PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Nutritional Consequences of Foraging in Primates: The Relationship of Nutrient Intakes to Nutrient Requirements [and Discussion[

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Phil. Trans. R. Soc. Lond. B 1991 **334**, 161-170
doi: 10.1098/rstb.1991.0105

The nutritional consequences of foraging in primates: the relationship of nutrient intakes to nutrient requirements

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SUMMARY

Many studies have examined the proportion of time that primates devote to feeding on various types of food, but relatively little is known about the intake rates associated with each food. However, the nutritional consequences of foraging can only be interpreted by comparing nutrient intakes with estimated nutrient requirements. The energy available to primates from ingested foods will depend both on the composition of the food and the extent to which various constituents, including fibre fractions, are digested. Both human and non-human primates have relatively low requirements for protein as a consequence of slow growth rates, small milk yields and relatively dilute milk. Because the nutrient demands of growth and reproduction are spread out over time, it appears that primates do not need to seek out foods of particularly high nutrient density, except perhaps during weaning. Although food selection in some species of primates appears to be correlated with the protein concentration of foods, it is unlikely that high dietary protein levels are required, at least when foods of balanced amino acid composition (such as leaves) are included in the diet.

1. INTRODUCTION

Most primates are omnivores and consume a complex variety of foods. In a review of field studies of the diets of 131 primate species, Harding (1981) concluded that fruit was consumed by 90% of the species, soft plant foods (immature leaves, buds, shoots, flowers) by 79%, mature leaves by 69%, invertebrates by 65%, seeds by 41% and other animal foods (including eggs) by 37%. Yet despite the wide variety of foods eaten, the particular items selected represent but a fraction of the 'potential foods' available. The causal factors that have moulded the patterns of food selection and avoidance are undoubtedly diverse. Food choice may be influenced by energy needs, requirements for specific nutrients, constraints of the digestive system, digestion-inhibiting or toxic constituents in foods, difficulties in removing inedible components, degree of food clumping and dispersal, intra- and interspecific competition, and predation (see, for example, Milton (1980, 1984); McKey *et al.* (1981); Glander (1982); Altmann *et al.* (1987); Janson (1988)).

Regardless of the factors underlying food choice, foraging behaviour can be considered successful only if the diet obtained provides sufficient amounts of energy and other nutrients to fulfil the nutritional requirements of the forager. However, this seemingly simple criterion is hard to evaluate for free-ranging primates. In this paper I shall discuss some of the complexities in evaluating the nutritional consequences of foraging patterns in primates.

2. THE PROPORTIONAL CONTRIBUTION OF DIFFERENT FOODS

The seasonal pattern of food consumption by primates is usually determined by direct observation, unless dense vegetation so limits observation that other methods become necessary (see Calvert 1985). For example, in a study of feeding by red howler monkeys (*Alouatta seniculus*) in the llanos of Venezuela, we found that mature leaves accounted for 30% of the time spent feeding on major foods in the dry season, increasing to 67% in the wet season (M. S. Edwards, S. D. Crissey, O. T. Oftedal & R. Rudran, unpublished data). Flowers and young leaves were important in the dry season (31 and 14%, respectively) but not in the wet season (0 and 3%), whereas fruits were equally important in both the dry (25%) and wet (30%) seasons.

Although botanical categories are appropriate for ecological description of feeding behaviour, they may have little value in predicting nutritional composition. For example, the common notion that fruits are lower in fibre fractions and thus of 'higher quality' than leaves does not always hold (table 1; Calvert 1985; Barton *et al.* 1992). On a dry-matter basis the mean concentrations of neutral-detergent fibre (NDF), acid-detergent fibre (ADF), lignin and several minerals were remarkably similar among the various food categories consumed by red howlers (table 1). Moreover large variation occurred among foods in each category, especially with respect to protein, lignin, and calcium.

Phil. Trans. R. Soc. Lond. B (1991) **334**, 161–170
Printed in Great Britain

Table 1. *Percentage composition of the major food plants eaten by red howlers*[a]

	flowers ($n = 3$)	fruit ($n = 9$)	mature leaves ($n = 20$)	young leaves ($n = 5$)
dry matter	25.1 ± 4.86	23.7 ± 1.07	36.5 ± 2.23	32.2 ± 2.28
water	74.9 ± 4.86	76.3 ± 1.07	63.5 ± 2.23	67.8 ± 2.28
protein	14.4 ± 3.06	7.0 ± 1.12	16.6 ± 1.25	21.2 ± 3.76
fibre (NDF)	50.6 ± 3.22	53.8 ± 5.00	57.2 ± 1.89	54.4 ± 5.64
fibre (ADF)	35.8 ± 3.22	35.2 ± 4.55	40.5 ± 1.91	36.4 ± 6.28
acid lignin	17.1 ± 3.51	16.6 ± 2.43	20.4 ± 1.99	21.1 ± 5.34
calcium	0.49 ± 0.22	0.64 ± 0.17	1.36 ± 0.22	0.29 ± 0.07
phosphorus	0.30 ± 0.01	0.16 ± 0.05	0.14 ± 0.01	0.28 ± 0.06

[a] Major food plants are defined as those that collectively comprise 80% of observed feeding time in a particular month (M. S. Edwards, S. D. Crissey, O. T. Oftedal & R. Rudran, unpublished data). Data presented as mean ± s.e.m. Young leaves were distinguished from mature leaves on the basis of size, shape, colour and texture. NDF = neutral-detergent fibre, ADF = acid-detergent fibre (see Van Soest 1982); n = number of species, protein = (total nitrogen) × 6.25.

