Using Carbon Isotopes to Track Dietary Change in Modern, Historical, and Ancient Primates

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ABSTRACT   Stable isotope analysis can be used to document dietary changes within the lifetimes of individuals and may prove useful for investigating fallback food consumption in modern, historical, and ancient primates. Feces, hair, and enamel are all suitable materials for such analysis, and each has its own benefits and limitations. Feces provide highly resolved temporal dietary data, but are generally limited to providing dietary information about modern individuals and require labor-intensive sample collection and analysis. Hair provides less well-resolved data, but has the advantage that one or a few hair strands can provide evidence of dietary change over months or years. Hair is also available in museum collections, making it possible to investigate the diets of historical specimens. Enamel provides the poorest temporal resolution of these materials, but is often preserved for millions of years, allowing examination of dietary change in deep time. We briefly discuss the use of carbon isotope data as it pertains to recent thinking about fallback food consumption in ancient hominins and suggest that we may need to rethink the functional significance of the australopith masticatory package. Am J Phys Anthropol 140:661–670, 2009.   © 2009 Wiley-Liss, Inc.

There has been increasing interest of late in the importance of fallback foods in primate ecology and evolutionary biology. It has been argued that fallback, rather than preferred or more frequently consumed foods, have often strongly influenced the masticatory anatomy of diverse taxa such as Malagasy lemurs (Yamashita, 1998), Old World monkeys (Lambert et al., 2004), and our hominin antecedents (Ungar, 2004; Laden and Wrangham, 2005). In general, these insights have been gleaned by wedding observational field studies with ecomorphological analysis, although the short-term dietary information manifest in dental microwear has been an important source of hypothesis generation (e.g., Scott et al., 2005; Grine et al., 2006b). Here, we discuss how stable isotope analysis can be used to investigate short-term dietary change from modern, historical, and fossil specimens and thus may test and generate hypotheses about the importance of fallback foods in primate ecology and evolution.

When fallback and preferred foods are isotopically distinguishable, stable isotope analysis may provide important data about fallback food consumption. One great benefit of stable isotope analysis is that death and geography provide few barriers to retrieving dietary information. The hair of a baboon that was shot and displayed in a museum a century ago faithfully records short-term dietary excursions, as can a 3-million-year old hominin tooth unearthed only recently, although the information in this latter case will have poorer temporal resolution. But in addition to the significance of stable isotope techniques for investigating the diets of animals from the recent and deep past, there are many instances where stable isotope studies can elucidate short-term dietary change in modern taxa. For instance, when one wishes to examine dietary change in spatially discrete populations over the same time period, stable isotope analysis might be used where traditional observational studies would prove impractical. Of course, long-term observational studies can document dietary ecology in greater detail than can stable isotope analysis, but that does not diminish the utility of stable isotope studies for a variety of applications.

We begin this article by giving a brief overview of how one can elucidate dietary change through time using

stable isotope analysis of feces, hair, and enamel. Other tissues have been studied and offer similar promise for resolving temporal dietary variation, though we do not discuss them here, as they are either not directly relevant to the study of primates (baleen; Lee et al., 2005; Caraveo-Patino et al., 2007; hoof and horn; Harrison et al., 2007; Zazzo et al., 2007) or less generally available for analysis (dentine; Koch et al., 1995; Balasse et al., 2001). Our discussion of the materials and techniques will be brief perforce, but we reference papers with greater detail for the interested reader. We then briefly discuss the potential significance of fallback foods in hominin evolution, with an explicit focus on integrating data from dental microwear, ecomorphological, and stable isotope studies.

BACKGROUND ON MATERIALS
Feces

Fecal analysis has long been used as a tool to investigate primate diets (e.g., Moreno-Black, 1978; Tutin and Fernandez, 1985; McGrew et al., 1988; Yamagiwa and Basabose, 2006), and feces are of great potential utility for stable isotope studies as they can provide highly resolved temporal dietary data. Although mean retention time of undigested particulate matter is variable between primate taxa (e.g., ~13 h and ~40 h for *Callithrix* and *Pan*, respectively; Caton et al., 1996; Milton and Demment; 1988) and within primate taxa (e.g., 38 h and 48 h for *Pan troglodytes* on low- and high-fiber diets, respectively; Milton and Demment, 1988), one can generally assume that primate feces reflect the last few days' diet (see Lambert, 1998 for a review). Feces are also fairly easy to obtain in field situations from live animals and can often be collected from rare and difficult to observe nocturnal species without inducing stress. However, there are only two published studies of which we are aware in which stable isotope analysis has been carried out on primate feces, both of which focused on South African chacma baboons (*Papio ursinus*) (Codron et al., 2005a, 2008). Both studies found great variability in the percentage of ^{13}C-enriched foods (e.g., tropical C_4 grasses, some sedges, and succulents) consumed by *Papio* populations, ranging from about 5% to over 35%. Perhaps more significantly, however, one of these studies showed that baboons from the Northern Basalt Plains of Kruger National Park vary their diets dramatically from month to month, with more than 60% C_4 foods consumed in March to less than 5% consumed in October (Codron et al., 2008). From one month to the next, C_4-food consumption differed by as much as 35% (see Fig. 1).

