Subsistence Strategies of Two "Savanna" Chimpanzee Populations: The Stable Isotope Evidence

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Twenty-two chimpanzee hair samples collected from night nests at two different "savanna" sites were analyzed for carbon and nitrogen stable isotope ratios represented as $\delta^{13}C$ and $\delta^{15}N$ values. The first at Ugalla, Tanzania is a miombo woodland with grass groundcover and small patches of forest. The second at Ishasha, Democratic Republic of the Congo is a habitat composed of riverine gallery forest, semideciduous thicket forest, wooded grassland, and grassland. Based on comparative data from other primates, Ugalla hair $\delta^{13}C$ values suggest that the chimpanzees are feeding primarily in the woodland rather than in forest patches or on grassland foods (grasses or grammivorous fauna). Similar comparisons indicate that the Ishasha chimpanzees are feeding within the forests and not in more open areas. In addition, the Ugalla chimpanzees had $\delta^{15}N$ values that indicate extensive ingestion of leguminous flowers, seeds, and/or leaves. The Ishasha samples show a range encompassing three trophic levels. Two samples with the most positive values may indicate a nursing signal or vertebrate-feeding. Three individuals with intermediate values are similar to those in omnivorous nonhuman primate species. The four individuals with the lowest values are very similar to those in herbivorous monkeys. Stable isotope ratios permit time-averaged and habitat-specific dietary comparisons among sites, even without habituation or detailed foraging observations. Am. J. Primatol. 49:297–314, 1999.
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INTRODUCTION

Chimpanzees (*Pan troglodytes*) have been reported from nearly 40 sites across Africa [Wrangham et al., 1994] including closed canopy rainforests [Boesch & Boesch-Achermann, 1991] and woodlands [Goodall, 1986; Nishida & Uehara,

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1983], as well as habitats dominated by grassland [McGrew et al., 1981]. Across these sites, large variations occur in diet, social patterning and tool use [McGrew et al., 1996]. While some of this variation may be due to chance [McGrew et al., 1997], site ecology apparently plays an important role in other cases [Boesch, 1994b]. Choosing among possible explanations requires site specific knowledge of behavioral and ecological variables; yet, only 5 of the 40 chimpanzee sites have long-term data on known individuals [Goodall, 1994] and all studies of habituated individuals come from woodland or forest regions [McGrew et al., 1988]. At open "savanna" sites [sensu Moore, 1992], population densities of lower than one chimpanzee per km^2 [Collins & McGrew, 1988; Moore, 1992] provide few observations (367 sightings in 4 years at Mt. Assirik, Senegal [McGrew et al., 1988]) as the animals actively avoid observers. Multiseason field studies in such sites are extremely rare [Suzuki, 1969; McGrew et al., 1988] with general ecological data compiled through shorter-term studies of nest site and floral mapping [Nishida, 1989; Sept, 1992]. Still, we lack basic subsistence information necessary for testing hypotheses about chimpanzee behavioral ecology in open sites, and by extension, in other sites as well.

Tree fruits are considered their basic food [Wrangham, 1977; Teleki, 1981; McGrew et al., 1988], but actual intake levels are uncertain even at better studied sites because methods of diet assessment vary widely from feeding time [Isabirye-Basuta, 1989; Wrangham et al., 1992; Chapman et al., 1994] to fecal composition [Suzuki, 1969; Tutin & Fernandez, 1985; Tutin et al., 1991] to food types [Wrangham, 1977; Nishida & Uehara, 1983; Goodall, 1986; McGrew et al., 1988]. The uncertainty is compounded when preferred fruits are less available. At such times, social groups can fission and some individuals can continue feeding on fruit [Ghiglieri, 1984; Tutin et al., 1991], but diet breadth can also increase to include food requiring greater processing (e.g., hard seeds [Suzuki, 1969]) or with lower caloric concentration (e.g., stems [McGrew et al., 1988] or pith [Wrangham et al., 1991]). In open country sites, seasonal availability is expected to be more variable than in better watered forests [Moore, 1996], although it has not been possible to test this hypothesis.

Also, whereas leaves generally provide the main source of protein for large-bodied primates [Hladik & Chivers, 1994], chimpanzees use many alternatives including hard seeds [Suzuki, 1969] and insects or meat [McGrew, 1983; Boesch, 1994a; Stanford, 1996] with marked variation within and between sites [Wrangham & van Zinnicq Bergmann-Riss, 1990; Stanford, 1998; Boesch & Boesch, 1999]. As with fruit-eating, actual intake levels of these protein sources is uncertain. Meat-eating, when based on fecal evidence, may be underestimated [McGrew, 1992] due to sampling error [Boesch & Boesch, 1989] or completeness of digestion [Stanford, 1996]. At the well-studied site of Gombe, only 5.8% of feces contained mammalian remains [McGrew, 1992] even though meat is known to be an important part of the diet for some individuals [Stanford, 1996]. Similarly, no fecal incidence data are available for Tai (data in Table 7.1 in McGrew, 1992 are probably based on a misinterpretation of Boesch & Boesch, 1989), another well-studied site where meat-eating has been observed for over 10 years [Boesch & Boesch, 1999]. At open country sites, the few indirect data suggest little dependence on vertebrates and variable dependence on insects [Suzuki, 1966, 1969; McGrew, 1983; Moore, 1992] but the accuracy of this interpretation cannot be assessed.

Site composition probably affects food choice and behavior (Boesch, 1994b) even though the exact relationships are far from clear. Many chimpanzee home ranges encompass several ecological zones, which are used differentially [Suzuki,

1969; Nishida, 1989; Tutin et al., 1991; Sept, 1992; Malenky et al., 1994]. At Mt. Assirik, forest and woodland account for 40% of the chimpanzees' range but over 80% of the food species chimpanzees are known to consume [McGrew et al., 1988]. In contrast, at Kasakati in Tanzania, forest and woodland account for 70% of the total area and 95% of fecal volume [Suzuki, 1969].[1] Forest and woodland food species are overrepresented in both regions but the two regions apparently differ from one another although actual intakes are unknown in both regions.