Table 2. *Examples of calculated ingestion rates of adult male red howlers at Hato Masaguaral, Venezuela*[d]

part…	flowers	ripe fruit	simple leaves	compound leaves
species…	*Pithecellobium saman*	*Mangifera indica*	*Ficus pertusa*	*Pithecellobium tortum*
rank[b]…	DS 1	DS 2	WS 1	WS 4
food intake[c]				
bite rate/(bite min^{-1})	14.3	7.8	12.6	6.4
bite size/(g per bite)	0.75	2.39	0.45	0.39
intake/(g min^{-1})	10.7	18.7	5.7	2.5
food composition				
dry matter (DM) (%)	20.2	20.3	30.2	39.2
protein (% DM)	19.8	4.1	12.2	22.0
fibre (NDF) (% DM)	47.4	21.0	49.1	59.2
calcium (% DM)	0.16	0.11	3.06	0.52
phosphorus (% DM)	0.30	0.04	0.08	0.08
nutrient intake				
dry matter (g min^{-1})	2.17	3.81	1.71	0.97
protein (g min^{-1})	0.43	0.16	0.21	0.21
fibre (NDF) (g min^{-1})	1.02	0.80	0.84	0.57
calcium (mg min^{-1})	3.5	4.2	52.3	5.0
phosphorus (mg min^{-1})	6.5	1.5	1.4	0.8

[a] Unpublished data of M. S. Edwards, S. D. Crissey, O. T. Oftedal and R. Rudran.

[b] Rank refers to relative importance in terms of percent of feeding time in dry (DS) and wet (WS) seasons: 1 = most important, 2 = second most important, etc.

[c] Bite rate data from field observations; bite size data from measurements on captive adult males at Hato Masaguaral (10–14 intake trials per plant part, greater than 10 bites per intake trial).

Within a plant species immature leaves are usually lower in fibre than are mature leaves (Milton 1979; McKey *et al.* 1981). However many primates appear to select leaves that are low in fibre fractions, regardless of the growth stage of the leaves (for examples, see Milton (1979); Oates *et al.* (1980); Glander (1981); McKey *et al.* (1981); Calvert (1985)). Thus there may be little difference in the fibre concentrations of the young and mature leaves actually ingested (table 1; Glander 1981).

3. MEASUREMENT OF FOOD INTAKE

Data on time spent feeding do not take into account the considerable differences in intake rate that may occur during feeding on different foods (Hladik 1977; Milton 1984). Food intake rates certainly vary in red howlers (table 2): in 1 min of feeding on large, ripe mangoes (*Mangifera indica*), red howlers ingest as much food (by mass) as when feeding on compound leaves of *Pithecellobium tortum* for 7.5 min. The high intake rate when feeding on ripe mangoes reflects the large bite size (2.4 g per bite). Flowers of the saman tree (*Pithecellobium saman*) are both large and quickly consumed (14 bites per minute). The twofold difference in intake rate of the two leaf types is due to the difference in bite rate (12.6 versus 6.4 bites per minute), not bite size.

Nutrient intake rates can be calculated from data on food intake and composition (table 2). Dry matter intake rate was highest for mango fruit, protein and phosphorus intake rates were greatest for saman flowers, and calcium intake rate was highest for fig (*Ficus pertusa*) leaves (table 2). Fibre intake rates were lowest when the monkeys were feeding on *Pithecellobium* leaves. These examples illustrate that maximum intake rate of a nutrient does not always occur when a primate feeds on the food item with the highest concentration of the nutrient. For example, red howlers feeding on fig leaves containing 12% protein achieved the same protein intake rate as when feeding on leguminous leaves containing 22% protein, although the howlers simultaneously ingested more dry matter, one third of which was NDF (table 2). The potential cost or benefit of the additional dry matter and fibre consumed depend on the digestibility of this material, whether it contains potentially toxic compounds, and whether the indigestible component exerts a negative, bulk-limiting effect on overall food consumption (Van Soest 1982).

4. THE ENERGY AVAILABLE FROM PRIMATE FOODS

Nutrient intake rates need to be related to the intake of metabolizable energy (ME), as maintenance of energy balance is the ultimate determinant of food intake (National Research Council 1978). Although total gross energy is easily measured in plant materials by bomb calorimetry, the proportion of this energy available to the animal may be highly variable, depending to a large extent on the amount, type and fermentability of fibre. Fibre fractions are resistant to mammalian digestive enzymes, but may be fermented by symbiotic microorganisms in the digestive tract, leading to net production of volatile fatty acids. Volatile fatty acids are undoubtedly an important energetic substrate for many primates, especially those species with specialized fore- or hind-gut fermentation areas (Bauchop & Martucci 1968; Milton & McBee 1983; Martin *et al.* 1985).

