

Measuring food intake in wild animals: primates

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The last 30 years have seen the rapid accumulation of large quantities of data on the diets and feeding behaviour of free-ranging primates in all continents. Much is known about what, when and where different primates eat through the seasons, on their activity patterns and use of space, but in the wild it is difficult to quantify actual amounts of food and of primary and secondary nutrients ingested.

Diet

The commonest method to deduce diet is based on the time spent eating different food types: fruit pulp (ripe and unripe), seeds, flowers, leaves (young, mature, buds, stems), exudates (gum, sap), animal matter (invertebrate and vertebrate; see Chivers, 1991). Such data are invaluable in ecological terms, in relation to activity budgets and the importance an animal attaches to a particular activity. In relation to metabolism, one needs to know the actual weights of each food ingested; this has to be based on the time spent eating each item and/or food type in each day, the weight of each item and the rate of intake (which may vary through a feeding bout). One also needs to know the composition of each food item, in terms of sugars, protein, fats, mineral, vitamins and secondary compounds, such as alkaloids (toxins) and tannins (digestion inhibitors). In this way one can calculate the food intake, preferably on a daily basis. Such data are very difficult to collect, however, even in open habitats where visibility is good and dietary diversity lower; in forest habitats, where most primates reside, the problems are much greater, often insuperable.

Dietary types

Primates are unusual among mammals in having avoided the dietary and anatomical specializations that characterize most other orders of mammals (Chivers & Hladik, 1980). Mammals generally evolved either to perpetuate the ancestral strategy of insectivory (or to develop that into carnivory) or to specialize on foliage, which is much more abundant but difficult to digest. Hence, faunivores (animal eaters; this term is used to avoid the taxonomic connotations of insectivores or carnivores), consuming the most nutritious and digestible of foods, are relatively small with simple guts dominated by the small intestine. Folivores

have had to become much larger, to accommodate voluminous guts with enlarged fermenting chambers in the stomach (foregut) and/or large intestine (caecum and primitive right colon; midgut). Similarly, also requiring the breakdown of long-chain carbohydrates, gumnivory requires an elaborate gut compartment for fermentation (caeco-colic).

Frugivores, typified by primates, have occupied the 'middle ground', which gives them an unique dietary flexibility (Fig. 1). Animals cannot live by fruit alone, since certain amino acids are missing; hence, they must procure animal or plant protein. The smaller primates supplement their fruit staple with animal matter or tree exudates, the larger ones consume foliage. This flexibility is not just shown between species, but within species. Add to this dietary flexibility the reproductive flexibility conferred on haplorhine primates (monkeys, apes and man) by the menstrual cycle, with a capacity for year-round breeding, and you have the recipe for real success, as evidenced by the profusion of primate species and the emergence of man. One might note here the critical bottleneck of meat-eating, through which ancestral man probably passed; the only way to economize on organ energetics was to eat the most nutritious and digestible foods and use the spare energy to fuel the unique brain expansion that characterizes man (Aiello & Wheeler, 1994).

Primates

There are clear patterns among the primates (Fig. 2), which radiated in relation to the evolution of more complex and diverse angiosperm vegetation, with elaborate flowers and fruit, and more edible leaves than those found in gymnosperms, and with increasing seasonality. The main split, probably way back in the Eocene, led to an initial retention of the ancestral insectivorous form and nocturnal habit (the strepsirhines) and the development of larger body size and more varied diet and positional behaviour (locomotion and posture; below branch as well as above branch), with increasing diurnality (the haplorhines).

The Strepsirhini uniquely span the spectrum from extreme faunivory (*Arctocebus*) to extreme folivory (*Lepilemur*) and gumnivory (*Phaner*), a relatively recent radiation, mainly in isolation on Madagascar (Fig. 3;

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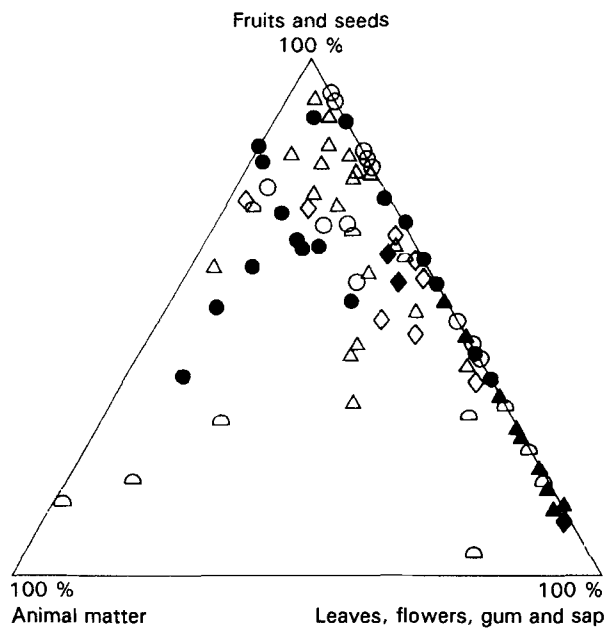


Fig. 1. Diets of primates, in terms of percentage of fruit (and seeds), leaves, flowers and exudates, and animal matter. Diets can be represented in the form of a triangular diagram, with 100% faunivory, 100% folivory and 100% frugivory at the three corners. The average diets of eighty primates are shown, with fauni-frugivores to the left and foli-frugivores to the right; prosimian species are particularly variable in their diets. (○, ●), New World monkeys; (▲), colobines and (△), cercopithecines (Old World monkeys); (◇), gibbons; (◆), great apes; (▽), lemurs and lorises. (From Chivers, 1992.)

Hladik, 1979; Barrett, 1984). Positional behaviour is almost as diverse as that seen in haplorhine primates. The *Arctocebus* is small with a very simple gut dominated by the small intestine; the *Lepilemur* has a much enlarged caecum and colon for the fermentation of cellulose (it is not very large and has to re-ingest the first faeces to maximize digestion). It is very difficult to quantify the diets of these mainly nocturnal primates. In Africa and Asia, smaller species are faunivorous, (*Arctocebus perodicticus* and *Loris tardigradus*), whereas the larger species are frugivorous (*Perodicticus potto* and *Nycticebus coucang*). Galagos, in Africa, vary from small faunivorous species to larger frugivorous and gumnivorous ones.

Apart from the exclusively faunivorous tarsiers (*Tarsius*), the Haplorhini are distinguished by, initially, exceeding 1 kg in body weight, thereby needing to add plant material (fruit) to the animal matter consumed. Thus, monkeys and apes are distinctly frugivorous, even in the New World, where marmosets and tamarins are secondarily small. In the Old World, while the cercopithecids are emphatically frugivorous, the larger colobids have diverged into a niche where leaf-eating predominates, augmented in many cases by seeds. The stomach is enlarged and sacculated into a fermenting chamber (Chivers & Hladik, 1980). In other primates the caecum and/or primitive right colon are enlarged into a fermenting chamber (Fig. 4). Fruit dominates the diets of apes (gibbons, orang-utans, chimpanzees and gorillas, except in the large mountain gorilla (*Gorilla gorilla*) in the montane forests on the edge of the Rift Valley where fruit are scarce).

Faunivorous and folivorous primates (the latter absolutely larger with respect to body size and tooth size) have small cutting incisors, and crested, cutting cheek teeth with thin enamel for dividing food items as small as possible to maximize the surface area for digestion (Kay, 1975). Frugivores have broad incisors for scraping, large canines for gouging, and large, relatively flat cheek teeth with thick enamel for grinding fruit.

Thus, smaller primates eat more animal matter, larger ones eat more foliage; the main fruit-eaters are of intermediate size (Fig. 5). Apes, cercopithecids and ceboids stand out as the main frugivores, strepsirhines as the main faunivores, and colobids as folivores, although there is considerable variation within each group (Fig. 6).