The combination of observational difficulty, lack of methodological standardization, and spatio-temporal environmental complexity makes quantitative comparative analyses of chimpanzee diets difficult. Since relatively small differences in diet may have profound evolutionary consequences (e.g.. [Wrangham et al., 1996]), this is a serious problem for socioecologists. It is especially acute for paleoanthropologists interested in ape models of hominid evolution, who would like to gain an understanding of modern ape adaptation to savanna environments despite the absence of habituated chimpanzees at such sites [McGrew et al., 1988; McGrew, 1992; Moore, 1992; Moore, 1996].

For this reason, we undertook a stable isotope study of chimpanzee hair from animals living in two open country sites. Stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in animal tissues are determined by the ratios in their diets [DeNiro & Epstein, 1978, 1981]. The ratios vary across food items [Schwarcz & Schoeninger, 1991] in patterned, predictable ways, which underlie their increasing use in various ecological investigations [Rundel et al., 1989; Lajtha & Michener, 1994; Proceedings, 1996]. The patterns occur because the natural abundance ratios of the isotopes ($^{13}C/^{12}C=1.1/98.9$; $^{15}N/^{14}N=0.36/99.64$) change as plants incorporate carbon dioxide and various nitrogen compounds from the atmosphere and soil followed by subsequent changes between plants and animals [Hoefs, 1987]. The alterations are consistent and predictable because the stable isotopes with the heavier mass (e.g., ^{13}C and ^{15}N) react faster in chemical reactions than the ones with the lighter mass (^{12}C and ^{14}N). The changes in the ratios are very small (commonly 10^{-5}) and partially for this reason, the ratios in samples (e.g., chimpanzee hair) are compared directly to an international standard.[2] The difference between the sample and standard (i.e., the delta or δ as in $\delta^{13}C$ and $\delta^{15}N$) is expressed in per thousand or per mil notation (i.e., ‰).

METHODS

Our study focused on two regions containing unhabituated chimpanzees. The Ugalla region of the Tongwe Forest Reserve is located approximately 60–80 km east of Lake Tanganika, just east of Kasakati, and about 100 km northeast of the Mahale research area (Fig. 1) where long-term study has been conducted [Nishida & Uehara, 1983]. The area receives about 1,000 mm rain/year with a single 5 month dry season (defined as <60 mm rainfall/month) during which most seasonally flowing streams are dry. As such, it is similar to Kasakati which has approximately 962 mm rain/year with a 6 month dry season [Moore, 1992]. Both Kasakati and Ugalla are "miombo" woodlands dominated by leguminous species

[1]Suzuki's annual figure is the average of monthly percentages [Suzuki, 1969; Table IV]. Recalculation as percent of total made no discernible difference.

[2]A δ value is defined as: $d = R_{sample}/R_{std} - 1 \times 1,000$ ‰ read as per mil or parts per thousand, where R is the isotope ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$ and the standard is the internationally recognized standard. The international standard for carbon, $^{13}C/^{12}C$, is Pee Dee Belemnite (PDB), a marine carbonate; the standard for nitrogen, $^{15}N/^{14}N$, is atmospheric nitrogen (AIR).
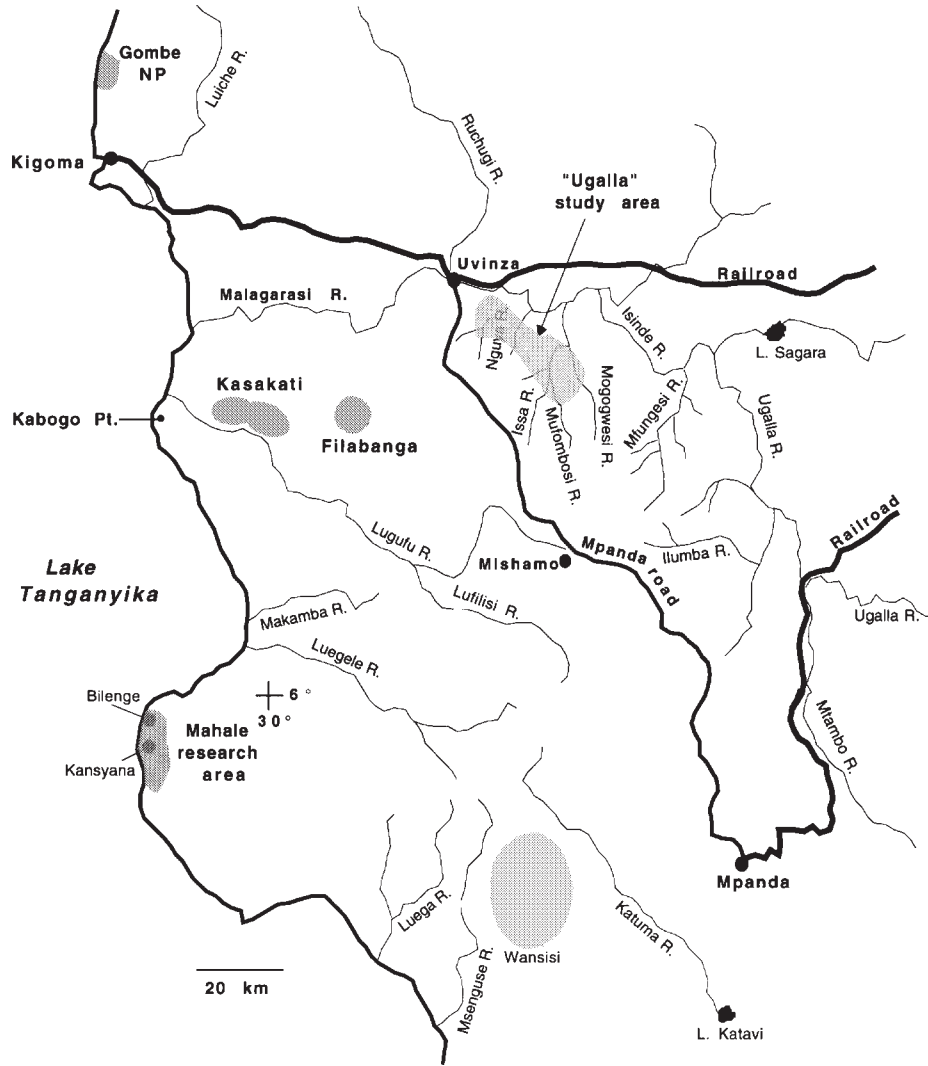
Fig. 1. Map of the Ugalla study area with Gombe National Park and the Mahale research area shown as references. The shaded areas indicate places where chimpanzees have been studied or surveyed.