The fibre in plant materials is chemically complex, often including some readily fermentable carbohydrate (e.g. pectin), partially fermentable structural carbohydrate (e.g. cellulose and hemicellulose) and polyphenolic compounds that are thought to be completely indigestible (e.g. lignin). In the detergent fibre method of analysis, the NDF fraction represents the entire plant cell wall (other than pectin and some minor components that are solubilized in neutral detergent), whereas the ADF fraction represents cellulose and lignin (Van Soest 1982). Both fractions can constitute a large proportion of primate foods (table 1), making measurement of fibre digestibility an essential step in the assessment of metabolizable energy.

In captivity, folivorous or omnivorous primates consuming diets of relatively low fibre concentration (15–25% NDF, dry matter basis (DMB)) have been shown to be able to digest a large proportion of the fibre. For example, black and white colobus (*Colobus guereza*) digested 68–81% of NDF and 68–69% of ADF, whereas chimpanzees (*Pan troglodytes*) digested 71% of NDF and 57% of ADF (Oftedal *et al.* 1982; Watkins *et al.* 1985; Milton & Demment 1988). On higher fibre diets, digestibility of fibre fractions may be reduced, apparently due to more rapid passage of digesta through the tract. NDF and ADF digestibilities were only 54% and 33%, respectively, when chimpanzees were fed a manufactured diet containing 34% NDF (Milton & Demment 1988).

The manufacture of dry primate feeds involves mixing of ground ingredients, introduction of steam, and expression through an extruder under pressure. In the digestive tract, these feeds disintegrate into small particles, providing large surface area for attachment of microbes, thereby facilitating fermentation. The difference in physical form and the higher fibre concentration of many natural foods suggests that primates in the wild may not be able to digest fibre nearly as completely as the above experimental values suggest. Milton *et al.* (1980) estimated that mantled howlers (*Alouatta palliata*) digested only 24–42% of NDF when they were fed diets comprised of mixtures of natural foods (leaves and fruit).

Because human foods are typically low in fibre and high in digestibility, it is common in the United States to apply energetic factors of 4 kcal (16.7 kJ) per g protein and carbohydrate and 9 kcal (37.7 kJ) per g fat in estimating physiologically available energy in human diets (National Research Council 1989). In this system 'carbohydrate' percentage is estimated by difference (100 − (% water + % fat + % protein + % ash)) and hence includes fibre fractions. This system overlooks differences in the digestibility and fibre concentration of foods and is inappropriate for the natural foods eaten by primates. Even flowers and fruits may be quite high in fibre fractions (table 1). Insects also contain significant but variable amounts (8–27% of dry matter) of the relatively indigestible structural carbohydrate, chitin (Allen 1989).

Ideally, digestion trials should be conducted with each primate food to measure the amount of energy that can be extracted via digestive processes. We have been able to capture troops of free-ranging red howlers and adapt them to long-term studies in specially constructed cages in the field (Crissey *et al.* 1991; see also Milton (1980)). Unfortunately digestion trials are laborious and impractical for foods that are difficult to collect in the large amounts required for the trials. *In vitro* fermentation assays with rumen innocula or enzymic procedures that employ proteases and cellulases have been used to generate theoretical indices of digestibility for plant materials eaten by ruminants (Barnes 1973; Van Soest 1982). These procedures have also been applied to plants ingested by primates (see, for example, Oates *et al.* (1980); McKey *et al.* (1981); Calvert (1985)), with the implicit assumption that folivorous primates with fore- or hind-gut fermentation will digest foods in a similar fashion and to the same extent as a ruminant. However *in vitro* assays do not take into account important differences in tooth structure and function, gut morphology, rates of digesta passage, particle size segregation and other aspects of the digestive process. It is essential that *in vitro* indices be validated by digestion trials with the primate species of interest.

Any particular food will not be digested equally well by all primates. For example, Power (1991) has shown that the energy digestibility of an artificial diet may range from 71% to 86% among different species of

Table 3. *Comparison of recommended nutrient levels (on a dry matter basis) for human and non-human primates when consuming equivalent diets*[a]

	human			
	infant	young woman	lactating woman	non-human primates (all stages)
age/years	0.5–1	19–24	1st 6 months	—
energy/(kcal d^{-1}) intake	850	2200	2700	—
dry matter/(g d^{-1}) intake	179	550	675	—
protein (%)	7.8	8.4	9.6	16.3
calcium (%)	0.34	0.22	0.18	0.54
phosphorus (%)	0.28	0.22	0.18	0.43
magnesium (%)	0.034	0.051	0.053	0.16
iron (p.p.m.)	56	27	22	196
zinc (p.p.m.)	28	22	28	11
iodine (p.p.m.)	0.28	0.27	0.30	2.2
selenium (p.p.m.)	0.08	0.10	0.11	—
vit. A/(IU kg^{-1})	6985	4848	6420	10900
vit. D/(IU kg^{-1})	2235	727	593	2170
vit. E/(IU kg^{-1})	22	15	18	54
vit. K (p.p.b.)	56	109	96	—
vit. C (p.p.m.)	196	109	141	109
thiamin (p.p.m.)	2.2	2.0	2.4	—
riboflavin (p.p.m.)	2.8	2.4	2.7	5.4
niacin (p.p.m.)	33.5	27.3	29.6	54
vit. B_6 (p.p.m.)	3.4	2.9	3.1	2.7
folate (p.p.b.)	196	327	415	217
vit. B_{12} (p.p.b.)	2.8	3.6	3.9	—

