

Plant Foods Consumed by *Pan*: Exploring the Variation of Nutritional Ecology Across Africa

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ABSTRACT It has been shown that differences in resource density and nutrient supply affect variation in ranging patterns, habitat use, and sociality. Among nonhuman primates, chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) have often been used as models for the link between social system and habitat ecology. Field reports suggest that resource density is higher in habitats occupied by bonobos (compared to chimpanzee habitats), and in the West (compared to the East) of the range of chimpanzees. In this study we compared diet quality at the level of species and populations using information from nutritional analyses of fruit and leaves consumed by chimpanzees (three) and bonobos (one population). Quality of plant foods was assessed on the basis of a) the concentration of macronutrients, fiber, and anti-feedants, and b) associations of different

nutrient components. Overall plant samples collected at each site differed in terms of macronutrient content. However, nutritious quality and gross energy content of food samples were similar suggesting that dietary quality reflects selectivity rather than habitat ecology. The quality of plant foods consumed by bonobos was within the range of chimpanzees and the quality of plant foods consumed by western chimpanzees was not higher than that of eastern chimpanzees. While the results showed significant variation across forests inhabited by *Pan*, they did not match with geographical patterns between and within *Pan* species as proposed in previous studies. This suggests that the nutritional quality of the habitat is not always a reliable predictor of the quality of the diet. *Am J Phys Anthropol* 141:476–485, 2010. © 2009 Wiley-Liss, Inc.

The diet of medium or small body sized vertebrates tends to include relatively large amounts of fruit and the preference for a fruit-based diet is usually related to the high content of easily digestible macronutrients, such as nonstructural carbohydrates and lipids, and to low levels of indigestible fibers and antifeedants (Milton, 1987). Despite these nutritional advantages, frugivory tends to be facultative in vertebrates, even among so-called fruit specialists, with constraints such as the spatio-temporal distribution of reproductive plant parts limiting the extent to which animals can subsist on an entirely fruit-based diet (Rode and Robbins, 2000). Large body size generally permits a low-energy, low-nutrient density diet (Clauss et al., 2008). As a consequence, large animals can subsist on low-quality plant foods with a high fiber content and relatively low nutrient density while smaller animals have to search for higher quality items (Dement and van Soest, 1985). In this regard chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) are exceptional. In spite of their large body mass (Smith and Jungers, 1997) they are among the most consistently frugivorous primates, in that they maintain their frugivorous habits even at times of low fruit availability (White and Lanjouw, 1994; Wrangham et al., 1998). This adherence to frugivory requires flexibility in ranging and grouping patterns, and the fission-fusion system of *Pan* is likely to be one adaptation for exploiting food patches

that fluctuate in time and space (Hashimoto et al., 2004; Lehmann et al., 2007).

Information on the feeding ecology of *Pan* has been reported from a large number of sites across Africa, including deciduous, woodland, and evergreen forests in West, East, and Central Africa (Nishida and Uehara, 1983; Newton-Fisher, 1999; Hunt and McGrew, 2002; Morgan and Sanz, 2006). Corresponding information from bonobos comes from sites in the North (Badrian and Malenky, 1984; Kano, 1992), and South (Sabater Pi and Veà, 1993; Hohmann et al., 2006) of the species' dis-

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tributional range, which is entirely restricted to the Democratic Republic of Congo.

Habitats occupied by *Pan* differ in terms of their floristic composition (Rodman, 2002) and resource abundance (Doran et al., 2002) and this variation is thought to affect habitat use, diet composition, and sociality both within and between the species (Wrangham, 1986; Boesch, 1996). Comparison of hair samples from two populations of savanna chimpanzees revealed different isotope signatures which were related to foraging behavior and nutrient intake (Schoeninger et al., 1999). The two chimpanzee populations at Gombe and Mahale differ in terms of food selection and food processing (Nishida et al., 1983) and similar differences in the use of plant foods have been reported from other communities (Newton-Fisher, 1999; Boesch et al., 2006). Although other factors are likely to be involved, ecological parameters are thought to be the key underlying the observed variation. Despite the considerable attention given to the influence of food distributional patterns in space and time as key ecological determinants of these intra- and interspecific variations (Chapman et al., 1995; Doran et al., 2002), no explanatory patterns have yet emerged. Assessments of spatial and temporal patterns of resource abundance within and between sites are frequently based on rainfall data and phenological accounts such as leaf flushing and fruit production (Tutin and Fernandez, 1993). While these approaches address some quantitative aspects of food availability, an often overlooked source of variability among sites is the nutrient content and nutrient density of plant foods. Studies on herbivores have shown how variation of food quality can promote or constrain activity budgets, ranging patterns and sociality, such as female gregariousness, in a similar manner as food distribution and predation pressure (Hamel and Cote, 2007; Bailey and Provenza, 2008). The ideal free theory offers a framework that explains the relationship between habitat quality, population density and resource competition (Fretwell and Lucas, 1970; Fretwell, 1972). The model assumes that spatial distribution of individuals is a function of habitat quality, that is, individuals prefer habitats with high resource density and compete for access to them while avoiding poor habitats. The consequence of habitat selection is a skew in population density and equal gains by all individuals. In the context of nutritional ecology, the model predicts that in spite of consistent differences in ecology and habitat characteristics, the intake of nutrients is similar across habitats.

