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Evolutionary Implications of Non-human Primate Diets



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Abstract and Keywords

Extant non-human primates are our closest living relatives and knowledge of their diets serves as a focus for hypotheses about past diets. We now know that the diets of extant primates vary from almost total folivory to considerable faunivory. Subsistence strategies of extant primates and stable isotope ratio data constrain dietary scenarios for fossil primates, including hominins. Among extant primates, significant faunivory occurs only in species of <1 kg body weight. Among those >1 kg body weight, smaller primates feed on fruit or fruit with insects, and larger ones on fruit and foliage, including leaves, pith, stems, flowers, and bark. Fossil hominins fall into the size range for fruit and foliage-eating.

Keywords: stable isotopes, adaptation, subsistence strategies, body size, digestion

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Extant primates feed on C₃ plants and display C₃ $\delta^{13}\text{C}$ values in tooth enamel. The C₄ and CAM (crassulacean acid metabolism) plants eaten are restricted to plants introduced by humans, including crops, and some sedges, grasses, and cacti and other succulents. Sometimes minimal amounts of C₄ or CAM appear in faeces and hair, which record times up to one week. No extant primate taxa eating native vegetation record significant (>20%) amounts of C₄ or CAM foods in tooth enamel or bone $\delta^{13}\text{C}$ values. In marked contrast, some fossil hominin $\delta^{13}\text{C}$ values indicate reliance on C₄ or CAM foods. Of interest is how these fossil hominins lived on high-fibre, low-calorie, and low-protein dense C₄ or CAM foods, with little evidence for reliance on a significant source of calories or protein.

Extant non-human primates are our closest living relatives and knowledge of their diets serves as a 'central conceptual focus' (Moore 1996) for hypotheses about past diets (Wood and Schroer 2012). This chapter combines observations of the subsistence strategies of extant primates and stable isotope data on many species. We emphasize the plethora of stable isotope studies on primates, many of which can be difficult to observe across seasons and years, because they are wary of human observers, or inhabit dense forests, or forage at night. Dietary reconstructions of fossil primates, including hominins, rely heavily on findings from such work.

Scientific observations of wild-living non-human primates began in the 1930s (Nissen 1931), and these, tempered by knowledge of anatomy, marked the beginning of the modern compilations of dietary information on primates. We now know that the diets of extant primates vary from almost total folivory (e.g. black-and-white colobus monkey, *Colobus guereza*, eats mature leaves) to total faunivory (e.g. tarsiers, *Tarsius* spp.), while the majority of species ingest a mixed diet consisting of fruit and foliage or fruit and insects (Fleagle 2013). They live in a variety of tropical environments, from open regions lacking trees (e.g. gelada baboon, *Theropithecus gelada*), to swamps and seasonally flooded forests (e.g. Allen's swamp monkey, *Allenopithecus nigroviridis*). Some species (e.g. chimpanzee, *Pan troglodytes*) live across a wide range of habitats, from rainforest to savanna (Hunt and McGrew 2002). As is true for all animals, diet is crucial for survival; food availability and competition for select food items impact both reproductive success and overall social organization (Wrangham 1980).

Since Washburn's time, concepts or principles have emerged that describe relationships between most primate species and their diets (Fleagle 2013). We focus on general principles because our ancestors and fossil relatives differed morphologically, and we assume behaviourally, from living humans or any single non-human primate species living today (Wood and Schroer 2012).

General Principles: Body Size Constrains Diet

Primate foods vary seasonally in type and abundance and at intra- and inter-species levels. All diets must provide adequate energy (Pontzer et al. 2014), and protein. Energy, which supports basic metabolism, growth, movement, and reproduction, comes mainly from carbohydrates (digestible fibre and sugars with trivial amounts of starch) in fruit and foliage (i.e. non-reproductive parts including pith, underground storage organs) or lipids (e.g. fats, fat-soluble vitamins) mainly in nuts and seeds, and some animal matter. Protein, for tissue synthesis during growth and for turnover, comes mainly from foliage supplemented by seeds and nuts; however, animal matter, usually in the form of invertebrates and small vertebrates, is taken by some species (McGrew 2014). Meat intake by baboons (*Papio* spp.) (Strum 1981), capuchins (*Cebus* spp. and *Sapajus* spp.) (Rose 2001), and chimpanzees (Wrangham and van Zinncq Bergmann-Riss 1990) has received particular attention for generating hypotheses relating to the evolution of meat-eating in hominins. Chimpanzees, bonobos, and orangutans eat mammals (Hohmann and Fruth 2008; Utami and Van Hooff 1999; Wood and Gilby 2018), but faunivory contributes a small proportion of their total diet (Carmody 2018).

