

Stable isotope evidence of meat eating and hunting specialization in adult male chimpanzees

Geraldine E. Fahy^{a,b,1}, Michael Richards^{a,c}, Julia Riedel^b, Jean-Jacques Hublin^a, and Christophe Boesch^b

Departments of ^aHuman Evolution and ^bPrimates, Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany; and ^cDepartment of Anthropology, University of British Columbia, Vancouver, BC, Canada V6T 1Z1

Edited by Frans B. M. de Waal, Emory University, Atlanta, GA, and approved March 4, 2013 (received for review December 17, 2012)

Observations of hunting and meat eating in our closest living relatives, chimpanzees (*Pan troglodytes*), suggest that among primates, regular inclusion of meat in the diet is not a characteristic unique to *Homo*. Wild chimpanzees are known to consume vertebrate meat, but its actual dietary contribution is, depending on the study population, often either unknown or minimal. Constraints on continual direct observation throughout the entire hunting season mean that behavioral observations are limited in their ability to accurately quantify meat consumption. Here we present direct stable isotope evidence supporting behavioral observations of frequent meat eating among wild adult male chimpanzees (*Pan troglodytes verus*) in Taï National Park, Côte d'Ivoire. Meat eating among some of the male chimpanzees is significant enough to result in a marked isotope signal detectable on a short-term basis in their hair keratin and long-term in their bone collagen. Although both adult males and females and juveniles derive their dietary protein largely from daily fruit and seasonal nut consumption, our data indicate that some adult males also derive a large amount of dietary protein from hunted meat. Our results reinforce behavioral observations of male-dominated hunting and meat eating in adult Taï chimpanzees, suggesting that sex differences in food acquisition and consumption may have persisted throughout hominin evolution, rather than being a recent development in the human lineage.

dietary ecology | stable isotope analysis | human evolution

Comparisons with extant primates and other mammals are essential to understanding the varied ecological niches occupied by early hominins. Data from chimpanzees (*Pan troglodytes*) indicate that populations living in different forest habitats have different food repertoires (1–4). Variation in hunting behavior and meat consumption has been observed between populations, with chimpanzee communities acquiring and consuming meat with varying levels of importance, from those who hunt rarely and largely opportunistically for slow-moving small mammals (4) to more regular, systematic hunting of medium-sized prey (2, 3, 5). As all chimpanzee populations rely heavily on various plants, nuts, and invertebrates for their daily energy requirements, the disparity in vertebrate meat consumption across populations has led some researchers (6, 7) to suggest that meat is an occasionally consumed, nonessential dietary supplement.

The chimpanzees (*Pan troglodytes verus*) of the Taï National Park, Côte d'Ivoire, are known to be some of the most specialized chimpanzee hunters, consuming large quantities of meat annually, predominantly from Western red colobus (*Procolobus badius*) and, occasionally, Western black-and-white colobus (*Colobus polykomos*) monkeys (3,8). Hunting at Taï is cooperative among the male chimpanzees, and after capture, division of the resultant prey rewards participation in the hunt, rather than nepotism (2, 8). A significant adult male sex bias is also evident, with adult males reported to consume almost seven times more meat daily than their female counterparts (8). Therefore, although the unique hunting style of the Taï chimpanzees is well known (2), how this translates into the amount of meat digested and incorporated in body tissues is unknown. Furthermore, variation in meat sharing at

Taï and among other chimpanzee populations (1–3, 8, 9), along with different hunter-gatherer populations (10), raises the question of why hunters hunt. Does being the most successful hunter result in more meat consumption? Is meat consumption significant enough to register, and be detected, in body tissues?

The detection of hunting in chimpanzee populations, particularly unhabituated populations, is difficult (11). Although analysis of food remains in feces can indicate consumption of a particular food type, the quantity consumed or frequency of consumption is more problematic to identify. No data exist reflecting the amount of meat digested and integrated into the body by an individual chimpanzee, or its nutritional function (12). Fecal sampling is not always a reliable indicator of hunting and can often underestimate the rate of fauna consumed (11), and constraints on continual direct observation throughout the entire hunting season mean that behavioral observations are limited in their ability to accurately quantify the amount of meat consumed. Observational data are further limited in that they are nutritionally incomplete, as they capture only a short period in the life of a long-lived individual.

