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Methods in Primate Nutritional Ecology: A User's Guide

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Abstract An important goal of primatology is to identify the ecological factors that affect primate abundance, diversity, demography, and social behavior. Understanding the nutritional needs of primates is central to understanding primate ecology because adequate nutrition is a prerequisite for successful reproduction. Here, we review nutritional methods and provide practical guidelines to measure nutrient intake by primates in field settings. We begin with an assessment of how to estimate food intake by primates using behavioral observations. We then describe how to collect, prepare, and preserve food samples. Finally, we suggest appropriate nutritional assays for estimating diet nutritional quality and point to the merits and limitations of each. We hope this review will inspire primatologists to use nutritional ecology to answer many unresolved questions in primatology.

Keywords Energy · Feeding ecology · Near-infrared reflectance spectroscopy · Protein

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Introduction

An important goal of primatology is to decipher the ecological factors that influence primate abundance, diversity, life history, and social behavior. Nutritional ecology is at the core of these questions because primates must acquire adequate nutrition under a suite of environmental and social constraints to reproduce successfully (Cameron 1996). For example, insights into nutritional ecology not only provide understanding of determinants of diet selection or patch choice (Leighton 1993), but also contribute to broader questions, including hypotheses about the diversity of primates across continents (Ganzhorn *et al.* 2009) and primate niche separation (Conklin-Brittain *et al.* 1998; Ganzhorn 1988; Milton 1981). Further investigation into nutritional ecology may lead to new insights with respect to competitive regimes and sociality (Isbell 1991; Janson and van Schaik 1988; Sterck *et al.* 1997). For example, higher ranked female gray-cheeked mangabeys (*Lophocebus albigena*) did not compete over fruit but did show agonism when eating bark, which is sodium rich (Chancellor and Isbell 2009; Rode *et al.* 2003). Knowledge of a species' or a population's specific nutritional goals can be important in the construction of informed conservation or restoration plans for endangered species (Chapman *et al.* 2004; Felton *et al.* 2010). For example, the protein-to-fiber ratio of mature leaves in a habitat is a good predictor of the biomass of colobines across forests (Chapman *et al.* 2004; Fashing *et al.* 2007), and forest managers could use information about a species' nutritional needs to pinpoint specific trees and areas to protect (Chapman *et al.* 2004; Felton *et al.* 2010).

We here review the methods for measuring nutrient intake by wild primates. We begin with an assessment of how to estimate food intake by primates. We then describe how to collect, prepare, and preserve food samples. Finally, we suggest appropriate nutritional assays for estimating diet nutritional quality. This article is not intended to be a complete manual of primate nutritional ecology and associated laboratory methods, but rather to point readers to potentially valuable approaches and methods. We stress that it is important to outline the exact question that will be addressed so that methods can be tailored (Felton *et al.* 2009a). For further information we suggest a few excellent textbooks: Van Soest (1994), Barboza *et al.* (2009), and Robbins (1993).

Before embarking on research that involves collecting and processing primate foods for nutritional analysis, it is important to realize that most countries require explicit permission to collect, export, and import wildlife samples, including plants. It is critical to obtain this proper documentation; otherwise samples can be held up at country borders, or confiscated and destroyed. Unfortunately, obtaining proper permits takes time. For example, we work in Uganda, and import plant, insect, fecal, and urine samples to the United States and Canada. In Uganda, in addition to obtaining permits to conduct research, explicit written permission is required before collection of wildlife or their products. When exporting samples, a material transfer agreement is needed and fees are paid according to the amount of material removed. After collection and before export, the samples must be inspected. After inspection, it takes ≥6 wk for an application to be approved. These are all reasonable requests made by the host country, just as obtaining Animal Care approval is appropriate for the study of primates (Fedigan 2010). Primatologists should inquire about the

procedures in their country of interest and budget their travel itineraries accordingly. If researchers do not follow rules and export samples illegally, it impacts all of the research community because countries will be reluctant to allow any samples to be exported in the future. To import samples into the United States, one needs permits from the United States Department of Agriculture (USDA) for plants and insects, and there are similar requirements for Canada. Primate fecal material requires a separate permit from the Centers for Disease Control (USA) and Public Health Agency of Canada. In our experience, it can take 3–4 mo for such permits to be processed. Similar regulations are probably applicable in other countries. We found that the more physically processed the samples are, the easier it is to obtain permits. At present in the United States and Canada, if plant samples are dried and milled before import, a permit is not needed, though a letter stating this from the appropriate agency is helpful for export and at customs. Similarly, if fecal samples are not infectious, a permit is not necessarily required, though a letter stating this is again helpful. Thus, we suggest drying and milling samples before export. In addition, this advance processing also helps to prevent mold and pathogens that can affect analyses.

In the Field

Behavioral Methods

The selection of methods to quantify a behavior represents a tradeoff between the amount and quality of the data that can be obtained. There are many descriptions of the costs and benefits of different approaches (Altmann 1974; Martin and Bateson 1986), and we do not attempt to describe these methods. Full-day continuous focal follows are ideal to obtain a robust sample of the daily nutrient intake (Felton *et al.* 2009a; Knott 1998). However, this method is dependent on the ability to obtain a large sample of complete days for each subject under study because if a day is not representative of the study period, e.g., it is raining or the subject is sick, it may be misleading and obtaining more samples during shorter periods of time might be more appropriate. Frequently it is logistically unfeasible to conduct a full-day follow because of poor visibility or government regulations (Rothman *et al.* 2008b). In these instances it may be appropriate to conduct short focal follows with quantified food intake combined with scan samples (of the group or individual or both) to estimate the overall amount of time feeding (Janson and Vogel 2006; Rothman *et al.* 2008b).