Studies on nonhuman primates have explored the principles determining the form of social relations in relation to resource distribution (van Schaik, 1989; Isbell, 1991). Some species have served as models of the socioecology of hominines (humans and their ancestors) and chimpanzees and bonobos, in particular, have received considerable attention in this regard (Wrangham, 1986; Ghiglieri, 1987; Lambert, 2007).

Early field studies and work on captive bonobos has revealed remarkable and unexpected differences in sociality and gregariousness compared to chimpanzees. For decades, scientific wisdom has held that the consistently observed differences between chimpanzee and bonobo social systems, particularly in attributes of female behavior, grouping and non-kin bonding, and female dominance or co-dominance with regard to males, can be traced to differences in habitat ecology (Wrangham, 1986). Several hypotheses have suggested variations on the exact nature of these differences, focus-

ing on the abundance, distribution, and quality of available plant foods, ranging from fruit to herbaceous vegetation (Malenky et al., 1994; Wrangham, 2000; Lambert, 2007). However, the original model that emphasized consistent disparity between the two sister species (Wrangham, 1986) is not unchallenged. First, although a comparison of Lomako bonobos with chimpanzees from Gombe (Tanzania) suggested that bonobos have access to larger food patches of tree fruits than chimpanzees (White & Wrangham, 1988), a comparison of Lomako bonobos with chimpanzees from Kanyawara (Uganda) did not confirm the proposed differences in grouping and food distribution (Chapman et al., 1994). Similarly, though Malenky (1990) proposed that the quality of fruit consumed by Lomako bonobos exceeds that consumed by East African chimpanzees, nutritional analyses of food from a bonobo population from Salonga and a population of Nigerian chimpanzees from Gashaka (Nigeria) indicated both similarities and differences (Hohmann et al., 2006). While plant foods of the two species were similar in terms of their overall composition, they differed in terms of how macronutrients and antifeedants were associated. Results from this study indicate that it is not nutrient content but the association of macronutrients with antifeedants that affects fruit quality between the two species.

Second, recent information from long-term chimpanzee study sites has yielded a complex scenario and has shifted key assumptions of previous models (Mitani et al., 2000; Lehmann and Boesch, 2004; Murray et al., 2006). There is considerable variation in the grouping patterns and bonding relationships between and within the sexes among populations of chimpanzees. The variation in chimpanzee sociality has been related to differences in resource distribution (Balcomb et al., 2000; Lehmann et al., 2007), and demography (Lehmann and Boesch, 2004), leading to a proposed dichotomy between East and West African chimpanzees (Doran et al., 2002). While the ecological differentiation fits the original model, the geographic location alone is not sufficient to predict patterns of resource density and sociality.

Third, information from bonobos is biased to few populations and does not account for the heterogeneity in climate, forest composition, and resource abundance that characterizes the central Congo basin (Bergmans, 1998), making existing theories of the socioecology of this *Pan* species preliminary.

Previous studies have explored the links between social structure and the distribution and abundance of food resources and this work has significantly influenced our understanding of the socioecology of primates and other social mammals (Pusey and Packer, 1997). However, regarding the two *Pan* species, some of the key questions remain: In what ways do chimpanzee habitats differ from each other, and from bonobo habitats, and are these differences sufficient to explain the differences in behavior and social patterns observed between the two species? Are differences between East and West African chimpanzees based on differences in regional habitats or do they reflect contrasting geographic differences in landscape ecology?

Previous studies have proposed consistent differences in food abundance between West and East Africa (chimpanzee range), and between the forest south (bonobo range) and north (chimpanzee range) of the Congo River. This study uses data from four *Pan* populations to test whether or not differences in the quality of plant food follow the proposed geographic pattern and whether