Stable isotope analysis of body tissues and ecosystems can be used in ecological investigations of diet to provide quantified, or semiquantified, measures of diet (13). Carbon isotopes estimate dietary dependence on plants growing under particular ecological conditions and can be used to differentiate between C₃- and C₄-based diets (14). Stable isotope ratios of nitrogen are used to estimate the trophic position of an organism (15), with an estimated stepwise trophic enrichment of ~3‰ from herbivore to omnivore and omnivore to carnivore commonly used (15, 16). Therefore, using the “you are what you eat” principle, stable isotope ratios of carbon and nitrogen in body tissues provide a way to quantitatively distinguish between long-term dominant plant versus animal consumption, thus identifying the level of animal-derived protein in the diet (17, 18).

Varying turnover rates mean that different body tissues record dietary information at different intervals of an individual's life (19). A hair strand contains a chronological record of an individual's diet along its length (18). Average monthly human scalp hair growth is 1 cm (20), but as yet, hair growth in chimpanzees and other nonhuman primates is not well characterized. However, this study, and previous nonhuman primate research by Schoeninger et al. (17, 18), Sponheimer et al. (16), and Oelze et al. (12) assumes that hair growth in *Pan* is similar to that in humans. This assumption is further validated by Rosen (21), who compared human scalp hair with a range of primate head hair and found no significant distinctions between them.

Because of its continuous, but slower, turnover, long-term (multiyear) dietary information is recorded in bone (19). Research

Author contributions: M.R., J.-J.H., and C.B. designed research; G.E.F. performed research; J.R. contributed new reagents/analytic tools; G.E.F. analyzed data; and G.E.F., M.R., and C.B. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. E-mail: geraldine_fahy@eva.mpg.de.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1221991110/-DCSupplemental.

has also indicated no significant differences in histological bone development between humans and chimpanzees (22). Collagen from bones with higher proportions of cancellous bone, such as ribs, provides dietary information encompassing a more recent time frame compared with those with higher proportions of compact bone, such as femora and humeri, which record long-term dietary information.

Using observational information gathered during a 20-y period, we compared stable isotope data of chimpanzee hair keratin and bone collagen with behavioral observations on the dietary ecology of the Tai chimpanzees. Our study compares isotope data with known individual behavior of wild chimpanzees in their natural habitat. Our aim was to determine whether meat eating is regular enough in Tai chimpanzees to be detectable with isotopic measurements and whether observed sex differences in meat eating are detectable, on a short- and long-term basis, using stable isotope analysis. Furthermore, given the unique nature of hunting at Tai, we also investigated whether an individual's role in the hunt results in increased vertebrate meat consumption identifiable through protein-associated $\delta^{15}\text{N}$ values.

Results

A range of environmental samples was analyzed to determine the baseline isotopic ecology of the Tai National Park (Tables S1 and S2). The inherent isotopic variability expected in a closed-canopy tropical evergreen forest is reflected in our environmental $\delta^{13}\text{C}$ results; however, even with this variability, the study site is predominantly a C_3 ecosystem. The $\delta^{15}\text{N}$ variability of the faunal samples generally reflects the increasing stepwise trophic enrichment expected of herbivores, omnivores, and carnivores.

