

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

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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

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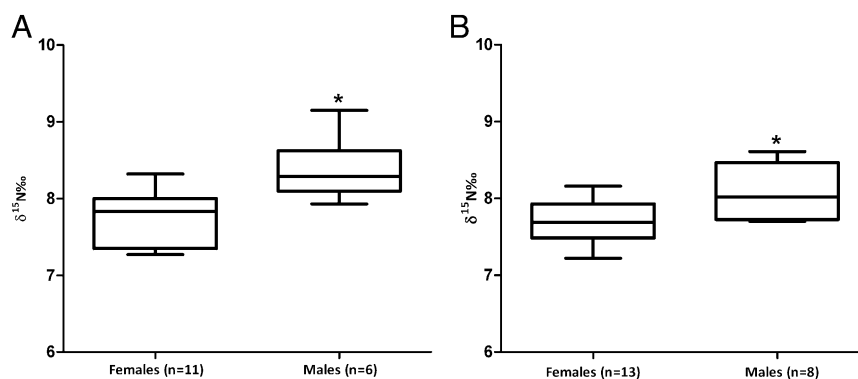


Fig. 3. $\delta^{15}\text{N}$ values for chimpanzee rib (A) and femora (B). Adult male chimpanzees have significantly higher rib ($t_{19} = -3.553$; $P = 0.002$) and femora ($t_{22} = -2.856$; $P = 0.009$) $\delta^{15}\text{N}_{\text{coll}}$ values compared with those of adult females.

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

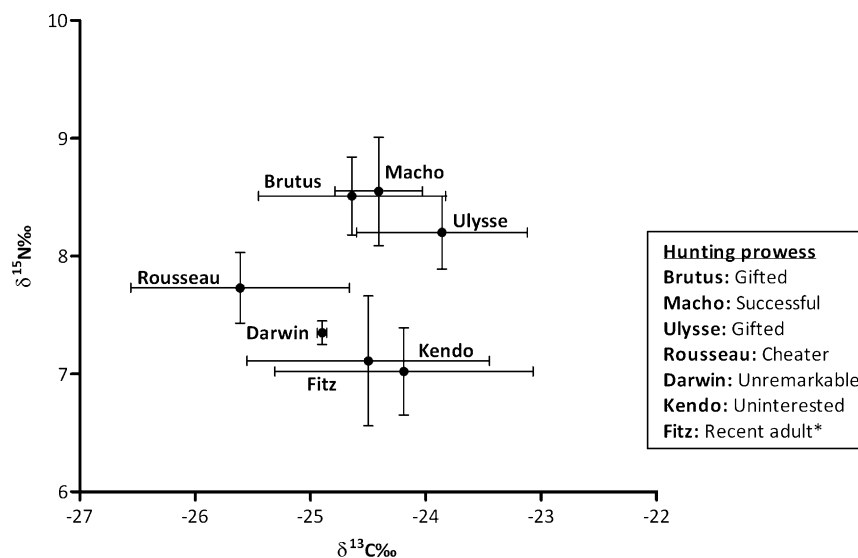


Fig. 4. Isotopic meat levels according to North Group adult male hunting prowess. Irrespective of rank, a significant difference was found in $\delta^{15}\text{N}_{\text{keratin}}$ values, with chimpanzees known to be gifted and successful hunters being $\sim 1.0\text{‰}$ higher in $\delta^{15}\text{N}_{\text{keratin}}$ 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-Finnegan) 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).

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Supporting Information

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SI Materials and Methods

Materials. The Taï National Park, Côte d'Ivoire lies ~100km from the Liberian border. Sample collection for this study encompassed a span of 22 y. Hair samples were collected noninvasively from fresh chimpanzee night nests; information on the identity of the nest owner came from observations made the previous evening. All skeletal material is housed at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany.