Hladik & Chivers (1978) showed that the proportions of animal matter, fruit and leaves in the diet correlate more closely with biomass density than with body size, i.e. it is the total weight of a species in an area that relates most closely to dietary proportions. Thus, colobid monkeys are more folivorous than the largest primates, the great apes. They also showed (Chivers & Hladik, 1980) how much variation there can be around the mean annual diet (Fig. 7), according to food availability and the flexibility conferred by the biology of primates, the key to their evolutionary success.

The aim is, therefore, to review the information available on primate diets in the wild, and efforts to extrapolate from data for feeding time to those for food weight; there have been some attempts to assess the amounts of nutrients in various foods and/or diets. What an animal consumes depends to a considerable extent on (1) its dentition for the mechanical tasks of food processing, and (2) its gastrointestinal tract for the chemical processes of digestion, absorption and excretion.

Diet in terms of feeding time

Given the difficulty of quantifying the diverse diets of strepsirhine primates, and the heterogeneity and incompleteness of data on the diets of the frugivorous Old World cercopithecoid monkeys, the focus here will be on (1) New World monkeys which vary the frugivorous diet markedly according to their considerable differences in body size, (2) the supposedly folivorous colobid monkeys, mostly found in Asia, and (3) the frugivorous apes, especially the gibbons of South-east Asia.

Ceboidea

New World monkeys, Ceboidea, as haplorhine primates, are thought to have increased in size from an ancestor the size of a capuchin monkey (*Cebus*), consuming fruit as well as animal matter (Rosenberger, 1981). This challenges the traditional view that the ancestral ceboid was small and insectivorous, like the callitrichines (Hershkovitz, 1977). They subsequently diverged into the larger Atelidae, the larger fruit- (atelines) or seed-eating (pithecine) specialists, with increasing amounts of foliage supplement (*Alouatta* and *Lagothrix*), and the Cebidae, with decreasing body size and increasing amounts of exudates (*Callithrix*) or animal

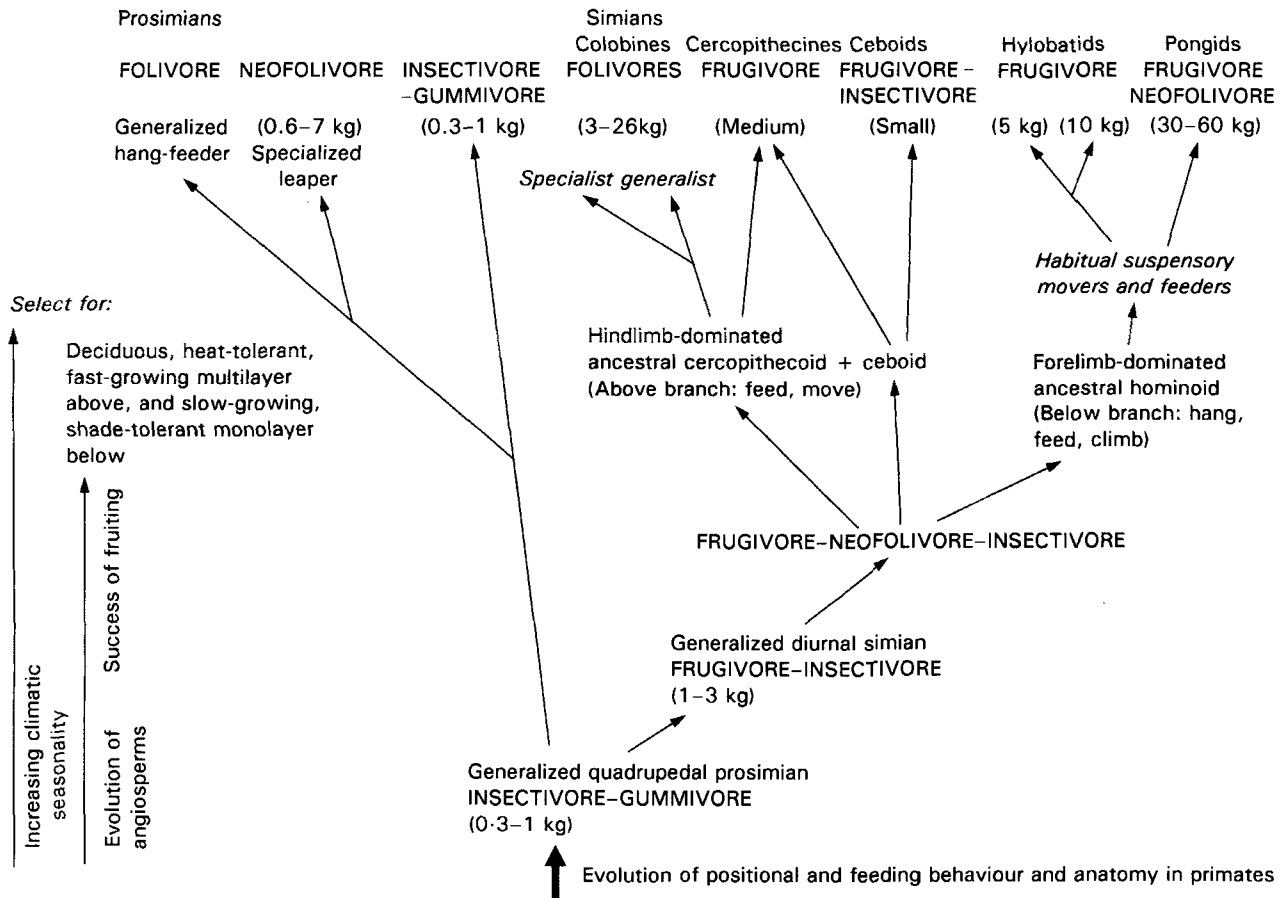


Fig. 2. The primate radiation; the evolution of positional and feeding behaviour in primates. (Based on Ripley, 1979.)

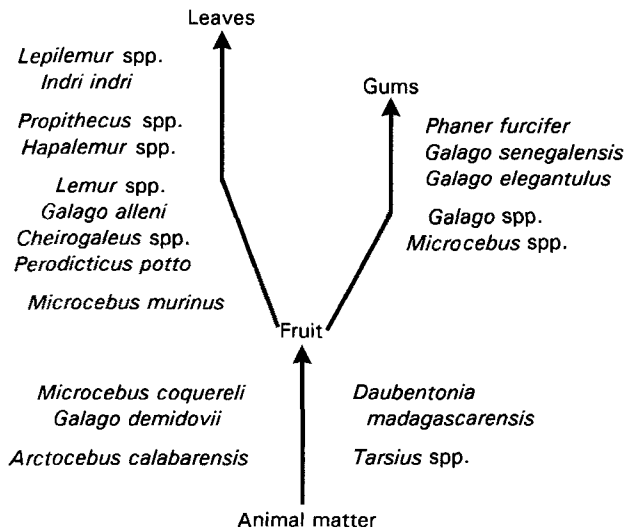


Fig. 3. Prosimian (strepsirhine) diets; relative preponderance of species consuming animal matter, fruit and leaves or gums.

matter (*Saguinus*, cebines) in addition to fruit (Rosenberger, 1981; Ford, 1986; Table 1). Even the smallest ceboids eat fruit for more than 60% of their feeding time. *Aotus*, the night monkey, and *Callicebus*, the titi monkeys, along with *Cebus*, the capuchins, perhaps have changed least from the ancestral ceboid, callitrichines and atelines the most. They

exhibit a dramatic range of positional behaviours, from the small, scurrying short-limbed callitrichines (0.3 kg), through the quadrupedal cebines and aotines, to the climbing pithecines (3 kg) and the suspensory and acrobatic atelines (6–8 kg) with long limbs and a prehensile tail. Since all species are almost exclusively arboreal, it is in these ways that forest niches have been partitioned to allow a high degree of sympatry between species.