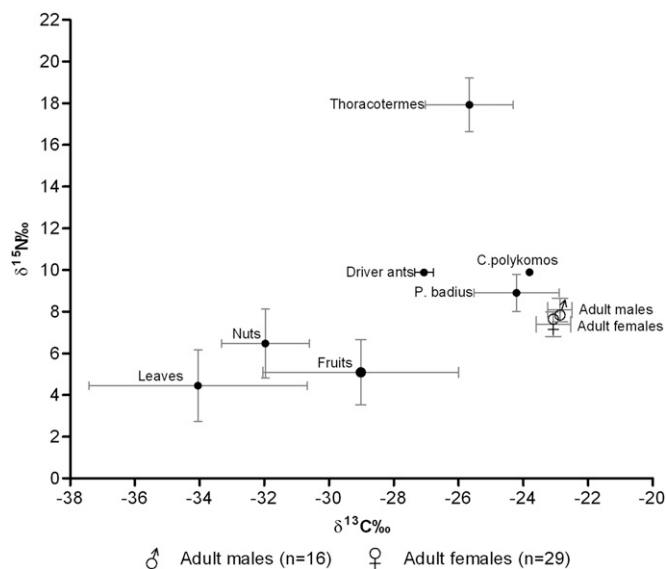


Fig. 1. Isotopic values of predominant chimpanzee foods, bone collagen, and hair keratin. Fruit is the dominant food resources for the Tai chimpanzees (see Table S3 for isotope data of some frequently consumed fruits). They also consume large quantities of nuts, mainly *Coula edulis* and *Panda oleosa*, during the nut cracking season (December–March). Further dietary supplements include driver ants (*Dorylus* sp.) once or twice weekly during the rainy season and large amounts of geophagic termites (*Thoracotermes* sp.) for a short, 4-wk period in early April. Hunting of western red colobus (*P. badius*) and, occasionally, black and white colobus (*C. polykomos*) occurs annually, taking place every 3 d before increasing to daily hunts during the hunting season (September–October). Colobine values include average bone collagen for adults and infants. Plotted mean \pm SD data for adult male ($8.1 \pm 0.6\%$) and adult female ($7.4 \pm 0.6\%$) chimpanzee data includes bone collagen ($n = 24$) and hair keratin ($n = 30$) data for all adults analyzed. $\delta^{13}\text{C}_{\text{keratin}}$ values were adjusted by $+2\%$ (15) for comparability with $\delta^{13}\text{C}_{\text{coll}}$ values.

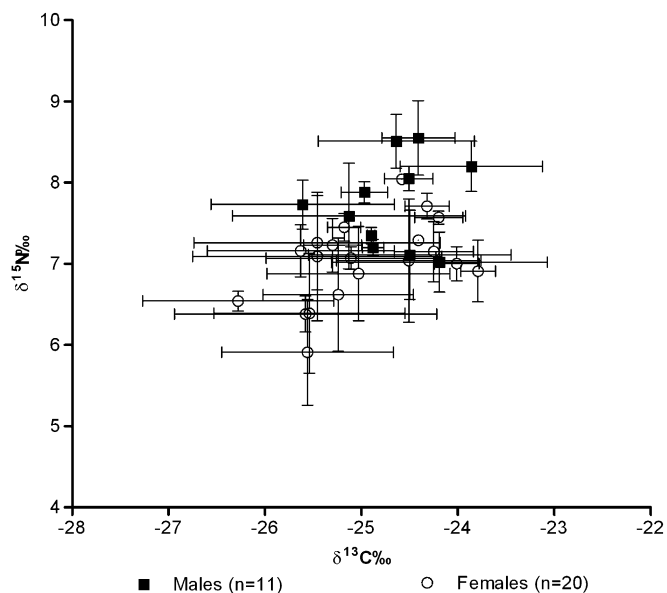


Fig. 2. Isotopic values for adult male and female Tai chimpanzee hair. No significant difference was found between adult male and female chimpanzees in their $\delta^{13}\text{C}_{\text{keratin}}$ values ($t_{29} = 1.231$; $P = 0.228$), but a significant difference in $\delta^{15}\text{N}_{\text{keratin}}$ ($t_{29} = 0.474$; $P = 0.001$) values was found, with males having significantly higher $\delta^{15}\text{N}_{\text{keratin}}$ compared with females. Plotted data are mean \pm SD of sectioned hair, representing a bulk hair keratin value of approximately 6 mo for each individual.

Included in the environmental sample analysis were samples of predominant flora and fauna in the diet of the Tai chimpanzees; namely, certain fruits and seasonal supplements of nuts, ants, and termites, along with both species of colobus monkey (Table S3). Fig. 1 plots male and female chimpanzee bone collagen and hair keratin isotope values in their environmental context. When adjusted for tissue type ($\delta^{13}\text{C}_{\text{keratin}}$ values were adjusted by $+2\%$ (15) for comparability with $\delta^{13}\text{C}_{\text{coll}}$ values), average chimpanzee $\delta^{13}\text{C}$ values ($-22.9 \pm 0.5\%$) reflect their regular consumption of fruit and are similar to those reported for the Ganta chimpanzee collection from neighboring Liberia (23). However, both males and females had $\delta^{15}\text{N}$ values higher than 7% , which indicates a level of dietary protein higher than could be obtained from fruit alone, suggests some level of insectivory or carnivory (17, 18, 23, 24).

