

Selecting and processing food

Most primates, including humans, obtain some part of their food from plants. Only tarsiers (*Tarsius* spp.) are absolutely carnivorous. Meat generally presents few problems for primate digestive tracts. However, plant foods call for adaptive changes in behaviour and anatomy to allow this widely available, but chemically complex, energy source to be used. Special mechanisms have evolved to deal with the poisonous secondary compounds in many plant parts. Every part of a plant may be eaten by primates, but leaves make up the bulk of vegetable matter consumed by many species.

Plants vary widely in their chemical composition. The main components are complex structural carbohydrates (cellulose and hemicellulose) and related polymers (lignins). These are the most abundant potential source of energy, but primates (and other mammals) cannot utilise them directly because they lack the enzymes required for their digestion. To make use of this abundant resource, primates and other mammals have evolved a co-operative or symbiotic relationship with micro-organisms such as bacteria and single-celled organisms called protozoans that live in the gut and provide the enzymes needed to digest the cellulose.

Digestion of cellulose

Microbial fermentation occurs either in the enlarged foregut (stomach) or in the caecum. Among non-human primates, there is known to be foregut fermentation in langurs (*Presbytis*) and colobus monkeys (*Colobus*), and caecal fermentation in howler monkeys (*Alouatta*). Foregut fermenters have large stomachs with many pouch-like parts or sacs, whereas caecal fermenters have simple stomachs but a large, divided caecum.

The products of fermentation in both foregut and caecal fermenters are volatile fatty acids, carbon dioxide, methane and microbial cells. The gases (carbon dioxide and methane) are waste products, while the energy-rich fatty acids and microbial cells are used by the host. In mammals with caecal fermentation, food is digested in the stomach before microbial fermentation takes place. This means that the simple structural carbohydrates (from fruit and nectar) are digested and absorbed in the stomach and small intestine before the complex carbohydrates are acted on in the caecum by the gut's microbial inhabitants.

Fermentation in the caecum may have an advantage over fermentation in the foregut because plant toxins are not broken down (they remain biologically inactive) until after the food and any toxins it contains have passed through the small intestine with its highly absorptive walls. This means

that the breakdown of toxins is carried out primarily by the micro-organisms in the caecum and not by the host's liver, which could get damaged as a result. Also, because the large intestine (colon) is less absorptive, there is less chance of the by-products of the toxins being taken up by the body. Of course, this may also mean that absorption of nutrients is reduced. Gorillas and the sportive lemur (*Lepilemur*), which are both caecal fermenters, ingest their own faeces in the wild so that there is a second passage of food material, this time newly detoxified, through the intestine.

The long intestine of some herbivores delays the passage of food through it but may increase the efficiency of the gut micro-organisms. In primates, the time taken for food passage is positively correlated with body size; in other words, the larger the primate the slower the rate of passage. Although large primates need absolutely more food, metabolic costs per unit body weight decrease as body size increases. Thus, small primates have relatively higher energetic costs per unit body weight and must select high-quality food because they do not have the space in their gut to process large amounts of low-quality food. Large primates do not have this problem.

How primates deal with toxic chemicals

Plant parts are more than convenient packets of nutrients waiting to be unwrapped by micro-organisms in the digestive tracts of primates. Plants can and do defend themselves from hungry primates by using chemical defences, based on secondary compounds. These evolved as a defence against insects. In turn, insects evolved methods of handling the new plant chemicals and thus were able to maintain their association with their plants: an evolutionary 'arms race'. The fact that some plant secondary chemicals are also toxic, and serve as a deterrent to primates (which evolved much later than insects), is incidental but is nevertheless of value to the plant that contains them.

Plant-eating primates must deal with these rapidly evolving chemicals, which range from compounds that reduce digestibility (e.g. protein-binding tannins and enzymes) to toxins (e.g. alkaloids, cyanogenic glycosides and non-protein amino acids). Both physiology and behaviour are involved in helping primates to deal with the secondary compounds of plants.

Mammals use two main methods to detoxify such compounds. They can be degraded by microsomal enzymes in the liver and kidneys or by the gut micro-organisms. Indeed, the need to detoxify the secondary compounds of plants may have led to the evolution of foregut fermentation in the first place. For example, the micro-organisms

FOOD IN A PRIMATE'S LIFE

In order to survive and reproduce, a primate must find enough to eat and yet avoid being eaten itself. Much is now known about primate diets, especially about how primates select food items and how different species living in the same forest divide up its resources. Less clear, but equally important, is the link between the spatial and temporal distribution of the food available and the social organisation of primates.

The diets of most primates are made up predominantly of plant parts. Some species also eat insects and a few, particularly macaques and baboons, occasionally prey on nestling birds, lizards, or even the odd frog or crab. Baboons and chimpanzees hunt mammals as well, but meat is not a major item in their diet. Only the little tarsiers of Southeast Asia have never been seen to eat plants: they feed exclusively on insects and other small animals.