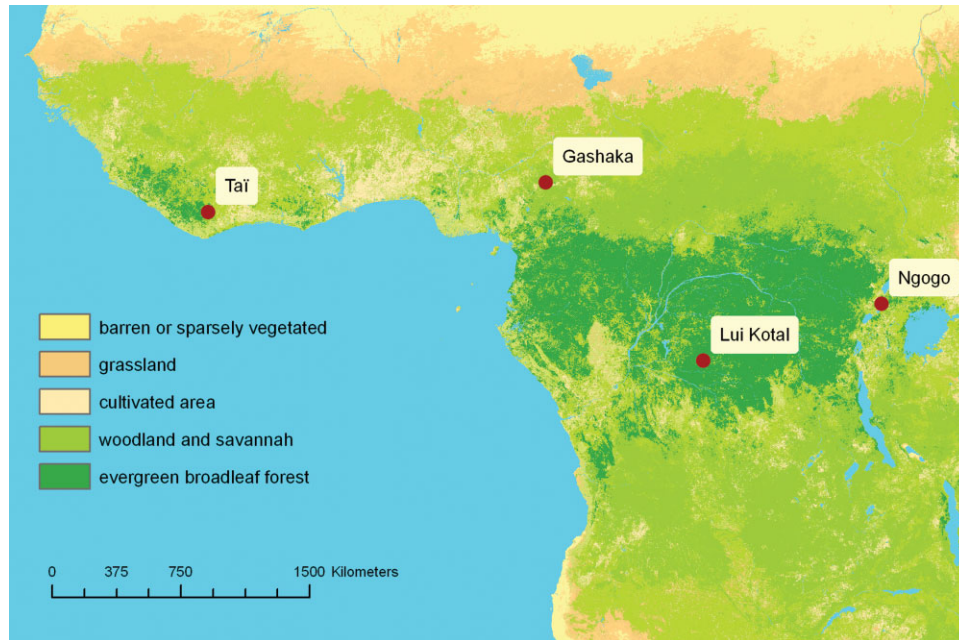


Fig. 1. Location of study sites.

such differences in habitat ecology affect the quality of food items. To this aim we compare the patterns of diet quality on the level of species (bonobos vs. chimpanzees) and populations (East African vs. West African chimpanzees). We analyzed the content of macronutrients, fibers, phenols and tannins of fruit and leaves consumed by chimpanzees (three sites) and bonobos (one site) to identify variation in nutritional ecology. To assess the nutritional quality of plant foods we used measurements of the major components of plant foods such as macronutrients, fiber, and antifeedants. To evaluate the accessibility of nutrients, we also explored the association between nutrients and antifeedants, and the relationship between nutrients and fiber. To identify possible variation in terms of energy supply, we investigated the relationship between protein and nonstructural carbohydrates, and the relationship between macronutrient content and energy.

METHODS

Study sites and subjects

This article presents original data collected from three field sites where long-term studies on wild populations are conducted: West African chimpanzees (*Pan troglodytes verus*) at Tai National Park, Ivory Coast; East African chimpanzees (*Pt. schweinfurthii*) at Ngogo in Kibale National Park, Uganda; and bonobos (*P. paniscus*) at LuiKotal at Salonga National Park, Democratic Republic of Congo (see Fig. 1). All three sites are characterized by moist, evergreen forest with a closed canopy and a rich and partly endemic flora. Information on the climate, topography, and ecology of the sites is summarized in Table 1. To relate findings from this study to similar work, the data from the three sites were compared to information from Nigerian chimpanzees (*Pt. vellerosus*) from Gashaka Gumti National Park, Nigeria (Sommer et al., 2003) that had been analyzed in a previous study (Hohmann et al., 2006).

Behavioral observations

Chimpanzees and bonobos at the four sites differed in terms of their tolerance toward human observers. At Tai and Ngogo, individuals were fully habituated to the presence of humans, thus allowing focal animal observations and all-day follows. In Salonga and Gashaka, habituation was in progress and observations of feeding behavior varied in terms of the frequency of encounters, number of contact hours, and observation distance. However, macroscopic analyses of fresh feces from habituated individuals and from individuals that did not tolerate direct observations suggested that the effect of habituation status was negligible (Bauer, 2006).

Collection of plant samples

Data collection covered 13 (Ngogo), 14 (Gashaka), 25 (Salonga), and 35 months (Tai) and followed the same protocol in terms of collection, processing, and storage of plant samples. Overall, 246 different plant species contributed to the dataset. The total sample set analyzed in this study included 169 (69%) fruits and 21 (9%) leaves that were known to be eaten by *Pan* at the respective sites, as well as 48 fruits and 8 leaves (together 23%) known or suspected to be avoided, as a comparison (Table 2).

Samples were preferably collected from plants that were visited by *Pan* and, whenever possible, samples came from feeding patches while the animals fed in them. When this was impossible, we collected a sample either from the same feeding patch after the animals left, or from a patch similar in size and phenophase. Most samples were made up of intact items that fell to the ground incidentally as subjects moved through a feeding tree. Items that were clearly discarded by a feeding animal were not collected, as their nutritional content likely differs from that of selected items. Other samples were taken directly from feeding trees. Samples were placed in plastic or paper bags in the forest and brought back to camp within a few

TABLE 1. Information on topography and climate of the four study sites

Site	Terrain	Altitude (m above sea level)	Temperature (°C) (min–max)	Annual rain fall (mm)	Number of dry months ^a
Gashaka	Hilly	300–2,419	23.2–32.2	1,859	4
Ngogo	Hilly	1,200–1,500	16.6–24.2	1,492	0
Salonga	Flat	320–413	20.7–26.9	2,480	0
Tai	Flat	100–240	21–33	1,747	1

Source of information: Sommer et al. (2003) for Gashaka, Struhsaker (1997) for Ngogo, unpublished data from the LuiKotale Bonobo Project for Salonga, de Rouw et al. (1990) for Tai.

^a Dry months refers to months without any rain.