Hair strands averaging 6 cm were used in this study, providing bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data representative of a 6-mo period before hair collection (Fig. 2). The $\delta^{13}\text{C}$ values indicated, in agreement with the environmental sampling, that the diets were predominantly C_3 -based. No significant difference was found between adult male ($-24.7 \pm 0.5\%$) and adult female ($-25.0 \pm 0.7\%$) chimpanzees in their $\delta^{13}\text{C}_{\text{keratin}}$ values, but a significant difference in $\delta^{15}\text{N}_{\text{keratin}}$ values was found. Although both sexes had $\delta^{15}\text{N}_{\text{keratin}}$ values above 7% , adult male chimpanzees ($7.8 \pm 0.5\%$) had significantly higher $\delta^{15}\text{N}_{\text{keratin}}$ values compared with adult females ($7.0 \pm 0.5\%$) (Fig. 2).

To identify whether this sex difference was also a long-term occurrence, bone collagen from adult and juvenile (not plotted) chimpanzee ribs and long bones was analyzed (Fig. 3). Similar to hair keratin, no significant difference was found between adult male ($-23.0 \pm 0.3\%$), adult female ($-23.2 \pm 0.3\%$), and juvenile ($-23.3 \pm 0.6\%$) chimpanzees in their average $\delta^{13}\text{C}_{\text{coll}}$ values in either rib or long-bone bone collagen (Table S4). Average $\delta^{15}\text{N}_{\text{coll}}$ values of the adult females (ribs, $7.7 \pm 0.4\%$; femora, $7.7 \pm 0.3\%$) and juveniles (ribs, $7.9 \pm 0.3\%$; femora, $7.7 \pm 0.3\%$) indicate that their main protein sources were fruit and nuts. In contrast, a number of adult males (ribs, $8.4 \pm 0.4\%$;

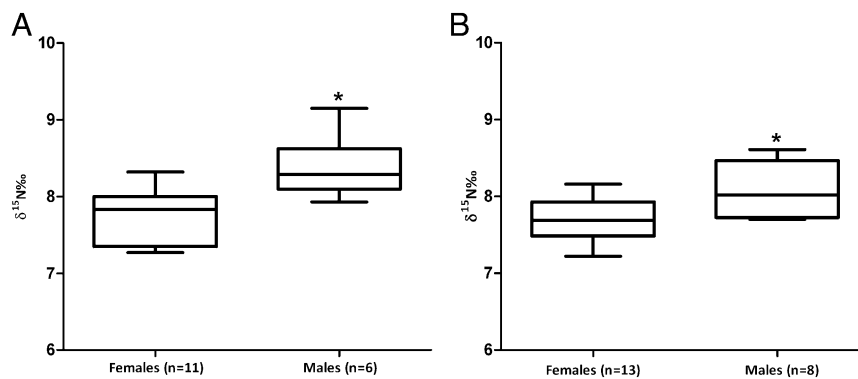


Fig. 3. $\delta^{15}\text{N}$ values for chimpanzee rib (A) and femora (B). Adult male chimpanzees have significantly higher rib ($t_{19} = -3.553$; $P = 0.002$) and femora ($t_{22} = -2.856$; $P = 0.009$) $\delta^{15}\text{N}_{\text{coll}}$ values compared with those of adult females.

femora, $8.1 \pm 0.4\text{‰}$) were significantly more enriched in $\delta^{15}\text{N}_{\text{coll}}$ in both ribs and long-bones compared with adult females and juveniles, further validating our hypothesis that they consume another trophic level source of protein in addition to their daily fruit and seasonal nut consumption (Fig. 3 and Table S4).