Sample Analysis. Plant samples were freeze-dried, homogenized, and weighed into tin capsules (≥ 2.0 mg). All faunal (except bone) samples were purified before isotopic analysis by rotation in a mixture of chloroform-methanol (2:1, vol/vol) for 24 h (1) and then transferred to an evaporator overnight at 40°C. Hair samples were weighed using a microbalance (≥ 0.4 mg) and

transferred to tin capsules for isotopic measurement. In one case, no femur was available for sampling and a sample from the distal end of the anterior surface of the left humeral shaft was sampled. Before sampling, the surface of the bones was cleaned by air abrasion with Al_2O_3 ; ~100–300 mg, depending on the nature of the bone (bones that had been buried in the forest before their removal to Germany had undergone some obvious demineralization, and therefore less bone was needed to obtain the necessary amount of collagen for isotope analysis), of bone was collected. Collagen extraction was done following refs. 2–4.

Data Analysis. Means and SDs were calculated in Excel (Microsoft). Where the data displayed homogeneity and normality, independent sample *t*-tests were run using SPSS (v.20).

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Table S1. Baseline flora samples

Scientific classification	Family	Sample	$\delta^{13}\text{C}\text{‰}$	$\delta^{15}\text{N}\text{‰}$	%C	%N	C:N
<i>Berlinia grandiflora</i>	Caesalpiniaceae	Flowers	-26.9	5.7	50.16	1.51	38.80
<i>Pentaclethra macrophylla</i>	Fabaceae	Flowers	-28.1	2.6	53.01	3.44	17.98
<i>Pentadesma butyracea</i>	Clusiaceae	Flowers	-27.3	6.2	53.75	1.11	56.38
<i>Halopegia</i>	Marantaceae	Flowers	-33.1	5.4	41.60	1.01	47.92
<i>Sacoglottis gabonensis</i>	Humiridaceae	Fruit	-27.5	1.4	47.12	0.33	164.77
<i>Ficus elegance</i>	Moraceae	Fruit	-30.3	2.9	53.29	1.88	33.00
<i>Cola nitida</i>	Sterculiaceae	Fruit	-28.8	2.9	45.71	1.24	43.01
<i>Chrysophyllum taiense</i>	Sapotaceae	Fruit Juice	-28.5	5.7	48.50	1.63	34.70
<i>Haloplegia</i>	Marantaceae	Fruit pith	-37.2	5.6	37.84	2.55	17.30
<i>Haloplegia</i>	Marantaceae	Fruit pith	-39.4	7.7	46.15	4.20	12.82
<i>Eremospatha macrocarpa</i>	Arecaceae	Fruit pith	-38.2	5.0	43.82	2.49	20.52
<i>Hypselodelphis violacea</i>	Marantaceae	Fruit pith	-30.3	7.4	39.96	1.59	29.32
<i>Hypselodelphis violacea</i>	Marantaceae	Fruit pith	-31.2	7.1	45.15	4.59	11.48
<i>Mammea africana</i>	Guttiferae	Fruit pulp	-26.8	3.5	48.92	1.07	53.56
<i>Chrysophyllum taiense</i>	Sapotaceae	Fruit pulp	-28.2	6.0	53.86	2.15	29.26
<i>Dialium aubrevillei</i>	Caesalpiniaceae	Fruit pulp	-25.4	5.4	39.13	1.32	34.69
<i>Diospyros mannii</i>	Ebenaceae	Fruit pulp	-31.5	5.0	39.61	0.73	63.08
<i>Mammea africana</i>	Guttiferae	Fruit pulp	-26.7	4.1	43.67	0.83	61.64
<i>Nauclea diderichii</i>	Rubiaceae	Fruit pulp	-28.9	4.5	46.72	0.58	93.86
<i>Sacoglottis gabonensis</i>	Humiriaceae	Fruit pulp	-27.5	4.2	50.90	0.58	102.68
<i>Treculia africana</i>	Moraceae	Fruit pulp	-26.1	4.3	47.19	1.85	29.73
<i>Chrysophyllum taiense</i>	Sapotaceae	Fruit pulp	-27.6	5.0	51.73	1.79	33.73