Colobidae

The colobus monkeys of Africa, the langurs and odd-nosed monkeys of Asia, Colobidae, are often called leaf-monkeys (especially in Asia), but they neither look like leaves nor eat leaves exclusively! They do have the capacity to break down cellulose by bacterial fermentation in their sacculated stomach, more than other primates, which have to depend on an expanded caecum and colon. They can also neutralize toxins (e.g. alkaloids) more effectively and also digestion inhibitors (e.g. tannins and other phenolic compounds); this increases the range and quantities of foods that they can consume, but even colobids select the more digestible leaves (Oates *et al.* 1980). This enables them to overcome the chemical protection of seeds, in contrast to the New World pithecine monkeys that break their way into mechanically-protected seeds, with their large, procumbent incisors and canines.

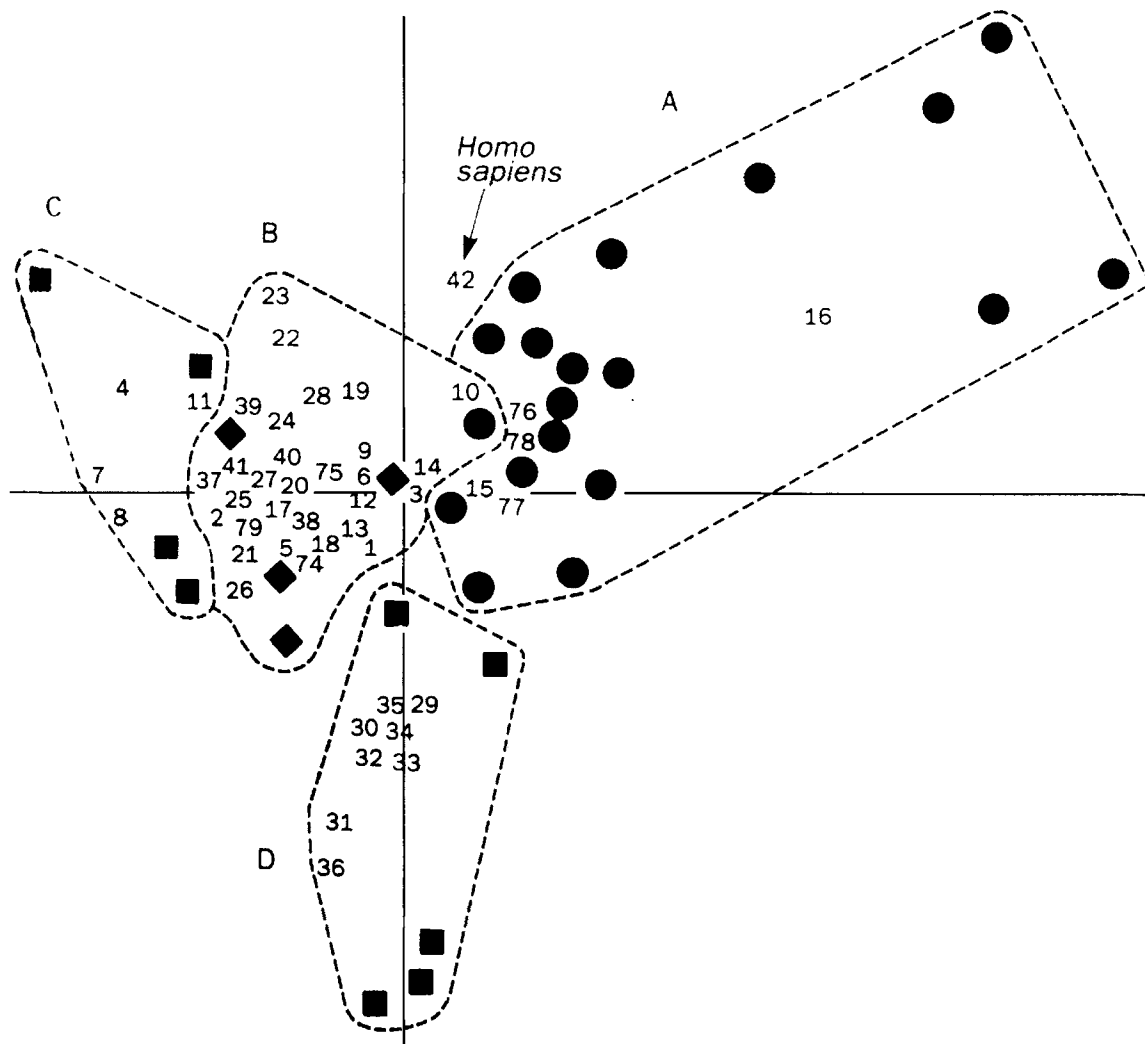


Fig. 4. Multi-dimensional scaling of gut compartments (plot of indices for surface areas of stomach, small intestine and caecum + colon) for eighty primates and other mammals, showing the radiation of morphology from a more generalized frugivorous gut, or from the specialized faunivorous gut (dominated by small intestine), to folivorous guts dominated by caecum and colon, or by a sacculated stomach. (A), Faunivores spreading to the upper right, with 'insectivores' and cetaceans more extreme than 'carnivores'; (B), frugivores, with most primates in the 'central' cluster; (C), midgut-fermenting folivores, with primates near to the frugivore cluster and the horse most extreme; (D), foregut-fermenting folivores, with ruminants more extreme than colobine monkeys. (●), Carnivores (carnivora), whales and dolphins (Cetacea), insectivores (Insectivora), seals (Pinnipedia), pangolins (Pholidota); (■), even-toed ungulates (Artiodactyla), anteaters (Edentata), hyraxes (Hydrocoidea), odd-toed ungulates (Perissodactyla), rabbits (Lagomorpha), marsupials (Marsupalia); (◆), rodents: squirrels (Sciuridae); 1, 2, 3, 4 etc, primates. (From MacLarnon *et al.* (1986).)

Old World monkeys, unlike those of the New World, have radiated out of the forest in the face of competition, into savannah, desert edge, and mountains, and maintained more similar body size and shape. Since many are terrestrial, their diets are more difficult to quantify, despite better visibility, since they spend much time rooting around on the ground for roots, grasses (? seeds) and invertebrates (Davies *et al.* 1984). The colobids are larger (6–10 kg), long-limbed and long-tailed, with a bounding quadrupedal gait and marked ability to leap around and between trees, with better developed forelimbs helping in landing.

McKey *et al.* (1978) showed that *Colobus satanas* ate large amounts of seeds, because the trees were growing on very poor soils and the leaves were very well protected chemically. Similar switches from eating leaves to seeds occur in Asia among *Presbytis* spp. in and around Borneo,

and, to a lesser extent, among *Trachypithecus* spp. in the seasonal forests in Bangladesh (Table 2; Davies & Oates, 1994). Young leaves are generally preferred to mature leaves, and flowers are often eaten when available. In consuming seeds, colobid monkeys are working against the seed-dispersing role of cercopithecoid and hominoid primates in the Old World, and against contributing to the natural regeneration of forest.