Combining the hair keratin and bone collagen data for the adult males ($8.1 \pm 0.6\text{‰}$) and adult females ($7.4 \pm 0.6\text{‰}$), adult male chimpanzee $\delta^{15}\text{N}_{\text{coll}}$ values average 0.8‰ higher than those of adult females. As all of the chimpanzees consume fruit daily, and seasonal nuts and termites are consumed by all chimpanzees, with females and juveniles consuming more nuts than males (8), these cannot be the source of the enriched male $\delta^{15}\text{N}_{\text{coll}}$ values. Therefore, the only difference between the diet of adult males and adult females and juveniles, and consequently the most likely contributor to the increased $\delta^{15}\text{N}_{\text{coll}}$ values of the adult males, is the regular consumption of colobus monkey flesh. When looking at the $\delta^{15}\text{N}_{\text{keratin}}$ values alone, it may appear that the difference between adult males and females is a reflection of a few adult males with high $\delta^{15}\text{N}_{\text{keratin}}$ values; however, given the different turnover rates between keratin and collagen, the fact that a significant sex difference is also seen on a long-term basis in bone collagen confirms sex differences in protein-associated $\delta^{15}\text{N}$

values in these chimpanzees that is not merely a reflection of the inclusion of some unique individuals.

It was possible to further investigate these unique individuals with extremely high $\delta^{15}\text{N}_{\text{keratin}}$ values, using observational data on hunting prowess among the Taï chimpanzees that were available for 7 adult males with corresponding hair keratin isotope data (Fig. 4). No effect of male dominance rank was found, but individuals described as being some of the most gifted hunters ($8.4 \pm 0.2\text{‰}$) at Taï (based on observational data detailed in ref. 8) were enriched in $\delta^{15}\text{N}_{\text{keratin}}$ by more than 1.0‰ compared with their less-successful counterparts ($7.3 \pm 0.3\text{‰}$) (Fig. 4).

When combined with observational data (8), the individual differences in $\delta^{15}\text{N}_{\text{keratin}}$ values can be clearly explained: Brutus ($8.6 \pm 0.3\text{‰}$), the oldest male analyzed, was an extremely successful hunter and the best meat provider in his community, and even as his rank fell with age, he continued to dominate meat-eating episodes. In addition, he had a close relationship with Macho ($8.6 \pm 0.5\text{‰}$), a successful alpha male and an extremely good hunter. Ulysse ($8.2 \pm 0.3\text{‰}$) was also a very gifted hunter, and as a result had frequent access to meat. At the other end of the scale are the less-successful hunters: Rousseau ($7.7 \pm 0.3\text{‰}$), Darwin ($7.4 \pm 0.1\text{‰}$), and even Kendo ($7.1 \pm 0.5\text{‰}$), who was alpha male at the time his hair sample was collected, are all

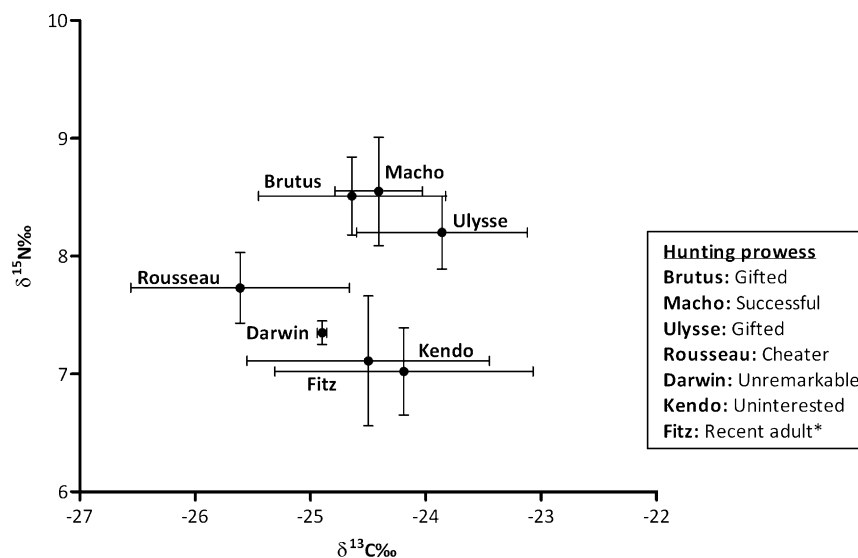


Fig. 4. Isotopic meat levels according to North Group adult male hunting prowess. Irrespective of rank, a significant difference was found in $\delta^{15}\text{N}_{\text{keratin}}$ values, with chimpanzees known to be gifted and successful hunters being $\sim 1.0\text{‰}$ higher in $\delta^{15}\text{N}_{\text{keratin}}$ compared with those observed as being uninterested or unremarkable hunters and adult females ($7.5 \pm 0.3\text{‰}$; not plotted).

noted as being uninterested or unsuccessful hunters who sometimes received meat through cheating or begging but who did not consume as much meat as those who actively participated in the hunt (8). Interestingly, Fitz ($7.0 \pm 0.4\text{‰}$), who was subsequently a successful alpha and a gifted hunter, has a relatively low $\delta^{15}\text{N}_{\text{keratin}}$ value compared with the other hunters. This can be attributed to the fact that at the time of sample collection, Fitz had just turned 15 y old and was a recently adult male.