Food Intake

To measure nutrient intake, it is essential to determine the amount of food, i.e., in grams, an individual consumes rather than the time it takes to consume a particular food item. Time spent feeding is an excellent indicator of foraging effort but a poor indicator of nutrient intake (Chivers 1998; Zinner 1999). Measures of feeding time can be misleading because an easily processed food item may take little time to prepare in relation to mass consumed, or conversely, a hard to chew item might take a longer time to consume with little mass intake. Accordingly, various field studies have demonstrated the discrepancy between feeding time and ingestion amounts

(Chivers 1998). Researchers have used various ways to estimate the mass of food consumed; the most popular are bites (Oftedal 1992; Rode *et al.* 2006; Watts 1984) and units (Altmann 1998; Muruthi *et al.* 1991; Rothman *et al.* 2008b; Vogel 2005). To estimate the number of bites, the observer counts the number of times the subject takes a bite of food, and estimates the mass of bite size. Because bite sizes can be variable among individuals, i.e., larger males may have bigger bites than females and juveniles (Perry and Harstone-Rose 2010), we recommend using unit counts instead of bites. With unit counts, the observer uses a predefined measurement (a leaf, fruit, particular length of bark, etc.) and notes each time the subject consumes the measured quantity. When intake data are not available for every observation, mean feeding rates can be used, or a functional response curve can be used to estimate feeding rates (Rode *et al.* 2006; Shipley *et al.* 1994; Spalinger and Hobbs 1992). Feeding rates differ not only among food items, but also as primates deplete patches or become satiated or as a function of dominance; thus counting the number of bites/units over the duration of the feeding bout will provide more precise estimates (Chivers 1998; Snaith and Chapman 2005).

After consumption, representative samples of the same unit are collected and weighed to the nearest 0.01 g. For example, if a primate eats a leaf, a single leaf may be considered a unit. Similarly a single fruit, or a cluster of fruit, can be considered a unit for analysis. For bark, stems, and pith the approximate dimensions of the food eaten are estimated from food remains left behind, e.g., the length and width of bark removed from a tree trunk (Knott 1998). The mean unit weight provides an estimate of the mass of the food item, and we suggest recording ≥30 individual unit weights for each food item to assess the variance of the mass. To account for seasonal variation in unit mass and intraspecific variation in plant morphology, we suggest this measurement be taken at least once a month for long-term nutritional ecology studies, particularly those assessing seasonal and spatial variability, if the food item is a staple component of the diet. These weights should be collected immediately after collection, providing a wet mass, so that nutrients can be determined on an as eaten basis and moisture can be calculated.

To measure nutrient intake, the numbers of food units per unit of time are converted to dry weight intake and multiplied by the food's nutritional composition, which is expressed as a percentage of dry or organic matter. These values are summed for the day or scaled to the appropriate time frame. If primates are feeding during travel or other activities, this should be factored into estimates of nutrient intake; e.g., mountain gorillas (*Gorilla beringei*) "snack" while traveling (Rothman *et al*. 2008b). Several primate studies have estimated nutrient intake and provide equations for doing so (Knott 1998; McCabe and Fedigan 2007; Rothman *et al.* 2007; 2008b), and outlining the calculations employed in these estimations is essential (Harrison *et al.* 2009).

Collecting Samples

Whenever possible, samples should be collected from the same plants eaten by the primates under study because the nutrient content of plants within a single species can vary over different spatial and temporal scales. For example, depending on location, young leaves of the same species eaten by monkeys in Kibale National

Park, Uganda varied in protein content from 22% to 47% (Chapman *et al.* 2003) and the fat content of a single species of ripe fruit varied seasonally from 0.3% to 30.0% (Worman and Chapman 2005). Fruits in Kibale also varied in dry weight according to canopy height (Houle *et al.* 2007), and in Madagascar, sun-exposed leaves had more protein than shaded leaves (Ganzhorn 1995). The nutritional components of terrestrial herbaceous vegetation eaten by mountain gorillas are highly variable (Rothman *et al.* 2009a). For example, depending on its location, samples of *Triumfetta tomentosa* collected in a single month over a range of locations varied in protein from 17.4% to 28.2%, and neutral detergent fiber from 26.1% to 44.8% on a dry matter basis (Rothman *unpubl. data*; Fig. 1). This striking intraspecific

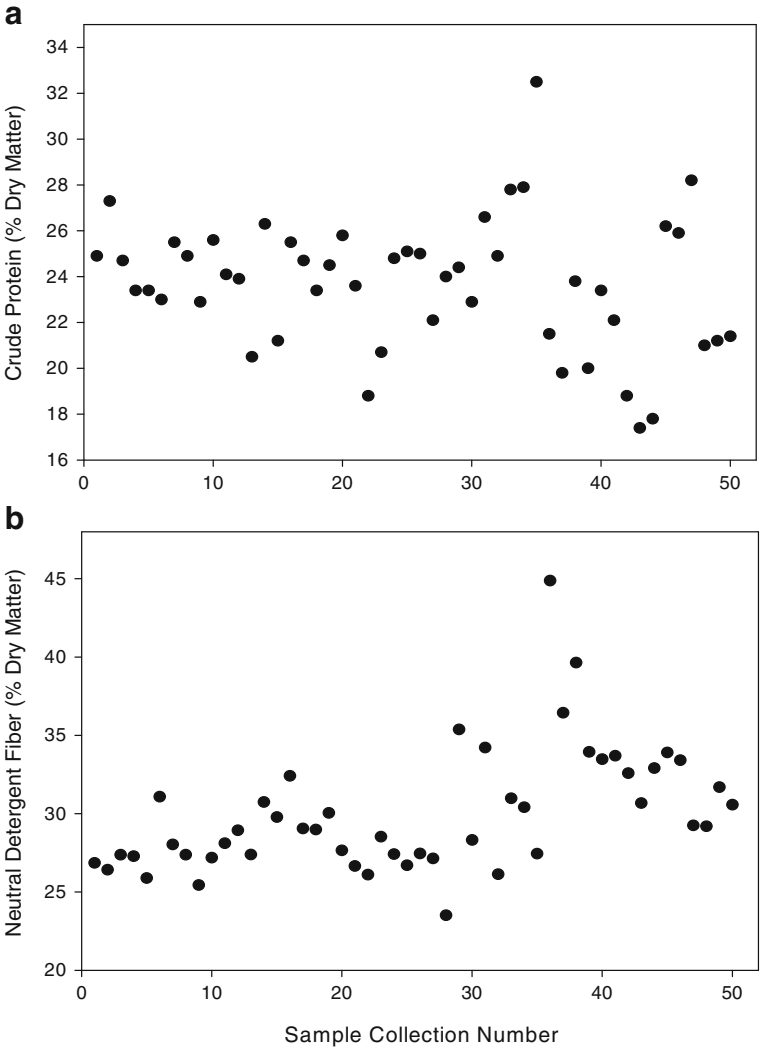

Fig. 1 Intraspecific variability in the **(a)** crude protein and **(b)** neutral detergent fiber concentrations of 50 samples of *Triumfetta tomentosa*, a staple food of *Gorilla beringei*. We collected these samples in a variety of areas throughout the home range in June 2003.