Hylobatidae

The gibbons (or lesser apes) are fruit-pulp specialists (Chivers, 1984), like the spider monkeys (*Ateles* spp.) of the Neotropics, and chimpanzees (*Pan* spp.) of Africa, but, unlike most primates, especially cercopithecoids (*Macaca*

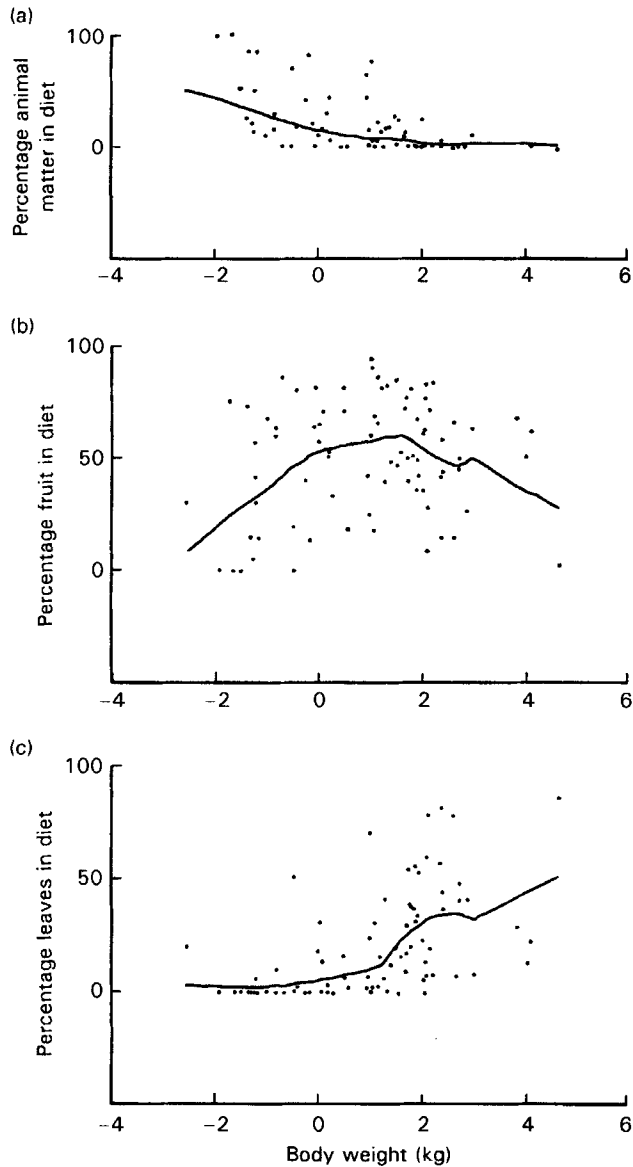


Fig. 5. Body size (kg) in primates and percentages of (a) animal matter, (b) fruit and (c) leaves in their diets. (Prepared by JMC Ayres.)

spp. of Asia), they compete more with large birds, such as pigeons and hornbills, for the small, colourful, sugary fruit. The monogamous family groups focus on small fruiting trees, to avoid competition with the large multi-male, multi-female groups of macaques and the large orang-utan (*Pongo pygmaeus* in Borneo and north Sumatra, Indonesia). At least 60% of feeding time is spent eating fruit pulp (often seeds are swallowed and dispersed in faeces) by gibbons, except for the large siamang (*Hylobates syndactylus*, 10kg v. 5kg) in Malaya and Sumatra, and the concolor gibbon (*H. concolor*) in the seasonal forests of Indo-China, at least in some seasons (Table 3). Young leaves are commonly eaten, especially by the siamang, but the Kloss gibbon (*H. klossi*) lives in trees on very poor soils on the Mentawai islands, off the west coast of Sumatra. Gibbons cannot cope with secondary compounds like

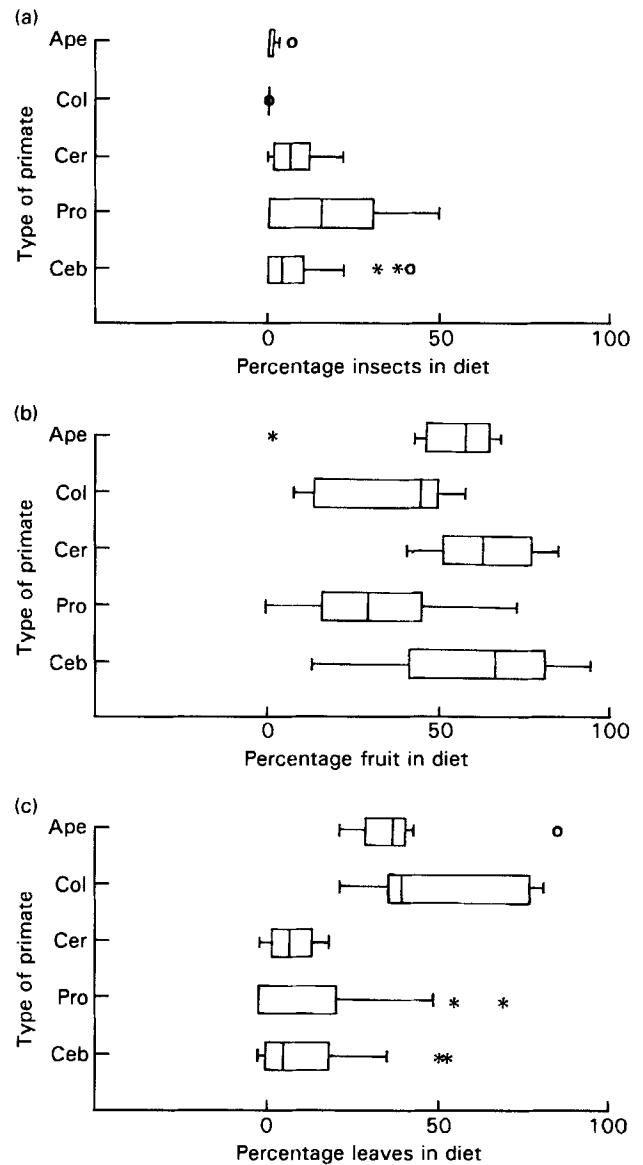


Fig. 6. Percentage of (a) animal matter, (b) fruit and (c) leaves in the diets of apes, colobids (Col), cercopithecids (Cer), prosimians (strepsirhines; Pro) and ceboids (Ceb). (Prepared by JMC Ayres.) Values are means (vertical bars) with their standard errors (□) and ranges (horizontal bars). *, O, Outlying species which were unusual and excluded from statistical analysis.

monkeys can, and they seek animal, rather than plant, protein under such circumstances (Vellayan, 1981).

Pongidae

The orang-utan of Borneo and north Sumatra is highly frugivorous for most of the year, depending on sufficient large fruiting trees in their home range (Table 4). Their absence from parts of Borneo is best explained by too low a density of such trees. Foliage is an important supplement, given their large body size (male 70 kg, female 35 kg), especially in certain seasons when fruits are scarce.