[a] Calculated from National Research Council (1978, 1989), based on the following assumptions.
1. Manufactured primate diets contain 92% dry matter, so primate requirements as given in National Research Council (1978) have been divided by 0.92.
2. A human diet equivalent to a manufactured primate diet would contain 4 kcal per g dry matter, so energy allowances have been divided by 4 (4.75 for infant fed some milk) to calculate equivalent dry matter intakes.
3. Bioavailability of nutrients in mixed human diets and primate diets are comparable, so no adjustments in nutrient levels are necessary.

callitrichids (marmosets and tamarins). With an interspecific decline in body mass from 680 to 310 g, callitrichids exhibit a decrease in the transit time of marked food through the digestive tract and a corresponding decrease in energy digestibility. However the smallest callitrichid, the pygmy marmoset (*Cebuella pygmaea*), appears to be an exception to this pattern, for transit time is relatively long and energy digestibility is high (84%). This difference in the digestive function of pygmy marmosets may reflect specialization on gums that require fermentation (Power 1991), and illustrates the importance of species-specific data on the digestibility of foods.

5. PRIMATE NUTRIENT REQUIREMENTS

The relative advantage or disadvantage associated with a high or low intake rate of a particular nutrient will depend on the total intake and bioavailability of the nutrient in relation to requirements of the animal. There may be a significant premium in terms of survival and ultimate reproductive success for a primate that is able to augment the intake of a limiting or deficient nutrient, but little if any benefit in increasing the intake of a nutrient that is already present in sufficient amounts to meet requirements.

It has been shown that laboratory and farm animals require about 45–47 nutrients (vitamins, minerals, amino acids, fatty acids), depending on the species. Although the Panel on Nonhuman Primate Nutrition of the Committee on Animal Nutrition, U.S. National Research Council was only able to estimate quantitative requirements for 24 nutrients (National Research Council 1978), there is little doubt that primates require most if not all the nutrients known to be required by other mammals.

The estimated nutrient requirements of non-human primates may be compared with recommended nutrient levels for humans by expressing both sets of estimates on a dry matter basis (table 3). The human recommendations are not minimal requirements since they include allowances for the bioavailability of nutrients in typical diets, and have been increased to encompass expected variability among individuals. Even with these adjustments, the human recommendations for most nutrients are lower than the estimated requirements of non-human primates. Most of the non-human primate requirements are not well defined, leading to a reliance on 'practical levels' as best estimates of requirements. 'Practical levels' are those thought to be sufficient based on experience with primate colonies, but may be considerably higher than minimal requirements.

In formulation of manufactured feeds it is usually safer to err on the high side for a given nutrient, adding a margin of safety to cover losses during manufacture

Table 4. *Comparison of nutrient composition of commercial primate diets to nutrient requirements of non-human primates as estimated by the U.S. National Research Council (1978)*[a]

	primate requirement[b]	commercial primate diets		
		mean	range	*n*
dry matter (dry diets) (%)	—	91.7	89.2–93.6	5
dry matter (canned diets) (%)	—	41.7	41.1–42.3	2
fat (%)	—	5.5	2.7–9.8	7
protein[c] (%)	16.3	21.2	16.0–26.1	7
neutral detergent fibre (%)	—	20.9	14.0–25.7	6
acid detergent fibre (%)	—	8.0	4.9–14.0	6
acid lignin (%)	—	1.7	0.8–2.4	6
ash (%)	—	6.8	5.6–8.3	7
gross energy/(kcal g^{-1})	—	4.63	4.43–4.89	5
metabolizable energy[d]/(kcal g^{-1})	—	3.91	3.49–4.24	7
calcium (%)	0.54	1.29	0.98–1.84	7
phosphorus (%)	0.43	0.66	0.40–0.92	7
magnesium (%)	0.16	0.18	0.10–0.29	7
sodium (%)	—	0.40	0.19–0.71	7
potassium (%)	—	1.05	0.83–1.44	7
iron (p.p.m.)	196	492	111–1140	7
copper (p.p.m.)	—	17.6	14.0–22.6	7
zinc (p.p.m.)	11	196	106–505	7
manganese (p.p.m.)	—	89	31–176	7
selenium (p.p.m.)	—	0.36	0.07–0.59	7

[a] All values (except dry matter), expressed on a dry matter basis. Protein = total nitrogen × 6.25. Analytical data on commercial primate diets provided by Dr Mary E. Allen, Allen and Baer Associates, Olney, Maryland 20832.

[b] Requirements for primates converted to a dry matter basis assuming an average dry matter concentration of natural ingredient diets of 92%.

[c] The National Research Council (1978) notes that New World primates may require up to 27% protein (DM basis). Commercial diets marketed for New World primates usually have 25–26% protein.