variability implies that it will introduce considerable error when a single collection of a particular species is used to represent the nutritional parameters of multiple food items, as subjects may discriminately select foods with specific nutrient qualities. Thus, to estimate nutrient intake, we strongly advocate, where possible, collecting samples from the same plant from which the subject was feeding, at the same time of day, and within a few days of when it was consumed. It is essential to collect the exact stage of food eaten because differences in, e.g., fruit ripeness can have strong effects on nutritional composition. For example, ripe fruits eaten by chimpanzees (*Pan troglodytes*) and cercopithecines are higher in sugar and fat than unripe fruits (Conklin-Brittain *et al*. 1998).

Because accurate sampling requires numerous samples to be collected, we suggest primatologists consider using near-infrared reflectance spectroscopy to process a large number of samples effectively and reduce time and laboratory costs (Rothman *et al.* 2009a). If time and finances are not available to process individual samples, we suggest numerous collections be combined to get a representative sample of foods in different seasons and microhabitats. Taking subsamples and mixing them means that some sources of variance are not estimated, but this will likely approximate the average nutritional composition of a food item.

The physical collection of primate food samples can be logistically difficult. Terrestrial foods can be easily collected using a machete or plant pruners. Tree saws and poles can be used to extract arboreal foods. We also recommend opportunistic collection when primates drop branches from which food samples can be obtained. There are also various tree climbing techniques that can be used to collect samples (Houle *et al.* 2004). Insects comprise a high portion of some primate diets (Dammhahn and Kappeler 2008; Isbell 1998), but they are rarely analyzed for their nutritional composition because they are very difficult to collect (*cf.* Deblauwe and Janssens 2008). Insect collections are typically opportunistic but other methods can be employed (Janson and Chapman 1999; Ozanne *et al*. 2011). Primatologists should collaborate with entomologists to ensure proper identification of insects. In addition, entomologists often fog areas with insecticide and sort samples (Stork 1991); primatologists could then sample insects used as primate food for nutritional analysis after the samples are sorted, as the insecticide will likely not impact the nutritional chemistry of the insects.

Estimating the amount of material to collect is dependent on the types of analyses needed. We suggest that researchers collect ≥30 g of dry weight of material for analysis. This provides 1–2 g for each macronutrient assay, with some to spare in case of loss of sample during milling, the need to run samples multiple times to obtain an accurate assessment, or accidents during the analysis. It is always better to have more sample than less. To collect 30 g of dry weight may require collections of up to 500 g wet weight depending on the food item's moisture content. Based on our experience, pith/stems contain the most moisture, whereas bark/wood contains the least (Rothman *et al.* 2006a).

Processing Samples

Researchers should process the samples in the way they were processed by the consumer. For example, if the consumer eats the leaf lamina, but not the leaf petiole, the petiole should be removed before weighing and nutritional analysis. If the consumer eats

only the pith of a stem and discards the outer herbaceous covering, this covering should be removed. This requires careful observation and meticulous, and often very time consuming, processing. Some items are more difficult to process; gorillas suck and spit out wood (Rothman *et al.* 2006b), and chimpanzees make wadges or quids whereby they extract (suction) juices from fruits, pith, and bark, and discard the fibrous component (Goodall 1986; Malenky and Wrangham 1994; Reynolds *et al.* 1998).

Whether to remove seeds from fruit in nutritional analysis should be dependent on the subject's feeding behavior and nutritional questions asked. If primates spit seeds then they should be removed before analysis. If the primates chew the seeds and puncture the seed coat, they are likely obtaining nutrients from the seeds, and so the seed should be included in the assessment of the fruit's nutritional quality. However, if the primate swallows the seed, the decision to include the seed is less clear. Although there is evidence that a portion of the seed is altered as it is passed through primate guts (Chapman 1995; Wrangham *et al.* 1994), the majority of the seed is not. Because seeds are typically high in protein and lipid, and the seed coat high in fiber, estimations of seeds in fruit samples will probably elevate estimations of fiber, lipid, and protein intake (Conklin and Wrangham 1994; Milton 2008; Urquiza-Haas *et al.* 2008). In addition, seeds fill the gut and reduce the amount of additional food the consumer can obtain. Where studies of diet digestibility are of interest, if seeds are included in the fecal sample (output) but not the diet intake (input), this will confound analysis (Rothman *et al.* 2008b). As we have stressed repeatedly, here again, fruit samples should thus be processed according to the question posed. In general, we recommend that primatologists obtain the total mass of the fruit, and the masses of the pulp and seed separately for each fruit to differentiate the contribution of seed in the fruit (Leighton 1993; Milton 2008). We also recommend that samples of the whole fruit, pulp, and seed are separated for analysis even when fruits are consumed whole. However, if is known that the seed is crushed and masticated along with the pulp, the entire fruit should be analyzed. It is important to note the processing procedure, and the rationale for this separation should be discussed when presenting nutritional data.

Drying Samples

It is rare to be able to analyze fresh samples because laboratories are typically unavailable at field sites, and so drying the sample before transport to the laboratory is necessary. The goals of drying primate foods are to inhibit enzymatic activity rapidly to prevent chemical and physical shifts and preserve the sample's nutritional attributes. In the agricultural and food science industry, freeze drying is thought to be the best way to preserve a sample in its current state. In this process, a sample is placed in liquid nitrogen, where it is stored until it can be dehydrated with a freeze dryer. However, the procedure requires a supply of liquid nitrogen, the ability to carry a liquid nitrogen tank to the field site, storage facilities for the liquid nitrogen, and a dry shipper, which keeps samples frozen at cryotemperatures during transport. The storage of large numbers of samples often makes freeze drying prohibitive. Consequently, few primate field studies have been able to freeze dry their samples (*cf.* Ganas *et al.* 2008; Hohmann *et al*. 2006; Sommer *et al*. 2011).