Although these results were unsurprising given the large literature showing dietary versatility in baboons (e.g., DeVore and Hall, 1965; Altmann and Altmann, 1970; Norton et al., 1987; Altmann, 1998), they nevertheless demonstrated the potential of fecal isotope analysis for studying short-term dietary change amongst savanna primates. They also reveal why baboons may prove interesting models for early hominins, as both consume(d) C_4 resources to various extents, while extant African apes rarely do so even when they are locally abundant (Schoeninger et al., 1999; Sponheimer et al., 2006a; Codron et al., 2008; Fig. 2). Such studies might reveal some of the reasons that the C_4 components of *Papio* diets differs so much from season to season, and
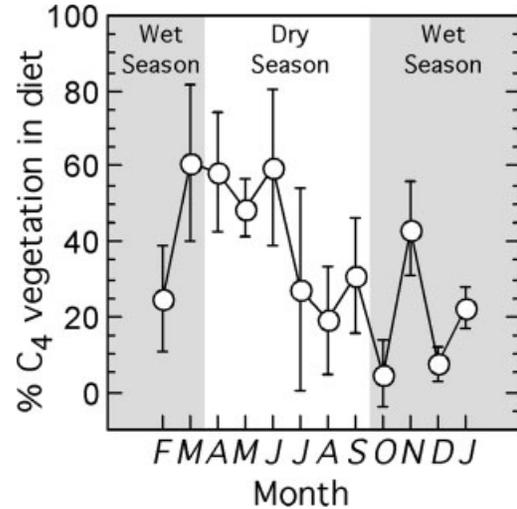

Fig. 1. Monthly percent C_4 vegetation consumed by chacma baboons from the Northern Basalt Plains of the Kruger National Park, South Africa in 2003–2004. Percent C_4 is calculated assuming a −0.9‰ diet-feces fractionation and by using plants collected monthly to establish monthly C_3 and C_4 endmembers. The data are from Codron et al. (2008).

in fact from month to month, as they require far less effort than long-term observational studies (samples need only be collected a few days a month and then prepared and analyzed in a few days). This would make it possible to realistically study variability in several groups simultaneously and might allow one to better understand how small differences in plant availability, precipitation, and nutrient content affect dietary behavior (so long as such data are available or collected in tandem with isotopic data). The potential benefits of this approach are evident in a recent study of bovid feces from the Kruger National Park, where it was shown that impala (*Aepyceros melampus*) on the southern basalts ate large quantities of grass throughout the year, with mean monthly C_4 grass consumption ranging from about 60–85% (Codron et al., 2006) (see Fig. 3). However, less than 25 km away on granite substrates in the same park, impala diets differed enormously during the same year, with mean monthly C_4 grass consumption ranging from over 80% (March) to about 15% (July), with a maximum month to month change of over 30%. By collecting and determining $\delta^{13}C$, $\delta^{15}N$, and %N values for both feces and plants from different areas of the park throughout the year, the authors observed that impala diet choice is probably not driven by the relative availability of grass or browse in the environment, nor by the nutritional quality of available tree foods, but largely by the nutritional quality of local grasses (see Codron et al., 2006, 2007 for related nutritional analyses). It is in such spatially dispersed and/or diachronic studies that fecal stable isotope data are likely to prove most rewarding.
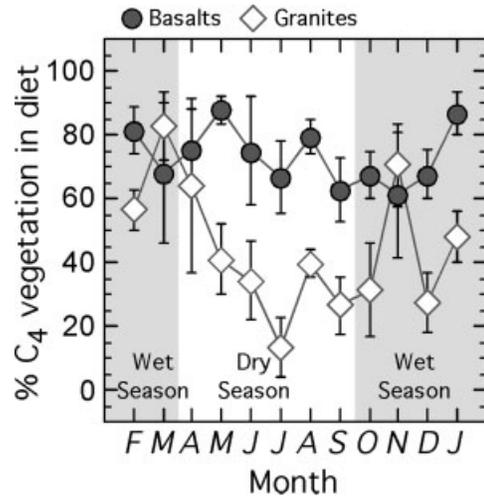
Hair

Although several stable isotope studies of hair have provided us with insights into primate dietary ecology (Schoeninger et al., 1997, 1998, 1999; Sponheimer et al., 2006a), very few have used hair's great potential as a
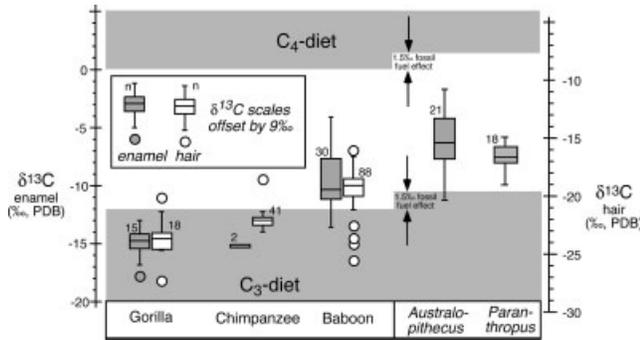
Fig. 2. $\delta^{13}C$ values of modern gorillas (*Gorilla gorilla*), chimpanzees, baboons, and South African australopiths. Note that both the hair and enamel of chimpanzees and gorillas are consistent with nearly pure C_3 diets, even though many of the chimpanzee samples were from areas where C_4 resources abound. In contrast, many baboon and most australopith $\delta^{13}C$ values are consistent with the consumption of various degrees of C_4 vegetation. The C_3 and C_4 endmembers (shaded areas) have been shifted around the australopith data to compensate for the effect of fossil fuel utilization on the $\delta^{13}C$ values of modern fauna (Friedli et al., 1986). The data are from Codron et al. (2005b, 2008), Sponheimer et al. (2006a), and Cerling (unpublished data).