Communities of chimpanzees (*Pan troglodytes*; male 50 kg, female 40 kg) range widely in search of fruit

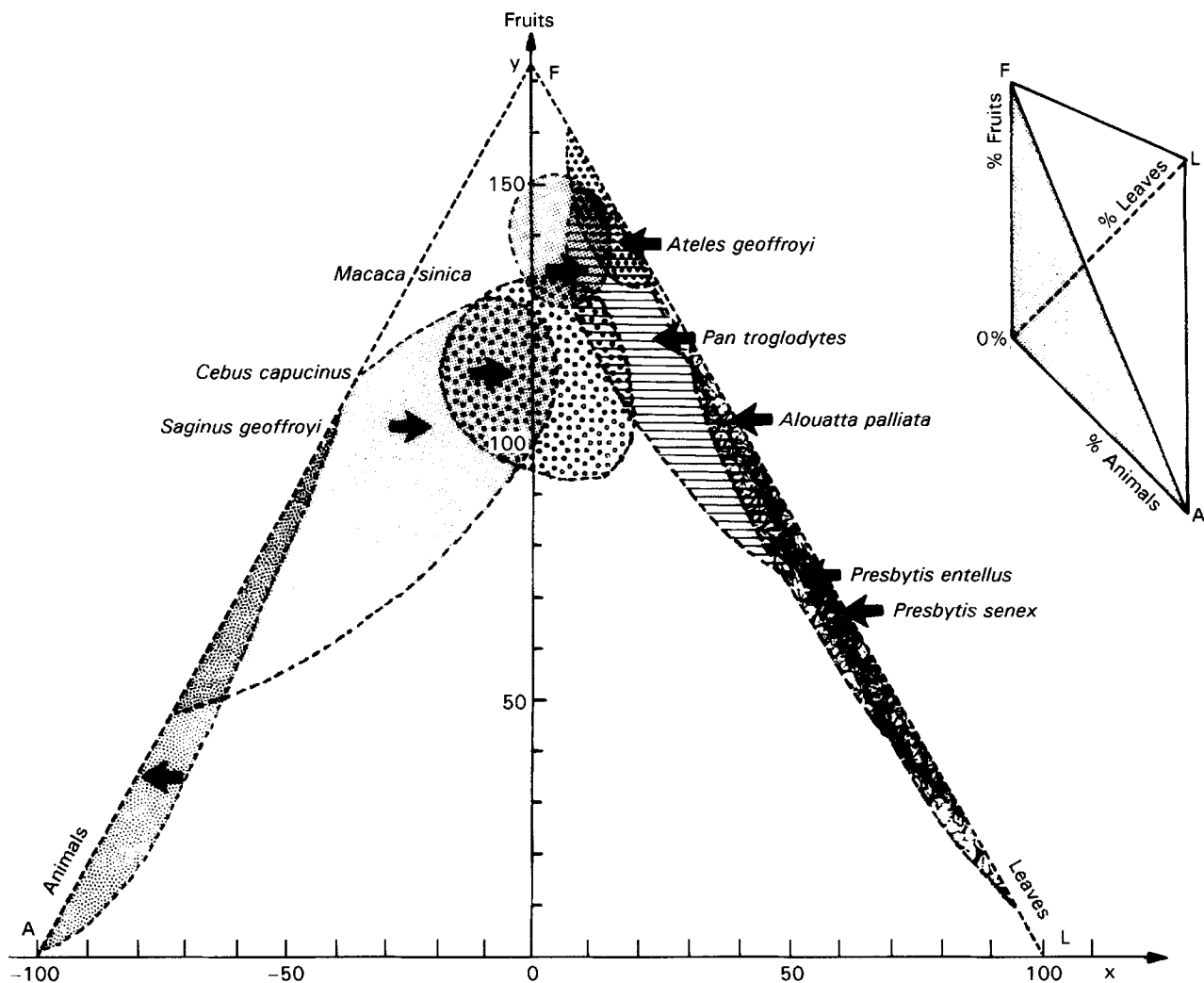


Fig. 7. Plots of mean annual diets and extent of annual variation for nine primate species in Panama, Sri Lanka and Gabon, indicating calculation of a dietary index, from -100 (100% faunivory), through 0 (peak of frugivory) to $+100$ (100% folivory). (From Chivers & Hladik, 1980.) $x = (\% \text{ leaves}) - (\% \text{ animals})$; $y = 1.732 (\% \text{ fruits})$. \longrightarrow , area of plot associated with means and ranges for individual primates.

(Wrangham, 1977), obtaining animal protein from colonial invertebrates and the occasional hunt for mammals (e.g. pig and colobus monkey), a time-consuming process (Table 4). The mean fruit-eating score for the pygmy chimpanzee (*Pan paniscus*) may be inflated by being presented as a proportion of fruiting trees, rather than relative to feeding time (which may be closer to 50% than 80%; see Susman, 1984). While the mountain gorilla (male 160 kg, female 90 kg) in Rwanda and Zaire consumes foliage almost exclusively (Fossey & Harcourt, 1977), the lowland gorilla in the west (Gabon and Cameroun) spends nearly 50% of its feeding time eating fruit, at least at certain seasons (E Rogers, personal communication).

Diet in terms of food weight

Food intake by weight is difficult to assess, even for particular feeding bouts. The problem is not only to estimate the weight of each mouthful, but to record the rate of ingestion. Similar food items are collected from the ground or trees for weighing. The number of mouthfuls

(easier for whole fruit than a bundle of leaves or flowers) has to be counted throughout a feeding bout, since the rate is highest at the start of a bout, slowing down in the middle, to rise to a secondary peak at the end (Chivers, 1974). Thus, the average rate through a bout has to be computed, and the duration of each bout needs to be recorded.

Few data are available for feeding through complete days. Some data are available for howler monkeys (*Alouatta seniculus*), langurs (*Presbytis senex* and *P. entellus*) and gibbons (*Hylobates agilis x muelleri*; Table 5), based on a few days here and there. These show that feeding time consistently underestimates the intake of fruit by weight; the weight of leaves and flowers (and animal matter) take disproportionately longer to ingest. Knowledge of feeding time, ingestion rate, and bite size of fruit, leaves, flowers and animal matter, allows extrapolation to intake by weight. From such values for each bout, Chivers & Raemaekers (1986) calculated daily totals from four gibbon studies (two of siamang, and one each of lar (*Hylobates lar*) and agile (*H. agilis*) gibbons; Table 6). Predicted values derived from body size and energy expenditure suggest that

Table 1. Diets of ceboid monkeys (From Hladik & Hladik, 1969; Klein & Klein, 1977; Kinzey, 1978; Milton, 1980; Mittermeier & van Roosmalen, 1981; Gaulin & Gaulin, 1982; Rylands, 1982; Estrada, 1984; Ayres, 1989; AD Johns, personal communication)

Species	Percentage of feeding observations						
	Leaves	Flowers	Fruit		Exudates	Animals	
			Pulp	Seeds			
<i>Callithrix humeralifer</i>		8		68		14	10
<i>C. penicillata</i>		1		57		28	14
<i>Leontopithecus rosalia</i>		10		68		8	14
<i>Saguinus geoffroyi</i>	10			60			30
<i>S. fuscicollis</i>		6		74		14	6
<i>S. mystax</i>		13		67		5	15
<i>S. oerstedii</i>	2			60	20		18
<i>S. sciureus</i>				66	17		17
<i>S. vanzolini</i>		8		40	12		40
<i>Cebus capucinus</i>	15			60	5		20
<i>C. apella</i>	2	8		65	5		20
<i>Aotus trivirgatus</i>	5	11			64		20
<i>Callicebus moloch</i>	26	1			72		1
<i>C. torquatus</i>	13			58	9		14
<i>Pithecia pithecia</i>		7		47	46		
<i>P. albicans</i>	31			50	19		
<i>Cacajao calvus</i>		6		18	67		5
<i>C. melanocephalus</i>		5		20	70		5
<i>Chiropotes satanas</i>		11		9	63		
<i>C. albinasus</i>		3		54	36		
<i>Alouatta palliata</i>	50	6		44	0		
<i>A. seniculus</i>	52	6		42	0		
<i>Ateles geoffroyi</i>	20				80		1
<i>A. belzebuth</i>	16	1			83		
<i>A. paniscus</i>	6	4		84	5	1	

Table 2. Diets of colobid monkeys (From Davies & Oates, 1994; Gupta, 1997)

Species	No. of studies	Percentage of feeding observations				
		Leaves		Flowers	Fruit	
		New	Mature		Pulp	Seeds
<i>Procolobus badius</i>	6	49	16	17	15	10
<i>P. verus</i>	3	37	13	11	20	16
<i>Colobus guereza</i>	1	65	13	2		15
<i>C. satanas</i>	2	20	20	4	2	57
<i>C. polykomos</i>	1	30	26	3	3	32
<i>Semnopithecus entellus</i>	3	22	28	7		30
<i>Presbytis comata</i>	1	59	6	7	14	1
<i>P. melalophos</i>	1	28	8		24	26
<i>P. rubicunda</i>	2	37	1	11	19	30
<i>P. thomasi</i>	1		32	8		58
<i>Trachypithecus obscurus</i>	2	33	15	9	28	6
<i>T. johnii</i>	1	31	27	9		25
<i>T. auratus</i>	2	55	2	12	15	11
<i>T. vetulus</i>	1	20	40	12		28
<i>T. pileata</i>	3	34	30	6	15	13
<i>T. phayrei</i>	2	52	2	7	13	18
<i>Nasalis larvatus</i>	3	43	12	6	30	13

animals should consume 10–15% of their body weight daily, and both larger and small gibbons come close to this expectation, at 1.45 and 0.8 kg/d.