Because freeze drying facilities are not often available, numerous studies have evaluated the analytical biases encountered when using various drying methods and,

depending on the nutrient of interest, these should be consulted before deciding on a drying method. Samples should be quickly dried at or near 55°C to stop enzymatic activity and prevent the Maillard reaction, in which amino groups react with sugar (Deinum and Maassen 1994). This reaction, responsible for the toasting of bread and roasted coffee, will cause an overestimate of fiber and underestimate of soluble sugars (Van Soest 1994). If electricity is available at the field site, a drying oven may be used. We also recommend the use of inexpensive food dehydrators, such as Nesco® models, which have adjustable temperature control and multiple trays to hold and sort samples. Where electricity is not available, ovens can be made by storing samples in metal boxes over a charcoal stove where temperature is carefully controlled (Conklin-Brittain *et al*. 1998; Powzyk and Mowry 2003; Wrangham *et al*. 1998).

When samples will be analyzed quantitatively for secondary compounds such as flavonoids, tannins, and silicates, if freeze-drying is not possible, drying at ≤45°C out of sunlight is preferable (Julkunen-Tiitto and Sorsa 2002; Mueller-Harvey 2001; Palmer *et al*. 2000; Stewart *et al*. 2000). Light and heat can alter secondary compound composition (Cork and Krockenberger 1991; Waterman and Mole 1994), though ≥1 study demonstrated no differences in the stability of polyphenols dried at 60°C (Muetzel and Becker 2006). Qualitative tests (presence/absence) of secondary compounds are not as sensitive to temperature adjustments.

When samples are dried at ambient temperature, great care must be taken to avoid samples from molding, as its inclusion will dramatically alter sample nutritional composition. When there is no choice but to dry at ambient temperature, a desiccant with a color moisture indicator should be included in a sample container. This desiccant can be regenerated by heating in a cooking pan to restore function. However, this method has limited applicability for succulent fruits. Another method is to place samples directly in a preserving solvent, such as ethanol or methanol. Although some primate studies have successfully preserved samples in solvents (Powzyk and Mowry 2003; Remis *et al.* 2001), we do not recommend it because a liquid extract containing ethanol soluble carbohydrates is produced, and analyzing both the extract and sample is difficult. After drying, samples should be weighed to the nearest 0.01 g so that moisture can be estimated (see section on Dry Matter), and should be stored in plastic bags with desiccant in a dark area with low humidity, and labeled with a chemical-resistant marker. Ensure that the desiccant is packed within a permeable cloth (paper or cotton) so that it does not directly mix with the samples. We recommend that a small label be included inside the sample bag. There is no particular recommended shelf life for dried plant samples, and protein, carbohydrates, and minerals should be stable. Unsaturated fatty acids and some secondary compounds may oxidize during storage. However, we analyzed the same samples using the same methods after 10 yr and they retained the same results for protein, fiber, fat, and sugar (Rothman *unpubl. data*).

Laboratory Analysis

Milling Samples

Particle size is important in nutritional analysis because the size of a food particle will affect the reaction surface and thus the outcome of analyses (Hall and Mertens

2008; Mertens 1992). Samples can be ground by hand (with gloves to avoid inflating fat and salt values) to reduce bulk for storage, but need to be milled to a uniform size for analysis. Samples should not be ground via a mortar and pestle, or coffee grinder, because they will not produce uniform and known particle sizes.

Consideration should be taken in the type of mill used (Mertens 1992). Cutting mills such as the Wiley® mill control for particle size by allowing free fall of ground material through a uniform sieve. Cyclone mills such as the Udy® mill force grind plant material through a sieve at an angle. For standardization, most nutritional procedures suggest a Wiley® mill fitted with a 1-mm screen or delivery tube. It should be noted that the Wiley® mini-mill does not come standard with a 1-mm delivery tube; it must be specially ordered (no. 20 screen is 0.85 mm, and no. 16 is 1.19 mm). Because cyclone mills force material through a sieve, they tend to produce an average particle size that is smaller than cutting mills; thus when a cyclone mill is used, samples should be milled to 2 mm to achieve a similar particle size to samples ground with a Wiley® mill (Mertens 1992). Sample sorting will occur as the sample is handled. Sometimes very tough or "fluffy" material takes longer to go through the sieve. All efforts should be taken to obtain a milled sample that is representative of the original sample, so if some material does not go through the sieve, it should still be mixed in with the rest of the milled sample and analyzed regardless of particle size. Samples that are especially oily could be frozen in liquid nitrogen first, so that they will easily go through the sieve. If the samples are not mixed properly, sub-sampling can introduce very large errors in analysis. When milling the sample, as the material is passing through the sieve, one should use a bag or jar that is large compared to the size of the resulting sample. In this way, there is room to stir sample contents thoroughly to ensure uniformity. After the samples are milled, they should be stored in tightly sealed plastic bags or glass jars to avoid moisture and insect consumption. If a plant sample is particularly oily, samples should be stored in brown jars because sunlight can affect the oxidation of some fatty acids.

Measuring Macronutrients and Energy

Here, we review some of the recommended measures for estimating macronutrients in primate foods. We view our discussion as complementary to a review by Ortmann *et al.* (2006). We also direct readers to the AOAC Official Methods of Analysis, which provides detailed step-by-step protocols for most nutritional analyses and is currently available on the Internet. Before conducting any nutritional analysis, milled samples must be thoroughly mixed. During storage, heavier particles tend to settle toward the bottom of the container. Stirring a sample is much more effective than shaking it.

Dry Matter and Organic Matter

Moisture and the dry portion (or dry matter) of a food sample make up its weight. However, animals receive protein, energy, minerals, and vitamins only from dry matter. In addition, because a variety of factors can affect the moisture of a food sample, e.g., humidity, sample characteristics, it is necessary to account for any adsorbed moisture during nutritional analysis. Sample moisture should be calculated

so that an estimate of wet weight intake can be attained; this weight is the fresh weight as eaten, or is often termed the "as-fed" weight in agriculture. In addition, some primates may choose foods based on their water content, particularly if they are faced with a water-limited environment (Camperio Ciani *et al.* 2001). The moisture of food samples can vary greatly; e.g., gorilla foods vary from 7% to 97% (Rothman *et al.* 2006a).