Fig. 3. Monthly percent C_4 vegetation consumed by impala on the southern basalts and southern granites of the Kruger National Park, South Africa in 2004–2005. Percent C_4 is calculated assuming a $-0.9‰$ diet-feces fractionation and by using plants collected monthly to establish monthly C_3 and C_4 endmembers. Note the very different monthly responses of these two populations which live within 25 km of each other. The data are from Codron et al. (2006).

recorder of temporal dietary information (but see Wilson et al., 2007; Codron et al., 2008; and below). Hair, the main constituent of which is the protein keratin does not exchange carbon or nitrogen after it is formed, and thus each individual strand of hair represents an archive of an individual's diet that can be sampled incrementally to provide high-resolution dietary information [particularly of dietary protein as in Tieszen and Fagre (1993)]. In the first such attempt, White (1993) sampled and analyzed the hair (about 15 strands of hair per individual) of Nubian mummies in 2-cm increments. She found intraindividual variability in $\delta^{13}C$[1] values of nearly 4‰ (nearly one-third the change from a pure C_3 to a pure C_4 diet) over about 8 months of hair growth. She thus argued that the ancient Nubians practiced seasonal crop rotation similar to that used in the region today, where C_3 plants (e.g., wheat and barley) are planted during the winter and C_4 plants (e.g., sorghum and millet) are planted in the summer. Subsequently, O'Connell and Hedges (1999) carried out a natural experiment wherein they analyzed ~2-cm sections of a woman's hair who had moved from Texas to the United Kingdom, and who also changed from an omnivorous to a vegan diet at about the same time. People living in the United States typically consume a good deal of C_4-derived carbon because corn (*Zea mays*, a tropical C_4 grass) tends to be fed to livestock, corn syrup and other corn products are ubiquitous, and because sugar in the United States is generally derived from C_4 grasses (*Saccharum* spp.). In the United Kingdom, by contrast, corn is rarely fed to livestock and most sugar is derived from the sugar beet (*Beta vulgaris*), which is a C_3 plant. Thus, one would

expect the woman's hair $\delta^{13}C$ values to have decreased after her arrival in the United Kingdom. As for hair $\delta^{15}N$ values, they were also expected to decrease through time after she adopted a vegan diet, given the well-established relationship between trophic level and $\delta^{15}N$ values (e.g., Schoeninger and DeNiro, 1984). The observed hair $\delta^{13}C$ and $\delta^{15}N$ values both decreased through time as expected.

These studies amply demonstrated the potential of hair as a tissue for investigating dietary change through time using stable isotope analysis. However, they also had limitations. They were quite coarse so far as sampling interval goes and thus had limited temporal resolution (they were capturing about 2-month snapshots per analysis). More importantly, however, tightly controlled studies of just how long it takes for hair stable isotope compositions to fully reflect dietary changes were lacking (although the O'Connell and Hedges, 1999 study was an important step in this direction), making interpretation of such diachronic data problematic. It was clear from a pioneering study by Jones et al. (1981) that cattle hair patch $\delta^{13}C$ values did not immediately reflect dietary values, and Schwertl et al. (2003) followed this up with a semicontrolled study of individual cattle hair strands, which suggested that the body's metabolic pool feeding hair growth had a half-life of about 20 days (based upon turnover of hair $\delta^{15}N$ values). Ayliffe et al. (2004) first showed how diet changes were reflected in individual hair strands for animals on tightly controlled, experimental diets. In this study, horses were changed between C_3 and C_4 hay diets, and individual strands of their tail hair were sampled at very short increments (as small as 1 mm, if only C and not N isotope analysis was sufficient). Ayliffe et al. (2004) showed that dietary changes are apparent rapidly in tail hair, with about ~30% of the dietary change in $\delta^{13}C$ values visible within the first day, and a 55% change within the first week (see Fig. 4). Yet, they also demonstrated that hair $\delta^{13}C$ values did not fully equilibrate with dietary $\delta^{13}C$ values for many
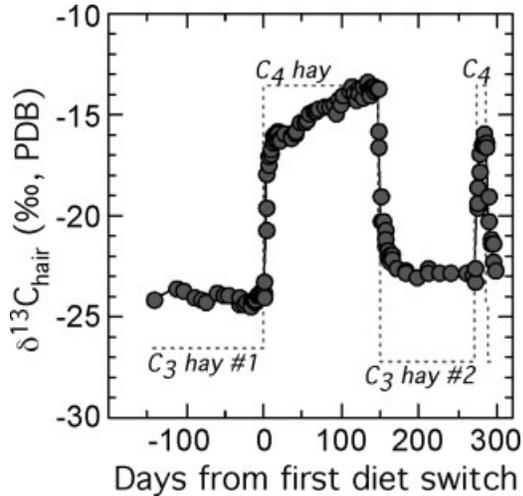
[1] By convention, stable carbon and nitrogen isotope ratios are expressed as δ values relative to international standards in parts per thousand (per mil) as follows in an example for carbon isotopes: $\delta^{13}C$ (‰) = $(R_{sample}/R_{standard} - 1) \times 1000$, where $R = {}^{13}C/{}^{12}C$ and the international standard is Vienna Peedee Belemnite (VPDB). The standard for nitrogen (15N/14N) is atmospheric nitrogen (AIR).
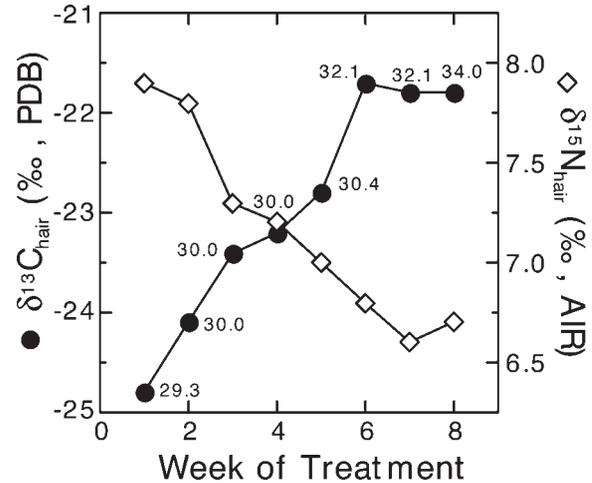
Fig. 4. Horse tail hair $\delta^{13}C$ data from Ayliffe et al. (2004). Horses underwent a series of four dietary changes during this experiment. Tail hair $\delta^{13}C$ values captured the dietary changes within a single day and about 55% of the amplitude of the dietary change was manifest within the first week. However, after more than 100 days, tail hair $\delta^{13}C$ values did not fully reflect the new diet due to recycling of amino acids. Thus, while hair provides fairly high-resolution dietary data, the dietary signal is significantly attenuated.