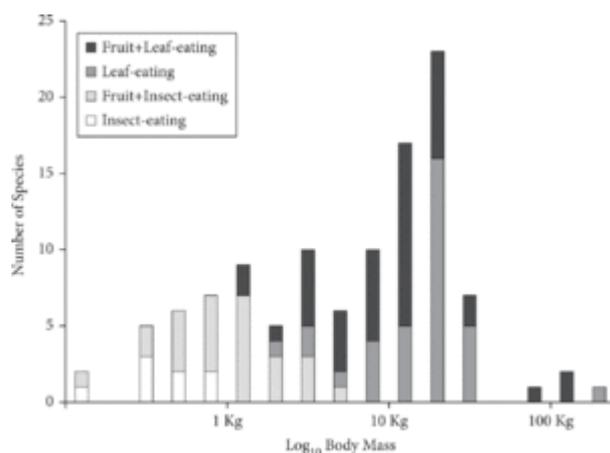


Figure 2.1. Species average body weight in kg plotted against diet in living non-human primate species (based on Fleagle 2013). Large primates may be totally folivorous and small primates (<1 kg) may be completely faunivorous. Most primates eat fruit for energy and insects or leaves for protein. Larger primates tend to be fruit and leaf-eating, while smaller primates tend to be fruit and insect-eating. Fossil hominins and most hominoid species fall into the size range of expected fruit and leaf-eating.

In general, primate diets vary according to the expectations of the Jarman-Bell model and exemplify the established relationship between overall caloric requirements per kg of body mass and total body mass, whereby larger animals require fewer calories per kg of body mass than do smaller ones (Gaulin 1979 and see Figure 2.1). According to Kay and Covert's (1984) calculations, the largest primate that could rely completely on insects for energy could weigh only

250–300 g as an adult. Thus, although insects provide much energy per gram, large-bodied primates cannot ingest enough insects to meet energy requirements on a regular basis. Invertebrates, however, may provide required minerals such as bioavailable iron (Deblauwe and Janssens 2008). The aye-aye (*Daubentonia madagascariensis*), at 2.5 kg in females (Glander 1994), has specialized adaptations for insectivory—i.e. a reduced dental

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formula, ever-growing incisors, and a long, slender third digit. In contrast, the smallest primate that could be completely folivorous is 700 g, due to the digestive constraints of extracting energy from indigestible cellulose and hemi-cellulose in leaves. *Lepilemur* spp. (sportive lemurs), which falls just at this limit (Nash 1998), have physiological adaptations that facilitate its adaptation. Sportive lemurs practice high levels of coprophagy, have large caeca relative to body size, and have the lowest metabolic rate in primates that, in combination, doubles the length of the gastrointestinal (GI) tract, lowers energy requirements, and slows passage of food through the GI tract (Hladik and Charles-Dominique 1974).

Dietary distinctions become obvious during periods of food scarcity, when primates rely on fallback foods—i.e. ‘resources of relatively poor nutritional quality [that are eaten] when preferred foods are scarce’ (Marshall et al. 2009: 140, although see Lambert and Rothman 2015). Great apes prefer high-energy, ripe fruit, but they fall back on foliage and other plant parts when these become less available (Harrison and Marshall 2011). The largest living primate, the mountain gorilla (*Gorilla g. berengei*), with females weighing around 80 kg and males around 180 kg, relies almost entirely on foliage to provide calories and protein throughout the year; lowland gorillas (*Gorilla g. gorilla*, *Gorilla g. graueri*) increase intake of such foods during fruit scarcity and always ingest larger amounts of vegetative foods when compared with sympatric chimpanzees (Malenky et al. 1994; Tutin and Fernandez 1993; Yamagiwa et al. 1996). The extensive folivory and overall toughness of gorilla diets associate with relatively thick molar enamel compared with chimpanzees, although thin when compared with orangutans (*Pongo* spp.) who have the thickest occlusal enamel in hominoids (Constantino et al. 2009). Gorillas also show greater development of enamel crests (Kay and Hylander 1978 and see Chapter 5 in this volume).