To calculate a sample's moisture and dry matter, a 2-step process should be used including field and laboratory drying. In the field, the total sample should be weighed shortly after collection and before drying. This initial or field moisture content should be calculated by subtracting the sample dry weight from the fresh weight obtained shortly after collection in the field. Immediately before nutrient analysis, a portion or subsample (0.5–1.0 g) of the field-dried samples should then be dried at 105°C for 16 h in a forced air oven to remove any adsorbed atmospheric water to calculate a coefficient for determining the 100% dry matter of a sample (Goering and Van Soest 1970). This coefficient typically varies between 88% and 95% of the total sample weight. It is important that the dry matter coefficient be calculated on each day that the sample is prepared for analysis because local weather varies, which will affect adsorbed moisture.

Ash, or inorganic matter, represents the portion of the sample that does not contain organic matter. The same subsample used for dry matter calculations should be used to calculate the organic matter, or ash-free portion of the sample. This subsample is placed in a weighed, labeled (etched) beaker. It is then burned at 500–550°C and reweighed to provide an estimate of the minerals, soil, and dust contamination. Nutrient values can be expressed as a percentage of the dry matter, or organic matter (DM or OM basis, respectively).

Protein

Milton (1979) observed that howlers (*Alouatta palliata*) selected leaves that were higher in protein and lower in fiber than those avoided, suggesting that protein was an important criterion for leaf choice in folivores. To estimate protein intake by primates, it is important to consider not only crude protein, but also its digestibility and quality. Because animals do not require crude protein, but amino acids, the best approach to examine protein intake by primates is to estimate the amounts and types of amino acids in primate foods. Amino acid composition is analyzed via high-performance liquid chromatography (HPLC), which is based on separation of different amino acids based on their polarity. Few studies have analyzed the amino acid composition of primate foods (Curtis 2004), probably because amino acid analysis is quite expensive and requires a specialized technique. Most primate studies measure the crude protein, which is a measure of all the nitrogen in a sample. Because pure protein is typically 16% nitrogen, a conversion value of 6.25 is typically used to convert the amount of nitrogen in sample to its crude protein content; however, this value overestimates the amount of digestible protein. Only 60–70% of the crude protein in domesticated plant species is "true protein" that is composed of amino acids (Van Soest 1994), and in wild plants, the true protein content is probably even less (Milton and Dintzis 1981). Some of the nitrogen may be bound to the plant cell wall, i.e., fiber-bound nitrogen (Rothman *et al.* 2008a), and it is resistant to digestion by animal and microbial enzymes. Other nitrogen can

be bound to secondary compounds, particularly tannins, and thus rendered indigestible (Robbins *et al.* 1987a). Plants may also contain considerable amounts of nonprotein nitrogen in secondary compounds, i.e., alkaloids, glucosinolates, and cyanides, in nucleic acids or ammonia, or as products of amino acid catabolism. When crude protein is measured, all of these different types of nitrogen are counted as protein, even though they are not necessarily digestible. Because the 6.25 protein conversion is inaccurate in accounting for nonamino forms of nitrogen, studies have proposed adjustments to this factor to separate other N-containing fractions from true protein (Levey 2000; Milton and Dintzis 1981). However, it is not known whether these other conversion factors are too restrictive: in a study of tropical foliage, Conklin-Brittain *et al*. (1999) noted that a 4.3 correction factor probably underestimates protein digestibility. Thus, they consider a fiber-free protein an "optimist's" view of available protein estimation and a crude protein coefficient of 4.3 as a "pessimist's" view. Without better measures of nitrogen balance through carefully controlled feeding experiments, it is difficult to know how much protein is available. Fortunately, new methods are being developed to assess protein intake by primates and provide complementary approaches (Vogel *et al*. 2012).

To make good approximations of protein availability and quality, we recommend a few steps be employed. First, it is important to obtain an estimate of the crude protein in a sample through the Kjehdahl assay or combustion (AOAC methods 984.13 and 990.03; AOAC 1990). Second, researchers should estimate the portion of protein bound to fiber and indigestible (Licitra *et al.* 1996; Rothman *et al.* 2008a). This is accomplished by first following the steps to estimate acid detergent fiber (ADF) and then measuring the nitrogen that remains in the sample via Kjehdahl or combustion. Third, whenever possible, other nonprotein nitrogenous compounds should be measured using stabilized tungstic acid (Licitra *et al*. 1996; Martinek 1964). However, estimating the amino acids in a sample provides the most information about the quality of protein.

It is also worth mentioning that colobines, which have foregut fermentation, probably can subsist on lower quality protein than simple-stomached primates. Their forestomach provides a rich source of microbial protein, and microbes can use may many sources of protein that are unavailable to animals (Van Soest 1994). For example, in a study of protein utilization in hamsters and rats, the foregut-fermenting hamsters did not respond to amino acid supplementation while the rats did, suggesting that hamsters are less dependent on dietary protein quality than rats (Banta *et al*. 1975). A common assumption in the literature is that colobines should select high-protein diets (Chapman and Chapman 2002; Mowry *et al.* 1996); digestive physiology should factor more readily into these discussions.

Protein digestibility may be affected by tannins (Robbins *et al.* 1987a; Robbins *et al.* 1987b). Both condensed tannins (Glander 1982; Wrangham and Waterman 1981) and hydrolyzable tannins (Marks *et al.* 1988) have been shown to affect primate feeding behavior (*cf*. Barton and Whiten 1994; Chapman and Chapman 2002). However, the role of tannins in primate nutrition is not clear. Some primates, including humans, have adaptations to deal with tannins, such as proline-rich salivary proteins that bind tannins (Mau *et al*. 2009; 2011; Mole *et al.* 1990), and others host tannin-degrading microbes in the gastrointestinal tract (Frey *et al.* 2006; Kay and Davies 1994). To complicate this, discrepancies in analytical techniques make it

difficult to assess the quantities and biological activity of tannins. Several recent reviews highlight these challenges and offer ways forward (Foley and Moore 2005; Rautio *et al.* 2007; Rothman *et al.* 2009b). A popular practice in primatology is to use the acid-butanol assay (Chapman and Chapman 2002; Powzyk and Mowry 2003), but the standard used, "Quebracho," is not usually similar to the tannins within primate foods, leading to erroneous results (Rothman *et al.* 2009b). If this assay is employed, we suggest that primatologists purify tannins from plant species of interest, or report tannins in a qualitative fashion (Rautio *et al.* 2007; Rothman *et al.* 2006a; 2009b). Such qualitative methods can apparently be performed in the field (Lucas *et al.* 2011). A newly developed assay uses fungal cellulases to simulate gut microbes and polyethyene glycol to account for the potential effects of tannins on digestibility (DeGabriel *et al.* 2008; Felton *et al.* 2009b). This measure may provide a useful estimate of food digestibility when tannins are present. However, it should also be viewed cautiously because it is still unclear what physiological adaptations primates have for coping with tannins (such as salivary proteins), and fungal cellulases do not necessarily have functions similar to those of gut microbes (Mould *et al.* 2005).