Why does a primate select particular kinds of food in preference to others? Body size and specialisations of the teeth and gut strongly influence choices. Large-bodied primates, for instance, need bulky and abundant foods to meet their energy, protein and other nutritional needs. Leaves, a major source of protein, figure importantly in their diet, and fleshy fruits provide energy in the form of fruit sugar. Leaves are difficult to process, and leaf-eating primates have teeth specialised for shearing and grinding leaf blades, and guts specialised for digesting them. In contrast, small-bodied primates tend to seek out insects, which constitute a high-quality, though sparse, source of protein, and they supplement their diet with energy-rich fruit or gums.

In the early days of field research, primates were considered wasteful, clumsy feeders because they frequently drop food, particularly fruit, from the trees in which they are feeding. Subsequent work has shown that in fact they are highly selective, and the fruit raining down has been discarded as either unripe or too ripe. The nutritional qualities of fruit and leaves vary from one plant species to another, and from one season to another, and primates

use taste, vision and smell to choose amongst them. For example, almost all leaf-eating primates have a strong preference for immature leaves, which tend to be higher in protein and lower in fibre and poisons than mature ones.

The discovery of poisonous compounds in some leaves has encouraged research on primate-plant relationships from the plants' point of view, and a whole array of defensive strategies used by plants against herbivores, including primates, has now been uncovered. Some plants use primates to disperse their seeds: they produce fleshy fruits that attract primates, but the seeds pass unharmed through the digestive tract of many of these fruit-eaters, and are then deposited in faeces, often far from the parent tree.

The dietary choices of primates are influenced by their own attributes and those of the plants and animals potentially available as food. It has been suggested that competition for food between primate species living in the same forest may also help determine diet, by preventing one species from eating food that is important in the diet of another. The role of competition in establishing and maintaining ecological differences among primates (*niche separation*) is still unclear, but niche separation itself has been found wherever it has been sought: from South American rainforest communities contain-



Capped langurs (*Presbytis pileata*) on a fruit tree in Assam, India.

ing 11 primate species, through African communities with as many as 15, to Malaysian communities of 6. No two primate species use the forest in identical ways.

A primate's diet affects many aspects of its life. Primates with leafy diets tend to be less active than those preferring fruit, moving shorter distances each day and occupying a smaller home range. Determining the ways in which the ecology of a primate species influences its social organisation is a particularly challenging problem.

We know that insect-eating primates tend to be solitary or to live in small social groups, probably because it is easier to hunt insects alone, and that fruit-eating primates often live in social groups that fragment and rejoin, depending on the size of fruiting patches. But many factors influence social organisation and it is difficult to evaluate their relative influence.

For instance, in order to survive, a primate must not only find food but also avoid predators. Species (e.g. savanna baboons) living where predators are abundant usually live in larger social groups than their relatives occupying a forest environment: the old maxim of 'safety in numbers' contains some real truth. Against this, large group size presents a potential disadvantage for its members, because competition for food is likely to be greater than in a small group.

A final complicating factor in attempts to sort out the relationship between primate ecology and social organisation is the possibility that ecological influences affect males and females differently. For example, it has been suggested that female chimpanzees distribute themselves primarily in relation to the distribution of food, but that males distribute themselves primarily in relation to females.

In sum, it is clear that food plays a much larger part in the life of a primate than merely providing the means for staying alive and healthy. Less clear is precisely how diet is linked to other spheres of a primate's life. A.F. Richard

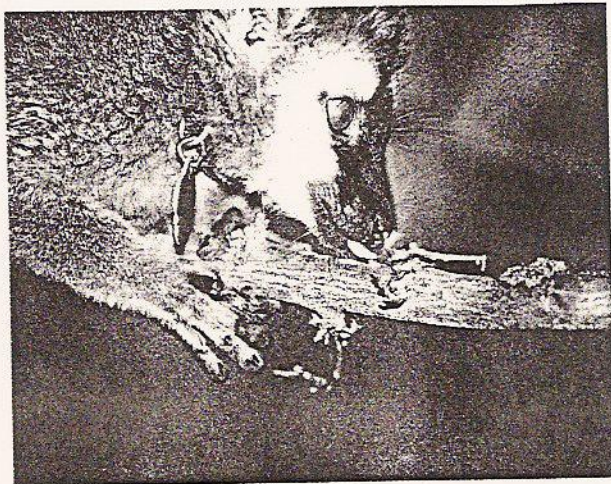
in the stomach of the Hanuman langur (*Presbytis entellus*) may protect this primate from the large amounts of alkaloids in the fruit of the clearing nut (*Strychnos potatorum*).

Very little is known about the biochemical pathways used by non-human primates to detoxify plant chemicals. Comparative studies of drug metabolism in primates suggest that non-human primates metabolise drugs much as humans do. The relative importance of enzymes and gut micro-organisms in detoxifying foreign substances is unknown for most plant secondary compounds. No single species of primate can possibly have all the mechanisms needed to handle every kind of plant poison. They must

also depend on behaviour to cope with the toxic chemicals produced by plants.