In contrast, chimpanzees and bonobos fall back on less-preferred fruits, such as figs (*Ficus* spp.), and they increase daily travel time to obtain them (Conklin-Brittain et al. 1998). Frugivores generally have larger home ranges and day ranges than folivores, because fruits, in contrast to foliage, are more patchily distributed across time or space (Fleagle 2013). These behavioural adaptations in chimpanzees associate with the smallest post-canine teeth across large-bodied hominoids (Constantino et al. 2009).

Fallback foods of orangutans tend to be both hard and tough. Bornean orangutans (*Pongo pygmaeus*) eat bark and cambium, as well as foliage and unripe fruit, while Sumatran orangutans (*P. abelii*) rely more on various parts of strangler figs (Wich et al. 2006). The eating of these hard, tough foods associates with very large teeth (Constantino et al. 2009).

Gastrointestinal Morphology, Food Transit Times, and Diet

Diets in mammals also associate with different types of GI tracts (Chivers and Hladik 1980). Insectivorous primates with diets containing little fibre have simple tracts with long, small intestines and simple colons. Insect/fruit-eating primate species tend to have simpler GI tracts than do foliage/fruit-eating species. Humans and other large-bodied hominoids have similar GI morphologies with simple stomachs and small intestines; but they differ in the much larger hindguts of the other large-bodied hominoids (Darwin 1871; Milton 1987). Because primates lack endogenous enzymes for hydrolysing cellulose (e.g. cellulases) leaf-eating primates rely on a fermentation process of cellulose hydrolysis by gut microbiota in the colon (Ley et al. 2008) to release protein and produce free fatty acids that provide energy. Colobines, many of whom feed extensively on foliage high in structural carbohydrates (i.e. indigestible fibre), have expanded stomachs with multiple chambers (foregut fermentation) which increase assimilative efficiency of such diets compared to hindgut fermentation, and may also serve to detoxify foods with chemical defences (Lambert 1998). Foregut fermentation restricts feeding on acidic fruits because stomach acidity is detrimental to its resident microbiota (Janson and Chapman 1999). In contrast, humans (Marleb and Hoehn 2010) and most other primates (Chen et al. 2008) have highly acidic stomachs. Folivores spend much of the time resting and digesting, which constrains day ranges and activity levels (Snaith and Chapman 2007).

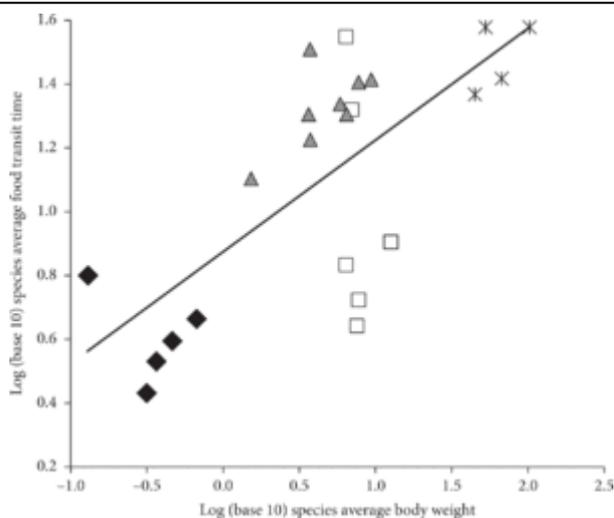


Figure 2.2. Species average body weight in kg plotted against species average food transit time in hours (both Log base 10, based on Lambert 1998). Species above the line have longer than expected transit times based on body size; those below the line have shorter than expected transit times. Open squares are Atelines, closed diamonds are Callitrichines, closed triangles are Cercopithecines, and stars are Hominoids. See text for discussion of the distribution.