Hladik *et al.* (1971) also estimate from Kleiber's (1961) Law that there are 1260 kJ available/kg body weight for the larger *Alouatta* (8 kg, consuming 1.2 kg/d), and 1720 kJ/kg body weight for the smaller *Cebus* (3 kg,

consuming 0.4 kg/d; the latter is more active and needs relatively more energy.

Diet in terms of nutrient intake

Analyses of the composition of wild primate foods are equally scarce. Hladik and colleagues (Hladik & Hladik,

Table 3. Diets of gibbons (*Hylobates* spp.) (From Chivers, 1984, 1997; Ahsan, 1994)

Species	No. of studies	Percentage of feeding observations			
		Leaves	Flowers	Fruit	Animals
<i>H. syndactylus</i>	5	40	7	49	10
<i>H. lar</i>	5	25	3	62	10
<i>H. agilis</i>	1	39	3	58	1
<i>H. muelleri</i>	1	32	4	62	2
<i>H. agilis x muelleri</i>	3	35	10	51	3
<i>H. klossi</i>	1	2	5	67	25
<i>H. pileatus</i>	1	13	7	64	15
<i>H. concolor</i>	1	72	7	21	0
<i>H. hoolock</i>	5	25	7	66	1

Table 4. Diets of great apes (From Fossey & Harcourt, 1977; Hladik, 1977b; Rodman, 1977; Galdikas, 1978; Rijksen, 1978; Susman, 1984)

Species	Percentage of feeding observations			
	Leaves	Flowers	Fruit	Animals
<i>Pongo pygmaeus</i>	33	3	58	6
<i>Pan troglodytes</i>	49		14	37
<i>Pan paniscus</i>	24	3	71	2
<i>Gorilla gorilla</i>	86	2	2	0

Table 5. Measures of food intake by time (%; T) and weight (%; W) for howler monkeys, langurs and gibbons (From Hladik, 1977a,b; Gaulin & Gaulin, 1982; N Rooney and J Ekstrom cited in Chivers, 1997)

Species	Leaves				Flowers				Fruit			
	T	W	T:W	Ingestion rate (g/min)	T	W	T:W	Ingestion rate (g/min)	T	W	T:W	Ingestion rate (g/min)
<i>Alouatta seniculus</i>	52	24	2.2		6	3	2.0		44	73	0.6	
<i>Presbytis senex</i>	92	91	1.0	3.0	5	5	1.0	0.3	3	4	0.8	4.0
<i>P. entellus</i>	33	25	1.3	5.2	15	10	1.5	3.7	52	65	0.8	11.2
<i>Hylobates agilis x muelleri</i> :												
Group 1	31	30	1.0	5.6*	21	4	5.3	0.2*	47	67	0.7	8.3*
Group 2	51	54	0.9		21	4	5.3		27	42	0.6	
<i>Pan troglodytes</i>	49	33	1.5					14	63	0.2		

*Mean for the two groups.

1969; Hladik *et al.* 1971) pioneered such studies on Barro Colorado Island (Smithsonian Tropical Research Institute), Panama Canal Zone, and then in Sri Lanka (Hladik, 1977a), calculating the proportions of primary nutrients (Table 7). These showed the importance of sugars, and adequate protein and fats, and how cellulose was avoided, especially by the smaller species; seeds are the main source of lipids.

A second wave of activity was focused on secondary compounds, to understand why the black colobus (*Colobus satanas*) ate seeds in profusion instead of leaves. McKey *et al.* (1978) showed how they were avoiding the unusually high level of chemical defences in the leaves of many tree species at Douala-Edea in Cameroun, compared with Kibale, Uganda (*C. badius*). They selected foliage lower in phenolics and fibre (Table 8); otherwise, they consumed mostly seeds (Table 2). Similar behaviour has been observed in Asian colobids on poorer soils (Davies *et al.* 1988), selecting the more digestible leaves, and eating seeds. The red langur (*Presbytis rubicunda*) in Borneo is a

prime example of this, but the banded langur (*P. melalophus*) also eats large amounts of seeds, even though the leaves in Peninsular Malaysia are not especially indigestible.

The intake of tannins is variable (Davies *et al.* 1988). They may not be digestion inhibitors in the sacculated colobid stomach, but may enhance protein digestion. It seems that seeds are selected for high protein level, and that toxin levels have a marked effect, but there is a paucity of information even for colobid species. The key common factors in Africa and Asia are the avoidance of fibre and the quest for protein.

Vellayan (1981) performed similar analyses on gibbon foods, showing their almost total avoidance of alkaloids and tannins. Apes (and man) and the spider monkey (*Ateles*) lack the enzyme uricase (EC 1.7.3.3), present in all other haplorhine primates, and so cannot deal with tannins as effectively. Gibbons selected their foods, mainly fruit low in fibre (except for fig (*Ficus* spp.) receptacles), high in protein and sugars, and low in fats (Table 9).

Table 6. Various measures of food intake by gibbons (From Chivers & Raemaekers, 1986)

	Siamang (<i>Hylobates syndactylus</i>)		Lar gibbon (<i>H. lar</i>)	Agile gibbon (<i>H. agilis</i>)
Feeding time (min/d)	354	310	217	196
Food intake (kg dry wt)				
Fruit	0.16	0.16	0.15	0.15
Leaves	0.22	0.14	0.05	0.06
Flowers	0.05	0.03	0.01	0.01
Food intake (kg wet wt)				
Fruit	0.57	0.56	0.55	0.54
Leaves	0.95	0.61	0.21	0.25
Flowers	0.15	0.09	0.02	0.01
Insects	0.01	0.04	0.02	0.01
Total	1.66	1.30	0.80	0.80
Predicted intake*		1.58	0.83	
Percentage of feeding time (T)				
Fruit	32	43	69	68
Leaves	58	47	26	31
Flowers	9	6	7	3
Insects	2	15	13	1
Percentage of food weight (on wet wt basis; W)				
Fruit	34	43	69	68
Leaves	57	47	26	31
Flowers	9	7	3	1
Insects	0.4	3	3	0.3
T:W				
Fruit	0.94	0.84	0.72	0.85
Leaves	1.02	0.91	1.16	1.26
Flowers	1.00	0.86	2.33	3.00
Insects	5.00	5.00	5.58	3.33
W:T				
Fruit	1.06	1.19	1.38	1.17
Leaves	0.98	1.09	0.90	0.79
Flowers	1.00	1.17	0.43	0.33
Insects	0.20	0.20	0.23	0.30

* Derived from body size and BMR.