<i>Dialium aubrevillei</i>	Caesalpiniaceae	Fruit pulp	-27.5	5.3	42.16	1.08	45.40
<i>Diospyros mannii</i>	Ebenaceae	Fruit pulp	-32.7	5.8	35.73	0.31	133.48
<i>Parinari excelsea</i>	Chrysobalanaceae	Fruit pulp	-29.6	6.0	44.99	0.33	158.40
<i>Uapaca esculenta</i>	Euphorbiaceae	Fruit pulp	-29.7	4.0	39.16	0.20	233.90
<i>Dacryodes klaineana</i>	Burseraceae	Fruit pulp	-29.7	5.6	41.18	0.78	61.23
<i>Klainedoxa gabonensis</i>	Irvingiaceae	Fruit pulp	-28.0	5.1	48.26	0.54	103.40
<i>Chrysophyllum taiense</i>	Sapotaceae	Fruit pulp	-27.4	6.0	61.99	1.80	40.15
<i>Dialium aubrevillei</i>	Caesalpiniaceae	Fruit pulp	-26.5	5.2	40.87	0.64	74.12
<i>Ficus vogelii</i>	Moraceae	Fruit pulp	-28.5	4.6	50.10	0.69	84.88
<i>Hiterla buteii</i>	UID	Fruit pulp	-28.3	5.7	45.67	0.50	105.85
<i>Irvingia grandifolia</i>	Irvingiaceae	Fruit pulp	-29.4	5.7	45.98	0.61	87.67
<i>Landolphia dulcis</i>	Apocynaceae	Fruit pulp	-28.2	1.7	47.89	0.77	72.48
<i>Nauclea diderichii</i>	Rubiaceae	Fruit pulp	-26.2	5.2	46.08	0.51	106.18
<i>Nauclea xantophylon</i>	Rubiaceae	Fruit pulp	-27.3	6.7	46.63	0.25	215.18
<i>Parinari excelsea</i>	Chrysobalanaceae	Fruit pulp	-29.7	5.5	48.92	0.50	113.66
<i>Sacoglottis gabonensis</i>	Humiriaceae	Fruit pulp	-27.8	2.5	50.48	0.39	152.56
<i>Strychnos aculeata</i>	Loganiaceae	Fruit pulp	-28.8	7.1	42.38	0.89	55.40
<i>Treculia africana</i>	Moraceae	Fruit pulp	-28.8	3.1	52.01	0.93	65.06
<i>Uapaca esculenta</i>	Euphorbiaceae	Fruit pulp	-27.3	3.6	39.31	0.22	205.35
<i>Chrysophyllum taiense</i>	Sapotaceae	Leaves	-30.9	5.7	57.22	2.56	26.06
<i>Dialium aubrevillei</i>	Caesalpiniaceae	Leaves	-32.1	7.1	48.04	2.33	24.06
<i>Dichapetalum Heudeloti</i>	Dichapetalaceae	Leaves	-37.7	7.9	50.87	3.14	18.87
<i>Diospyros mannii</i>	Ebenaceae	Leaves	-34.6	6.2	55.63	2.07	31.38
<i>Parinari excelsea</i>	Chrysobalanaceae	Leaves	-29.3	5.4	50.38	1.37	42.99
<i>Xylia evansii</i>	Mimosaceae	Leaves	-32.0	4.0	52.88	2.38	25.96
<i>Coula edulis</i>	Olacaceae	Leaves	-34.8	6.1	52.64	2.04	30.06
<i>Chrysophyllum taiense</i>	Sapotaceae	Leaves	-30.1	4.4	55.00	1.95	32.83
<i>Diospyros mannii</i>	Ebenaceae	Leaves	-33.0	4.4	52.92	1.49	41.52
<i>Sacoglottis gabonensis</i>	Humiriaceae	Leaves	-37.3	2.3	52.24	1.33	45.84
<i>Dialium aubrevillei</i>	Caesalpiniaceae	Leaves	-37.2	1.7	45.41	1.67	31.78
<i>Tarrietia utilis</i>	Sterculiaceae	Leaves	-35.3	2.8	52.06	1.47	41.37
<i>Diospyros mannii</i>	Ebenaceae	Leaves	-37.5	3.0	54.47	2.47	25.78
<i>Diospyros manaii</i>	Ebenaceae	Leaves	-37.4	3.3	53.03	1.89	32.68
<i>Calpocalyx aubrevillei</i>	Mimosaceae	Leaves	-30.0	4.8	51.82	3.01	20.05
<i>Calpocalyx brevibracteatus</i>	Mimosaceae	Leaves	-27.9	3.1	59.89	2.72	25.65
<i>Chrysophyllum taiense</i>	Sapotaceae	Leaves	-29.4	4.7	56.87	2.14	31.01
<i>Cola heterophylla</i>	Sterculiaceae	Leaves	-38.2	3.8	48.23	2.51	22.46
<i>Dialium aubrevillei</i>	Caesalpiniaceae	Leaves	-28.7	6.0	52.48	1.46	41.99
<i>Dichapetalum Heudeloti</i>	Dichapetalaceae	Leaves	-35.5	6.1	50.36	3.45	17.02
<i>Ficus barteri</i>	Moraceae	Leaves	-36.1	0.2	45.62	2.04	26.08
<i>Glyphea brevis</i>	Tiliaceae	Leaves	-34.3	5.2	46.68	3.20	17.02