TABLE 2. Number of samples of foods and nonfoods collected at the four sites

Site and sample size	Species	No. of fruit samples		No. of leaf samples	
		Food	Nonfood	Food	Nonfood
Gashaka (73)	<i>P. t. vellerosus</i>	44	29	0	0
Ngogo (35)	<i>P. t. schweinfurthii</i>	23	4	4	4
Salonga (82)	<i>P. paniscus</i>	58	15	5	4
Tai (55)	<i>P. t. troglodytes</i>	44	0	11	0

hours, where fruits and seeds were measured and weighed as soon as possible. For all plant food items, multiple samples were collected and results of nutritional analyses were pooled. There was within-species variation in terms of nutritional quality, which may have been caused by differences in the stage of ripeness, the location of food trees within the forest, and the location of fruit within trees (Chapman et al., 2002). The determination of the causes of within-species variation in phytochemistry would have required a different approach and was not addressed in this study. To prevent molding and other types of degradation such as bacterial-induced changes in the chemical content of fresh material, samples were stored in liquid nitrogen and later lyophilized before sending them to the nutritional labs of the Leibniz Institute for Zoo and Wildlife Research in Berlin and Hamburg University.

Phytochemical analyses

Macronutrient analyses of all samples were performed at the Nutritional Lab of the Leibniz Institute for Zoo and Wildlife Research (Berlin). Samples were ground prior to analysis with an IKA A11 basic mill (IKA, Staufen, Germany). Dry matter content (DM) was determined by drying a portion of the sample at 105°C overnight and all data are given as % dry matter. Samples were analyzed using standard techniques for the following macronutrients: nitrogen was determined by complete combustion (Dumas combustion) at high temperature (about 950°C) in pure oxygen, using a Rapid N III analyzer (Elementar Analyser Systeme, Hanau, Germany) and the traditional factor of 6.25 was used for conversion into protein (crude protein (%DM) = 6.25 × N (%DM)), although studies on tropical forage indicate that this might overestimate the crude protein content and factors between 4.3 (Milton and Dintzis, 1981; Conklin-Brittain et al., 1999) and 5.64 (Levey et al., 2000) are recommended. Lipids were extracted with ethyl ether using a fully automatic Soxhlett-system (Gerhardt Laboratory Systems, Königswinter, Germany). Energy content was assessed using bomb calorimetry which gives the “gross” energy of food items, a value that is considerably larger than the metabolizable energy due to energy losses via feces and urine. Energy losses increase with decreasing digestibility of forage

and it has been shown in chimpanzees that fiber digestibility is a function of fiber content of the diet (Milton and Demment, 1988). The higher the fiber content the lower is the fiber digestion coefficient. However, the gross energy value provides a basis for investigating the relative contribution of various macronutrients to the overall energy content of plant items. Gross energy was determined by burning a sample of dry matter in pure oxygen atmosphere in a bomb calorimeter (C5003 bomb calorimeter; IKA, Staufen, Germany). The heat produced is measured in kJ g⁻¹ DM. Sucrose, D-glucose, D-fructose, and starch were determined with commercialized enzymatic tests (R-Biopharm, Darmstadt, Germany; UV method). Detergent fiber analysis was performed following van Soest (1994) with NDF (neutral detergent fiber), ADF (acid detergent fiber), and ADL (acid detergent lignin) being determined sequentially from each sample using an Ankom Fiber Analyser 220 (Ankom Technology, Macedon, USA). Hemicellulose (NDF-ADF) and cellulose (ADF-ADL) were calculated by weight difference.

Analyses of antifeedants such as phenols and tannins were carried out at Hamburg University following the protocol described in Hohmann et al. (2006). These methods were applied to allow comparisons with data collected previously. Phenolic components and tannins (as either toxins or digestion inhibitors) are extremely variable chemically as well as with respect to their biological activities in different consumer species (Waterman and Mole, 1994; Wrangham et al., 1998; Schofield et al., 2001; Rautio et al., 2007). It may be futile to try to find a general procedure which will allow standard analyses of these components across species. Possible solutions to this problem could either be to simply analyze the availability of “digestible nitrogen” to account for digestibility reducing tannins (DeGabriel et al., 2008) or to analyze specific toxic components which could act either on endosymbiotic microbes or be toxic for the consumer itself (Stolter, 2008, 2009).

Temporal variation in nutrient supply

Measurements of the temporal variation in the availability of different macronutrients require data on fruit production, number of fruit bearing trees per month and

species, crop size, and nutritional quality of food items. Although each site collected some of this information, variation of sampling techniques did not allow a quantitative comparison between sites. Therefore we used simple criteria to identify temporal patterns of nutrient supply between three sites (data from Tai were excluded because of the lack of corresponding information). Assessments on the presence/absence of fruit from a given food species came from monthly phenology records. Using the calculated median value for each macronutrient at each of the three sites, the different food species were classified as containing high values (above-median) or low values (below-median). Assignment of these data to the presence/absence of given species per month of field work produced a matrix of high or low supply for each macronutrient and for each month. For example, the presence of one or more food species with an above-median score for protein was considered to indicate sufficient protein supply. When all food species contained below-median scores, protein supply was considered to be constrained.