with regularly spaced trees providing a thin, but nearly continuous, canopy over broad areas underlain mainly by grass groundcover [Suzuki, 1969; Moore, 1992; Moore, 1994]. Ugalla also contains approximately 1% evergreen forest [Kano, 1972], which, based on other regions, we thought might contain important foods. At Mt. Assirik, 3% of the area is forest but it contains 30% of food species [McGrew et al., 1988]. Also, at Kasakati, dense forest covers only 10% of the habitat but forest foods contribute nearly 80% of fecal volume [see Table I, Suzuki, 1969]. In a single, 9 day dry season survey at Ugalla, nearly 80% of observed night nests were located in woodland [Nishida, 1989] but it is not known whether feeding location associates with night nests and is woodland-focused or if it is forest-focused as at Mt. Assirik and Kasakati. We used hair $\delta^{13}C$ values, which correlate with forest canopy cover in arboreal monkeys and prosimians [Schoeninger

TABLE I. Fecal Evidence for Diet in "Savanna" Chimpanzees

Vegetatin type	Percent of total	Volume in feces % by season		Legumes are dominant in % of area	Legumes in droppings % of annual
		Wet	Dry		
Savanna	30%	—	—	—	—
Woodland	60%	07%	36%	>90%	11%
Riverine	10%	93%	64%	60%	—

*Data from [Suzuki, 1969] rounded to nearest whole percent.

et al., 1997, 1998] to determine whether the Ugalla chimpanzees feed largely in closed canopy forest or in open woodland.

Once the location of feeding was determined using $\delta^{13}C$ values, we used chimpanzee hair $\delta^{15}N$ values, which correlate with feeding on legumes and with trophic position in several primate species [Schoeninger et al., 1998], to indicate overall dependence on leguminous plants and omnivory (vertebrate versus insect-feeding cannot be distinguished). At Kasakati, 11% (by volume) of 194 scat, collected over 15 months, was leguminous with significant seasonal variation, one contained a presumed bone [Suzuki, 1969] and the incidence of insect remains was less than 10% [Suzuki, 1966]. Only two scat have been recovered at Ugalla; both contain leguminous seeds and one of the two also contained mammal hair [Nishida, 1989]. The vertebrate fauna at Ugalla includes species typical of both open grassland (e.g., zebra, *Equus burchelli*) as well as forest (e.g. blue monkey, *Cercopithecus mitis*) and insect species are abundant [Itani, 1979; Nishida, 1989; Moore, 1994; Moore, unpublished].

The second region lies along the small perennially flowing Ishasha River, which flows north into Lake Rutanzige, and forms part of the national boundary between Uganda (Rwenzori National Park) and the Democratic Republic of the Congo (ex-Zaire: Parc National des Virunga) (Fig. 2). The average annual rainfall is 750 mm per year with an average of 5 dry months each year (December–February and June–July). A small population of chimpanzees (10–25, based on nest counts [Sept, 1992; Steklis et al., 1992]) lives along the river, along with baboons and other primates [Rowell, 1966]. The habitat consists of closed-canopy, semideciduous (mixed evergreen and deciduous) gallery forest along much of the river grading to dry forest or thicket and open wooded grasslands on the surrounding plains and plateaus. Thirty-five belt transects along a 10 km stretch of the river were surveyed during the dry season in July–August 1989 and the wet and dry season in March–August 1990 [Sept, 1992; Steklis et al., 1992]. Nesting evidence showed over 80% of chimpanzee nests were located in the riverine gallery forest during the 6 months represented by survey [Sept, 1992, 1994]. The analyses of 113 fecal samples [Steklis et al., 1992] taken during the 1990 field season indicate that fleshy fruits from forest trees were the most common foods with fruits from forest margin trees and shrubs also frequent. This is similar to Kasakati where the majority of fecal volume came from dense riverine forest which covers only 10% of the habitat [Suzuki, 1969]. Since the number of fecal samples from Ishasha is small (4–10 per animal), however, and represents only half the annual cycle, we used carbon stable isotope analysis to determine the annual use of woodland versus forest.