Table S1. Cont.

Scientific classification	Family	Sample	$\delta^{13}\text{C}\text{‰}$	$\delta^{15}\text{N}\text{‰}$	%C	%N	C:N
<i>Panda oleosa</i>	Pandaceae	Leaves	-36.9	3.1	52.11	2.92	20.82
<i>Strychnos aculeata</i>	Loganiaceae	Leaves	-30.0	5.2	44.02	1.38	37.13
<i>Treulia africana</i>	Moraceae	Leaves	-30.2	3.9	52.21	1.12	54.41
<i>Desplatsia chrysochlamys</i>	Tiliaceae	Leaves	-32.0	5.5	53.16	1.18	52.47
<i>Coula edulis</i>	Olacaceae	Leaves	-28.2	2.6	53.72	1.44	43.48
<i>Desplatsia chrysochlamys</i>	Tiliaceae	Leaves	-31.9	3.6	43.33	3.10	16.32
<i>Pouteria aningeri</i>	Sapotaceae	Leaves	-35.1	3.5	49.00	2.24	25.50
Unknown tree	UID	Leaves	-33.2	6.6	44.92	1.51	34.80
<i>Haloplegia</i>	Marantaceae	Leaves	-39.4	8.2	42.73	2.08	23.99
Herb II	UID	Leaves	-38.1	6.7	47.52	1.61	34.48
Herb I	UID	Leaves	-37.6	3.2	44.35	1.74	29.67
<i>Eremospata macrocarpa</i>	Arecaceae	Leaves	-37.9	3.2	44.88	3.97	13.19
<i>Uapaca esculenta</i>	Euphorbiaceae	Leaves	-35.5	3.6	45.87	1.40	38.22
Unknown leaves	UID	Leaves	-37.1	4.3	52.68	2.88	21.32
Unknown leaves	UID	Leaves	-35.4	3.8	50.28	2.49	23.51
Unknown leaves	UID	Leaves	-36.2	4.0	44.82	2.64	19.79
<i>Auricularia auricula-judae</i>	Auriculariaceae	Mushrooms	-24.6	5.7	44.54	2.91	17.89
<i>Agaricus bisporus</i>	Agaricaceae	Mushrooms	-25.9	9.2	44.69	5.58	9.34
<i>Auricularia auricula-judae</i>	Auriculariaceae	Mushrooms	-24.4	3.9	40.97	4.93	9.70
<i>Auricularia auricula-judae</i>	Auriculariaceae	Mushrooms	-24.4	3.9	37.90	4.74	9.33
<i>Auricularia auricula-judae</i>	Auriculariaceae	Mushrooms	-26.0	4.5	42.62	2.72	18.28
<i>Coula edulis</i>	Olacaceae	Nut shell	-28.6	5.9	53.38	0.34	183.86
<i>Coula edulis</i>	Olacaceae	Nuts	-30.4	6.5	53.73	1.70	36.87
<i>Panda oleosa</i>	Pandaceae	Nuts	-32.7	4.8	67.28	4.10	19.14
<i>Panda oleosa</i>	Pandaceae	Nuts	-32.8	8.1	69.38	4.54	17.83
<i>Parinari excelsea</i>	Chrysobalanaceae	Nuts	-29.0	6.3	44.08	0.54	95.22
<i>Xylocarpus evansii</i>	Mimosaceae	Seeds	-27.4	6.2	50.18	5.20	11.25
<i>Irvingia gabonensis</i>	Irvingiaceae	Seeds	-29.1	3.7	62.41	1.27	57.39
<i>Calpocalyx aubrevillei</i>	Mimosaceae	Seeds	-26.3	7.9	41.69	6.79	7.17
<i>Gilbertiodendron spelndidum</i>	Caesalpiniaceae	Seeds	-26.5	5.1	45.86	0.84	63.92
<i>Xylocarpus evansii</i>	Mimosaceae	Seeds	-28.6	7.8	45.89	3.67	14.60
<i>Calpocalyx aubrevillei</i>	Mimosaceae	Seeds	-27.2	5.4	48.25	5.85	9.62
<i>Calpocalyx brevibracteatus</i>	Mimosaceae	Seeds	-25.4	2.1	48.28	7.04	8.00
<i>Cola heterophylla</i>	Sterculiaceae	Seeds	-34.5	5.8	47.27	1.92	28.69
<i>Strychnos aculeata</i>	Loganiaceae	Seeds	-28.3	6.6	42.69	1.82	27.31
UID	UID	Tree bark	-28.3	1.2	50.08	0.61	96.47

