991). Stronger support for the australopith/chimpanzee C<sub>4</sub> dichotomy comes from a study of stable carbon isotopes in hair from two

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chimpanzee populations in semi-arid woodlands (Schoeninger et al., 1999). This study revealed no evidence for the consumption of  $C_4$  resources despite their local abundance at these sites; nevertheless, this finding must be tempered by the fact that one of these sites has nearly continuous canopy cover, affording fairly consistent access to preferred arboreal resources. Sites with more extensive non-woodland components are inhabited by chimpanzees in southeastern Senegal (McGrew et al., 1981; Pruett et al., 2002). Among them are Mt. Assirik and Fongoli, which receive about half the rainfall ( $\sim 950$  mm) of most chimpanzee habitats (Moore, 1996) and are the northernmost free-ranging chimpanzee sites yet recorded. Importantly, although woodland is the dominant vegetation type at these sites, grassland and wooded grassland are major components of these ecosystems (McGrew et al., 1981; Pruett, in press). Chimpanzees in this region are reported to consume primarily fleshy fruits like their forest brethren, but have somewhat restricted dietary repertoires due to the limited availability of preferred foods (McGrew et al., 1988; Pruett, in press). As a result, they consume some foods that are tedious to obtain or process (e.g., seeds, pods) (McGrew et al., 1981). Given the dietary constraints in these environments, we reason that significant consumption of  $C_4$  resources is more likely in these chimpanzee communities than in those utilizing more strictly forested habitats. Here, we test this hypothesis by examining the stable carbon isotope compositions of chimpanzee hair samples collected from the Fongoli community of chimpanzees in southeastern Senegal ( $12^\circ 39' N$   $12^\circ 13' W$ ).

## Methods

A total of 36 chimpanzee hair samples were collected from abandoned chimpanzee night nests over an area of  $\sim 64$  km<sup>2</sup> during wet and dry seasons from 2001 to 2003 (Table 1). In an effort to best constrain carbon isotope values for  $C_3$  and  $C_4$  plant consumption, and in the absence of a comparative faunal hair collection from Fongoli, we also analyzed hair samples from 49 known  $C_3$ - and 126 known  $C_4$ -consuming modern herbivores (Table 2). These were collected from a variety of field sites and exhibits throughout South Africa, with the majority coming from the Transvaal Museum (Northern Flagship Institution) and the Kruger National Park. Hair samples ( $\sim 700$   $\mu$ g) were cleaned with ethyl alcohol or acetone, combusted in an elemental analyzer (Carlo-Erba, Milan, Italy), and analyzed for stable carbon and nitrogen isotope abundances using a flow-through inlet system on a continuous flow isotope ratio mass spectrometer (Finnigan, Bremen, Germany). Stable light isotope ratios are expressed as  $\delta$  values in parts per thousand (‰) relative to international standards, which are PDB (a marine carbonate) and atmospheric  $N_2$  for carbon and nitrogen, respectively. For the sake of completeness,  $\delta^{15}N$  data are included in Table 1, but as they are not relevant to the present discussion, they will receive no further mention herein. All hair samples were run with non-hair working standards for which the standard deviation of replicate measurements of  $\delta^{13}C$  was  $<0.1$ ‰.

The standard deviation of replicate measurements of hair samples in our lab is  $<0.2$ ‰. We tested for differences in the  $\delta^{13}C$  of the three groups (chimpanzees,  $C_3$  consumers, and  $C_4$  consumers) using analysis of variance (ANOVA) and performed pairwise comparisons using the Scheffé test.