Discussion

Our results represent unique stable isotope data on the wild chimpanzees of Taï National Park, Côte d'Ivoire, for which corresponding behavioral data are also available. Previous research on unsexed (16, 24) and sexed (23) chimpanzees, habituated sexed bonobos (12), and other primate species (17, 18) indicated that significant sex differences in adult $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are unlikely. We found no significant sex differences in $\delta^{13}\text{C}$ in the Taï chimpanzees; however, our $\delta^{15}\text{N}$ values support behavioral observations of significant meat eating among some adult males at Taï compared with adult females and juveniles. This sex difference is reflected on a short- and long-term basis and suggests that humans are not the only primate for which meat is an important dietary staple. The indication that, for adult males at Taï, meat is a frequently sought-after protein resource and not merely, as previously suggested (3), an infrequent luxury item in the chimpanzee dietary repertoire poses some questions as to why meat eating appears to be important for some and less important for others.

Given that animal protein is rich in important nutrients, it has long been suggested that its consumption helped sustain the evolution of large human brains (25). With this caveat, the fact that vertebrate protein consumption is so important in adult male Taï chimpanzees suggests some advantages, such as the development of collaborative abilities that were proposed to be important in territorial and predator defense in both human and chimpanzee societies (26, 27). Sharing etiquette is often seen as the distinguishing factor between human and chimpanzee hunting (7), and one of the main differences between species and populations occurs in the nature of food distribution after capture. Our isotopic data provide independent support for long-term observations of the unique hunting strategy used by the Taï chimpanzees (2, 5).

To enable stable cooperation, the benefit to the hunter must exceed that of cheaters (2). To this end, the Taï chimpanzees have developed elaborate meat-sharing rules in which the role an individual plays in prey-capture is highly correlated with the amount of meat that individual consumes. Behavioral (2) and isotopic evidence demonstrates that Taï chimpanzee hunters obtain, and consume, significantly more meat than bystanders or latecomers. Further, although adult females are present at almost all hunting sites (8), these meat-sharing rules mean that they have limited access to large amounts of meat. This male sex bias in meat consumption seen in Taï chimpanzees distinguishes itself from meat eating in most human hunter-gatherer societies, where females receive large amounts of meat as well as spoils (10, 28).

Many researchers have reported that chimpanzee parties experience increased hunting success when particular individuals are present (1, 8, 9); the term "impact hunters" was coined by Gilby et al. (29), describing specialized male hunters at Kanyawara, Kibale National Park, Uganda, who often initiate hunts and in whose absence hunts rarely occur. Similarly, at Taï, such gifted individuals have been recognized (8), and a clear separation in $\delta^{15}\text{N}_{\text{keratin}}$ values is evident between male chimpanzees with known hunting skills and those noted as being not especially gifted (Fig. 4), as well as adult females. High rank is not necessarily a prerequisite for hunting ability (29); a variety of nonspecific special qualities or characteristics also may result in an individual chimpanzee being an impact hunter (29). The three gifted hunters

at Taï stood out as being self-confident (Brutus), keen (Macho), and intelligent (Ulysse) (8).

Aside from the nutritional benefits of increased meat consumption (high energy source, nutritionally rich in vitamins and minerals) (8), there are some potential benefits of being a good hunter in both hunter-gatherer societies and nonhuman primate societies. Among hunter-gatherers, reputations men earn from their hunting abilities are beneficial in terms of their social standing with other men and access to younger, more fertile, and harder-working wives (10). At Taï, observational evidence suggests some females are more successful at obtaining prey because of their affiliative behavior with hunter males; the major role of these females is to enforce the social rules favoring hunters (2), and therefore, gaining meat becomes a common interest for these females and the hunter males. Gomes and Boesch (30) also found that female chimpanzees at Taï copulated more frequently with males who shared meat with them in the long-term. In addition, Mitani and Watts (3) suggested that the risk-taking demonstrated during a hunt enables males to assess each other's reliability; correspondingly, hunting likely played a role in the development of collaborative abilities, which are important in strategic territorial and predator defense in both chimpanzees and humans (8).