A range of flora samples ($n = 99$) was analyzed to establish the baseline isotopic ecology of the Tai National Park. UID, unidentified.

Table S2. Baseline fauna samples

Common name	Scientific name	Diet	Type	Sample	$\delta^{13}\text{C}\text{‰}$	$\delta^{15}\text{N}\text{‰}$	%C	%N	C:N
Tree ants	<i>Pseudomyrmecinae</i> (subfamily)	H	Insect	Multiple insects	-26.3	6.4	51.74	10.55	5.72
Black driver ants	<i>Dorylus nigricans</i>	C	Insect	Multiple insects	-26.9	9.8	49.02	9.87	5.79
Red driver ants	<i>Dorylus helvulus</i>	C	Insect	Multiple insects	-27.3	10.0	49.59	12.46	4.64
True bugs	<i>Hemiptera</i> (order)	O/I	Insect	Multiple insects	-27.6	6.9	42.37	11.91	4.15
Tsetse fly	<i>Glossinidae</i> (family)	C	Insect	Whole insect	-26.3	9.9	48.57	9.76	5.81
Tsetse fly	<i>Glossinidae</i> (family)	C	Insect	Whole insect	-26.3	10.0	48.37	12.58	4.49
Antlion	<i>Myrmeleontidae</i> (family)	O/I	Insect	Segment	-26.3	9.2	30.66	6.00	5.96
Caterpillar I	<i>Lepidoptera</i> (order)	H	Insect	Segment	-35.3	5.2	50.35	10.37	5.66
Caterpillar II	<i>Lepidoptera</i> (order)	H	Insect	Segment	-30.7	8.1	48.78	9.41	6.05
Centipede	<i>Chilopoda</i> (class)	C	Insect	Segment	-25.1	5.8	24.77	3.83	7.54
Grasshopper I	<i>Caelifera</i> sp. (suborder)	H	Insect	Segment	-26.5	5.0	57.66	11.92	5.65
Grasshopper II	<i>Caelifera</i> sp. (suborder)	H	Insect	Segment	-32.7	4.5	55.67	12.12	5.36
Leopard	<i>Panthera pardus</i>	C	Other	Hair	-23.3	11.8	52.55	15.00	4.09
Prince Demidoff's Galago	<i>Galagoides demidovii</i>	I/Frg	Other	Hair	-25.2	10.2	55.10	14.59	4.41
Elephant	<i>Loxodonta african cyclotis</i>	H	Other	Bone	-26.3	8.0	41.76	14.72	3.31
Rat	<i>Muridae</i> (family)	O/I	Other	Hair	-24.1	10.0	54.65	15.19	4.20
Snake	UID	C	Other	Skin	-25.7	9.1	5.15	1.24	4.85
Western red colobus	<i>Procolobus badius</i>	Fr/Fo	Primate (adult)	Hair	-24.1	8.7	42.27	13.55	3.64
Western red colobus	<i>Procolobus badius</i>	Fr/Fo	Primate (adult)	Bone	-25.9	7.6	46.20	12.42	4.34
Western red colobus	<i>Procolobus badius</i>	Fr/Fo	Primate (baby)	Hair	-24.6	9.2	50.99	14.12	4.21
Western red colobus	<i>Procolobus badius</i>	Fr/Fo	Primate (baby)	Bone	-23.0	8.9	41.87	14.87	3.28
Western red colobus	<i>Procolobus badius</i>	Fr/Fo	Primate (baby)	Bone	-23.6	9.7	39.76	13.99	3.31
Western red colobus	<i>Procolobus badius</i>	Fr/Fo	Primate (baby)	Bone	-24.6	9.2	44.08	13.74	3.74
Western red colobus	<i>Procolobus badius</i>	Fr/Fo	Primate (baby)	Bone	-22.8	9.1	40.06	14.65	3.19
Western black & white colobus	<i>Colobus polykomos</i>	Fr/Fo	Primate (UID)	Bone	-24.3	10.5	42.30	15.20	3.25
Western Black & White colobus	<i>Colobus polykomos</i>	Fr/Fo	Primate (UID)	Bone	-23.3	9.3	41.75	14.82	3.29
Termite	<i>Cubitermes</i>	Geophagic	Termites	Multiple insects	-29.5	5.1	7.29	0.44	19.54
Termite	<i>Cubitermes</i>	Geophagic	Termites	Multiple insects	-26.0	14.7	14.81	2.45	7.06
Termite	<i>Thoracotermes</i>	Geophagic	Termites (soldiers)	Whole insect	-25.6	15.4	35.76	9.40	5.52
Termite	<i>Thoracotermes</i>	Geophagic	Termites (winged)	Whole insect	-24.7	18.8	46.86	11.54	4.74
Termite	<i>Thoracotermes</i>	Geophagic	Termites (workers)	Whole insect	-28.5	15.7	7.55	0.98	9.02
Maxwell's Duiker	<i>Philantomba maxwelli</i>	Fr/Fo	Ungulate	Bone	-22.9	11.0	41.84	15.31	3.19