The Ishasha fecal data also included seeds and pods from several leguminous species in the closed gallery forest where leguminous trees are among the dominant species and from one species in the dry forest margins. There was no
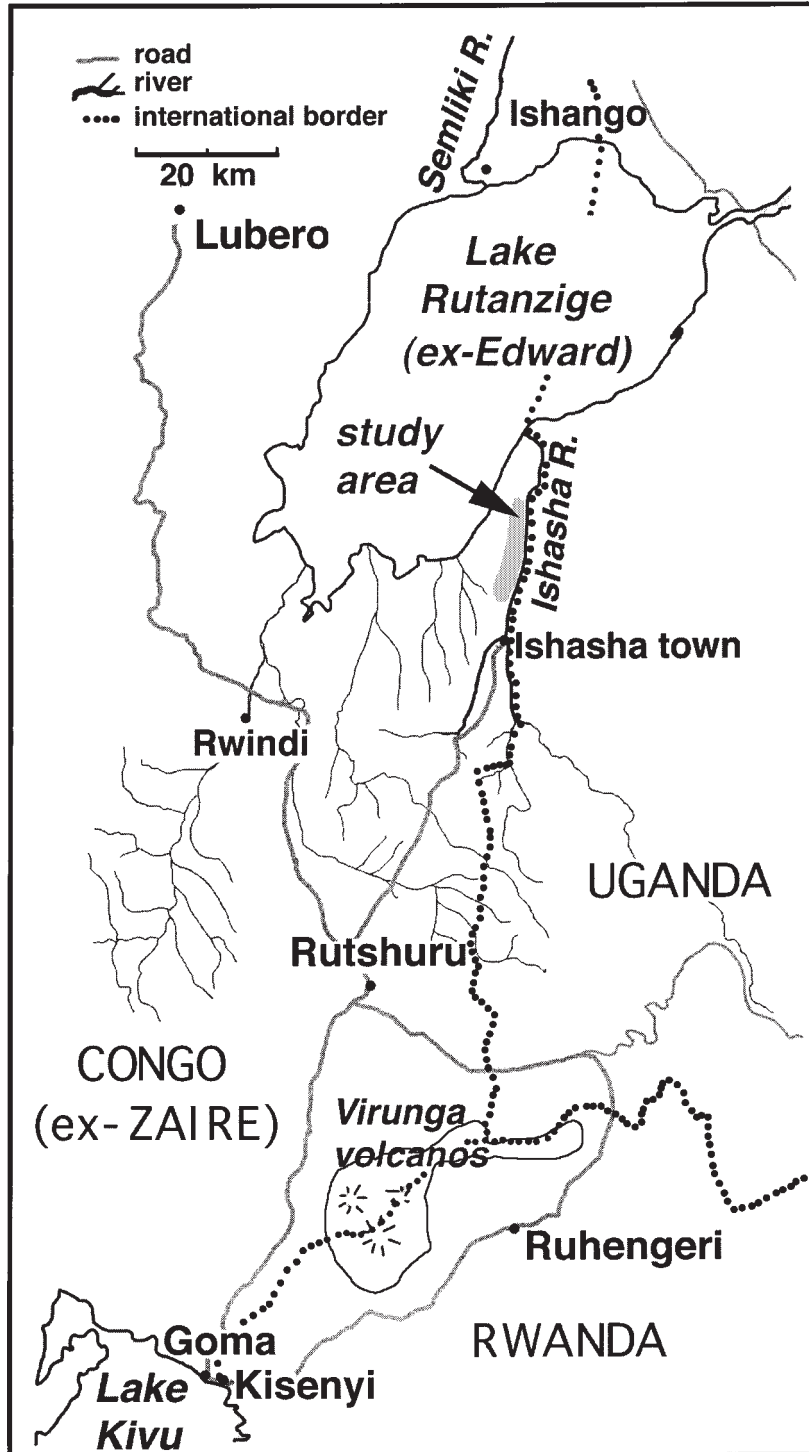
Fig. 2.   Map of the Ishasha region. The study area is on the Congo (ex-Zaire) side of the perennially flowing Ishasha river.

evidence of meat-eating or insect-eating in either survey. The extent of foraging away from the forest is unclear although observations by park rangers and local informants, fresh feeding remains, food species distribution, and nests encountered during surveys indicate that such foraging occurs. We used nitrogen stable isotope analyses to estimate dependence on leguminous plants and the level of omnivory.

Stable isotope analysis was performed on twelve hair samples, collected by JM at Ugalla, and ten hair samples, collected by JS at Ishasha. All samples came from night nests except for one hair recovered from a fecal sample at Ishasha. Samples were taken from widely dispersed nests to avoid sampling the same individual more than once although some multiple sampling may have occurred at Ishasha and the origin of the hair taken from the fecal sample is unknown. In addition, two plant samples showing evidence of chimpanzee feeding and hair from a red tail monkey (*Cercopithecus ascanius*) carcass were collected at Ishasha by J.S. and analyzed for comparison. Hair growth in chimpanzees is not well characterized and we assume a similarity to humans since chimpanzee hair grows long and is not the result of seasonal molting (although observations on other, smaller-bodied primate species suggest that hair may grow rapidly after the dry season, Nash personal communication). In humans, individual hair follicles are in a growing phase for approximately 3 years and in transitional or resting phases for a total of about 4 months [Valkovic, 1977]. Single hairs, such as were analyzed in this study, should reflect an average of 3 years of diet unless there are spurts to hair growth (we have found no reports, even anecdotal, that spurts occur in chimpanzee hair growth). Assuming that chimpanzee hair grows in a manner similar to humans, seasonal variation will be averaged out as will annual variation over a 3 year period.

Animal hair $\delta^{13}C$ values estimate dietary dependence on particular plants growing under particular ecological conditions [Minson et al., 1975; Nakamura et al., 1982; DeNiro & Epstein, 1978; Jones et al., 1981; Tieszen et al., 1983; White & Schwarcz, 1994]. Across all plant species there is a bimodal distribution of $\delta^{13}C$ values. Herbaceous vegetation and trees, called C_3 plants in reference to the number of carbon atoms in the first metabolite formed during photosynthesis, have $\delta^{13}C$ values between –31‰ and –23‰ [O'Leary, 1988; Farquhar et al., 1982]. Those growing in closed-canopy forests have values at the more negative end of the range because the available CO_2 is ^{12}C-enriched due to input from biomass degradation [van der Merwe & Medina, 1989; Broadmeadow et al., 1992] and because light levels are low [Yakir & Israeli, 1995]. Plants of the same species growing in open environments have values at the less negative end of the range and those growing under drought conditions have the least negative values [O'Leary, 1981; Garten & Taylor, 1992].

In correlation with plant variation, hair values in non-human primates from evergreen forests have the most negative values, those from deciduous forests are intermediate, and those from a drought afflicted forest are the least negative [Schoeninger et al., 1997, 1998]. This pattern holds true across a wide geographic range and primate taxa (Table 2); therefore extremely negative chimpanzee hair $\delta^{13}C$ values (–25‰) would indicate that the majority of their diet comes from the evergreen forest portions of their habitats. Less negative values (–24 to –23‰) would indicate that the majority of feeding occurs in forested, but not evergreen, portions of their habitats. If the hair $\delta^{13}C$ values are close to the least negative values (–21‰), it would indicate that the majority of chimpanzee diet came from open woodland portions of their habitats.