Statistics

Prior to testing for differences between sites and fruit parts we tried to reduce the number of variables (i.e., macronutrients and antifeedants) using Principal Component Analysis (PCA). Before subjecting variables to PCA, we checked their distributions for normality, and, in case of deviations from normality, we transformed variables using log (protein, ADL, cellulose, hemicellulose, fructose, glucose), squareroot- (NDF, ADF), fourth root (fat, total phenols, total tannins, condensed tannins), or sixth root-transformations (starch, sucrose). We also ensured that the pattern of correlation between two variables was similar within and across sites by visual inspection of scatter plots. Based on the distribution of missing data, patterns of correlations between variables and formal checks of whether PCA was justified (Kaiser-Meier-Olkin measures of sampling adequacy and Bartlett's test of sphericity; McGregor, 1992) we chose to run separate PCA on subsets of variables. These were i) NDF, ADF and ADL, ii) the monosaccharide's, and iii) total phenols and total tannins. All three PCA revealed a single principal component (PC) explaining 86, 96, and 99% of the total variance, respectively.

We tested for differences in nutritional value of mesocarp between sites using one-way ANOVA of the transformed variables (see above) or PC-factor scores as response variables. Because of a lack of data we could not include Gashaka when comparing sugars and antifeedants in this analysis. When the data did not fulfill the assumptions of this test (see below) we repeated the analysis using Kruskal-Wallis H-test but got essentially the same results.

We tested for differences in nutritional value of mesocarp between food and nonfood using two-way ANOVA (with site as the second factor) applied separately to each transformed variable or PC-factor score. Because of a lack of data we could include only data from Ngogo and Salonga in this analysis and also could not analyze condensed tannins and antifeedants. When the data did not fulfill the assumptions of this test we compared food with nonfoods, separately for the two sites, using Mann-Whitney U-tests but got largely comparable results.

We conducted ANOVA separately for each variable (or factor score). We checked for assumptions using Levene's

test of equality of error variances and by visual inspection of plots of residuals against predicted values. For post-hoc comparisons we used LSD multiple comparisons.

We tested for relations between variables using Pearson correlations applied to the potentially transformed variables (see above) and separately for each site. We tested whether correlations differed between sites using the procedure described in Zar (1999), which results in a χ^2 -distributed variable with degrees of freedom equaling the number of correlation coefficients minus one.

We controlled for multiple testing using Fisher's omnibus test. This procedure combines a number of P -values into a single χ^2 -distributed variable with degrees of freedom equaling twice the number of P -values (Haccou and Meelis, 1994). In case of correlations we also derived a combined P -value by testing whether correlation coefficients were on average zero using one-sample t -tests.

We calculated ANOVA, PCA, and correlations using SPSS 15.0 for Windows, tests comparing correlations using a self-written script for R (R Development Core Team, 2008) and Fisher's Omnibus test by hand.

RESULTS

Nutritional quality of fruits

Overall, sites clearly differed with regard to nutritional parameters of fruit samples (Fisher's Omnibus test combining one-way ANOVA: $\chi^2 = 50.6$, $df = 22$, $P < 0.001$). Individual tests revealed significant differences between the sites in the concentrations of protein ($F_{3,97} = 3.96$, $P = 0.01$), sucrose ($F_{2,86} = 8.43$, $P < 0.001$), starch ($F_{3,95} = 3.39$, $P = 0.021$), and condensed tannin ($F_{3,61} = 2.78$, $P = 0.048$). Pairwise post-hoc comparisons showed that samples from Ngogo contained more protein and less sucrose than samples from Salonga and Tai, and samples from Salonga more starch than samples from the other three sites (Fig. 2a). The concentrations of other macronutrients were not statistically different across sites (Fig. 2a) nor were the concentrations of digestible and nondigestible fiber components (Fig. 2b), and concentrations of antifeedants other than condensed tannins (Fig. 2c). Concentrations of condensed tannins were higher in Gashaka compared to the other three sites (LSD: all $P < 0.05$; all other comparisons: $P > 0.05$; Fig. 2c). In spite of the multiple differences in nutrient composition, the average gross energy content of fruits was similar across sites, ranging between 18.2 ± 1.48 kJ g^{-1} dry matter at Ngogo and 20.0 ± 4.78 kJ g^{-1} dry matter at Gashaka.

Leaves had a higher protein content than fruit (Fisher's omnibus test: $\chi^2 = 58.3$, $df = 6$, $P < 0.001$). However, compared to fruit eating, records on the consumption of leaves from trees and woody climbers were relatively rare (Ngogo: $N = 29$, Salonga: $N = 62$, Gashaka: $N = 11$), and thus the contribution of leaves to dietary protein may be limited in these populations.

Food versus nonfood items

Comparison of food items and nonfood samples was constrained by our ability to identify those species that were never eaten and those that were not eaten during the time of sampling but might be consumed at other times. Overall nutritional contents of food and nonfood species differed (Fisher's omnibus test: combining ANOVA: $\chi^2 = 37.6$, $df = 18$, $P = 0.004$) and there was no