A range of fauna samples ($n = 32$) was analyzed to establish the baseline isotopic ecology of the Taï National Park. C, carnivore; Fo, folivore; Fr, frugivore; H, herbivore; I, insectivore; O, omnivore; UID, unidentified.

Table S3. Common chimpanzee food items

Species	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	%C	%N	C:N	Frequency
Fruits							
<i>Diospyros mannii</i>	2	-32.1	5.4	37.67	0.52	98.28	Regular diet
<i>Chrysophyllum taiense</i>	3	-27.9	5.7	54.02	1.84	34.46	
<i>Klainedoxa gabonensis</i>	1	-28.0	5.1	48.26	0.54	103.40	
Termites (<i>Thoracotermes</i> sp.)							
<i>Thoracotermes</i> (winged)	1	-24.7	18.9	19.29	4.34	7.64	Seasonal
<i>Thoracotermes</i> (workers)	3	-26.6	17.0	46.86	11.54	4.74	
Driver ants (<i>Dorylus</i> sp.)							
<i>D. gerstaeckerii</i>	1	-27.3	10.0	49.59	12.46	4.64	6-mo period
<i>D. nigricans</i>	1	-26.9	9.8	49.02	9.87	5.79	
Nuts							
<i>Coula edulis</i>	1	-30.4	6.5	53.73	1.70	36.87	3-mo period
<i>Parinari excelsa</i>	1	-29.0	6.3	44.08	0.54	95.22	
<i>Panda oleosa</i>	2	-32.6	6.5	68.33	4.32	18.49	
Colobus monkey (bone)							
<i>Procolobus badius</i>	5	-24.0	8.9	42.39	13.93	3.57	Year-round
<i>Colobus polykomos</i>	2	-23.8	9.9	42.0	15.0	3.3	

Fruit makes up the predominant daily diet of the Taï chimpanzees. They supplement this with seasonal nuts, ants, and termites throughout the year. Meat of adult and baby western red colobus monkeys, and occasionally black and white colobus monkeys, is the preferred vertebrate meat of the Taï chimpanzees. Colobine values include average bone collagen values for adults and infants.