In general, larger animals take longer to pass food through the GI tract, allowing them to consume a lower-quality diet than smaller animals (Remis 2000). Body size, however, explains only 31% of the variance in food transit time among primates (Lambert 1998), in part due to intra-species variation in diet across seasons and years (Lambert and Rothman 2015). Large-bodied hominoids and squirrel-sized Callitrichines fall, as expected, at the high and low end of the scale respectively (Lambert 1998); but there are many

exceptions that appear to be diet-related (see Figure 2.2). Among the Atelines, howler monkeys have longer transit times than expected based on body size, reflecting their extensive folivory. They also spend over half of their diurnal time resting (Gaulin and Gaulin 1982). Spider monkeys (*Ateles* spp.), woolly monkeys (*Lagothrix* spp.), and muriqui monkeys (*Brachyteles* spp.) have shorter passage times than expected, which associate with their extensive fruit-eating (Strier 1992). Interestingly, nine analysed cercopithecine species show longer than expected passage times for their body sizes, placing a premium on food absorption (Lambert 1998: 15).

Stable Isotope Data

The following is a brief introduction to carbon and nitrogen stable isotope biogeochemistry and some examples of how it has been applied in non-human primate studies. The focus is mostly on carbon and nitrogen. Oxygen stable isotope values have recently been used (Carter and Bradbury 2015; Krigbaum et al. 2013), and although they hold great promise and indicate habitat ecology in extinct species of non-human primates and hominins (White et al. 2009a), they will not be discussed further due to space restrictions (see Nelson and Hamilton 2018 for a recent overview of oxygen stable isotope ratios).

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Park and Epstein (1960) reported fractionation of carbon during photosynthetic fixation of atmospheric carbon dioxide (CO_2), and Bender (1968) recognized the association between photosynthetic pathway and plant $\delta^{13}\text{C}$ values. These findings now are applied to many dietary queries when direct observation is not possible or adequate. Of the three photosynthetic pathways, C_3 , C_4 , and CAM, C_3 plants (trees, herbaceous plants, cool season grasses, and the vast majority of other plants) have lower $\delta^{13}\text{C}$ values, which do not overlap the values in C_4 plants (arid adapted and dry season grasses, some sedges: Peters and Vogel 2005). Cacti and other succulents use the third photosynthetic pathway, CAM, with $\delta^{13}\text{C}$ values that fall between C_3 and C_4 plants or overlap with C_4 plants (Ting and Gibbs 1982). The specific $\delta^{13}\text{C}$ value in C_3 plants correlates negatively with mean annual precipitation (MAP), as does biomass density (Kohn 2010). Consequently, plants growing in closed canopy forests have the lowest $\delta^{13}\text{C}$ values, while those in open habitats have higher values (van der Merwe and Medina 1991). Animals eating C_3 or C_4 plants (or CAM plants), or a mixture, record those diet sources in their tissues (DeNiro and Epstein 1978). Primates that eat animal tissue incorporate the $\delta^{13}\text{C}$ values of the animals, in addition to those from ingested plants (e.g. Fahy et al. 2013; Oelze et al. 2011; Schoeninger et al. 1998).

Stable nitrogen isotope ratios in plants vary widely based on their source of nitrogen and metabolic factors (see table 2 in Shearer and Kohl 1986). Legumes have $\delta^{15}\text{N}$ values close to zero when their symbiotic microorganisms fix atmospheric nitrogen ($\delta^{15}\text{N}=0$, by definition). Most plants use soil nitrogen and have $\delta^{15}\text{N}$ values of 3–7‰ (Virginia and Delwiche 1982) especially in nutrient-poor, acidic, sandy soils (Schmidt et al. 2005). The available data on African soil $\delta^{15}\text{N}$ values show variation of less than 3‰ (Amundson et al. 2003); therefore, plant metabolic factors should play a significant role in plant $\delta^{15}\text{N}$ values across the continent. Globally, plant $\delta^{15}\text{N}$ values exhibit significant negative correlations with MAP (Amundson et al. 2003), and some animals show $\delta^{15}\text{N}$ values that vary in concert with such plant values (e.g. Pate and Anson 2008). In general, herbivorous animals, which obtain their protein from plants, have bone collagen $\delta^{15}\text{N}$ values approximately 3‰ higher than the plants on which they feed; carnivores are 3‰ higher, on average, than herbivores, which supply their protein (Schoeninger and DeNiro 1984).