Fat

High-fat foods are important energy sources for primates; their caloric value exceeds that of carbohydrates, protein, and any energetic returns from fiber (National Research 2003). Most plant foods do not have appreciable quantities of fat, aside from some fatty fruits and seeds, such as palms (Norconk and Conklin-Brittain 2004; Norconk *et al.* 2009), and fruits of *Virola* (>30%) (Milton 2008). The best way to assess the fat contents in a sample is to estimate its fatty acid composition, whereby fats are placed in a hydrophobic solvent, purified, esterified, and then analyzed via gas chromatography (Sukhija and Palmquist 1988). However, few studies have analyzed the actual fatty acid composition of primate foods (Chamberlain *et al.* 1993; Reiner and Rothman 2011), probably because this analysis is time consuming and expensive. Ether extract is a simple method that is commonly employed to estimate the crude fat in a sample. Although ether extract gives a crude measure of fats and is appropriate for the measurement of triglycerides, plants have nonfat components that are extracted by ether, such as wax, cutin, galactose, essential oils, chlorophyll, glycerol, and other compounds that cannot be saponified and that are frequently indigestible (Palmquist and Jenkins 2003). Forage leaves contained 5.3% fat as determined by ether extract, but 57% of the ether extract was composed of non-nutritive substances (Palmquist and Jenkins 2003). Thus, in the agricultural industry, it is recommended that one is subtracted from the percentage of ether extract in forage leaves to account roughly for these compounds when fatty acid analysis is not available (Palmquist and Jenkins 2003), and some have adopted this technique in primatology (Rothman *et al.* 2011). Using this method, if the ether extract of a sample is below 1%, it should be converted to 0.

Carbohydrates and Lignin

Carbohydrates are a major source of energy in primate diets. They fall into 3 umbrella categories: simple sugars, which include glucose and fructose, and their

conjugates; storage reserve compounds, which include starch, sucrose, and fructans; and the structural polysaccharides, which include the pectins, hemicelluloses, and celluloses (Van Soest 1994). In the animal nutrition literature, these plant compounds are divided into 2 categories: nonstructural carbohydrates and structural carbohydrates (plant cell wall). It is important to recognize that the nonstructural carbohydrates include both the storage reserve compounds and the simple sugars, but water-soluble carbohydrates include only the rapidly digestible part of this fraction that are soluble in water, including all of the simple sugars and a small fraction of the storage compounds (Van Soest 1994). Of the nonstructural carbohydrates, simple sugars are fully digested by animal enzymes and starches have high digestibility, whereas structural carbohydrates are indigestible by animal enzymes but may be fermented with the aid of symbiotic gut microbes.

Dietary fiber is typically considered the carbohydrate portion that animal enzymes cannot digest (Van Soest 1996). This portion includes structural carbohydrates that occur in the plant cell wall and are either insoluble (hemicellulose and cellulose) or soluble (gums, pectin, β-glucans, and various other carbohydrates such as fructans). The soluble fibers are probably completely available to most primates through fermentation. The fermentation of hemicellulose and cellulose varies with gut morphology and physiology and attributes of gut microbes hosted. The insoluble fiber, including hemicelluloses, i.e., 5-carbon sugars, is heterogeneous in its composition, whereas celluloses, 6-carbon sugars, are fairly homogeneous. Lignin is a structural component of the cell wall that is not well characterized chemically, but can be considered "the most significant factor limiting the availability of plant cell wall material to animal herbivores" (Van Soest 1994). A detailed overview of the carbohydrates and lignin is available elsewhere (Van Soest 1994), as well as a glossary of nutritional terminology (Conklin-Brittain *et al.* 2006).

Measuring the quantities of specific simple sugars such as glucose and fructose is usually performed via HPLC (Reynolds *et al.* 1998; Riba-Hernandez *et al.* 2005; Simmen and Sabatier 1996). Colorimetric assays are not adequate to separate specific sugars, but do provide a quantitative estimate of sugars in a sample. A common approach is to assess the total water soluble carbohydrates using colorimetric assays with a sugar standard such as the phenol–sulfuric acid assay (Dubois *et al.* 1956), which was developed for examining sea water. In animal nutrition applications, the protocol is typically modified; we suggest the modification of boiling a dry sample for 6 min in distilled water. Protocols are available for partitioning of most nonstructural carbohydrates and soluble fiber, such as starch and sugars (Hall *et al*. 1999). The current methods for estimating starch are outlined in Hall (2009), but researchers should also consider confounding compounds, such as antioxidants and tannins that affect results (Hall and Keuler 2009). To estimate the concentrations of soluble and insoluble fiber, the TDF total dietary fiber (TDF) method that is used widely in human nutrition can be used; it may be particularly helpful in identifying the portions of carbohydrates available to frugivores (Conklin-Brittain *et al.* 2006; Food and Nutrition Board 2005; Lee *et al.* 1992). Methods for particular soluble fibers, such as pectins, which are widespread in fruits and some tropical leaves, are also available (Milton 1991). In addition, we recommend using a specific analysis for total nonstructural carbohydrates (TNC: Hall *et al.* 1999). The TNC measure is frequently estimated by subtraction, whereby the grams or

percentages of neutral detergent fiber, protein, fat, and ash are subtracted from the total mass of the plant, or 100% on a percentage basis. This approach is adequate for a rough estimation of the nonstructural carbohydrates, but does not consider the secondary compounds, vitamins, and other minor components of foodstuffs. Another problem with this crude estimate is that any errors associated with the analysis of each portion (protein, fiber, fats) accumulate in the difference. These errors may be major. For example, fiber-bound nitrogen is measured twice, once in the crude protein component and again in the portion of fiber, which might result in substantial underestimation of TNC. To remedy this, researchers should subtract the fiber-bound nitrogen from crude protein. In addition, in high-fat foods, if fatty samples are not preextracted before NDF analysis, some of the fat might be measured twice, once in the NDF and again in the ether extract portion. These challenges highlight the importance of understanding the limits and merits of various analytical techniques.