Table S4. Isotope data for all chimpanzee bone collagen analyzed

Name	Age, y	Sample	Weight, mg	Collagen mass, mg	Collagen, %	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	%C	%N	C:N
Adult males										
Léo	19	Rib	117.90	25.80	21.90	-23.2	8.2	41.57	15.05	3.22
Léo	19	Femur	119.40	24.50	20.50	-22.8	7.7	41.79	15.00	3.25
Kendo	25	Rib	126.50	24.90	19.70	-22.9	8.3	41.09	14.80	3.24
Kendo	25	Femur	142.20	23.80	16.70	-23.0	8.5	41.92	15.22	3.21
Fitz	20	Rib	151.70	35.60	23.50	-23.0	8.5	42.16	15.25	3.23
Fitz	20	Femur	182.60	36.50	20.00	-22.8	7.8	41.36	15.03	3.21
Rafiki	20	Rib	459.00	103.60	22.57	-23.0	8.3	51.33	18.71	3.20
Rafiki	19	Femur	317.00	34.20	10.79	-23.0	8.3	40.79	14.76	3.22
Brutus	46	Metatarsal	226	46.90	20.75	-22.8	9.2	48.05	16.93	3.31
Brutus	46	Humerus	278	49.40	17.77	-22.7	9.0	46.63	16.64	3.27
Unknown1	N/A	Rib	260.00	20.80	8.00	-23.0	9.2	45.46	16.44	3.23
Unknown1	N/A	Femur	459.00	37.00	8.06	-23.4	8.2	45.00	15.66	3.35
Unknown2	N/A	Femur	310.00	28.60	9.23	-22.6	8.6	45.44	16.23	3.27
Unknown3	N/A	Femur	347.00	41.60	11.99	-23.4	7.7	45.43	16.39	3.23
Unknown4	N/A	Femur	307.00	55.80	18.18	-23.3	7.7	46.53	16.75	3.24
Unknown4	N/A	Rib	306.00	21.40	6.99	-23.1	7.9	46.18	16.69	3.23
Adult females										
Agathe	15	Femur	249.00	42.50	17.10	-22.6	7.8	40.90	14.64	3.26
Bijou	19	Rib	524.00	133.50	25.50	-22.9	7.8	42.57	15.35	3.24
Bijou	19	Femur	285.00	21.40	7.50	-23.3	7.2	43.27	15.52	3.25
Bijou	19	Metatarsal	461.00	104.20	22.60	-23.1	6.9	43.73	15.84	3.22
Fanny	25	Rib	109.00	22.60	20.70	-23.1	8.0	41.54	14.98	3.24
Fanny	25	Femur	131.60	24.70	18.80	-22.7	8.0	42.28	15.25	3.24
Loukoum	27	Rib	118.30	18.90	16.00	-23.4	8.0	41.82	15.22	3.21
Loukoum	27	Femur	176.10	28.60	16.20	-23.0	7.9	41.33	14.96	3.22
Venus	27	Rib	100.80	18.90	18.60	-23.3	8.3	41.41	15.12	3.20
Venus	27	Femur	129.60	12.30	9.50	-23.6	8.2	39.09	13.31	3.43
Kiri	23	Rib	251.00	39.90	15.90	-23.2	7.3	44.50	16.28	3.19
Kiri	23	Femur	318.00	70.00	22.01	-23.3	7.5	64.13	23.02	3.25
Ondine	38	Rib	204.00	22.90	11.23	-22.7	7.9	43.98	15.88	3.23
Ondine	38	Femur	257.00	41.70	16.23	-22.7	8.0	46.51	16.30	3.33
Ondine	38	Metatarsal	265.00	58.80	22.19	-22.6	7.8	45.62	15.96	3.33
Tita	25	Rib	218.00	29.10	13.35	-23.7	7.4	43.75	15.94	3.20
Tita	25	Femur	353.00	30.00	8.50	-23.6	7.5	46.42	16.29	3.33
Unknown1	N/A	Rib	200.00	35.00	17.50	-23.3	7.3	45.39	16.35	3.24
Unknown1	N/A	Femur	276.00	50.20	18.19	-23.2	7.8	45.04	16.03	3.28
Unknown2	N/A	Rib	306.00	27.00	8.82	-23.5	7.4	46.31	16.45	3.29
Unknown2	N/A	Femur	305.00	45.00	14.75	-23.4	7.6	45.98	16.26	3.30
Unknown3	N/A	Rib	294.00	38.70	13.16	-23.7	7.6	43.91	15.50	3.30
Unknown3	N/A	Femur	280.00	55.00	19.64	-23.1	7.6	43.46	15.64	3.24
Unknown4	N/A	Rib	228.00	48.10	21.10	-23.6	8.0	43.75	15.84	3.22
Unknown4	N/A	Femur	296.00	38.80	13.11	-23.3	7.5	43.22	15.68	3.21
Juvenile males										
Max	6	Rib	277.00	78.80	28.45	-23.2	8.1	43.92	16.11	3.18
Oreste	6	Rib	255.00	67.20	26.35	-24.8	7.9	44.92	13.54	3.87
Oreste	6	Femur	312.00	59.3	19.00	-24.1	7.9	35.10	11.82	3.46
Lefkas	8	Femur	158.20	33.90	21.40	-23.3	7.4	43.40	15.27	3.32
Juvenile females										
Goshu	6	Rib	299.00	92.90	31.07	-23.1	7.4	41.74	15.20	3.20
Goshu	6	Femur	242.00	45.4	18.76	-23.0	7.4	45.11	16.16	3.26
Tina	9	Rib	199.00	22.50	11.31	-22.6	8.0	41.23	15.12	3.18
Dorry	10	Femur	253.00	64.1	25.34	-23.5	7.2	46.47	16.66	3.25