Fig. 5. Incremental $\delta^{13}C$ data from ~25 hair strands of patient F-D, a 25-year-old female who was suffering from anorexia nervosa, reflecting about 8 weeks of treatment. The numbers next to each datapoint are F–D's weight in kilos during each week of treatment. Clearly, as the patient's diet improved her weight increased as did her hair $\delta^{13}C$ values. In contrast, her hair $\delta^{15}N$ values decreased. These changes likely reflect an increase in protein consumption and reduced gluconeogenesis following the shift to a nutritionally adequate diet at the onset of treatment. The data are from Mekota et al. (2006).

months. Thus, although very short-term (even a single day) dietary changes can be captured through incremental sampling and analysis of tail hair, there is also an isotopic inertia as the body's large amino acid pool regularly contributes to hair $\delta^{13}C$ values and effectively attenuates the primary dietary signal. Nevertheless, models that take this attenuation into account have been developed, enabling more realistic estimates of dietary $\delta^{13}C$ values from hair $\delta^{13}C$ values (Ayliffe et al., 2004; Cerling et al., 2004).

Significantly, such incremental sampling of hair cannot only tell us about dietary change *per se*, but can also tell us about changes in the levels of nutritional stress experienced by primates. Mekota et al. (2006) showed that when patients suffering from acute anorexia nervosa are treated and gain weight the $\delta^{13}C$ and $\delta^{15}N$ values of their hair begin to change. They collected ~25 hair strands from patients after treatment, and these were, in aggregate, sectioned into 2.5-mm sections that reflected roughly 1 week's hair growth (assuming growth of about 1 cm per month; Valkovic, 1977). Figure 5 shows how the carbon isotopic composition of one patient's (patient F-D) hair changed week-to-week during the course of treatment. The increased $\delta^{13}C$ values and the decreased $\delta^{15}N$ values were interpreted as evidence of an increase in dietary protein consumption and a decrease in the catabolism of body protein that accompanies starvation (see Hobson et al., 1993).

Clearly, stable isotope analysis of hair shows much promise for studies of dietary change over time (e.g., seasonal differences in resource consumption and brief consumption of fallback foods). All in all, there are likely to be many primatological applications for this technique. They will probably prove most efficacious in ecosystems where C_3 and C_4/CAM resources are both present and variably consumed. Ring-tailed lemurs

(*Lemur catta*) come to mind as one possibility, as many live in C_3 dominated areas, but consume significant quantities of CAM plants (which can have $\delta^{13}C$ values similar to those of C_4 plants; Winter, 1979). Vervets (*Chlorocebus aethiops*), patas monkeys (*Erythrocebus patas*), and geladas (*Theropithecus gelada*) might also prove particularly illuminating, as would many of the Asian macaques (*Macaca* spp.).
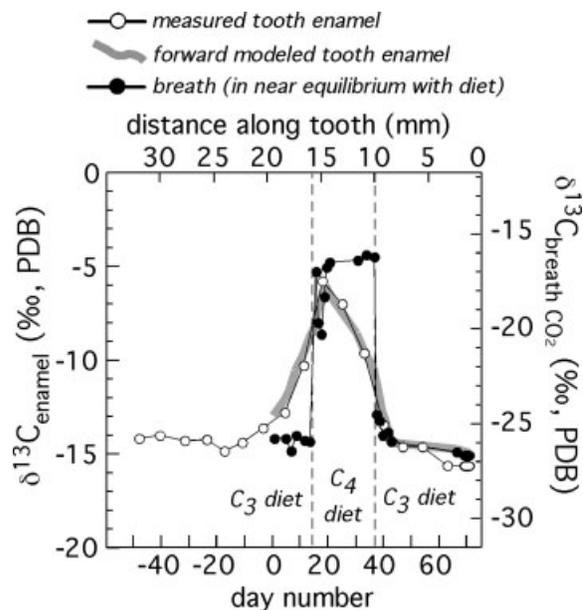
Enamel