Isotope data on non-human primates come from tissue (e.g. muscle, blood, hair, tooth enamel and dentine, bone apatite, and bone collagen) and excreta (faeces and urine) for carbon and nitrogen stable isotope ratios (Codron et al. 2008; Crowley 2012). Faecal material represents hours to days of ingestion, depending on food intake levels, digestibility of fibre, and throughput time (Codron et al. 2012; Lambert 1998). A single hair represents the diet during the months of its formation. Enamel records isotopic input during the months to years of formation. Bone remodels throughout life and represents years.

The information recorded varies across these materials depending on dietary source. The $\delta^{13}\text{C}$ values in highly organic tissues (collagen, keratin) are weighted slightly toward dietary protein values. Approximately 60% of carbon atoms in tissue proteins come from dietary protein (Froehle et al. 2010), apatite fractions represent an average of the total

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diet (protein and energy sources) (Kellner and Schoeninger 2007), and excreta represents material not incorporated into the body, but nearly isotopically equilibrated to whole diet (i.e. diet-faeces enrichment is typically small). The $\delta^{15}\text{N}$ values represent the protein portion (i.e. amino acids) of the diet in both plants and animal material. Not all nitrogen is in the form of useable amino acids; for example, many underground storage organs and fruit have nitrogen, but it is not metabolically available (Schoeninger et al. 2001b). Mode of sampling should be geared toward the timescale and the type of questions being addressed.

We limit discussion to relative comparisons describing diets as higher or lower in delta values or minimal, minor, or major portions of diet, rather than assigning a percent to specific food items, because the various mixing models published are as yet insufficiently precise in primate studies (Sandberg et al. 2012). Stable isotope data are constrained by equifinality, so that identical stable isotope data in tissues can result from different diets. For this reason, it is critical to keep the general principles outlined above in mind when interpreting stable isotope data for estimating diets in primates in the absence of direct observations.

Non-human Primate Carbon Stable Isotopes

Almost all extant non-human primates have tissue $\delta^{13}\text{C}$ values that are consistent with feeding on C_3 plants, such as fruits and foliage from trees and herbaceous vegetation, or C_3 -feeding insects or small vertebrates. However, some interesting exceptions may be useful for understanding C_4 -feeding in some fossil hominins (Lee Thorp et al. 2003). In *Microcebus*, an insect-eating prosimian (50–100 g, on average), virtually all hair $\delta^{13}\text{C}$ values fall within the range for C_3 diets (Crowley et al. 2011). One population, however, has values consistent with minimal ingestion of C_4 plants, CAM plants, or insects feeding on such plants (Rakotondranary et al. 2011). Such reliance on insects has also been suggested for some early hominins (Peters and Vogel 2005; Sponheimer et al. 2005).

In studies of Asian macaques (*Macaca* spp.) (see references in Sandberg et al. 2012; Schillaci et al. 2013; and see Schurr et al. 2012) evaluating dietary heterogeneity, environmental toxins, tourist feeding, and dietary changes through time, all taxa show a C_3 diet, except hair $\delta^{13}\text{C}$ values in one population. The latter reflects observations of seasonal crop raiding on maize (*Zea mays*) (O'Regan et al. 2008). Similarly, virtually all data from African cercopithecine tissues, collected as parts of larger ecological studies, are consistent with pure C_3 diets of mixed intake of foliage, fruit, and insects (see references in Krigbaum et al. 2013; Sandberg et al. 2012), except for some baboons.