## Results and discussion

Analysis of variance demonstrates a strong difference in the  $\delta^{13}C$  of known  $C_4$  consumers,  $C_3$  consumers, and Fongoli chimpanzees ( $F_{2, 208} = 1843.441$ ;  $P < 0.0001$ ). The  $C_4$  grazers ( $x = -10.4$ ‰, s.d. =  $1.6$ ‰,  $n = 126$ ) are enriched in  $^{13}C$  compared to the other two groups ( $P < 0.0001$ ), but Fongoli chimpanzees ( $x = -22.2$ ‰, s.d. =  $0.4$ ‰,  $n = 36$ ) and  $C_3$  browser/frugivores ( $x = -22.9$ ‰, s.d. =  $1.3$ ‰,  $n = 49$ ) are isotopically indistinguishable from one another ( $P = 0.11$ ) (Table 1; Fig. 1). This result strongly suggests that the Fongoli chimpanzees exploit  $C_3$  plant resources almost exclusively, despite the relative abundance of  $C_4$  resources in their local environment. Moreover, when we added the data from Schoeninger et al. (1999) to the analysis, we found the Fongoli chimpanzee  $\delta^{13}C$  values to be practically identical to those of the woodland chimpanzees of Ugalla, Tanzania ( $x = -22.0$ ‰, s.d. =  $0.3$ ‰,  $n = 12$ ) ( $P = 0.99$ ), and very similar to those from Ishasha, Democratic Republic of the Congo ( $x = -23.1$ ‰, s.d. =  $0.3$ ‰,  $n = 10$ ) ( $P = 0.55$ ) (Fig. 1), both of which were interpreted as being nearly pure  $C_3$  consumers (Schoeninger et al., 1999). That being said, we cannot conclusively rule out the consumption of small quantities of  $C_4$  resources ( $<10\%$ ) without performing a comprehensive study of Fongoli's plants and animals.

One of the most striking patterns evident in this and previous studies is the general lack of isotopic variability within and between "savanna" chimpanzee populations (but see Table 1). Indeed, chimpanzee intrapopulation variation barely exceeds that of mammals (*Bos taurus*, *Capra hircus*, *Lama pacos*, *Lama glama*, *Oryctolagus cuniculus*) in controlled feeding studies (s.d. =  $0.2$ ‰; Sponheimer et al., 2003a) and is usually associated with reputedly stenotopic taxa such as wildebeest. Eurytopic taxa such as baboons and impala exhibit far more isotopic heterogeneity (Cerling et al., 2003; Sponheimer et al., 2003b; Codron et al., 2005).

Stable isotope comparisons between modern and fossil samples are difficult, yet in this case, we believe a comparison between these results and those obtained previously from early hominins and associated non-hominin fauna may prove useful (data from Lee-Thorp et al., 1994, 2000; Sponheimer and Lee-Thorp, 1999; van der Merwe et al., 2003; Sponheimer et al., 2005) (Table 2). In order to effectuate this comparison, we converted the  $\delta^{13}C$  values for hair to their enamel equivalents. We also compensated for the recent depletion of atmospheric  $CO_2$  due to the burning of fossil fuels. Since enamel is fractionated by about 13‰ compared to diet, while hair is fractionated by 3.2‰ (see Lee-Thorp et al., 1989; Sponheimer et al., 2003a; Passey et al., 2005), this was accomplished by adding 9.8‰ to the hair values, and adding a further 1.5‰ to adjust for the fossil fuel effect (Truinger et al., 1999).

Table 1  
 $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , year, and season collected for the chimpanzee hair specimens analyzed for this study<sup>1</sup>