Tooth enamel is an incremental tissue, composed of biological apatite, that can be sampled to investigate temporal changes in both climate and diet using stable isotope analysis (e.g., Fricke and O'Neill, 1996; Wiedemann et al., 1999; Balasse, 2002; Nelson, 2005; Copeland et al., 2008). One conspicuous difference between enamel and hair as dietary archives is that while hair $\delta^{13}C$ values primarily reflect those of dietary proteins, the $\delta^{13}C$ values of biological apatites tend to closely track those of whole diets (Ambrose and Norr, 1993; Tieszen and Fagre, 1993). Another is that it is more difficult to extract high-resolution temporal data from enamel than from hair (or feces), for in addition to isotopic inertia problems wherein body stores are subtly influencing enamel $\delta^{13}C$ values, enamel suffers from the more serious problem of isotopic overprinting. When enamel is initially formed, it has only 20–33% of its mature mineral content. Mineralization then continues, in a somewhat complicated spatial and temporal pattern, for many weeks to months (see Suga, 1982; Balasse, 2002; Passey and Cerling, 2002). Thus, there is significant temporal mixing of enamel $\delta^{13}C$ values, effectively decreasing the resolution of enamel as a dietary archive. One particularly elegant illustration of this problem can be seen in Figure 6. Balasse (2002) changed the diets of steers from C_3 to predominantly C_4 vegetation and then analyzed the enamel formed during the study at ~4-mm
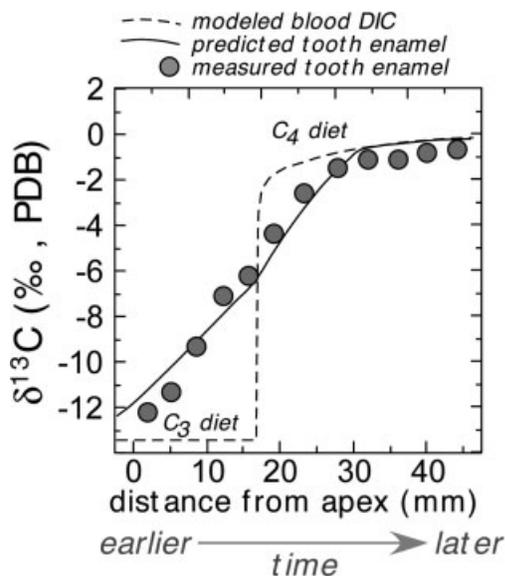
Fig. 6. Tooth enamel $\delta^{13}C$ data from steers whose diets were changed from C_3 to C_4 vegetation (Balasse, 2002). Each sample represents about 1 month's time. Note that the dietary change is evident in enamel that was initially deposited many months before the dietary change took place. Blood dissolved inorganic carbon (dashed line) reflects most of the dietary change within days, but given the protracted and complex process of enamel mineralization, enamel provides a greatly attenuated and temporally complex dietary signal. Yet, enamel $\delta^{13}C$ values can be predicted for a given dietary change as evidenced by the solid grey line, which is based upon the model of Passey and Cerling (2002).

Fig. 7. Incremental $\delta^{13}C$ values of rabbit incisor enamel (open circle), measured breath CO_2 values (black circle), and predicted $\delta^{13}C$ values of enamel (gray line) using the forward model of Passey and Cerling (2002). The forward model is in close accord with observed enamel $\delta^{13}C$ values demonstrating that, in continuously growing incisors, recovery of the primary dietary signal is a realistic objective. The data are from Passey et al. (2005).

intervals (representing about one month each). As Figure 6 shows, the dietary change is quite clear; however, the change is gradual rather than abrupt due to temporal mixing. Most notably, the diet change appears in enamel that was initially deposited about 6 months before the dietary change occurred! Thus, although enamel preserves dietary change through time, its use is not without complications. There has been significant progress in recovering primary dietary signals from time-averaged data, although this is only realistic when the growth and maturation parameters of teeth for the taxon being analyzed are well-characterized (Passey et al., 2005). For instance, Figure 7 shows the results of a forward model in which breath $\delta^{13}C$ values (which are in near-equilibrium with diet) were used to predict enamel $\delta^{13}C$ values for rabbit incisors over a 70-day period during which there were two diet changes. The predicted values (gray line) are in close accord with observed enamel $\delta^{13}C$ values (open circles) and show that, in continuously growing incisors, accurate recovery of the primary dietary signal is a realistic objective (see Passey et al., 2005 for the inverse model where observed enamel $\delta^{13}C$ values were used to reconstruct breath, and thus dietary $\delta^{13}C$ values).

This limitation obviously complicates the analysis of fossil primates, as in a recent study using laser ablation to sample along the growth trajectory of the external surface of *Paranthropus robustus* teeth (Sponheimer et al., 2006b). (It is worth noting that this was the only sampling protocol available at the time, as there were no sectioned teeth available for analysis.) The advantage of laser ablation compared to traditional sampling protocols is that it enables sampling at submillimeter increments, allowing one to provide a significant time-series while doing little visible damage to teeth. It also has drawbacks, including the fact that the teeth must be moved from the institutions where they are housed (traditional protocols allow in-house sampling with a small drill), lower precision in isotopic measurements, and difficulty in analyzing specimens much larger than *Paranthropus* teeth because of background CO_2 contamination associated with surface adsorption effects (see Passey and Cerling, 2006).