Baboons deserve separate mention among cercopithecines, because they have long been proposed as models for our ancestors, and they inhabit vast regions of Africa, in a wide variety of ecotypes and on a wide variety of diets (Codron et al. 2008; DeVore and Washburn 1963; Jolly 1970; Swedell and Plummer 2012). The majority of published $\delta^{13}\text{C}$

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values indicate little or no C₄ intake (see references in Crowley et al. 2010). For example, a recent compilation of δ¹³C values in non-human primate teeth from across Africa (Levin et al. 2015) presented data on forty-two modern *Papio spp.* Of these, over 80% had values consistent with eating 100% C₃ foods. In contrast, four individuals from Laikipia County, Kenya indicated feeding on >50% C₄ foods (see also Levin et al. 2008). The majority of these samples were collected the late 1990s, and roughly fifty years prior to the time of collection the region had witnessed the introduction of a non-indigenous prickly pear cactus (*Opuntia stricta*) (Strum et al. 2015). Unlike native succulents, this species has year-round fruits with sweet, low-acid pulp (Feugang et al. 2006) consisting of 65% simple sugars on a dry-weight basis (El Kossori et al. 1998). They are a baboon favourite (Strum pers comm and observation by MJS) and the animals spend hours rolling the fruits on the ground to remove its spines (personal observations). *Opuntia spp.* always use the CAM photosynthetic pathway and display δ¹³C values within the C₄ range irrespective of ecological variables (Sutton et al. 1976; Ting 1985). This introduced cactus is the most likely source of the C₄-like δ¹³C values reported by Levin and colleagues. No information was given on five remaining individuals who ingested 30–50% C₄ foods in diet (Levin et al. 2015); therefore crop raiding, provisioning by humans, or the presence of *Opuntia stricta* cannot be evaluated.

In addition, Thackeray and colleagues (1996) reported some South African baboons with bone collagen δ¹³C values indicating consistent ingestion of minor amounts of C₄ foods. Site specifics were not given, and the well-documented pattern of crop raiding by East African baboons (Strum 1987) could be occurring in South Africa as well. At another South African site, most baboon faeces had C₃ δ¹³C values, but a few, recovered under a *Euphorbia* plant, had δ¹³C values in the C₄ range suggesting short-term feeding on a CAM plant (Codron et al. 2006, 2008). Hair and bulk dentin data from baboons in the region indicated minimal C₄ intake (Codron et al. 2006, 2008). Perhaps the baboons in Thackeray's study also relied on CAM plants when preferred foods were not available.

Many studies comment on baboon reliance on grasses (e.g. DeVore and Washburn 1963 stated grass-feeding occurred daily, and all authors on this chapter have personally observed grass eating by baboons), which are virtually all C₄ at lower altitudes across Africa (Osborne et al. 2014). Of the detailed studies, Altmann (1998) reported feeding on the corms of unidentified grasses and on sedges in about 17% of feeding bouts. Based on these reports and on carbon and nitrogen (reported as crude protein without information on its molecular form) levels, scholars (Paine et al. 2018) have suggested recently that grass leaves should be considered as food sources for early hominins. It is possible that grass fermentation in the colon explains the slower than expected throughputs of food by baboons (Lambert 1998); but as reviewed above, few animals record C₄ in their tissues. Geladas are often reported as total grass eaters; but geladas living in an undisturbed habitat at high altitude ingest a wide variety of forbs and animal prey in addition to grass (Fashing et al. 2014). All the geladas in the region analysed thus far have tissue δ¹³C values consistent with pure C₃ diets, even though many plants analysed from the region are C₄ (Venkataraman et al. 2012; Schoeninger and colleagues, unpublished data). Given the range of dietary items in this high-altitude undisturbed habitat, and the range of

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baboon diets overall across Africa, a diet of geladas living in similarly undisturbed habitats at lower elevations cannot be proposed with any accuracy or reliability without further evidence. In summation, when the baboon data are evaluated in detail and with knowledge of local ecology and individual baboon group subsistence strategies, including crop raiding and feeding on introduced plants, baboons eat C₃ foods with a minor number of exceptions that are rational given body size, digestive constraints, and available food items. Early hominins eating C₄ or CAM plants must have had rational exceptions that consider their larger body sizes, social systems, and ecologies. Considering such exceptions is where we need to focus.

The emphasis on C₃ foods is repeated in the apes. Among the large number of studies devoted to chimpanzees, none indicates ingestion of C₄ foods (Crowley et al. 2010; Fahy et al. 2013; Macho and Lee-Thorp 2014; Nelson 2013; Phillips and O'Connell 2016; Schoeninger et al. 1999; Smith et al. 2010; Sponheimer et al. 2006). The same is true for western lowland gorillas, mountain gorillas (Blumenthal et al. 2012; Crowley et al. 2010; Oelze et al. 2014), bonobos (*Pan paniscus*) (Oelze et al. 2011), a single orangutan and a single gibbon (*Hylobates lar*) (Pushkina et al. 2010).