A second set of plants (referred to as C_4) is composed mainly of tropical grass

TABLE II. δ^{13}C in Hair Correlates With Canopy Cover*

Tropical forest type annual rainfall	Old World prosimians $\delta^{13}C_{PDB}$ ± s.d. (n)	New World monkeys $\delta^{13}C_{PDB}$ ± s.d. (n)
Drought deciduous <750mm[a]	−21.3‰ ± 0.89(9)	
Deciduous <1500 mm[b]	−23.1‰ ± 0.42(18)	−23.5‰ ± 0.32(19)
Evergreen 4,000 mm[c]		−24.8‰ ± 0.39(9)

*Data from: [Schoeninger et al., 1997, 1998].
[a]The species analyzed is *Lepilemur leucopus*.
[b]The species analyzed are *Galago garnettii*, *Galago zanzibaricus*, *Alouatta palliata*, and *Brachyteles arachnoides*.
[c]The species analyzed are *Cebus capucinus* and *Ateles geoffroyi*.

species with δ^{13}C values between −15‰ and −11‰ [O'Leary, 1988] because they are relatively unresponsive to environmental variations [Marino & McElroy, 1991]. Succulents commonly use a third photosynthetic pathway, CAM or Crassulacean Acid Metabolism [Kluge & Ting, 1978] and have values similar to C_4 plants in habitats like Ugalla and Ishasha [O'Leary, 1981; Ting & Gibbs, 1982]. Humans and other primates eating C_4 plants and succulents have hair [Schoeninger & Moore, 1992; Schoeninger et al., 1998] and bone protein [Ambrose & DeNiro, 1986] δ^{13}C values outside the range of animals feeding solely on C_3 plants. Hair from chimpanzees feeding on tropical grass seeds and corms or on grass-eating insects and vertebrates should show δ^{13}C values around −20‰ or less negative [although see Carter, 1998].

The δ^{15}N values in animal hair reflect diet [DeNiro & Epstein, 1981] distinguishing leguminous from non-leguminous plants [Virginia & Delwiche, 1982] and meat from plants [Schoeninger & DeNiro, 1984]. Leguminous plants have symbiotic bacteria in their roots that fix atmospheric nitrogen (0‰, by definition), directly [Virginia & Delwiche, 1982] and, with few exceptions [Vitousek et al., 1989], have lower δ^{15}N values than those common in other plants (5‰–7‰) [Shearer & Kohl, 1994]. Arboreal primates observed feeding on legumes have δ^{15}N values that are significantly lower than those of other primates (see Table III) and chimpanzee hair δ^{15}N values should be around 3‰ if legumes are a

TABLE III. δ^{15}N in Hair Correlates With Diet*

Diet	Prosimians $\delta^{15}N_{AIR}$ ± s.d. (n)	Monkeys $\delta^{15}N_{AIR}$ ± s.d. (n)
Insectivorous frugivore[a]	7.2‰ ± 1.02(18)	7.0‰ ± 0.14(4)
Frugivorous folivore[b]		5.4‰ ± 0.51(12)
Folivore[c]	5.5‰ ± 1.09(9)	
Frugivorous folivore with 40% legumes[d]		3.3‰ ± 0.49(12)

*Data from: [Schoeninger et al., 1997, 1998].
[a]Species: *Galago garnettii*, *Galago zanzibaricus*, and *Cebus capucinus*.
[b]Species: *Ateles geoffroyi* and *Brachyteles arachnoides*.
[c]Species: *Lepilemur leucopus*.
[d]Species: *Alouatta palliata*.

significant part of their diet. In the absence of legumes, an herbivorous chimpanzee should have $\delta^{15}N$ values around 5.5‰.

Carnivores typically have $\delta^{15}N$ values around 3‰ more positive than herbivores [Schoeninger & DeNiro, 1984; Minagawa & Wada, 1984] and omnivorous monkeys and prosimians have significantly more positive $\delta^{15}N$ values than herbivorous species [Schoeninger et al., 1997, 1998; see Table III]. Chimpanzee insect- or meat-eating should produce hair $\delta^{15}N$ values around 7‰.

Metabolic factors have been proposed as complicating these relationships but they should not affect the results of this study. Some ruminants eating low protein forage in arid regions had $\delta^{15}N$ values about 3‰ higher than expected [Ambrose & DeNiro, 1986; Heaton et al., 1986; Cormie & Schwarcz, 1996] and birds that had lost nearly 40% of their body weight had $\delta^{15}N$ values about 1‰ higher than expected [Hobson et al., 1993]. The effects of starvation and water stress have not been evaluated in any primate species but there is no reason to expect loss of 40% body weight in chimpanzees from either region and along the Ishasha river, water stress is highly unlikely.

As in previous studies, hair samples were cleaned in detergent to remove adhering soils or other material, rinsed with acetone to remove extraneous body oils, rinsed in double distilled H_2O, and freeze-dried. Complete hairs (>1 mg) were weighed into quartz tubes with excess cupric oxide, copper, and silver. The tubes were sealed under vacuum and the samples combusted at 900°C in a muffle furnace for 2 hours. Tubes were allowed to come to room temperature and then cracked on a glass vacuum line. Carbon dioxide and nitrogen gases were purified sequentially, collected cryogenically on the vacuum line (nitrogen gas was collected on molecular sieve), and analyzed on a Finnegan MAT 251 in M.J.S.'s laboratory. A glycine laboratory standard analyzed repetitively at the same time produced a standard deviation of 0.2‰ in $\delta^{13}C$ and 0.3‰ in $\delta^{15}N$. Some of the hair samples were too small to produce adequate nitrogen gas for mass spectrometric analyses and none were large enough for replicate analyses. Replicate $\delta^{13}C$ data are available on two samples. One showed identical $\delta^{13}C$ values and the second showed a 0.2‰ difference, well within precision limits.

RESULTS

The results (listed in Table IV and plotted in Fig. 3) show that neither of the chimpanzee populations has $\delta^{13}C$ values similar to primates living in closed canopy evergreen forests and that the two sites differ significantly from each other (P>.001 level in two-tailed test). The samples from Ishasha have $\delta^{13}C$ values that are 1‰ more negative than the samples from Ugalla and closely resemble those from prosimians and New World monkeys living in dry, semideciduous forests (see Table II). In contrast, the average δ^{13} value at Ugalla falls between those of primates living in semideciduous woodlands and those of prosimians living in a dry, open deciduous woodlands. Two individual prosimians, observed feeding only on C_3 plants (others ingested CAM plants [Nash, 1997]), had $\delta^{13}C$ values of –21.7‰ and –22.4‰. The chimpanzee values are equivalent (–21.6‰ to –22.3‰).