The laser ablation study found differences of greater than 5‰ within a given *P. robustus* tooth (see Fig. 8). Given the time averaging problem discussed above, this was an exceptional finding and suggested a switch from a diet dominated by C_3 vegetation to a diet dominated by C_4 vegetation. Another significant finding was that temporal variation was apparent at a variety of time-scales, with isotopic excursions appearing variously at intraseasonal, seasonal, and even interannual time-scales. Some of the changes in the carbon isotopic composition of *P. robustus* diet could be interpreted as fallback food consumption; but before addressing this possibility, we must first turn to recent thinking about the role of fallback foods in hominin evolution.

AUSTRALOPITHS AND FALLBACK FOODS

We preface this section by stating that it is not our intention to provide an overview of knowledge about australopith dietary ecology or even to fully discuss and assess the relevant carbon isotope data. Our purpose is
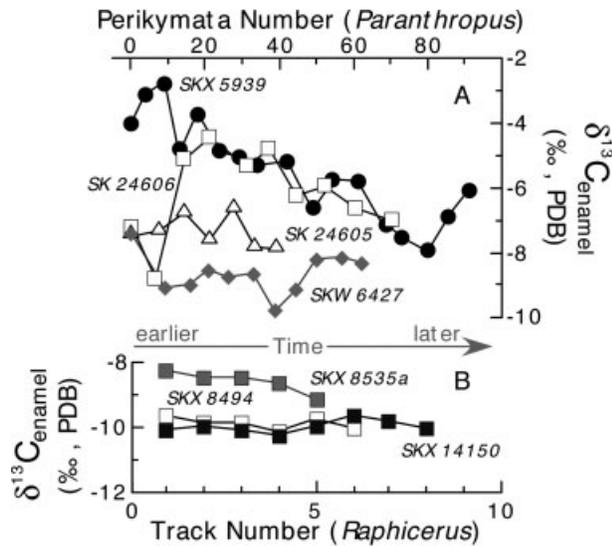
Fig. 8. δ^{13}C values for (**a**) *Paranthropus robustus* and (**b**) *Raphicerus* sp. obtained via laser ablation isotope ratio mass spectrometry (Sponheimer et al., 2006b). The δ^{13}C values of *Paranthropus* are highly variable, while there is little evidence for dietary change in the teeth of browsing steenbok.

to situate and discuss emerging thinking about the potential importance of fallback foods in australopith diets (e.g., Scott et al., 2005; Grine et al., 2006b; Ungar et al., 2008). It is our hope that this contribution enriches that dialog, however modestly, and suggests avenues for future research, both isotopic and otherwise.

The overall masticatory package of australopiths (e.g., postcanine megadontia, thick enamel, and robust mandibular corpora) has been interpreted as an adaptation for the consumption of harder and/or more abrasive foods (e.g., nuts and seeds) than those eaten by extant African apes, which tend to prefer fleshy fruits when available (Kay, 1985; Grine, 1986; Ward et al., 1999; Macho et al., 2005; White et al., 2006). Recently, however, several researchers have proposed that it was fallback foods, rather than typical or preferred diets, that drove hominin masticatory adaptations and that much of the time early hominins may have consumed foods similar to those eaten by chimpanzees (*Pan troglodytes*) or gorillas (*Gorilla gorilla*) (Ungar, 2004; Laden and Wrangham, 2005; Wrangham, 2005; Scott et al., 2005; Grine et al., 2006a,b; Ungar et al., 2008). One of the driving forces behind this idea has been a series of dental microwear studies (but see Laden and Wrangham, 2005 and Wrangham, 2005, which have an ecological focus). The first of this series used dental microwear texture analysis to investigate the diets of the australopiths *A. africanus* and *P. robustus* (Scott et al., 2005). It found that while there were observable differences in the dental microwear of these taxa, there was also considerable overlap, leading the authors to suggest that their diets were similar, possibly differing chiefly in the foods consumed during periods of resource stress.

This was followed by a study of 19 *A. afarensis* molars (Grine et al., 2006b), not one of which revealed evidence of hard-object feeding (e.g., high degree of pitting). The dental microwear of this hominin was actually quite similar to that of extant African apes, especially gorillas, which are not noted for their consumption of hard foods.

Most recently, Ungar et al. (2008) conducted a study of the dental microwear of *Paranthropus boisei*, the famous "Nutcracker Man" and the quintessence of the australopith masticatory package. They analyzed seven specimens that preserved antemortem microwear, not one of which preserved evidence of hard-object feeding; and in fact, the *P. boisei* microwear was very similar to that found in *A. afarensis*. Thus, of a total of 29 East African australopith specimens analyzed to date [3 specimens of *A. anamensis* were analyzed in Grine et al. (2006a)], not one retains evidence of hard-object feeding, despite australopith masticatory morphology being interpreted as an adaptation for hard-object consumption. How could this be?