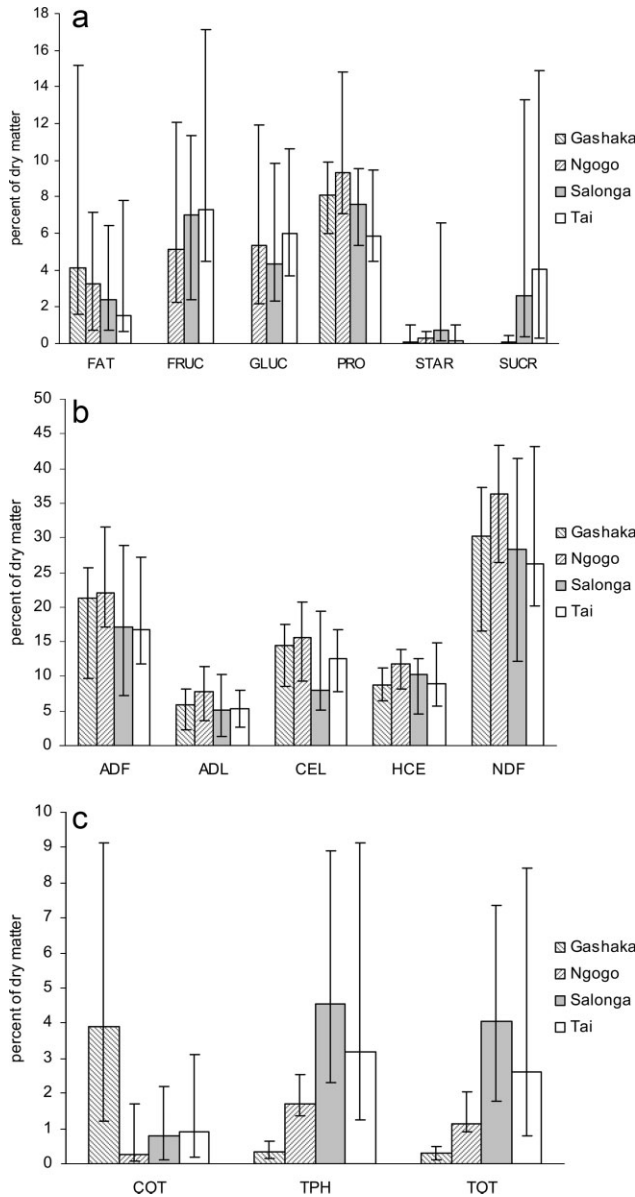


Fig. 2. a: Concentration of macronutrients in all fruit samples ($N = 217$) expressed as percent of dry matter in plant fruit samples collected at the four sites. Values are medians and quartiles. FAT = crude fat, FRUC = fructose, GLUC = glucose, PRO = crude protein, STAR = starch, SUCR = sucrose. b: Concentration of fiber components in all fruit samples ($N = 217$) expressed as percent of dry matter (ADF = acid detergent fiber, ADL = acid detergent lignin, CEL = cellulose, HCE = hemicellulose, NDF = neutral detergent fiber). c: Concentration of anti-feedants in all fruit samples ($N = 217$) expressed as percent of dry matter in plant food samples (COT = condensed tannin, TPH = total phenol, TOT = total tannin).

recognizable interaction between this factor and site ($\chi^2 = 22.3$, $df = 18$, $P = 0.22$). Food species contained higher amounts of sucrose (ANOVA: $F_{1,50} = 5.51$, $P = 0.023$) and monosaccharide (ANOVA: $F_{1,50} = 5.08$, $P = 0.023$), and lower amounts of fiber (ANOVA: $F_{1,42} = 5.59$, $P = 0.023$), and tended to contain lower amounts of anti-feedants (ANOVA: $F_{1,42} = 3.89$, $P = 0.055$).

Relationship between protein and nonstructural carbohydrates

The relationship between protein and nonstructural carbohydrates in those fruit samples eaten by *Pan* at Salonga, Ngogo, and Tai was explored with parametric correlations between a) protein and monosaccharide (i.e., the PC-factor score), b) protein and disaccharides, and (c) protein and starch. These analyses revealed that the concentration of protein was independent of that of mono-, disaccharides, and starch (Fisher's omnibus test: $\chi^2 = 18.45$, $df = 18$, $P = 0.43$).

Protein and fiber

There was no obvious correlation between protein and ADF (Fisher's omnibus test: $\chi^2 = 5.93$, $df = 8$, $P = 0.66$). At Salonga, ADF tended to increase with protein content (Pearson correlation: $r_p = 0.32$, $P = 0.09$, $N = 28$) but at the other sites, fiber content appeared to be independent of protein (Gashaka: $r_p = -0.18$, Ngogo: $r_p = 0.01$, Tai: $r_p = -0.01$; all $N \geq 10$, all $P > 0.6$).

Nutrient content and energy

Overall, there was a positive relationship between nutrient content and energy (Fisher's omnibus test combining correlation conducted separately for each site, and for fat, protein, starch, sucrose, and the monosaccharide: PC-factor-score: $\chi^2 = 106.3$, $df = 36$, $P < 0.001$; one-sample t -test of correlation coefficients: average $r_p = 0.23$, $t_{17} = 2.2$, $P = 0.042$). In food samples from all four sites, there was a significant positive correlation between energy and crude fat (average $r_p = 0.82$, Fisher's omnibus test: $\chi^2 = 65.6$, $df = 8$, $P < 0.001$, Fig. 3a) and there was also a consistent trend for a positive correlation between energy and protein (average $r_p = 0.50$, $\chi^2 = 17.2$, $df = 8$, $P = 0.028$, Fig. 3b). Correlations between gross energy content and various macronutrients did not obviously differ between sites (Fisher omnibus test, combining five tests comparing correlations: $\chi^2 = 7.69$, $df = 10$, $P = 0.66$). Also none of the individual comparisons between correlation coefficients obtained for different sites revealed significance (all $P > 0.1$).