Raw data from all of the adult and juvenile Taï chimpanzees analyzed.

Table S5. Hair keratin isotopic data

Name	Age, y	$\delta^{13}\text{C}\text{‰}$	$\delta^{15}\text{N}\text{‰}$	%C	%N	C:N
Males (<i>n</i> = 11)						
Bob	19	-24.9	7.2	42.39	13.17	3.79
Joé	20	-25.1	7.6	96.48	14.61	7.69
Kendo	21	-24.5	7.1	68.37	13.96	5.53
Ulysse	24	-23.9	8.2	64.01	14.52	5.18
Darwin	21, 23	-24.9	7.4	78.03	14.13	6.32
Fitz	15	-24.2	7.0	59.50	14.82	4.73
Rousseau	26	-25.6	7.7	85.10	13.41	7.32
Brutus	39, 41	-24.6	8.5	69.68	14.65	5.58
Macho	26, 35	-24.4	8.6	44.77	14.51	3.59
Léo	19	-24.5	8.1	45.24	14.72	3.59
Urs	30	-25.0	7.9	45.35	13.95	3.80
Females (<i>n</i> = 20)						
Perla	24	-24.2	7.6	43.86	14.60	3.51
Margot	25	-25.1	7.1	65.42	13.35	5.55
Castor	22	-25.6	7.2	93.08	14.69	7.32
Venus	19	-24.3	7.7	44.98	14.76	3.56
Yucca	27	-25.3	7.2	44.19	14.15	3.66
Rubra	29	-26.3	6.5	117.69	14.29	9.44
Julia	29	-25.6	5.9	64.45	13.61	5.44
Virunga	34	-25.5	6.4	69.05	14.37	5.55
Olivia	26	-25.6	6.4	95.32	14.65	7.50
Salomé	32	-24.0	7.0	43.74	14.13	3.61
Agathe	14	-25.2	7.5	44.20	14.63	3.52
Gala	27	-24.4	7.3	43.36	14.14	3.58
Gitane	41, 42, 44	-25.0	6.9	54.75	14.26	4.46
Loukoum	18, 25	-24.5	7.0	45.16	14.27	3.70
Ricci	31	-25.2	6.6	144.09	14.39	11.64
Fossey	14	-25.5	7.1	87.70	15.03	6.66
Belle	18	-25.5	7.3	93.54	14.33	7.59
Dilly	13	-24.6	8.0	44.61	13.84	3.76
Mystere	15	-23.8	6.9	46.75	13.96	3.91
Bijou	19	-24.3	7.2	46.06	14.19	3.79

Raw isotopic data from bulk hair samples for all adult chimpanzees analyzed are included.