It has been suggested that one way around this discordance between the microwear and morphology is fallback foods (Grine et al., 2006a,b; Ungar et al., 2008). The hypothesis holds that these taxa are morphologically like hard-object feeders because, in fact, hard objects were important components of their diets. It suggests, however, that these foods were consumed during short periods of resource stress, thus the invisibility of such behavior in the microwear record. We will call this idea the *fallback hypothesis*. The idea that fallback foods, rather than those eaten most regularly, so influenced hominin masticatory morphology represents a significant change in thinking to most students of human evolution [although hinted at previously as in Hatley and Kappelman (1980)]. Nevertheless, it is certainly true that during times of plenty one might consume abundant resources that prove little challenge to one's masticatory apparatus (such as ripe fleshy fruits), while during times of scarcity one might be forced to consume less favored and more mechanically challenging resources (such as nuts and seeds) [see Robinson and Wilson (1998)]. In short, having masticatory adaptations for the consumption of refractory materials does little or nothing to hinder consumption of soft and pliant foods (Wolpoff, 1988), but may prove of great import when such preferred foods are not available.

This phenomenon has often been noted in the primatological literature. For instance, Yamashita (1998) averred that the dental morphology of lemur species better indicates the hardest foods eaten than those consumed most frequently, and Lambert et al. (2004) found that despite large differences in the enamel thickness of *Lophocebus albigena* and *Cercopithecus ascanius*, their diets only differed in hardness during times of fruit scarcity. This is also evident in African apes, for when chimpanzees and gorillas are sympatric, they both tend to prefer fruits over herbaceous vegetation (Tutin and Fernandez, 1985; Stanford and Nkurunungi, 2003; Stanford, 2006; Yamagiwa and Basabose, 2006). During periods of scarcity, however, gorillas become much more reliant on terrestrial herbaceous vegetation, and this is reflected in the greater occlusal relief of their postcanine dentition. Hence, it might be argued that differences in the dentition of gorillas and chimpanzees are largely a function of their fallback foods and not a function of their preferred or even typical diets (Ungar, 2004).

The idea that australopiths preferred to eat ripe fruits, but that during times of resource stress they were able to access harder resources beyond the masticatory capabilities of extant apes, fits quite well with the South African australopith microwear datasets, as some specimens retain evidence of hard-object feeding. We are, however, less convinced by its applicability to the East African

australopiths for the reasons detailed below. It is well-known that dental microwear tells us primarily about the diets of individuals in the days just before they died (Grine, 1986), and it has also been observed that primate mortality is often greatest during times of resource stress (Cheney et al., 1981; Hamilton, 1985; Milton, 1990; Gould et al., 1999; Richard et al., 2002; Nakagawa et al., 2003; Hanya et al., 2004).[2] Because fallback foods are generally consumed when food is scarce, and because this is the time when mortality could well be highest, one might expect the consumption of fallback foods to be relatively over-represented in the fossil record. At the very least, one might expect fallback food consumption to reach the point of paleontological visibility. And yet, after 29 East African australopiths have been examined, not a single one preserves evidence of hard-object feeding.

Perhaps, this conundrum is the product of taphonomic bias, where fossil preservation is greater during periods of plenty when fallback foods were not consumed. We cannot deny this possibility, but neither can we adduce evidence in its favor. Or maybe the lack of a hard-object feeding signal is just a statistical anomaly. We would argue, however, that another interpretation may be more parsimonious: perhaps the East African australopiths show no evidence for hard-object feeding in their dental microwear because they did not in fact consume such foods. Is it possible that the East African australopith morphology represents an adaptation to a different kind of diet, possibly one of low-quality foods that required extensive mastication, and for which the prevention of fatigue failure would prove paramount (see Hylander, 1988)?

CONTRIBUTION OF STABLE ISOTOPES

What does the stable isotope evidence have to say about australopith fallback food consumption? Certainly, the dietary change during tooth mineralization in *Paranthropus robustus* (Sponheimer et al., 2006b)[3] is consistent with the *fallback hypothesis*. However, if fleshy fruits were their preferred foods as has been suggested, this might indicate that the australopith fallback foods were C_4 resources (e.g., tropical grasses, sedges, or animals eating these foods; see below with regard to CAM plants). And which of these might be considered "hard objects," and the morphological ramifications of their consumption, is not clear (but see Dominy et al., 2008). Additionally, the bulk carbon isotope compositions of the South African australopiths suggest that about 25% of the individuals analyzed had diets of nearly 50% or more C_4 foods during crown formation (Sponheimer

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[2]Note that resource stress can occur during the dry season, rainy season, or throughout the year in the case of drought, and that increased mortality during periods of food shortage is a general feature of herbivore populations as discussed in Young (1994).