[d] Metabolizable energy (ME) of diet calculated assuming ME values of 4 for protein and carbohydrate (NFE) and 9 for fat.

and storage as well as possible interspecific differences in requirements. Analytical data for commercial primate feeds illustrate that some nutrients are included at higher levels than the NRC estimated requirements (table 4). These feeds also vary considerably in composition, in part because some feeds have been targeted to specific types of primates (e.g. callitrichids, cebids or folivorous species) and also because the ingredients and mineral premixes used by various manufacturers are different.

It is not possible in this paper to review the importance, function and method of establishing requirements for all nutrients that are considered essential for primates. However, in evaluating compositional data on foods consumed by free-ranging primates, one must have some basis for judging the level of a nutrient to be high or low. The values in tables 3 and 4 provide benchmarks that may be used for comparison. Because food intake tends to decline with increasing energy density, somewhat higher nutrient concentrations may be appropriate for diets that are high in fat and energy. Conversely, the lower ME concentration of high-fibre diets may permit reduced nutrient levels without compromising nutrient intakes. It is important to recognize that the bioavailability of nutrients may differ greatly among foods. For example, compounds such as phytic acid, oxalic acid, protease inhibitors and tannins may reduce digestibility or bioavailability of particular minerals or protein (Swain 1979; Van Soest 1982; Cheeke & Shull 1985; Morris 1986). High levels of some minerals may also produce toxicity or interfere with the utilization of other minerals (National Research Council 1980).

6. ESTIMATES OF THE PROTEIN REQUIREMENTS OF PRIMATES

Protein has frequently been singled out as potentially beneficial to foraging primates (see, for example, Hladik 1977; Milton 1979, 1981; Glander 1981; McKey *et al.* 1981; Calvert 1985; Altman *et al.* 1987; Whiten *et al.*, this symposium). It has been suggested that primates exhibit preference for foods high in protein and essential amino acids, whether in selecting young leaves rather than mature leaves, in making choices among different species of leaves, fruits or seeds, or in supplementing fruit diets with a protein source such as leaves or insects.

The attention to protein status was probably inspired by the widespread view in the 1960s that human protein malnutrition was 'the major nutritional problem of the world', and that protein deficiency was 'common' in the less developed countries where primate field studies are usually undertaken (FAO 1965). Subsequently a more balanced view emerged in assessments of human nutrition, recognizing the predominant role of inadequate energy intake in protein–energy malnutrition (PEM) (Widdowson, this symposium). Even when protein intakes are low, clinical symptoms usually emerge in association with infection

Table 5. *Estimated protein requirements of primates*

						estimated protein requirements	
species	data source[a]	age class	body mass (kg)	type of protein	principal parameter	intake (g kg^{-1} BM)	in diet (% of ME)
Callithrix jacchus	1	adult	0.41	soybean[b]	N-balance	4.6	7.4
Saimiri sciureus	2	2–3 week infant	0.15	casin	growth	18	15
	2	2–3 month infant	0.3	casein	growth	7.3	7.1
	2	9 month juvenile	0.5	casein	growth	4.3	5.8
	3	subadult	0.7	soybean[b]	growth[c]	8.0	12.5
Cebus albifrons	4	5–6 week infant	0.4	lactalbumin	growth	5.2	7.0
	4	3 month infant	0.6	lactalbumin	growth	4.2	6.4
	4	7 month infant	1.0	lactalbumin	growth	3.3	5.2
	5	adult	2.8	lactalbumin	weight	1.8	7.5
	4	5–6 week infant	0.4	soybean	growth	10.4	14
	4	3 month infant	0.6	soybean	growth	6.8	11
	4	7 month infant	1.0	soybean	growth	6.1	9.7
Macaca mulatta	6	1–7 month infant	1.1	milk protein	growth	3.4	5.5
Homo sapiens	7	1–6 month infant	6	milk	growth	2.2	8.0
	7	6–12 month infant	9	mixed	factorial[d]	1.6	6.6
	7	1–3 year child	13	mixed	factorial	1.2	4.9
	7	7–10 year child	28	mixed	factorial	1.0	5.6
	7	young woman	58	mixed	factorial	0.8	8.4
	7	pregnant woman	58	mixed	factorial	1.0	9.6
	7	lactating woman (1st 6 months)	58	mixed	factorial	1.1	9.6

[a] Sources of data as follows: 1, Flurer *et al.* (1988); 2, Ausman *et al.* (1979); 3, De La Inglesia *et al.* (1967); 4, Samonds & Hegsted (1973); 5, Ausman & Hegsted (1980); 6, Kerr *et al.* (1970); 7, National Research Council (1989).

[b] Methionine added to diet.

[c] Serum chemistry and hepatic histology also examined.

[d] Factorial method based on various types of published data, including N-balance.

or energy deficits, both of which increase degradation of tissue protein and hence exacerbate nitrogen losses (Torun & Viteri 1988). PEM is embedded in a web of poverty that restricts access to food, sanitation, health care, agricultural improvements and education (Oftedal & Levinson 1977), and is as much a social disease as a nutritional one.