The two sites also differ significantly from each other in average $\delta^{15}N$ values (P>.001 level 2-tailed test) even when the two outliers from Ishasha are removed. The Ugalla data have a range of variation similar to that reported for animals raised on controlled diets [i.e., 2‰ DeNiro & Schoeninger, 1983], whereas at Ishasha, the range is much larger (5.4‰) and includes two outliers (10.2‰ and 10.4‰; perhaps the same individual). Most of the samples fall in the range of 5.0‰ to 7.1‰ in two, small, groups which differ from each other by 1.5‰ (6.7‰ ±

TABLE IV. Stable Isotope Data

Site
  species
    common name and material
	Lab number	$\delta^{13}C_{PDB}$ in ‰	$\delta^{15}N_{AIR}$ in ‰

Ugalla			
Pan troglodytes			
Chimpanzee hair	4,540	−22.2	3.3
	4,357	−22.2	3.1
	4,535	−22.1	2.5
	4,534	−22.2	2.4
	4,537	−21.8	2.3
	4,536	−22.2	2.0
	4,533	−21.7	1.7
	4,539	−21.7	1.2
	4,356	−22.3	—
	4,532	−21.6	—
	4,538	−21.6	—
	4,542	−22.0	—
Averages ± s.d.		−22.0 ± 0.31	2.3 ± 0.78
Ishasha			
Pan troglodytes			
Chimpanzee hair			
	4,062	−22.6	10.4
	4,055	−23.4	10.2
	4,060	−23.0	7.1
	4,347	−23.1	6.7
	4,061	−22.7	6.4
	4,346	−23.4	5.4
	4,350	−23.2	5.4
	4,348	−23.1	5.1
	4,345	−23.4	5.0
	4,349	−22.9	—
Average ± s.d.		−23.1 ± 0.31	6.9 ± 2.19
			5.9 ± 0.87
Cercopithecus ascanius			
Red tail monkey hair	3,983	−22.5	5.4
Ficus sp.			
Fig from chimp feces	3,985	−26.4	6.8
Unknown fruit			
Seed from chimp feces	3,986	−25.7	5.3

0.3 n=3 vs. 5.2‰ ± 0.2 n=4, P>.001 two-tailed test). The lower value is very similar to those reported for herbivorous monkeys and prosimians and the higher value is similar to those in omnivorous taxa. The Ugalla samples are 3‰ less positive, on average, than the Ishasha samples with removal of two outliers. They are also less positive than those from New World howling monkeys (*Alouatta palliata*) that spend an average 40% of feeding time on legumes (Fig. 4).

DISCUSSION:

The results from both open country sites support previous observations that chimpanzees are highly dependent on food from trees [reviewed in Peters & O'Brien, 1981; Kortlandt, 1983; McGrew et al., 1988] because all of the isotope
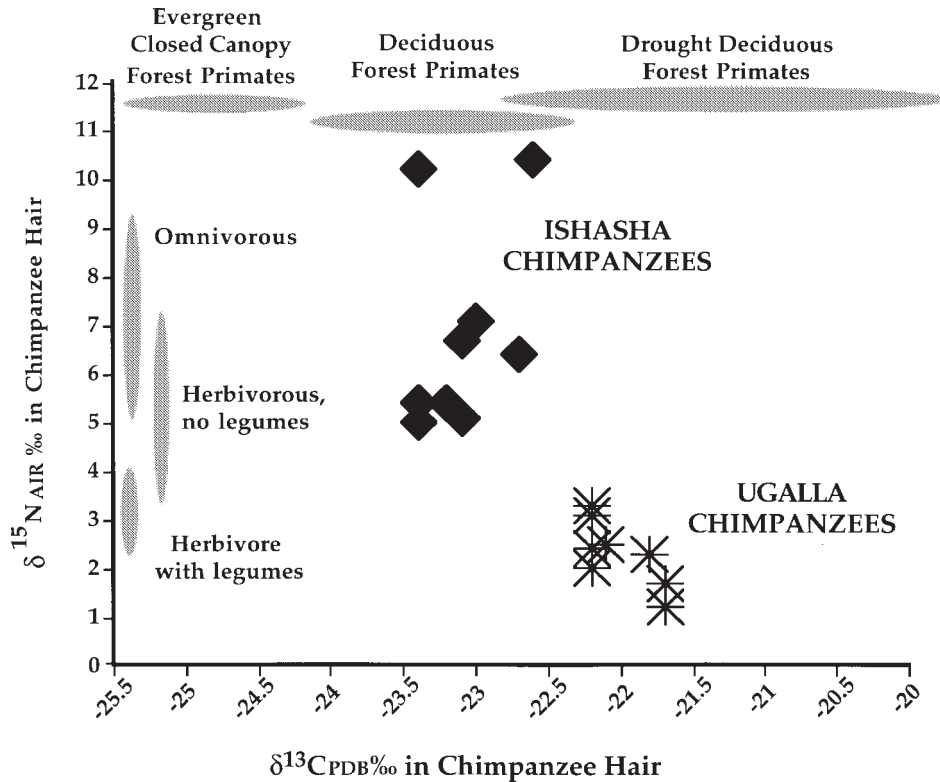
Fig. 3. Bivariate plot showing the $\delta^{13}C$ and $\delta^{15}N$ values in chimpanzee hair from Ishasha and from Ugalla. Across the top are indicated the ranges in $\delta^{13}C$ values previously reported for several primate species from a closed canopy evergreen forest in Costa Rica, three deciduous forests (Costa Rica, Kenya, and Brazil), and one drought deciduous forest in Madagascar [Schoeninger et al., 1997, 1998]. Along the Y axis, the ranges in $\delta^{15}N$ values for the same species are indicated: one species ate a significant amount of legumes; three ate little to none; and three were omnivorous species. The shading shows the ranges of individual values. The Ugalla chimpanzees are eating a lot of legumes in the open woodland region of their range whereas the Ishasha chimpanzees are eating little to no legumes. The highest $\delta^{15}N$ values at Ishasha may be a nursing signal while the values around 7‰ suggest omnivory and the rest appear herbivorous.