Table 7. Nutrient content (g/kg) of foods of some neotropical primates (From Hladik *et al.* 1971; Hladik, 1977a)

	Protein	Lipids	Reducing sugars	Cellulose	Complementary fraction [‡]	Minerals (g/kg dry wt ingested)		
						K	Ca	P
<i>Alouatta</i> spp.	100	30	220	140	520			
<i>Ateles</i> spp.	70	50	340	110	430			
<i>Cebus</i> spp.	140*	160	260	80	360			
<i>Saguinus</i> spp.	210*	90	290	70	340			
<i>Presbytis senex</i>	115	40	70–150 [†]			15–25	10–25	2–3
<i>P. entellus</i>	100–160	30–110	70–150 [†]			15–35	5–15	3–5

* 50 g Plant protein/kg.

[†] All values vary seasonally, according to fruit and flower availability.[‡] 1000-(protein + lipid + reducing sugars + cellulose).

Protein and mineral intake in chimpanzees has been quantified by Hladik (1977b). Animal protein is augmented significantly by ants (Formicidae) or termites (Isoptera) from some leaves and the earth of termite mounds.

Goodall (1977) analysed mountain gorilla foods in some detail, in relation to his socio-ecological study in the Kahuzi-Biega National Park in Zaire. He estimated net energy available to a male (200 kg) and a female (100 kg), showing an availability three times the predicted value for BMR. He also estimated water intake, and loss in dung, urine and evaporation, leaving, in the male, 14–17 litres

available for metabolism. They seem able to satisfy their nutritional needs from vegetation, simply eating more when necessary.

Concluding discussion

We have surveyed a wide spectrum of feeding in wild primates, from the parts of plants (and animals) eaten, in terms of feeding time and food weight, to the nutritional contents (primary and secondary compounds, minerals and energy). Treatment has been patchy, partly because of the nature and quantity of information available. Detailed study

Table 8. Food composition (g/kg) and digestibility (%) of some colobid diets (From Davies *et al.* 1988)

	Total phenolics		Condensed tannins		Acid-detergent fibre (ADF)		Digestibility		N		Crude protein (N × 6.25): ADF	
	A	W	A	W	A	W	A	W	A	W	A	W
Species												
<i>Colobus satanas</i>	79	89	80	66	470	400	37	45	29	38	5	6
<i>Colobus badius</i>	55	58	50	60	340	310	54	53	33	33	7	7
<i>Trachypithecus johnii</i>	77	64	76	56	350	370	40	45	24	23	5	5
<i>Presbytis melalophos</i>	38	28	39	20	440	410	45	46	26	26	4	5
<i>P. rubicunda</i>	76	63	104	94	450	340	41	51	29	30	5	7
Food item												
Leaves: Uneaten	40		49		470		39		21			
Eaten	38	37	31	30	440	440	49	49	30	35		
Flowers: Uneaten	86		90		410		40		17			
Eaten	12	12	1	1	410	390	49	49	23	24		

A, actual composition of all leaves; W, weighted according to intake (relative to uneaten and total leaf analysis).

Table 9. Nutrient composition (g/kg) of gibbon diets (Vellayan, 1981)

	Fibre	Protein	Carbohydrates	Fat	Tannins	Alkaloids
Young leaves	< 150	110–240	600	< 50	Low	0
Flowers	170–260	100–270	600–700		Very low	0
Fruit	65	High or Low	500–800	Low	Low (0.3–50)	0
Fig (<i>Ficus</i> spp) fruit	290–550	< 90	650–320 or 30–130	55	Low (0–45)	0

of nutrients from field collections are not always balanced by the required details of feeding behaviour, and they are not always carried out in the same way, so that comparison between studies are difficult. Some studies focus on primary compounds, others on secondary compounds, and still others on energy calculations.

Observational problems, in tropical forest in particular, impede comprehensive quantification of diets, even in terms of feeding time. Collection of weight data is even more problematic, but as data accumulates, so we can extrapolate from feeding time to food weight, at least in certain areas and for certain food types. Not much has been said about figs, which are a key component of many primate diets, because of their abundance and year-round availability. The wasps they contain provide some animal protein, even though the receptacle is fibrous and less digestible, but the pulp is high in sugars and protein. The family Leguminosae is also a major source of food for folivorous as well as frugivorous, primates, and population biomass density correlates positively with their abundance in the forest (Marsh & Wilson, 1981).

This analysis of food intake by primates has been set against the radiation of our closest relatives into a wide variety of habitats and niches, a success story based on their lack of the specializations characteristic of most other mammalian orders, and on their flexibility or adaptability to different environments. Thus, appreciation of the structure and composition of these habitats is crucial, as is an understanding of their anatomy (limbs for procuring food, teeth for mastication and guts for digestion). No primate is omnivorous, in the original sense of the term, since their guts, in particular, cannot deal with significant amounts of foliage and animal matter. Most 'omnivores' are, in fact, frugivores, or fauni- or foli-frugivores. Only man (thanks to food processing and cookery) and some versatile primate populations (baboons and chimpanzees) can cope with a truly mixed diet.

Dental anatomy is crucial in understanding how different foods may be broken down for digestion. Key features of the gastrointestinal tract relevant to the present discussion are the size of different compartments (surface area for absorption, volumes for fermentation, weight for muscular activity) and passage (retention) time, for which limited data are available in primates, but which is central to the processing of differing foods. Flowers are grouped with leaves in some analyses, since they pose similar digestive problems to guts. Some guts can deal with the more fibrous foods, others have to pass them through more rapidly; the distinction between differences in passage time between particles (the solid fraction) and fluids are of paramount importance (see Chivers & Langer, 1994).

As data accumulate, so we are able to understand this diversity. In particular, progress is being made, despite the difficulties, in quantifying primate diets and their selectivity in terms of nutrients and energy expenditure. Much has been done, but much remains to be done, especially at the physiological and biochemical end of this spectrum of biological, multi-disciplinary endeavour. We must hope that the gaps can be filled, and understanding completed, while the amazing diversity of primates still exists.

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References

- Ahsan MF (1994) Behavioural ecology of the hoolock gibbon (*Hylobates hoolock*) in Bangladesh. PhD Thesis, University of Cambridge.