Specimen	Taxon	Year	Season	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
FOC1	<i>Pan troglodytes verus</i>	2001	Dry	-22.6	2.8
FOC2	<i>Pan troglodytes verus</i>	2001	Wet	-22.2	2.6
FOC3	<i>Pan troglodytes verus</i>	2001	Wet	-21.9	2.7
FOC4	<i>Pan troglodytes verus</i>			-22.1	3.3
FOC5	<i>Pan troglodytes verus</i>	2002		-21.8	2.7
FOC6	<i>Pan troglodytes verus</i>	2002		-21.9	2.6
FOC7	<i>Pan troglodytes verus</i>	2002	Dry	-22.0	3.2
FOC8	<i>Pan troglodytes verus</i>	2002	Dry	-21.7	2.5
FOC9	<i>Pan troglodytes verus</i>	2002	Dry	-22.3	2.9
FOC10	<i>Pan troglodytes verus</i>	2002	Dry	-22.0	2.8
FOC11	<i>Pan troglodytes verus</i>	2002	Dry	-22.0	3.2
FOC12	<i>Pan troglodytes verus</i>	2002	Dry	-21.7	2.5
FOC13	<i>Pan troglodytes verus</i>	2002	Dry	-23.0	2.2
FOC14	<i>Pan troglodytes verus</i>	2002	Dry	-22.5	3.4
FOC15	<i>Pan troglodytes verus</i>	2002	Dry	-22.5	2.7
FOC17	<i>Pan troglodytes verus</i>	2002	Dry	-22.2	2.6
FOC18	<i>Pan troglodytes verus</i>	2002	Dry	-22.4	2.8
FOC19	<i>Pan troglodytes verus</i>	2002	Dry	-22.2	2.5
FOC20	<i>Pan troglodytes verus</i>	2002	Dry	-22.5	2.9
FOC21	<i>Pan troglodytes verus</i>	2002	Dry	-22.5	3.2
FOC22	<i>Pan troglodytes verus</i>	2002	Dry	-22.6	3.2
FOC23	<i>Pan troglodytes verus</i>	2002	Dry	-22.8	2.5
FOC24	<i>Pan troglodytes verus</i>	2002	Dry	-22.3	2.7
FOC25	<i>Pan troglodytes verus</i>	2002	Dry	-22.7	3.6
FOC26	<i>Pan troglodytes verus</i>	2002	Dry	-22.6	3.6
FOC27	<i>Pan troglodytes verus</i>	2002	Dry	-22.5	3.0
FOC28	<i>Pan troglodytes verus</i>	2002	Wet	-22.1	3.3
FOC29	<i>Pan troglodytes verus</i>	2002	Wet	-21.4	3.0
FOC30	<i>Pan troglodytes verus</i>	2002	Wet	-21.8	2.8
FOC31	<i>Pan troglodytes verus</i>	2002	Wet	-22.0	2.9
FOC33	<i>Pan troglodytes verus</i>	2002	Wet	-23.1	2.8
FOC34	<i>Pan troglodytes verus</i>	2002	Wet	-21.7	3.0
FOC35	<i>Pan troglodytes verus</i>	2002	Wet	-22.1	3.4
FOC36	<i>Pan troglodytes verus</i>	2002	Wet	-21.5	3.2
FOC37	<i>Pan troglodytes verus</i>	2002	Wet	-22.1	2.9
FOC39	<i>Pan troglodytes verus</i>	2003		-22.7	3.0
				-22.2 ± 0.4	2.9 ± 0.3

<sup>1</sup> These chimpanzees display remarkably little variation in  $\delta^{13}\text{C}$  compared to most eurytopic taxa (Sponheimer et al., 2003b; Codron et al., 2005). Nevertheless, our data betray a small (0.4‰) but significant seasonal difference in  $\delta^{13}\text{C}$  ( $P < 0.05$ ;  $t$ -test and Mann-Whitney  $U$ -test).

We then performed an ANOVA of converted (modern hair) and unconverted (fossil enamel)  $\delta^{13}\text{C}_{\text{enamel}}$  values for all groups in Figure 2 ( $F_{8, 415} = 745.895$ ;  $P < 0.0001$ ). The Scheffé test shows that the converted  $\delta^{13}\text{C}_{\text{enamel}}$  values for modern  $\text{C}_3$  consumers ( $x = -11.6\text{‰}$ ,  $\text{s.d.} = 1.3$ ,  $n = 49$ ) are nearly identical to the values of their fossil counterparts ( $x = -11.5\text{‰}$ ,  $\text{s.d.} = 1.3$ ,  $n = 61$ ) ( $P = 0.99$ ). The difference between modern and fossil grazer values is also quite small (1.5‰), even though the means are significantly different ( $P < 0.01$ ). Thus, the conversion provides good congruence between the modern  $\text{C}_3$  and  $\text{C}_4$  consumers and their fossil equivalents and has an accuracy of  $\sim 1.5\text{‰}$  or better.