data indicate ingestion of C_3 plants or of animals feeding on C_3 plants. Even so, at neither site are they focusing solely on dense forest patches for their food. At Ishasha, chimpanzee hair $\delta^{13}C$ values indicate that the animals are feeding both in the gallery forest closest to the river and the dry forest beyond. This conforms to the distribution of sleeping nests in the dry season [Sept, 1992] and suggests that wet season feeding is similarly focused on the two types of forest. As such, Ishasha is similar to Kasakati where fecal data indicated that the majority of feeding was restricted to the minor forest regions lining rivers [Suzuki, 1969]. In contrast, the Ugalla hair δ^{13} values indicate use of the "miombo" woodland with little or no use of the small area of forest within their habitat. This suggests a difference in the pattern of habitat use between Ugalla and Mt. Assirik where the 3% of the region that is forest is used heavily by chimpanzees [McGrew et al., 1988] but isotope data from the Mt. Assirik chimpanzees are needed before reaching final conclusions. The difference in habitat use between Ugalla and Ishasha could not have been predicted on ecological grounds.
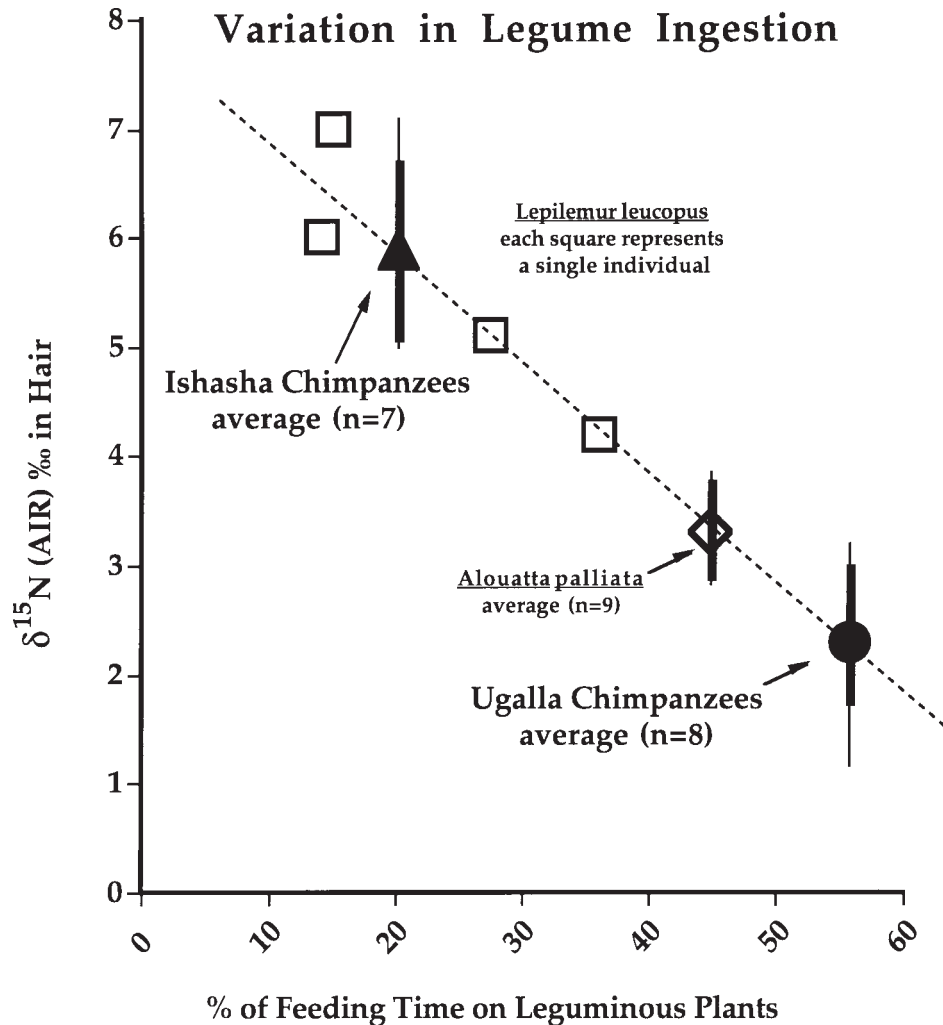
Fig. 4. Bivariate plot of $\delta^{15}N$ values and the percent of feeding time devoted to leguminous plants in four individual *Lepilemur leucopus* from Madagascar [Schoeninger et al., 1998] and the average for eight *Alouatta palliata* for which individual feeding data were not available [Glander, 1979]. The dashed line is fitted by eye to open symbols and chimpanzee points are placed on the line. No direct data on feeding time is available for any savanna chimpanzee (sensu Moore, 1992) population. Vertical bars indicate range and SD of ape and monkey $\delta^{15}N$ values.

The data from both Ugalla and Ishasha indicate little use of open grassland areas. For Ishasha, this suggests that non-survey observations, feeding remains, nest placement, and food species distribution are reflecting sporadic, not significant, use of such areas, perhaps because adequate, preferred food is available in the forest regions. At Ugalla, however, it is surprising that no grassland signal is apparent given the open, predominantly grassy groundcover. Insects or mammals that feed on grass (e.g., grasshoppers or infants of ruminant grazers) would have a grassland signal. The data suggest that these are minor parts of the diet if they are present at all. Thus, these chimpanzees survive in open, grassy woodland habitats similar to those in which the last common ancestor of apes and

humans probably lived [Kingston et al., 1994; Moore, 1996] but without taking advantage of C_4-based foods. The pattern of chimpanzee habitat use also contrasts with hominids living after the initial divergence. By 3 mya, *Australopithecus africanus* tooth enamel $\delta^{13}C$ values indicate routine dependence on resources from regions more open than Ugalla [Sponheimer & Lee-Thorp, 1999]. Such open regions, which chimpanzees apparently avoid because they provide no sleeping trees, include no required food items and/or expose them to large predators were successfully exploited by early hominids. A deeper understanding of the basis for these differences in resource exploitation and habitat use may help to clarify the processes behind the initial divergence of apes and hominids [McGrew, 1991; Moore, 1996] as well as subsequent adaptations within the hominid lineage.