Mounting evidence suggests that general habitat characteristics such as canopy cover and MAP affect non-human primate $\delta^{13}\text{C}$ values to a greater extent than do taxonomic group, dietary specifics, or geography. New World monkeys, African prosimians, and chimpanzees have $\delta^{13}\text{C}$ values similar to each other in cases where their habitats have structural similarities (Schoeninger et al. 1997, 1998, 1999). In contrast, chimpanzees from several different African countries show a range of over 3‰, similar to Thackeray et al.'s (1996) report on baboons across eastern and southern Africa, that correlate with MAP (Schoeninger et al. 2016). Bonobos at LuiKotale, Democratic Republic of Congo (Oelze et al. 2011) had $\delta^{13}\text{C}$ values that were virtually identical to those reported for chimpanzees in similar evergreen closed canopy forests. Loudon and colleagues (2007) reported one group of ring-tailed lemurs (*Lemur catta*) living in pristine forest with significantly lower hair $\delta^{13}\text{C}$ values compared to two other groups living in disturbed habitats. In some cases, specific diet items are associated with particular $\delta^{13}\text{C}$ values. For example, mountain gorilla faeces from Bwindi Impenetrable National Park, Uganda, revealed peaks in $\delta^{13}\text{C}$ values that coincided with observed increases in fruit intake (Blumenthal et al. 2012), and corroborated observed wet and dry season dietary differences between sympatric western lowland gorillas and chimpanzees in Gabon (Oelze et al. 2014). On the other hand, chimpanzee groups from across Africa showed no association between the amount of fruit eating and hair or faecal $\delta^{13}\text{C}$ values (Phillips and O'Connell 2016; Schoeninger et al. 2016).

Non-human Primate Nitrogen Stable Isotope Data

Virtually all of the $\delta^{15}\text{N}$ values in non-human primates are consistent with those of herbivorous mammals; but there are exceptions. Insect-eating capuchin monkeys (Schoeninger et al. 1997) and bush babies (Schoeninger et al. 1998) had significantly higher hair $\delta^{15}\text{N}$ values compared with sympatric leaf-eating primates. In the Taï Forest, male chimpanzees had significantly higher bone and hair $\delta^{15}\text{N}$ values than did females, and among the males $\delta^{15}\text{N}$ values correlated with male hunting rates (Fahy et al. 2013). In contrast, hair $\delta^{15}\text{N}$ values in bonobos at Lui Kotale were homogenous with no difference between males and females, and no correlation with observations of observed hunting (Oelze et al. 2011). This and other selective feeding probably explains why there is no correlation between MAP and chimpanzee hair $\delta^{15}\text{N}$ values across a range of rainfall levels (Schoeninger et al. 2016), as occurs in multiple kangaroo species, cows, and rabbits across Australia (Ayliffe and Chivas 1990; Pate and Anson 2008).

Several new studies suggest that it might be possible to obtain detailed information on non-human primate life-history patterns. Nursing, an example of a trophic level offset, can be monitored using $\delta^{15}\text{N}$ values. Faecal $\delta^{15}\text{N}$ values in a captive langur infant (*Trachypithecus francoisi*) revealed a longer nursing period than observations suggested (Reitsema 2012). Longitudinal dentin $\delta^{15}\text{N}$ values showed that male juvenile chimpanzees nursed longer than females (Fahy et al. 2014).

Significantly lower hair $\delta^{15}\text{N}$ values are correlated with time spent feeding on leguminous plant species in one of three sympatric social groups of ring-tailed lemur (Loudon et al. 2007), a troop of mantled howler monkeys (Schoeninger et al. 1997), among individual sportive lemurs (Schoeninger et al. 1998), and in locales where faecal analysis shows evidence of legume feeding by chimpanzees (Schoeninger et al. 1999). Cercopithecine monkeys as a group display low $\delta^{15}\text{N}$ values (Sandberg et al. 2012), which may be related to their relatively long digestive throughput time (Lambert 1998). More complete absorption of diet nitrogen would result in tissue values close to diet values (i.e. relatively low $\delta^{15}\text{N}$ values). More data are needed on plant $\delta^{15}\text{N}$ values and on how gut throughput times affect animal values.