Association between macronutrients and anti-feedants

There was no correlation between nutrient content and anti-feedants (correlations, separately for each combination of nutrient and anti-feedant and separately for each site, Fisher's omnibus test: $\chi^2 = 69.5$, $df = 62$, $P = 0.24$). Moreover, only 2 out of 31 such correlations revealed significance (Binomial test: one-tailed $P = 0.46$) and 19 of these correlations were negative whereas 12 were positive (Binomial test: $P = 0.28$).

Temporal variation in nutrient and energy supply

Information on the temporal variation of food species is available only for three sites. Independent of the type of macronutrient, consumers at Ngogo and Salonga had access to one or more high quality resources (percent dry matter value above median) for every month (Table 3). This contrasts with Gashaka where access to high quality sources was constrained. Here time periods with high quality food sources ranged from 10 months (for starch) to 6 months (for protein). At Salonga and Ngogo, high

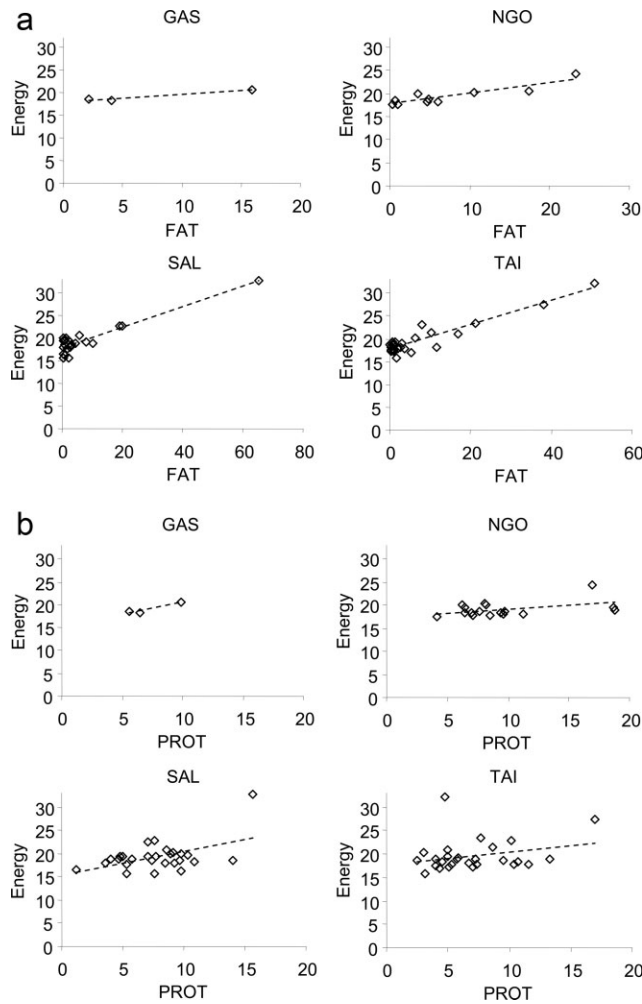


Fig. 3. a: Correlation between crude fat and energy in mesocarp of fruit consumed ($N = 169$). Regression lines are shown for illustrative purposes (tests conducted were correlations based on transformed data). b: Correlation between crude protein and energy content in fruits consumed ($N = 169$).

energy food sources were available throughout the year while at Gashaka the supply with high energy resources was restricted to 3 months.

DISCUSSION

The results of this study indicate significant differences in nutritional ecology across habitats. Samples from the four sites differed in terms of protein, nonstructural carbohydrates, and condensed tannins (Fig. 2a–c). However, these differences disappeared when we considered only samples from fruit that were actually eaten during the study periods. Food samples were also similar in terms of the association between different components (e.g., protein versus nonstructural carbohydrates) as well as in terms of the density of macronutrients, with crude fat showing the strongest positive correlation with crude energy of all macronutrients. Between-site differences were found in terms of the availability of high quality fruit over time but this difference did not separate eastern from western habitats. According to our data, the habitat occupied by bonobos fell into the range of those of chimpanzees. Samples from Ngogo (eastern

TABLE 3. Figures indicate the number of months offering one or more plant food sources containing above-median concentrations of macronutrients

	Gashaka	Ngogo	Salonga
Crude protein	6	12	12
Fructose	–	12	12
Glucose	–	12	12
Sucrose	–	12	12
Starch	10	12	12
Crude fat	8	12	12
Energy	3	12	12

chimpanzees) contained more protein than samples from any other site, while samples from Tai (western chimpanzees) and Salonga (bonobos) had higher concentrations of nonstructural carbohydrates.