The Ugalla values indicate a greater dependence on legumes than estimated from fecal evidence at Kasakati (11% [Suzuki, 1969]). It is not possible to calculate a specific intake level but comparative species' data suggest that it is around 50% of the diet (Fig. 4). Such a high level of dependence has several implications. Many legumes contain secondary compounds including protein digestion inhibitors [Glander, 1982; Stahl, 1984]. Unripe pods of *Acacia hockii* from the Ishasha region, for example, contain high concentrations of total phenolics and condensed tannins [Sept, 1990]. If the leguminous seeds at Ugalla contain any of these secondary compounds, it implies a trade-off is required for chimpanzees when eating the protein- and fat-rich legume seeds (Table V). Also, if, as we assume, chimpanzee hair grows throughout the year, the data suggest that legumes are eaten throughout the year. Even if they obtain excess protein from legumes during the 5 dry season months, protein is required for hair growth for the remaining 7 months since excess protein cannot be stored in the body. They are probably also eating legume leaves and flowers which might not be identified in scat. Feeding on leguminous flowers was proposed to account for observed seasonality in aspects of chimpanzee reproductive cycles at Gombe during years of high rainfall [Wallis, 1997] as legumes, in general., contain significant phytoestrogen levels [Kurzer & Xia, 1997]. Future fieldwork should be directed toward collecting feeding observations in leguminous woodlands and collection of foods for laboratory assessment of phytoestrogen and other secondary compound contents.

In contrast to Ugalla, two Ishasha samples have values above 10‰. We dis-

TABLE V. Nutritional Analyses of Representative Plant Food Samples

Species	Part	TNC[a]	Lipid	Protein	Source
Leguminous plants					
Acacia hockii	Green pods	7	1	17	[Sept, 1990]
Pterocarpus chrysothrix	Seeds	33	21	28	[Suzuki, 1969]
Julbernardia globiflora	Seeds	57	9	16	[Suzuki, 1969]
Cynometra sp.	Seeds	64	5	8	[Suzuki, 1969]
Isoberlinia angolensis	Seeds	65	3	11	[Suzuki, 1969]
Soybeans		27	18	34	[Suzuki, 1969]
Non-legumes					
Capparis tomentosa	Fruit flesh	37	0	7	[Sept, 1990]
Cucumis aculeatus	Fruit flesh	12	2	8	[Sept, 1990]
Grewia similis	Fruit flesh	23	0	8	[Sept, 1990]
Rice		72	2	7	[Suzuki, 1969]
Wheat		70	2	10	[Suzuki, 1969]

[a]TNC refers to Total Nonstructural Carbohydrate.

count nutritional stress as a likely explanation for these values because >40% weight loss in birds produced a mere 1‰ elevation in δ^{15}N values [Hobson et al., 1993] whereas our data are around 3‰ above expected values. The values could indicate omnivory although omnivorous nonhuman primates commonly show δ^{15}N values ~7‰. The red tail monkey (*Cercopithecus ascanius*) from Ishasha (5.4‰) is known to eat insects but the δ^{15}N variation in some species (Table III) indicates that more samples from this species are necessary to assess the significance of this individual value. In contrast to other primates, omnivorous humans typically have δ^{15}N values around 9 to 10‰ [Schoeninger & Moore, 1992] probably because vertebrates provide the majority of faunal prey and protein intake levels are generally high. At Gombe, some males can be expected to eat a level of meat approaching that in some humans [Stanford et al., 1994] and if this occurred at Ishasha, the high δ^{15}N values could be due to high vertebrate protein intake. Alternatively, the 3‰ elevation over other Ishasha chimpanzee δ^{15}N values is equivalent to that in the fingernails (a keratin protein, like hair) of nursing human babies relative to their mothers [Fogel et al., 1989]. In the absence of observational data regarding the age and sex of the individual(s) whose hair we analyzed, we cannot be more conclusive.

Three other samples have values that approach those in omnivorous nonhuman primates and it is tempting to suggest inclusion of insects or vertebrate fauna in the diet of some chimpanzee individuals. The remaining four samples have δ^{15}N values similar to those in general herbivores and to individual prosimians that include minimal amounts of legumes (10%) in their annual diet. This is consistent with feeding traces and fecal analyses in early dry season surveys [Steklis et al., 1992].

The Ishasha isotope data contrast with Ugalla where feeding on leguminous plants is a more significant part of diet, open woodland portions are emphasized, and there is no indication of omnivory. Apparently, 'miombo' woodland chimpanzees eat seeds requiring mastication and, quite possibly, secondary compound toleration in the dry season. In contrast, by 1.8 mya hominids were taking fairly complete animal carcasses in open areas [Bunn, 1999] as a dry season resource [Blumenschine, 1987]. Whether their use of such resources began earlier in the Pliocene with the spread of C_4 grasses and increased seasonality, either simply as an equiprobable alternative or because carcasses were more available than they are today [Marean, 1989], is highly debated. In either case, such a scenario replaces the "taste for meat" as a selective force with the need to increase diet breadth in the late dry season in a manner similar to open country chimpanzees [Wallis, 1995] or to gorillas [Tutin et al., 1991]. The use of such a resource would provide partial explanation for the success of our ancestors in open grassland savannas while chimpanzees are restricted to wooded savannas and gorillas are restricted to forests.

CONCLUSIONS:

1. Although both sites, Ugalla and Ishasha, fit the definition of 'savanna' by being relatively open with grass as the common ground cover, stable isotope evidence indicates that the two sites are used in different ways by the chimpanzees that inhabit them.

2. At Ishasha, the chimpanzees are feeding largely in the riverine forest with little feeding in the open, wooded grassland. In contrast, Ugalla chimpanzees are feeding largely in the open, "miombo" woodland rather than in available forest patches.

3. At both sites, the chimpanzees are feeding mostly on tree products rather than on open grassland shrubs or on animals (insects or infant mammals) feeding on such shrubs or on grasses. This failure to exploit some classes of available resources may be useful in interpreting the hominid-pongid divergence ca. 5 mya.

4. The chimpanzees at Ugalla are feeding on a significant quantity of legumes which have seeds that could provide energy and protein during the dry season. The potential need for detoxification of unripe legumes needs to be explored as does the possible significance of phytoestrogen ingestion in legume-feeding.

5. Among the chimpanzees at Ishasha, some individuals may have been nursing or eating significant amounts of insects and/or meat.

6. Because they average across seasons or years and are capable of showing dietary discriminations, such as those reported here for unhabituated primates, stable isotopes from hair and other tissues are of great potential utility for dietary studies of modern primates.

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