Summary and Conclusions

Across all body sizes, non-human primates primarily eat C₃ foods, even when they live in regions where C₄ and CAM plants are present. The exceptions include crop raiding on grains that have undergone intensive selection to increase seed size and numbers, and ingestion of non-native cactus fruits high in sugar and water, with some reliance on native succulents as fallback foods in some regions. Additional values indicating some C₄ and CAM plant ingestion come from sites with no ecological or other information. Such information is critical for understanding why the animals are eating C₄ and CAM plants (high in fibre and low in calorie and protein density) in contrast to the majority of primates. These examples underscore the flexibility of primates in incorporating dietary items under different circumstances of food availability and food scarcity, and emphasize the need for further investigations of grass and C₄ sedge feeding. Of the examples of extant primates eating C₄ and CAM plants, however, the fallback food option was the only choice available to our hominin ancestors and relatives. Unfortunately, fallback foods can be identified using $\delta^{13}\text{C}$ values only if they are distinct isotopically (Constantino et al. 2009; Marshall et al. 2009). Further, we need better assessments of how much of these foods must be ingested for them to impact the isotope values of bones and teeth (Daegling et al. 2013). More work is also needed on mixing models to determine which variables give the best information on this particular topic.

Most primates are herbivorous, with large-bodied primates taking only minimal amounts of animal material, at least by weight ingested. Primates weighing less than 250 grams feed primarily on insects for protein and energy; but for most primates, diets are largely a combination of insects and fruit (smaller primates) or foliage and fruits (larger primates). In insect and fruit-eating primates, protein comes from insects and energy comes from lipids (insects) and simple sugars and digestible fibre (fruit) with trace amounts of starch. In foliage and fruit-eating primates, protein comes from foliage fermentation while energy comes from simple sugars and digestible fibre in fruit, with trace amounts of starch (Fleagle 2013). By the early Pliocene, hominin ancestors and relatives achieved the body size of female chimpanzees (White et al. 2009b) yet, around 2.5 million years ago (mya), members of the hominin clade apparently began to favour animal matter (protein and lipids) sourced from larger vertebrate prey (Chapter 7 in this volume) to a diet of foliage and fruit-eating. Around that time, or soon thereafter, animal matter became a regular and significant portion of diet. Thus, there was a major change in energy source with the inclusion of animal lipids (Schoeninger et al. 2001a). Other members of the hominin clade relied on highly fibrous foods such as sedges and C₄ grasses of low energy density and, in the case of the sedges, low protein density (Dominy 2012, 2008). The foraging behaviours in these two disparate subsistence strategies may have been completely distinct, with the latter group completely different from any extant member of the Primate order.

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Extant primates continue to be used as validatory referential models for evolutionary hypotheses; but we also must consider effects of human encroachment. Loss of habitat may cause populations of a species to adapt their diet to a less varied repertoire, or to incorporate agricultural foods into their diet in crop raiding (e.g. McLennan 2012). Stable isotope analyses of tissues using archived specimens allows us to assess the adaptation of primates to fragmentation of habitat and to investigate the range of ecological systems inhabited by primates prior to human incursion (as suggested by Crowley et al. 2013; Gibson 2011; Schoeninger et al. 1997; Schurr et al. 2012).

Finally, we note that stable isotope analysis of primate tissues continues to expand as a field, as it has in bioarchaeology (Nelson and Hamilton 2018). Stable isotopes are useful not only to explore diets within and between groups, but also to address nutritional intake by infants (Katzenberg et al. 1996), other health issues (Fuller et al. 2005) related to nutritional intake (Reitsema 2012; Reitsema 2013), and additional life-history patterns. Oxygen and strontium isotope ratios may be applied in investigating the ecology of primates collected in the nineteenth and twentieth centuries without habitat information. We encourage additional applications of the method to fossil primates, in order to expand our understanding of a greater range of primate adaptations.

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