Conclusion

Our results support behavioral observations of high levels of meat eating among male chimpanzees at Taï and further support the observation that division of resultant prey rewards participation in the hunt, rather than nepotism. The confirmation of short- and long-term sex differences in $\delta^{15}\text{N}$ attributed to the contribution of meat consumption to metabolism highlights the potential to investigate male and female dietary differences on a short- and long-term basis in other populations. Further, these differences strongly suggest that sex differences in food acquisition and consumption may have persisted throughout hominin evolution, rather than being a recent development in the human lineage. Isotopic studies of chimpanzees at other sites, particularly those that vary in hunting frequency and those using different hunting strategies, along with detailed isotopic studies of hunter-gatherer populations, would further enhance our knowledge of the effect of different hunting strategies and meat-sharing habits and enable a more complete interpretation of the hominin isotopic record.

Materials and Methods

Study Site. The Taï Chimpanzee Project was established in 1979 (8). Collection of behavioral data have been ongoing since the start of the Taï Chimpanzee Project. Data collection in the field was in compliance with the requirements and guidelines of the Ministère de l'Enseignement Supérieure et de la Recherche Scientifique and adhered to the legal requirements of the Côte d'Ivoire.

Samples Analyzed. A range of floral and faunal samples was collected to construct the isotopic baseline of the Taï National Park (Tables S1 and S2). For details on environmental samples analysis, refer to *SI Materials and Methods*. Forty hair samples from 11 identified adult males and 64 hair samples from 20 identified adult females were analyzed (Table S5). Hair samples with an average length of 6 cm were used in this study, providing a bulk isotope signal for at least 6 mo before hair collection. Bone collagen from 21 chimpanzee ribs and 28 chimpanzee long bones was analyzed; samples also included six juvenile chimpanzees as well as adult male and female chimpanzees (Table S4). Only femoral cortical bone was sampled to avoid unnecessary destruction of the internal structure of the bones. Rib structure meant that the bone sample included a mixture of compact and cancellous bone. Details of laboratory analysis can be found in *SI Materials and Methods*. For stable carbon and nitrogen isotope analysis, duplicate 0.5 mg of the resulting dried collagen was weighed into tin capsules. Isotopic measurements were done using a Flash EA 2112 coupled to a DeltaXP mass spectrometer (Thermo-Finnigan) at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. The analytical precision, calculated from repeated analysis of internal and international standards, was better than 0.2‰ (1 σ) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Behavioral Observations. Collection of behavioral data has been ongoing since the start of the Taï Chimpanzee Project; data relevant to the determination of the level of meat eating, including age, dominance rank, hunting prowess, and cooperation and alliances, were extrapolated from these observations. A linear dominance hierarchy for the adult males at Taï for the period covering sample collection was determined by Boesch and Boesch-Achermann (8).

ACKNOWLEDGMENTS. We thank T. Deschner, A. Kalan, and the field assistants at Taï National Park for collection of environmental samples.

We also thank A. Rainer, S. Steinbrenner, and M. Mannino for their laboratory assistance and L. Luncz, S. Metzger, L. Wittiger, A. Kalan, and N. Eckhardt for invaluable comments and observations on the Taï chimpanzees. We thank L. Polansky for helpful advice on data analysis and S. Schnorr and R. C. F. Power for helpful comments on hunter-gatherer diets. We thank the authorities in Côte d'Ivoire, especially the Ministry of the Environment and Forests and the Ministry of Research, for allowing fieldwork in Taï National Park and for permitting the export of skeletal remains and environmental samples. This research was funded by the Max Planck Society.