Other between-site differences concern the high content of sucrose and starch, at Tai (western chimpanzees) and Salonga (bonobos) and the high levels of condensed tannins in Gashaka (Nigerian chimpanzees). Nonstructural carbohydrates are considered important sources for energy and there is ample evidence that foraging and food selection by primates and other frugivorous vertebrates is affected by the sugar content of fruit (Ungar, 1995; Remis, 2002). If the fruits of plants at Tai and Salonga do contain higher amounts of nonstructural carbohydrates, it is expected that chimpanzees and bonobos at these sites should exploit this source, as they appear to do. Starch also has generally been considered a rich source of energy, but recent studies suggest that low amylase activity may constrain the digestibility of this polysaccharide by *Pan* (Perry et al., 2007). Moreover, during ripening, starch and other components of cell walls undergo modifications (Prasanna et al., 2007), a source of variation that could not be considered in our datasets. Therefore, we cannot exclude the possibility that some of the differences observed between sites are due to sampling biases, based on differences in the specific stage of ripeness.

Foraging strategies reflect efforts to optimize the intake of nutrients and energy and in habitats that are variable in resource quality, individuals should move towards areas offering more profitable foraging areas (Partridge, 1978). While studies on social ungulates support the predicted relationship between resource distribution and travel patterns (Main, 2008), evidence from primates is still rare. Notable exceptions are positive correlations between population densities of folivorous lemurs and African colobines and protein content in leaves available in different forests (Ganzhorn, 1992; Wasserman and Chapman, 2003). Does the same relationship apply to the largely frugivorous populations of *Pan* described here? Information on population densities of the four *Pan* populations included in this study is incomplete, and exploring this question remains a topic for future work.

Although the results of this study do not match the proposed patterns of geographic differences in habitat quality, they nonetheless indicate significant variation in terms of nutritional ecology of *Pan* across habitats. Given the differences in nutritional ecology and the similarity of nutritional parameters of fruit that were eaten, habitat quality alone appears to be a poor predictor of diet quality. Comparing data from two geographically distinct gorilla populations, Rothman et al. (2007) found that, in spite of striking differences in habitat ecology,

the nutritional quality of foods was very similar. If consumers experience equal gains in spite of variation in ecology, one would expect to observe differences in population density and resource competition. Evidence for habitat-related variation in the social behavior of neighboring groups with overlapping home ranges comes from studies on lemurs and colobus monkeys (e.g., Curtis, 2004; Grassi, 2006; Harris and Chapman, 2007). Comparing data on social organization, activity budgets, and diet composition from a large number of savanna baboons, Kamilar (2006) found that variation of diet composition among geographically separated subspecies did not exceed variation within subspecies. This suggests that to demonstrate between-population differences, comparative data from multiple groups are required that represent the range of within population variation. Most studies on *Pan* represent information from a single community and data from the only site that offers information from multiple groups suggest variation in the behavior of neighboring communities (Boesch et al., 2006). Groups living in close proximity, such as chimpanzees at Kanyawara and at Ngogo, two sites that are separated by 10-km distance, seem to show more variation than groups that are separated by hundreds of kilometers. Taken together, although parameters of habitat ecology vary across landscapes, diet quality among *Pan* populations may be very similar. High quality habitats appear to exist across the African continent and the differences between bonobos and chimpanzees may be within the range of variation of different chimpanzee populations.

Although some of the results of our study require further verification, the data nonetheless shed new light on food habits of chimpanzees and bonobos, and on the nutritional ecology of forest habitats across Africa. Considering the differences in nutritional ecology between sites inhabited by *Pan* species one may ask what are the implications of these data for understanding and interpreting intra- and interspecific differences in behavioral ecology in *Pan*? Answering this question is beyond the goal of this study, but the information on the nutritional ecology of the four *Pan* populations presented here may aid future attempts to explain the differences in behavioral ecology of *Pan* among sites.

Other aspects have to be taken into account to assess the significance of variation of single diet components. Combining the information on the nutritional ecology with data on phenology and forest composition will facilitate quantitative assessments of nutrient supply and its temporal variation. Information on the protein requirements and the digestive efficiency of the two *Pan* species will also be required to explore variation in energy balance and the relationship between nutrition and population dynamics of bonobos and chimpanzees. In addition, data from other food items such as terrestrial herbs and animal food are required. Information on the chemistry of terrestrial herbs from the same sites that are currently analyzed by us will provide a more comprehensive picture of nutritional ecology and diet quality of these *Pan* populations.

Regardless of these drawbacks, the results of the current study do not suggest that bonobos and chimpanzees are exposed to a consistently different nutritional ecology, nor do they confirm the proposed dichotomy between East and West Africa. Given that fruits from trees and climbers constitute the largest proportion of plant food in the diet of both *Pan* species, differences in nutrient

supply, if they exist, must come from other food sources such as herbs and animal food. The results of our study do not prove the absence of between-population differences but highlight the importance of other aspects of food supply. Variation in the availability of macronutrients and other nutritionally relevant components adds to the complexity of the ecological framework that determines patterns of gregariousness, resource competition, and habitat use. Consideration of the quality of resources within existing models of primate socioecology will enhance our understanding of what resource members of a given community are likely to compete for and how this competition affects the fitness of consumers.

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