The verdict from primate foraging studies is equally mixed. Some studies have indicated a significant correlation between food choice and protein concentration, but others have not. For example, in a study of black colobus (*Colobus satanus*) McKey *et al.* (1981) found that selection among available seeds was significantly correlated with protein concentration, but selection among mature leaves was not. Choice of leaves appears to be related to protein concentration in mantled howler monkeys (Milton 1979; Glander 1981), but not in south Indian leaf-monkeys (*Presbytis johnii*; Oates *et al.* 1980). However, virtually all investigators agree that many factors underlie food choice, and that negative factors such as indigestible fibre, digestion-inhibiting phenolic compounds and potentially toxic secondary compounds may be as important as nutrient levels.

Ultimately the importance of high-protein foods depends upon levels of protein intake relative to requirements. Protein supplies both essential amino acids that primates are unable to synthesize (or, in the case of histidine, cannot synthesize at an adequate rate during infancy), and non-essential amino acids that are readily synthesized. The latter may be important as a source of organic nitrogen, but are not individually required. The foregut fermention system of colobine monkeys presumably entails microbial metabolism and synthesis of essential amino acids, so these primates may resemble ruminants in being relatively independent of the amino acid composition of protein (Van Soest 1982).

In human studies, protein requirements are usually established in relation to reference proteins such as egg and milk proteins that contain adequate levels of essential amino acids and are highly digestible (National Research Council 1989). Because nutritional research on primates has focused on them as models for human nutrition, emphasis has been placed on requirements for reference protein rather than the proteins consumed by primates in the wild. As discussed below, the two may differ considerably.

Several methods have been utilized in estimating the protein requirements of primates (table 5). Most commonly, a high-quality milk protein such as casein or lactalbumin is fed at graded levels to infant or juvenile monkeys, and growth responses are monitored. This method will only be accurate if other factors that influence growth (especially energy intake) are controlled. Another method involves measurement of nitrogen balance (the difference between nitrogen uptake from the diet and nitrogen excreted from the body), but this method has come under criticism because of errors that may generate biased results (Hegsted 1976). Primates tend to be particularly difficult to use in balance trials due to their propensity to scatter both food and excreta, leading to measurement errors that may have a major effect on nitrogen balance estimates. Some investigators have examined the response of serum proteins, other serum constituents, or specific tissues to changes in protein intake. In all cases, protein requirements may be overestimated if ingested diets do not provide sufficient energy, as animals typically catabolize protein as a source of energy when energy intakes are low.

Unfortunately some reviews of the protein requirements of primates (see Kerr 1972; National Research Council 1978) have accepted the conclusions of investigators without sufficient appraisal of experimental design, statistical methods or speculative statements. For example, the study of Robbins & Gavan (1966) is cited to show satisfactory nitrogen balance in adult rhesus even though individual values for nitrogen retention ranged from −31 % to +28 %. This was a very short study (4 days) with limited pre-adaptation of the rhesus to experimental conditions. Similarly, the statement of Hodson *et al.* (1967) that the lowest protein level that they fed to growing chimpanzees may have been marginal was accepted even though there were no treatment effects on growth rate, nitrogen balance or serum proteins. Many of the early studies on protein requirements of primates are difficult to evaluate as they include little or no statistical analysis.

The protein requirements of primates have typically been expressed in one of two ways, either as a daily intake in relation to body mass (grams per kilogram), or as a percentage of dietary metabolizable energy (table 5). Comparisons among species are complicated by differences in body size, age class and type of protein used in requirement studies. Within a species, the requirements of growing infants and juveniles appear to decline with an increase in age and body mass, whether protein requirements are expressed relative to body mass or as a percentage of dietary energy (table 5). Unfortunately there are relatively few data on protein requirements of adult primates. In humans, the estimated protein requirement of an adult female is lower (0.8 g kg^{-1}) than that of a child (1.0–1.2 g kg^{-1}) when expressed relative to body mass. However recommended energy intakes decrease even more (from about 90–100 kcal kg^{-1} in a young child to 38 kcal kg^{-1} in a young woman; National Research Council 1989) such that protein requirements expressed as a percentage of energy actually increase (from 4.9 to 8.4 %; table 5). A similar phenomenon has been observed in captive *Cebus* fed a reference protein (lactalbumin): relative to body mass the adult requirement (1.8 g kg^{-1}) is lower than that of the juvenile (3.3 g kg^{-1}), but as a percentage of energy the adult requirement is higher (7.5 % versus 5.2 %).

It is apparent that young infants have an especially high requirement for protein, but at this time they consume predominantly mother's milk. The proteins in primate milks are presumably equivalent or superior to the reference proteins (casein and lactalbumin from cow's milk) that have been tested, and typically supply 7–22 % of the energy (Oftedal 1984, O. T. Oftedal, unpublished data). It is not known whether the higher protein concentration (20–22 % of energy) observed in the milks of some primate species is indicative of particularly high protein requirements of infants, but it seems likely given the cost to the mother of producing milk that is high in protein.

Unfortunately, virtually no research has been conducted on protein requirements during pregnancy and lactation in primates, other than studies of the effects of pronounced protein deficiency on females and their infants (see, for example, Riopelle *et al.* (1975); Kohrs *et al.* (1980)). In humans it is estimated that protein requirements increase by more than one third (from 0.8 to 1.1 g kg^{-1} body mass; table 5) during early lactation, and an even greater increase probably accompanies the onset of lactation in species that produce milks higher in protein concentration. Human milk has the lowest protein concentration (about 7 % of energy) of any primate milk that has been studied. In general, it appears that primates produce small daily amounts of a relatively dilute milk (Oftedal 1984). Thus the protein and energy demands of lactation are probably low for primates by comparison to the demands experienced by many other mammals.