“Savanna” chimpanzee (converted Fongoli, Ishasha, and Ugalla data were pooled given their similarity)  $\delta^{13}\text{C}_{\text{enamel}}$  values are indistinguishable from the  $\delta^{13}\text{C}_{\text{enamel}}$  values of modern and fossil  $\text{C}_3$  consumers ( $P > 0.86$ ). In contrast, savanna chimpanzee  $\delta^{13}\text{C}_{\text{enamel}}$  is highly distinct from that of both *Australopithecus africanus* ( $x = -7.0\text{‰}$ ,  $\text{s.d.} = 1.8$ ,  $n = 20$ ) and *Paranthropus robustus* ( $x = -7.6\text{‰}$ ,  $\text{s.d.} = 1.1$ ,

$n = 18$ ) ( $P < 0.0001$ ). In fact, the chimpanzee mean is so different from that of *Australopithecus* (4‰), that there can be little doubt that this represents a real and significant ecological distinction (Fig. 2). To put this in perspective, it is nearly equivalent to the difference observed between grazing wildebeest and mixed-feeding impala in Kruger National Park (Sponheimer et al., 2003b), two creatures that are considered to be highly divergent ecologically (e.g., Kingdon, 1997; Cerling et al., 2003).

These results strongly support the contention that the diets of australopithecids and extant chimpanzees are fundamentally different. It appears that, for whatever reason, chimpanzees do not significantly exploit  $\text{C}_4$  resources even when they are abundant and preferred food resources are widely scattered (possibly resulting in extremely large home ranges for savanna chimpanzees; McGrew et al., 1981; Moore, 1996). This is not to say, however, that chimpanzees never consume  $\text{C}_4$  or  $^{13}\text{C}$ -enriched resources, for they demonstrably do. Members of the Fongoli community have been observed to consume grass

Table 2  
Taxonomic composition of modern and fossil C<sub>3</sub> and C<sub>4</sub> consumers used for comparative purposes in this study<sup>1</sup>

Modern C <sub>4</sub> consumers	Modern C <sub>3</sub> consumers
<i>Alcelaphus buselaphus</i>	<i>Cephalophus monticola</i>
<i>Ceratotherium simum</i>	<i>Cephalophus natalensis</i>
<i>Damaliscus dorcas</i>	<i>Diceros bicornis</i>
<i>Damaliscus lunatus</i>	<i>Raphicerus campestris</i>
<i>Hippotragus equinus</i>	<i>Tragelaphus scriptus</i>
<i>Hippotragus niger</i>	<i>Tragelaphus strepsiceros</i>
<i>Kobus ellipsiprymnus</i>	
<i>Redunca arundinum</i>	
<i>Redunca fulvorufula</i>	
<i>Syncerus caffer</i>	
Fossil C <sub>4</sub> consumers	Fossil C <sub>3</sub> consumers
<i>Connochaetes</i> sp.	<i>Aepyceros</i> sp.
<i>Damaliscus</i> sp.	<i>Ancylotherium hennigi</i>
<i>Equus burchelli</i>	<i>Antidorcas</i> sp.
<i>Equus capensis</i>	<i>Antidorcas recki</i>
<i>Eurygnathohippus lybicum</i>	<i>Cephalophus</i> sp.
<i>Hippotragus equinus</i>	<i>Diceros bicornis</i>
<i>Megalotragus</i> sp.	<i>Gazella vanhoepeni</i>
<i>Notochoerus capensis</i>	<i>Giraffa</i> sp.
<i>Parmularius braini</i>	<i>Neotragini</i> sp.
<i>Parmularius</i> sp.	<i>Oreotragus oreotragus</i>
<i>Phacochoerus antiquus</i>	<i>Sivatherium maurusium</i>
<i>Potamochoeroides shawi</i>	<i>Tragelaphus angasii</i>
<i>Redunca darti</i>	<i>Tragelaphus pricei</i>
<i>Metridiochoerus meadowsi</i>	<i>Tragelaphus scriptus</i>
	<i>Tragelaphus strepsiceros</i>

<sup>1</sup> The raw data for the modern animals will be published elsewhere, as they were originally obtained for an ungulate neocology study. Data for fossil specimens are from Lee-Thorp et al. (1994, 2000), Sponheimer (1999, unpublished data), and van der Merwe et al. (2003).

(although it often passes through their digestive tracts unmolested) and prey upon vervet monkeys (*Chlorocebus aethiops sabeus*) (Gasperi and Pruett, 2004), which are known to sometimes, if not regularly, eat grasses (Wrangham and Waterman, 1981; Harrison, 1984; Foord et al., 1994).