- Goodall J (1986) *The Chimpanzees of Gombe: Patterns of Behavior* (The Belknap Press of Harvard Univ Press, Cambridge, MA).
- Boesch C (1994) Cooperative hunting in wild chimpanzees. *Anim Behav* 48(3):653–667.
- Mitani JC, Watts DP (2001) Why do chimpanzees hunt and share meat? *Anim Behav* 61:915–924.
- Pruetz J (2006) *The Feeding Ecology of Great Apes and other Primates*, eds Boesch C, Hohmann G, Robbins M (Cambridge Univ Press, Cambridge, UK).
- Boesch C, Boesch H (1989) Hunting behavior of wild chimpanzees in the Taï National Park. *Am J Phys Anthropol* 78(4):547–573.
- Pruetz JD, Bertolani P (2007) Savanna chimpanzees, *Pan troglodytes verus*, hunt with tools. *Curr Biol* 17(5):412–417.
- Isaac GL (1978) The food-sharing behavior of protohuman hominids. *Sci Am* 238(4):90–108.
- Boesch C, Boesch-Achermann H (2000) *The Chimpanzees of the Taï Forest: Behavioural Ecology and Evolution* (Oxford Univ Press, Oxford, UK).
- Stanford C (1998) *Chimpanzee and red colobus* (Harvard Univ Press, Cambridge, MA).
- Hawkes K (2001) *Meat-Eating and Human Evolution*, eds Stanford CB, Bunn HT (Oxford Univ Press, Oxford, UK), p 225.
- Newton-Fisher NE (2007) Chimpanzee hunting behavior. *Handbook of Paleoanthropology*, eds Henke W, Tattersall I (Springer-Verlag, New York), pp 1295–1320.
- Oelze VM, et al. (2011) Does animal protein contribute to the diet of wild bonobo (*Pan paniscus*)? Evidence from stable isotope analysis. *Proc Natl Acad Sci USA* 108(24):9792–9797.
- Schwarz H, Schoeninger M (1991) Stable isotope analyses in human nutritional ecology. *Yearb Phys Anthropol* 34:283–321.
- Vogel J (1978) Isotopic assessment of the dietary habits of ungulates. *S Afr J Sci* 74:298–301.
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351.
- Sponheimer M, et al. (2006) Do “savanna” chimpanzees consume C4 resources? *J Hum Evol* 51(2):128–133.
- Schoeninger MJ, Iwaniec UT, Glander KE (1997) Stable isotope ratios indicate diet and habitat use in New World monkeys. *Am J Phys Anthropol* 103(1):69–83.
- Schoeninger MJ, Iwaniec UT, Nash LT (1998) Ecological attributes recorded in stable isotope ratios of arboreal prosimian hair. *Oecologia* 113:222–230.
- Hedges REM, Clement JG, Thomas CDL, O’connell TC (2007) Collagen turnover in the adult femoral mid-shaft: Modeled from anthropogenic radiocarbon tracer measurements. *Am J Phys Anthropol* 133(2):808–816.
- Tobin DJ (2005) The biogenesis and growth of hair. *Hair in toxicology. An important bio monitor*, ed Tobin DJ (The Royal Society of Chemistry, Cambridge, UK).
- Rosen SI (1974) Identification of primate hair. *J Forensic Sci* 19(1):109–112.
- Mulhern DM, Ubelaker DH (2003) Histologic examination of bone development in juvenile chimpanzees. *Am J Phys Anthropol* 122(2):127–133.
- Smith CC, Morgan ME, Pilbeam D (2010) Isotopic ecology and dietary profiles of Liberian chimpanzees. *J Hum Evol* 58(1):43–55.
- Schoeninger MJ, Moore J, Sept JM (1999) Subsistence strategies of two “savanna” chimpanzee populations: The stable isotope evidence. *Am J Primatol* 49(4):297–314.
- Aiello LC, Wheeler P (1995) The expensive tissue hypothesis: The brain and the digestive system in human and primate evolution. *Curr Anthropol* 36(2):199–221.
- Boesch C (2009) *The Real Chimpanzee: Sex Strategies in the Forest* (Cambridge Univ Press, Cambridge, UK), pp 40–41.
- Foley RA (2001) The Evolutionary Consequences of Increased Carnivory in Hominids. *Meat-Eating and Human Evolution*, eds Stanford CB, Bunn HT (Oxford Univ Press, Oxford, UK), pp 305–331.
- Hill K (1982) Hunting and human evolution. *J Hum Evol* 11:521–544.
- Gilby IC, Eberly LE, Wrangham RW (2008) Economic profitability of social predation among wild chimpanzees: Individual variation promotes cooperation. *Anim Behav* 75:351–360.
- Gomes CM, Boesch C (2009) Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS ONE* 4(4):e5116.