Proteins other than reference proteins are usually required at considerably higher levels to compensate for lower digestibility and shortfalls in essential amino acids. For example, the apparent digestibility of plant proteins consumed by humans may be as little as 78 % (beans) or as much as 96 % (refined wheat), but for most plant products is about 85–88 % (National Research Council 1989). In cebus monkeys (*Cebus albifrons*) the true digestibility of lactalbumin is about 100 %, but that of soy protein concentrate is only 83 % (Ausman *et al.* 1986). By complexing with proteins, tannins may reduce digestibility of plant proteins even further (Swain 1979). Although tannins are particularly abundant in leaves, they are also found in some fruits (including seeds), stems and flowers eaten by primates (see, for example, McKey *et al.* (1981); Calvert (1985); Barton *et al.* (1992)).

In any protein the essential amino acid that is in least supply relative to the levels in reference protein determines the amino acid score of that protein. A score of 50 % indicates that the amount of protein that must be consumed to meet protein requirements is twice (1/0.50) that of the reference protein. The protein in cereal grain can have an amino acid score of less than 50 % (owing to low lysine concentration) whereas the amino acid score of protein from legume seeds may be only 70 % (due to low concentration of the sulphur-containing amino acids, cysteine and methionine) (Munro & Crim 1988). Studies of young cebus monkeys have shown that soy protein concentrate has a potency of only 53–69 % (compared to lactalbumin) in supporting growth and nitrogen retention (Ausman *et al.* 1986). Thus estimated protein requirements for growing cebus are considerably higher when they are fed soy protein (without amino acid supplementation) in place of lactalbumin (table 5). However, even when soy protein is supplemented with methionine (a sulphur-containing amino acid), it is usually less potent than reference protein, presumably due to lower digestibility.

Relatively little is known about the essential amino acid patterns in foods consumed by wild primates. Glander (1981) reported higher levels of most essential amino acids in leaves eaten by mantled howlers than in leaves that were not eaten, but this difference disappears once the amino acid data are expressed as a percentage of protein. As a first estimate of amino acid adequacy, the amino acid composition of mature and young leaves eaten by howlers (Glander 1981) may be compared to the estimated amino acid requirements of 2-year-old-children (National Research Council 1989). Expressed as a percentage of protein, the average levels of histidine, isoleucine, leucine, lysine, phenylalanine + tyrosine, threonine, and valine all exceed the NRC figures for requirements. Methionine levels (1.8–2.0% of protein) are somewhat lower than total sulphur-containing amino acid requirements (2.5%), but cysteine was not measured. If the cysteine concentration of the protein in these leaves is similar to that of most leaf proteins (i.e. about 0.7–1.4%; Lyttleton 1973), the level of total sulphur-containing amino acids should not be limiting. Although tryptophan analysis was also omitted, leaf proteins usually contain 1.6–2.1% tryptophan (Lyttleton 1973), well above the NRC suggested requirement of 1.1%. Because leaves typically contain abundant levels of essential amino acids, the adequacy of leaf proteins for animal feeding is impaired more by the presence of tannins, growth depressants and toxic compounds than by amino acid imbalance (Allison 1973). Inappropriate amino acid levels are more likely to occur in storage organs such as tubers and seeds (Van Soest 1982).

What can we conclude about the protein requirements of primates in captivity and the wild? Once the period of milk dependency is past, growing and non-reproductive adult primates appear to require 5–8% of metabolizable energy as protein, if reference protein is fed (table 5). For manufactured feeds based on plant proteins but supplemented with limiting amino acids (e.g. methionine or lysine), this value should be increased to 6–9% of ME (7–10% of dry matter (DM)) on the assumption that protein digestibility is about 85%. A pregnant or lactating female may require at least 10% of ME as reference protein, equivalent to a level of not less than 12.5% protein (DM basis). The NRC recommendation is 15% protein (16% DM basis) for all stages of life (table 3). The suggestion that New World monkeys may require up to 25% protein (National Research Council 1978) is not supported by available data (table 5).

Estimation of the protein requirement of primates that feed on natural foods is complicated by uncertainties about protein digestibility, amino acid patterns and metabolizable energy concentration. Assuming a protein digestibility of 85%, an amino acid score of 100%, and a metabolizable energy concentration of only 3 kcal ME per gram DM (due to high fibre concentration and low fibre digestibility), a primate eating leaves would require 4–7% protein (DM basis) for growth and maintenance, and at least 8% (DM basis) for reproduction. However, with the same energy concentration and only 50% protein digestibility (due to severe effects of tannins), the estimated requirements would be 7–11% (DM basis) for growth and maintenance and at least 14% (DM basis) for reproduction. Given that the leaves eaten by primates usually average 12–16% protein (see, for example, Glander 1981; Calvert 1985; table 1), it is unlikely that protein deficiency will be a problem except perhaps for lactating females consuming leaves of high tannin content. Foods with unbalanced amino acid patterns may present a different picture. For example, if high-fat seeds have 85% protein digestibility, 60% amino acid score and 4.5 kcal per gram DM, the estimated requirements would be 10–16% and at least 20% protein (DMB) for growth and maintenance, and reproduction, respectively.