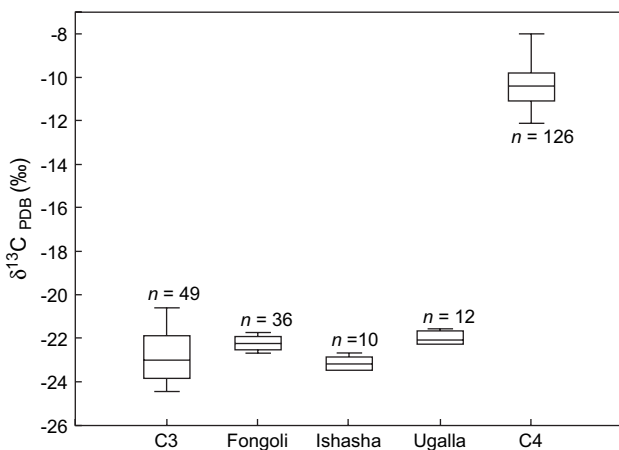


Fig. 1.  $\delta^{13}\text{C}_{\text{hair}}$  for modern chimpanzees from Fongoli, Ishasha, and Ugalla, as well as C<sub>3</sub>-plant consumers and C<sub>4</sub>-plant consumers (see Table 2). The boxes represent the 25th–75th percentiles (with the medians as horizontal lines) and the whiskers show the 10th–90th percentiles.

However, such trophic behavior makes a negligible contribution to their daily nutritional intake.

The most likely C<sub>4</sub> resources to be eaten by these chimpanzees regularly are termites, as it has been suggested that insectivory rates are higher (and meat consumption lower) in savanna chimpanzee populations than elsewhere (McGrew, 1983; McGrew et al., 1988; Moore, 1996; Pruett, in press). Individuals in the Fongoli community have been observed fishing for at least two termite species (*Macrotermes subhyalinus* and *M. bellicosus*) (Bogart et al., 2005). We have few data on whether or not these termite species consume C<sub>4</sub> plants (see Boutton et al., 1983 and Sponheimer et al., 2005 for other *Macrotermes* species), but preliminary analysis suggests they have C<sub>3</sub>-dominated diets ( $x = -24.6\text{‰}$ , s.d. =  $0.9\text{‰}$ ,  $n = 3$ ). It is clear, however, that consumption of these termites imparts little C<sub>4</sub> carbon to these chimpanzees, either because they consume relatively few termites compared to other foods or because the termites eat little C<sub>4</sub> vegetation themselves (which appears to be the case). Parenthetically, it is worth noting that if the Fongoli chimpanzees were consuming C<sub>4</sub>-specialist termites such as *Trinervitermes trinervoides* to any significant extent, then it would undoubtedly be manifest in their hair. This is because, unlike tooth enamel, which reflects the carbon isotope composition of the bulk diet, the stable isotope composition of body proteins such as hair keratin and bone collagen preferentially reflects dietary protein intake (Ambrose and Norr, 1993; Tieszen and Fagre, 1993). Thus, high protein foods such as termites would be over-represented in hair stable isotope ratios compared to fruits and other plant foods.

These results cast the australopith stable isotope data in an interesting light. To obtain the 35–40% C<sub>4</sub> dietary