[3] The study also suggests a relationship between the δ^{13}C and δ^{18}O values of *Paranthropus robustus*, with the former becoming lower as the latter values become higher. This relationship likely reflects a link between diet and environmental/climatic parameters, but as such links tend to be complex in the region (Smith, 2005), we hesitate to speculate on their nature at present. Moreover, as the precision, and especially accuracy, of the oxygen isotope measurements was relatively poor, utilization of such data remains problematic. A further complication is that laser ablation generates CO_2 with oxygen from at least two sources (phosphate and carbonate), the implications of which have not been subject to detailed study.
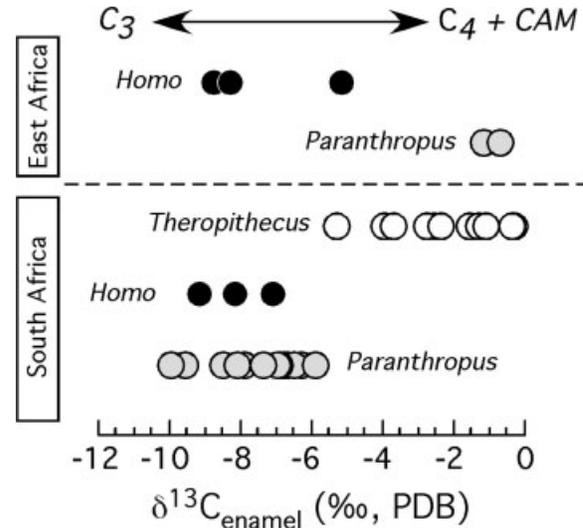
Fig. 9. δ^{13}C values of *Homo*, *Paranthropus*, and *Theropithecus* tooth enamel in South Africa and East Africa. Note the similarity in *Paranthropus* and *Homo* δ^{13}C values in South Africa as well as their collective dissimilarity to the δ^{13}C values of the grass-eating baboon *Theropithecus*. The East African data stand in contrast, with strong separation of *Homo* and *Paranthropus*, and the latter having less negative δ^{13}C values than most specimens of *Theropithecus*, suggesting a diet of perhaps 70–80% C_4 foods. The data are from Lee-Thorp et al. (1989), Codron et al. (2005b), Sponheimer et al. (2005), Fourie et al. (2008), and van der Merwe et al. (2008).

et al., 2005), which would represent a remarkable (and maybe unlikely) degree of reliance on fallback foods (but see Marshall and Wrangham, 2007 on staple fallback foods).

The scant carbon isotopic data from East Africa hint at more serious complications for the *fallback hypothesis*. van der Merwe et al. (2008) analyzed two specimens of *P. boisei* and three specimens of early *Homo*. Unlike the situation in South Africa, where *Homo* and the australopiths have similar δ^{13}C values, the data hint at very different dietary strategies for these genera in East Africa (see Fig. 9). The *Homo* δ^{13}C values suggest a mixed C_3/C_4 diet, with a significantly greater tendency towards consumption of C_3 food items. The *P. boisei* specimens, in contrast, suggest a diet of 70–80% C_4 vegetation, which puts them comfortably within the range of fossil *Theropithecus* (the grass-eating baboon) in C_4 environments. In fact, quite startlingly, the *P. boisei* numbers suggest greater C_4 consumption than most *Theropithecus* specimens analyzed to date (Lee-Thorp et al., 1989; Codron et al., 2005b; Fourie et al., 2008). It is virtually impossible to square these numbers with the idea that these individuals had diets similar to extant apes except in their fallback foods (unless they were "falling back" all the time as are mountain gorillas to a certain extent)—they suggest a fundamentally different dietary adaptation. Of course, these results may not be representative of *P. boisei* on the whole, but they are nevertheless suggestive. Perhaps we should be asking ourselves if there is in fact a C_4 resource that can produce the microwear observed in the East African australopiths and for which the robust masticatory apparatus of the australopiths is well-suited? This should not be an overly difficult question to address in practice, for tropical grasses or sedges

(either above or below ground portions) are by far the best possibilities, and both these foods would have been highly abundant in many *P. boisei* habitats [Hay, 1976; Bonnefille et al., 2004; and see Wrangham (2005) for a discussion of available foods in swampy areas such as the Eastern Lacustrine Plain at Olduvai; see Jolly (1970) with regard to the consumption of grass parts]. An outside possibility would be some sort of specialization on succulent vegetation using CAM photosynthesis such as *Euphorbia* spp. or the wild sisal plant "Oldupaai" (*Sansevieria ehrenbergii*), although this is difficult to imagine given their relative lack of abundance, suspect nutritional quality, and frequently significant secondary (i.e. toxic) compound loads. Baboons eat such CAM plants although they are not preferred and are not consumed in quantities sufficient to produce the *P. boisei* $\delta^{13}C$ values (Rhine et al., 1989; Barton et al., 1993; Codron et al., 2006a).

CONCLUSIONS

We argue that stable isotope analysis shows promise for investigations of short- and long-term dietary change in primates. Different tissues and sampling protocols allow one to address an assortment of questions about modern, historical, and paleontological primate diets that can be important supplements to traditional dietary studies, or which allow investigations where observation is impossible. Nevertheless, the application of stable isotopes to such questions is in its infancy, with small numbers of studies of any mammalian taxon, much less primates, for which only a handful of studies exist. Thus, we believe that judicious experimental and actualistic research may allow stable isotope analysis to make important contributions to our understanding of past and present primate dietary ecology (including fallback food consumption).

We further believe that stable isotopes should have an important role to play in future studies of early hominin dietary ecology. Application of laser ablation to examine carbon isotopic variability within individual teeth might prove important, especially among the East African australopiths. More crucially, however, the remarkable finding of van der Merwe et al. (2008) must be replicated (regardless of the methodology) with other *P. boisei* teeth, for if the reported $\delta^{13}C$ values are found to be broadly representative, they place important constraints on the potential diet range of *P. boisei*, and, by extension, possibly other East African australopiths. We clearly have much to learn about australopith diets and the functional significance of their distinctive craniodental morphology. Nevertheless, we have made great strides in the last few years, and while the resulting picture may not be clearer—and may be turbid by comparison to the picture a few years ago—it is certainly more accurate.

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