However, caution is required in interpreting analytical data on protein. Crude protein concentration is calculated, by convention, as total nitrogen (TN) times a factor (6.25) that assumes that protein contains 16% nitrogen. However, plants contain non-protein nitrogenous compounds, including alkaloids and non-protein amino acids, some of which cannot be metabolized by animals (Munro & Crim 1988). Some plant proteins have a higher concentration of nitrogen than 16%. The correct factor for calculating protein from nitrogen concentration is about 5.8 for many grains, 5.3–5.7 for some leguminous seeds (e.g. soybeans and peanuts), and 5.2–5.3 for other seeds and nuts (Watt & Merrill 1963). The appropriate factor for tropical leves may be even lower (*ca.* 4.0–5.0; Milton & Dintzis 1981). Thus crude protein (TN × 6.25) may substantially overestimate true protein.

7. CONCLUSION

Nutrients that are consumed at marginal or inadequate levels with respect to requirements may limit animal performance (and, ultimately, evolutionary fitness). Theoretically, animals should evolve feeding behaviours that enhance intakes of limiting nutrients. However, there may be little or no advantage to enhancing intake of a nutrient that is already abundant relative to requirements.

Despite the large number of studies that have been undertaken to relate food selection to food chemistry, very little information is available about the nutrient intakes of primates consuming natural diets or how these intakes relate to nutrient requirements. Further research is needed on feeding rates, digestibilities of foods, energy utilization and nutrient requirements, especially in relation to reproduction.

Because primates typically grow slowly and have low daily milk yields, age and reproductive effort probably have less effect on nutrient requirements than in most mammals. This reproductive strategy may be important in allowing primates to use foods of only moderate nutrient density on a year-round basis.

Research on the nutrition of red howler monkeys was funded by the Smithsonian International Environmental Studies Program. I thank M. Klein, M. Power, A. Rosenberg and A. Whiten for helpful comments on the manuscript.

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Discussion

A. Whiten (*Scottish Primate Research Group, University of St Andrews, U.K.*). Dr Oftedal lists nutritional factors known to affect the value of a food. Should not the occurrence of secondary compounds in plant foods, some of which influence digestibility directly, be added to that list?

O. T. Oftedal. Secondary compounds in plants may produce toxicity or reduce digestibility of fibre, protein or other nutrients in farm and laboratory animals, but little is known about their effects on primates. Unfortunately, adverse effects are hard to predict. Most screening tests for secondary compounds in foods are qualitative rather than quantitative, but toxic effects are dose-dependent. Moreover, most tests are for classes of compounds (e.g. alkaloids, saponins, tannins, cyanogenetic glycosides) even though toxicity or digestive effects may vary greatly between one compound and the next. The only way to ascertain the effects of secondary compounds is to conduct controlled toxicological and digestibility studies using the specific compounds and primate species of interest, but to my knowledge this has not been done.

D. A. T. Southgate (*AFRC Institute of Food Research, Norwich, U.K.*). I would like to reinforce the comments of Professor Altmann [comments not supplied] about the extent to which the complex carbohydrates in plant cell walls (fibre) are degraded in the large bowel of humans. It is important to distinguish between the different sources and composition of these complex carbohydrates, as these will influence the energy that the animal obtains. The acid lignin values may include other substances, for example cutin, and may exaggerate the extent to which the materials resist degradation.

O. T. Oftedal. The amount of energy that can be obtained by a primate from the complex carbohydrates in plant cell walls will depend both on the types of carbohydrates and the species of primate. Humans are probably not very representative of most primates because of their large body size. In mammals, large size usually correlates with slower passage rates of digesta with consequent increased opportunity for fermentation. However, some primates have evolved specialized fore- or hind-gut fermentation systems, and are undoubtedly more efficient at fibre fermentation than humans.

P. Van Soest (*324 Morrison Hall, Cornell University, New York, U.S.A.*). I comment on the high lignin content of leaves. It is probably not true lignin or cutin, but rather tannin, which often confounds crude lignin analysis. The effects of tannin upon reduction of fibre fermentation is low as compared with lignin, but much greater for the case of protein digestion. Sequential analysis can help resolve this contamination of crude lignin. Extractions in the sequential order: neutral detergent, acid detergent followed by lignin determination (yielding a maximum value) can be compared with the sequence: acid detergent, neutral detergent and lignin isolation. The difference between lignin values by the first sequence and second sequences gives some estimation of insoluble condensed tannins.

O. T. Oftedal. I agree that further investigation of the various fractions obtained with the detergent fibre system is needed, and believe the comparison Dr Van Soest suggests would be valuable.

P. Van Soest. Polysaccharides like pectins, fructans and galactans, which are soluble and highly fermentable, but not digestible by mamalian digestive enzymes, yield bacteria and volatile fatty acids from colonic fermentation and about 3 cal g^{-1} of metabolizable energy.

O. T. Oftedal. Such polysaccharides are of particular importance to primates that specialize on plant exudates, such as marmosets and some galagos.