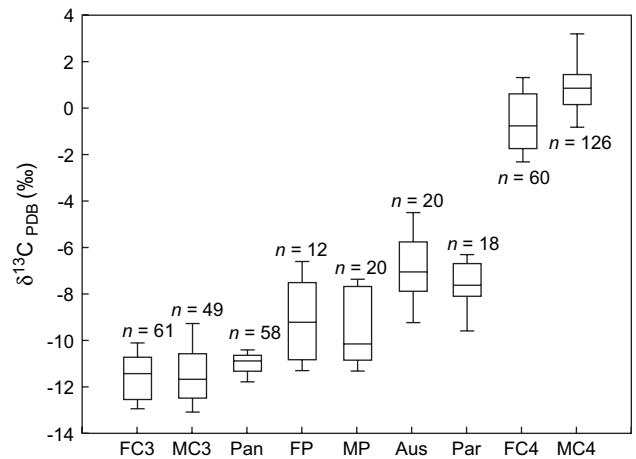


Fig. 2.  $\delta^{13}\text{C}_{\text{enamel}}$  of specimens analyzed for this study (converted from  $\delta^{13}\text{C}_{\text{hair}}$ ), as well previously analyzed hominin and non-hominin fossil fauna. The key is as follows: FC3 is fossil C<sub>3</sub> consumers, MC3 is modern C<sub>3</sub> consumers, Pan is all “savanna” chimpanzees, FP is *Papio hamadryas robinsoni*, MP is *Papio hamadryas ursinus* (includes 11 modern enamel values adjusted for the fossil fuel effect and 9 hair values converted for tissue differences and the fossil fuel effect), Aus is *Australopithecus*, Par is *Paranthropus*, FC4 is fossil C<sub>4</sub> consumers, and MC4 is modern C<sub>4</sub> consumers. The boxes represent the 25th–75th percentiles (with the medians as horizontal lines) and the whiskers show the 10th–90th percentiles.

contribution that has been reported (Sponheimer et al., 2005), australopiths would have had to have spent about a third of their daily foraging time on these resources. Alternatively, they could have focused on C<sub>3</sub> resources during one season and C<sub>4</sub> resources during another. Our current sampling methodologies do not permit ready discrimination between these alternatives. Regardless, the carbon isotope data do suggest that the disjunction between “savanna” chimpanzees and australopith carbon isotope values represents a fundamental shift in dietary strategies, which is supported by the marked differences in their craniodental morphologies (e.g., size and occlusal relief of their postcanine dentition; Grine, 1981; Teaford et al., 2002).

Finally, this brings us to the issue of ecological analogs for early hominins. After biochemical developments established our close phylogenetic relationship to chimpanzees (e.g., Goodman, 1963; Sarich and Wilson, 1967), and especially since evidence emerged that some australopiths may have inhabited heavily wooded environments and ate fleshy fruits (e.g., Grine and Kay, 1988; WoldeGabriel et al., 1994), there has been a tendency to envision the ecology of gracile australopiths as similar, although certainly not identical, to that of chimpanzees. Yet, some authors have argued that savanna-dwelling papionins present a more suitable ecological analog for early hominin behavioral ecology (Jolly, 1970, 2001; Dunbar, 1976), and from an isotopic standpoint, early hominins are more similar to modern and fossil baboons (*Papio* spp.) in two ways. First, while most modern and fossil *Papio* specimens that have been analyzed had predominantly C<sub>3</sub> diets, most also had a significant, if small, C<sub>4</sub> component. Consequently, the means of modern *Papio hamadryas ursinus* and fossil *Papio hamadryas robinsoni* are significantly enriched in <sup>13</sup>C compared to modern and fossil C<sub>3</sub> specialists ( $P < 0.001$ ) (Fig. 2; data from Codron, 2003; Codron et al., 2005). Second, while chimpanzee populations exhibit very little isotopic heterogeneity, modern and fossil *Papio* tend to fluctuate more widely temporally and spatially (Fig. 2; Thackeray et al., 1996; Codron et al., 2005, 2006). Similar variation has also been reported for *Papio* in modern observational studies (Devore and Hall, 1965; Dunbar and Dunbar, 1974; Rhine et al., 1989; Byrne et al., 1993; Altmann, 1998) and in a dental microwear study of fossil specimens (El-Zaatari et al., 2005). These facts, along with the long-recognized association between hominins and papionins (Dart, 1925; Delson, 1984), suggest that we might gain much by paying more attention to baboon ecology in our efforts to reconstruct the dietary behavior of australopiths.

This is not to argue that australopiths ate as baboons do today or as baboons once did. In fact, there is no reason to believe that any living primate shares more than a passing dietary resemblance to australopiths. We do contend, however, that modern and fossil baboons exhibit a flexibility and willingness to utilize <sup>13</sup>C-enriched savanna resources that appears to be absent in chimpanzees yet characteristic of australopiths. In short, based on our stable isotopic results, savanna and forest chimpanzees actually differ little in their dietary behavior, while savanna and forest papionin diets differ dramatically.

We surmise that this trophic flexibility was shared by early hominins, allowing them to colonize increasingly open and seasonal environments eschewed by chimpanzees. Further investigation into how climate, vegetational composition, demographics, and community interactions affect the diets of these quintessentially flexible primates may testify to the likely adaptive responses of hominins to changing conditions during the Plio-Pleistocene.

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