To estimate structural carbohydrates and lignin, we recommend the detergent system of analysis, which is widely used to estimate the fiber contents of primate foods. An excellent flow diagram of the procedure is found in Van Soest (1994) and details are outlined for the fiber procedure in Van Soest *et al.* (1991) and lignin in Van Soest (1963). Neutral detergent fiber (NDF) is composed primarily of hemicellulose, cellulose, and lignin, while acid detergent fiber (ADF) is composed of cellulose and lignin. Lignin is removed from cellulose and hemicellulose by treating the remaining fraction with 72% sulfuric acid. The detergent analyses can be performed in a sequential fashion, whereby NDF is analyzed first, followed by ADF and lignin. Alternatively, if lignin or ADF is the only desired fraction, then the NDF step can be omitted, but the results will not necessarily be comparable with those for sequentially analyzed samples. It should be noted that if ADF is completed directly, and its value is higher than NDF of the same sample, this is likely to be due to the confounding effects of tannins, which are mostly removed during the NDF step. High-fat samples (>10%) should be preextracted in ether or acetone before NDF because lipids can interfere with the detergent.

All of the fiber fractions include minor components in their residues. Neutral detergent residues include cutin (portion of the waxy plant cuticle), a minor portion of residual ash, and hydrolyzable tannins that are not dissolved in the detergent solution. Acid detergent residue includes cutin, pectin, total silica, and tannin complexes (Van Soest 1994). Lignin may contain a small amount of residual ash and cutin. The potential impact of ash on fiber estimates should be considered; high-ash foods, e.g., some exudates >25% ash (Smith 2000) and nuts >40% (Tsuji and Takatsuki 2008), may artificially inflate fiber estimates because ash is only partially removed.

Energy

Primates need energy for basal metabolism, growth, lactation, and reproduction, and energy intake has been related to fitness for some primate species (Altmann 1998; Altmann and Alberts 2005; Karasov 1986; Nagy and Milton 1979; NRC 2003). The acquisition of energy is viewed as a fundamental facet of female competitive regimes among primates (Janson 1988; Janson and van Schaik 1988; Snaith and Chapman 2007; Sterck *et al.* 1997; van Schaik 1989), and higher ranking individuals are often

able to obtain more energy than lower ranking individuals (Koenig 2000; Vogel 2005). Seasonal energetic shortfalls may have large consequences for primates (Knott 1998). An excellent step-by-step guide to estimating energetic contributions to primate diets is available (Conklin-Brittain *et al.* 2006). Accordingly, we briefly reiterate many of the points addressed in their article, placing emphasis on what we view are a few key points.

There are 2 methods used to estimate energy intake (Conklin-Brittain *et al.* 2006; NRC 2003): 1) via actual energy measurements of foods and excreta via bomb calorimetry after carefully controlled feeding experiments and 2) via estimation of food intake and the energetic contributions of fat, carbohydrates, and protein. There are 3 main classifications of energy.

Gross energy is the total energy content of a food, which may be calculated as energy released after combustion in a bomb calorimeter. The amount of energy released in a food is noted by a concomitant increase in water temperature within the bomb calorimeter. The problem with using gross energy of food items as an indicator of what energy is available to the consumer is that not all energy within a food is digestible. For example, wood has a higher energy content than the same mass of sugar, but it is far less digestible. Many primate studies have used gross energy as a measure of energy available to primates (Ganas *et al.* 2008; Gould *et al.* in press). However, this measure is misleading because without accompanying measures of fecal energy, gross energy measures do not provide any indication of the energy received. In addition, a standard estimate of the digestibility of all foods is not adequate because foods differ in their fiber and lignin contents. Digestible energy is the fecal energy subtracted from the gross energy. In this case, known quantities of each food ingested must be coupled with estimates of the energetic values of feces. These studies have rarely been conducted in primates (*cf.* Edwards and Ullrey 1999a,b). Metabolizable energy is the urinary energy subtracted from the digestible energy, which provides an even finer estimate of the energy consumed.

In cases where it is not possible to estimate digestible energy via bomb calorimetry on foods and excreta, an approximation of energy gain is provided from physiological fuel values derived from human diets, which estimate metabolizable energy as additive amount of calories provided by 4 kcal $\cdot$ g^{-1} for carbohydrates, 4 kcal $\cdot$ g^{-1} for protein, and 9 kcal $\cdot$ g^{-1} fats. Although this is an adequate approximation for human diets, these values may not necessarily be appropriate for primates that eat very different foods and have different digestive physiology (Lambert 1998; NRC 2003). In particular, the energetic contributions from fiber fermentation need to be considered as in Conklin *et al.* (2006), because depending on the digestive anatomy and physiology of primates, these energy gains may be substantial (Edwards and Ullrey 1999b; Lambert in press; Milton 1998; Milton and McBee 1983).

To estimate the energetic contributions from fiber fermentation, we need knowledge of the primates' digestive anatomy and physiology, fiber content of the diet, and ability of the hosted microbes to ferment fiber. These factors are considered in a study by Edwards and Ullrey (1999b) in which they fed multiple monkey species different diets with varying fiber contents, and noted their apparent digestibilities after a feeding trial. On a high-fiber diet, the hindgut fermenters digested a mean of 47% of NDF and the foregut fermenters digested 77% of NDF.