- Aiello LC & Wheeler P (1994) The expensive tissue hypothesis: the brain and the digestive system in human and primate evolution. *Current Anthropology* **36**, 199–221.
- Ayres JM (1989) Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. *Journal of Human Evolution* **18**, 697–716.
- Barrett EBM (1984) The ecology of some nocturnal arboreal mammals in the rain forest of Peninsular Malaysia. PhD Thesis, University of Cambridge.
- Chivers DJ (1974) The siamang in Malaya: a field study of a primate in tropical rain forest. *Contributions to Primatology* **4**, 1–335.
- Chivers DJ (1984) Feeding and ranging in gibbons: a summary. In *The Lesser Apes: Evolutionary and Behavioural Biology*, pp. 267–281 [H Preuschoft, DJ Chivers, WY Brockelman and N Creel, editors]. Edinburgh: Edinburgh University Press.
- Chivers DJ (1991) Species differences in tolerance to environmental change. In *Primate Responses to Environmental Change*, pp. 1–37 [HO Box, editor]. London: Chapman & Hall.
- Chivers DJ (1992) Diets and guts. In *The Cambridge Encyclopedia of Human Evolution*, pp. 60–62 [S Jones, R Martin and D Pilbeam, editors]. Cambridge: Cambridge University Press.
- Chivers DJ (1997) *Project Barito Ulu: The Role of Animals in Forest Regeneration, Quinquennial Report*. Jakarta: Ministry of Forestry.
- Chivers DJ & Hladik CM (1980) Morphology of the gastrointestinal tract in primates: comparisons with other mammals. *Journal of Morphology* **166**, 337–386.
- Chivers DJ & Langer M (1994) *The Digestive Systems in Mammals: Food, Form and Function*. Cambridge: Cambridge University Press.
- Chivers DJ & Raemaekers JJ (1986) Natural and synthetic diets of Malayan gibbons. In *Primate Ecology and Conservation*, pp. 39–56 [JG Else and PC Lee, editors]. Cambridge: Cambridge University Press.
- Davies AG, Bennett EL & Waterman PG (1988) Food selection by two South-east Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophus*) in relation to plant chemistry. *Biological Journal of the Linnean Society* **34**, 33–56.
- Davies AG, Caldecott JO & Chivers DJ (1984) Natural foods as a guide to nutrition of Old World primates. In *Standards in Laboratory Animal Management*, pp. 225–244 [J Remfry, editor]. London: Universities Federation for Animal Welfare.
- Davies AG & Oates JF (1994) *Colobine Monkeys: their Ecology, Behaviour and Evolution*. Cambridge: Cambridge University Press.
- Estrada A (1984) Resource use by howler monkeys (*Alouatta palliata*) in the rain forest of Los Tuxtlas, Vera Cruz, Mexico. *American Journal of Primatology* **5**, 105–131.
- Ford SM (1986) Systematics of the New World monkeys. In *Comparative Primate Biology. vol. 1, Systematics, Evolution and Anatomy*, pp. 73–136 [DR Swindler and J Erwin, editors]. New York: Alan R. Liss.
- Fossey D & Harcourt AH (1977) Feeding ecology of free-ranging mountain gorilla (*Gorilla gorilla berengei*). In *Primate Ecology*, pp. 415–447 [TH Clutton-Brock, editor]. London: Academic Press.
- Galdikas BF (1978) Orang-utan adaptation in Tanjung Puting Reserve, Central Borneo. PhD Thesis, University of California, Los Angeles.
- Gaulin SJC & Gaulin CK (1982) Behavioural ecology of *Alouatta seniculus* in Andean cloud forest. *International Journal of Primatology* **3**, 1–32.
- Goodall AG (1977) Feeding and ranging behaviour of a mountain gorilla group (*Gorilla gorilla berengei*) in the Tshibinda-Kahuzi Region (Zaire). In *Primate Ecology*, pp. 450–479 [TH Clutton-Brock, editor] London: Academic Press.
- Gupta AK (1997) Conservation ecology of primates and human impact in North-east India. PhD Thesis, University of Cambridge.
- Hershkovitz P (1977). *Living New World Monkeys (Platyrrhini) with an Introduction to Primates*, vol. 1. Chicago: University of Chicago Press.
- Hladik CM (1977a) A comparative study of the feeding strategies of two sympatric species of leaf monkeys: *Presbytis senex* and *Presbytis entellus*. In *Primate Ecology*, pp. 415–447 [TH Clutton-Brock, editor]. London: Academic Press.
- Hladik CM (1977b) Chimpanzees of Gabon and chimpanzees of Gombe: some comparative data on diet. In *Primate Ecology*, pp. 481–501 [TH Clutton-Brock, editor]. London: Academic Press.
- Hladik CM (1979) Diet and ecology of prosimians. In *The Study of Prosimian Behavior*, pp. 307–357 [GA Doyle and RD Martin, editors]. New York: Academic Press.
- Hladik CM & Chivers DJ (1978) Concluding discussion: ecological factors and specific behaviour patterns determining primate diet. In *Recent Advances in Primatology. vol. 1, Behaviour*, pp. 433–444 [DJ Chivers and J Herbert, editors]. London: Academic Press.
- Hladik CM & Hladik A (1969) Rapports trophiques entre végétation et primates dans la forêt de Barro Colorado, Panama (Trophic interactions between plants and primates in the forest of Barro Colorado, Panama). *Terre et Vie* **23**, 25–117.
- Hladik CM, Hladik A, Bousset J, Valdebouze P, Viroben G & Delort-Laval (1971) Le régime alimentaire des primates de l'île de Barro Colorado (Panama). Résultats des analyses quantitatives (The diets of primates on Barro Colorado Island (Panama). Results of quantitative analyses). *Folia primatologica* **16**, 85–122.
- Kay RF (1975) The functional adaptation of primate molar teeth. *American Journal of Physical Anthropology* **43**, 195–216.
- Kinzey W (1978) Feeding behaviour and molar features in two species of titi monkey. In *Recent Advances in Primatology. vol. 1, Behaviour*, pp. 373–385 [DJ Chivers and J Herbert, editors]. London: Academic Press.
- Kleiber M (1961) *The Fire of Life*. New York: Wiley.
- Klein LL & Klein DJ (1977) Feeding behaviour of the Colombian spider monkey. In *Primate Ecology*, pp. 153–181 [TH Clutton-Brock, editor]. London: Academic Press.
- MacLarnon AM, Chivers DJ & Martin RD (1986) Gastro-intestinal allometry in primates and other mammals including new species. In *Primate Ecology and Conservation*, pp. 75–85 [JG Else and PC Lee, editors]. Cambridge: Cambridge University Press.
- McKey D, Waterman PG, Mbi CN, Gartlan JS & Struhsaker TT (1978) Phenolic content of vegetation in two African rain forests: ecological implications. *Science* **202**, 61–64.
- Marsh CW & Wilson WL (1981) *A Survey of the Primates in Peninsular Malaysian Forests*. Kuala Lumpur: Universiti Kebangsaan Malaysia and University of Cambridge.
- Milton K (1980) *The Foraging Strategy of Howler Monkey*. New York: Columbia University Press.
- Mittermeier RA & van Roosmalen M (1981) Preliminary observations on habitat utilization and diet in eight Surinam monkeys. *Folia primatologica* **36**, 1–39.
- Oates JF, Waterman PG & Choo GM (1980) Food selection by the South Indian leaf monkey. *Oecologia* **45**, 45–56.
- Peres CA (1993) Diet and feeding ecology of saddle-back (*Saguinus fuscicollis*) and moustached (*S. mystax*) tamarins in an Amazonian terra firme forest. *Journal of Zoology, London* **230**, 567–592.
- Rijkssen HD (1978) *A Field Study on Sumatran Orang-utans (Pongo pygmaeus abelii Lesson, 1827)*. Wageningen: H. Veenman.

- Ripley S (1979) Environmental grain, niche diversification and feeding behaviour in primates. In *Food Acquisition and Processing in Primates*, pp. 33–72 [DJ Chivers, BA Wood and A Bilsborough, editors]. London: Plenum Press.
- Rodman PS (1977) Feeding behaviour of orang-utans of the Kutai Nature Reserve, East Kalimantan. In *Primate Ecology*, pp. 384–413 [TH Clutton-Brock, editor]. London: Academic Press.
- Rosenberger AL (1981) Systematics: the higher taxa. In *Ecology and Behavior of Neotropical Primates*, pp. 9–27 [AF Coimbra-Filho and RA Mittermeier, editors]. Chicago: University of Chicago Press.
- Rylands A (1982) The behaviour and ecology of three species of marmosets and tamarins (Callitrichidae, Primates) in Brazil. PhD Thesis, University of Cambridge.
- Susman RL (1984) *The Pygmy Chimpanzee: Evolutionary Biology and Behavior*. New York: Plenum Press.
- Vellayan S (1981) Chemical composition and digestibility of natural and domestic food of the lar gibbon (*Hylobates lar*) in Malaysia. MSc Thesis, Universiti Pertanian Malaysia.
- Wrangham RW (1977) Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In *Primate Ecology*, pp. 504–538 [TH Clutton-Brock, editor]. London: Academic Press.