To estimate the digestive coefficients (fraction of the ingested fiber that was fermented) of wild primates, we can use information gained from experimental feeding trials in which species are fed similar diet concentrations to that in the wild. For example, a feeding trial with chimpanzees on a diet of 34% NDF illustrated that they digested 54.3% of NDF (Milton and Demment 1988). This fiber coefficient can be used to estimate the energetic contributions from the fermentation of fiber in wild chimpanzees (Conklin-Brittain *et al.* 2006). When it is possible to estimate accurately estimate daily nutrient intake, feces can be collected, and dietary lignin is >5%, feces can be used as an internal marker to determine diet and fiber digestibility (Fahey and Jung 1983; Van Soest 1994). Using this approach, the diet and feces are analyzed for lignin content, and it is assumed that lignin is not digested. Consequently, NDF coefficients can be estimated and then incorporated into energy estimations (Rothman *et al.* 2008b). Another method is to culture and incubate fresh feces with food items as substrates to determine digestibility coefficients. This method has been used in studies of captive lemurs (*Varecia variegata*, *Eulemur fulvus*, *Hapalemur griseus*: Campbell *et al.* 2002), chimpanzees (Kisidayova *et al.* 2009), and orangutans (*Pongo abelii*: Schmidt *et al.* 2005). Here, fecal samples must be kept fresh so that microbial populations are preserved, which is challenging in the field.

Instead of using physiological fuel values derived from human diets, an alternative is to use the energetic equations developed for domestic animals. For example, for colobines, which have pregastric fermentation (Kay and Davies 1994), energetic equations based on small ruminants might be used (NRC 2007); however, without further research on colobine digestive ecology, we do not know if they are analogous to small ruminants (Milton 2006). For hindgut fermenters, humans are good models for comparison (Food and Nutrition Board 2005; Rothman *et al.* 2011), and energetic equations of swine might be helpful (NRC 1998; Rothman *et al.* 2008b).

Minerals and Vitamins

Little is known about vitamin and mineral requirements of wild primates, but recent work highlights their significance in primate diets (Fashing *et al.* 2007). For example, the soils of many tropical regions are sodium poor; thus primates in the tropics often have difficulty obtaining required sodium (Oates 1978; Rothman *et al.* 2006b). Sodium content of foods eaten by primates in Kibale National Park, Uganda was extremely low; no single food met the guidelines set by the NRC (2003), and sodium intake from the typical plant diet was well below suggested requirements throughout the year (Rode *et al.* 2003). Mineral analysis is typically preformed by ashing the sample and using atomic absorption spectroscopy. The principle of this method is that an aqueous solution of the minerals (sample ashed with acids) is heated to vaporize and atomize the minerals. Radiation beams are passed through the sample and the absorption of radiation is related to the amounts of different minerals in the sample, which can be differentiated by their absorption at different wavelengths. This technique requires specialized equipment, so primatologists usually send their samples to an outside laboratory.

The role of vitamins in primate diets is even less clear than that of minerals, but because primates eat diets that are fresh, and intentionally or accidentally consume

insects, they are probably not susceptible to vitamin deficiencies. Only a few studies have investigated a selection of vitamins in primate diets (Milton and Jenness 1987; Sterling *et al.* 1994), probably because vitamins are quite labile so samples need to be analyzed fresh. Liquid chromatography–mass spectrometry is now standard for vitamin analysis (Eitenmiller *et al.* 2007).

Near-Infrared Reflectance Spectroscopy

Given the diversity of primate diets and the intraspecific variability of foods within primate diets, methods used in agriculture and food sciences offer new options for primatologists for faster processing of primate foods. Near-infrared reflectance spectroscopy (NIRS) is a quick, nondestructive, and economical technology that can be used to assess the nutritional content of primate foods when large numbers of samples from the same habitat will be processed (Rothman *et al.* 2009a). The general principle of NIRS is that spectra are reflected based on the number and type of chemical bonds (C−H, N−H, etc.) in a sample when it is irradiated with near-infrared light. These spectra are then statistically calibrated against reference values, which are determined through traditional nutritional analysis, to develop multivariate regression equations that can then be used to estimate nutritional values for samples similar to those in the calibration set. With NIRS, up to 150 plant samples per day can be analyzed for multiple nutrients simultaneously after the spectrometer is calibrated with *ca.* ≥100 samples similar to those that will be analyzed. This offers a rigorous approach when sample sizes are numerous, and many similar samples need to be analyzed (Foley *et al.* 1998; Rothman *et al.* 2009a). In a preliminary study, NIRS was used to predict the N contents of bamboo eaten by lemurs (Ortmann *et al.* 2006), and in recent studies, NIRS was used to investigate the nutritional ecology of spider monkeys (Felton *et al.* 2009b) and mountain gorillas (Rothman *et al.* 2009a; 2011).

Conclusions

Milton's (1979, 1980, 1981, 1993) pioneering research on the differences in nutritional ecology of spider monkeys and howlers demonstrated that dietary adaptations had substantial implications for primate social behavior, sociality, and cognition. However, the field of primate nutritional ecology is still in its infancy. Despite the theoretical importance of energy in primate socioecological models, we know very little about primate energy intake (Conklin-Brittain *et al.* 2006; Vogel 2005) and the digestive ecology of both frugivorous and folivorous primates (*cf.* Campbell 2000; Caton 1999; Caton *et al.* 2000; Lambert 1998; Milton *et al.* 1980). Although protein-to-fiber ratios of the most common trees in the forest predict colobine abundance at multiple scales (Chapman *et al.* 2004), it is unclear what nutritional mechanism is driving this relationship because the protein content of mature leaves in these forests is high (Chapman *et al.* 2002) and primates do not require high-protein diets (Oftedal 1992); we need to unravel this "protein paradox" in the primate literature (Rothman *et al.* 2011). Tests of cognitive maps of a group's home range are often based on simple assumptions about nutrition, such as the

prediction that primates will choose the shortest distance between large high-energy fruit resources (Janson 2007). However, it is possible that animals are making deviations from expected patterns to be able to obtain particular nutrients (Harris and Chapman 2007; Link *et al.* 2011) or have complex decision rules dependent on both mental abilities and nutritional needs. Finally, we need to understand the role of ecology and phylogeny in shaping the evolution of primate feeding adaptations (Chapman and Rothman 2009). New frameworks of nutritional ecology such as nutritional geometry (Simpson and Raubenheimer 1999) and right angle mixture triangles (Raubenheimer 2011) will shed light on the nutritional priorities of animals; coupled with good nutritional methods and an understanding of physiological capabilities, these offer new approaches to understanding the patterns of nutrient intake by primates. We hope that researchers will use nutritional ecology to tackle new and longstanding hypotheses in primatology.

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