Selective feeding

A primate can either become a specialist and feed on only one or very few food species, or it can become a generalist and feed on a wide variety of plants. Extreme specialists, such as the marsupial koala bear, which feeds only on the leaves of the eucalyptus (and in some cases favours only one eucalyptus species, *Eucalyptus viminalis*), have to deal with only one or a few secondary compounds. However, because they feed on only a few plant species they could be



Most primates do not specialise on one or two plants but selectively feed on a variety of species. Here (above), a red-fronted lemur (*Lemur fulvus rufus*) is feeding on leaf buds of red maple (*Acer rubrum*) and (right) a mantled howler monkey (*Alouatta palliata*) is choosing new leaves of fig (*Ficus*). In this way, generalist feeders avoid plant parts containing toxic chemicals at certain times of the year and get a balanced diet.



in serious trouble should these become scarce. Generalists, on the other hand, are faced with a wide variety of chemicals and they cannot maintain detoxification systems for all of them. Therefore, they reduce the total number of chemicals or the amount of any one that they must process by selecting plants or plant parts that contain few chemicals or by ingesting small amounts of many foods. This varied diet provides generalists with a balanced intake of nutrients and protects them against a shortage of any one food.

Most primates are generalists, so most of the herbivorous species do not specialise on one or a few plants but selectively feed on a variety of species. For example, mantled howlers (*Alouatta palliata*) in Costa Rica and on Barro Colorado Island, Panama, prefer new leaves, fruits and flowers to mature leaves and thus avoid material containing certain secondary compounds. Black colobus monkeys (*Colobus satanas*) in Cameroon avoid the mature leaves of all common tree species and the new leaves of most of them, while feeding selectively on relatively rare tree species or on colonising plant species. The mature leaves of the common Cameroonian trees contain very high concentrations of toxic phenolic compounds. Black-and-white colobus monkeys (*Colobus guereza*) and vervets (*Cercopithecus aethiops*) are now known to behave in a similar way. Mountain gorillas (*Gorilla gorilla beringei*) on Mt Visoke, Rwanda, do not even sample balsam (*Impatiens*), one of the most common plants in their home ranges.

Medicinal uses of plants

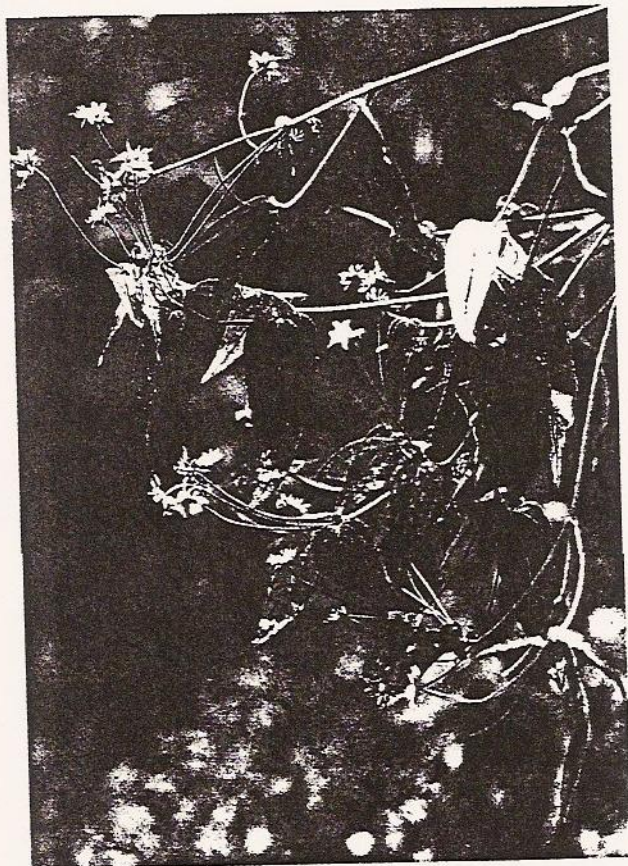
Consumption of plants with known medicinal properties have been observed in chacma and Hamadryas baboons (*Papio ursinus* and *P. hamadryas*) and in common chimpanzees (*Pan troglodytes*). The leaves and berries of *Balanites aegyptiaca*

could be eaten by the baboons as a protection against schistosomiasis. A female chimpanzee in the Mahale Mountains, Tanzania, has been seen chewing and then sucking the juice of bitter leaf (*Vernonia amygdalina*). She appeared ill with an influenza-like sickness from which she gradually recovered after swallowing the astringent juice of a bitter leaf. Bitter leaf is used by people throughout Africa for parasites and gastrointestinal disorders. Given this ethnomedicinal use of plants by humans, it is not unreasonable to assume a similar use by other primates.

Plant poisons and human evolution

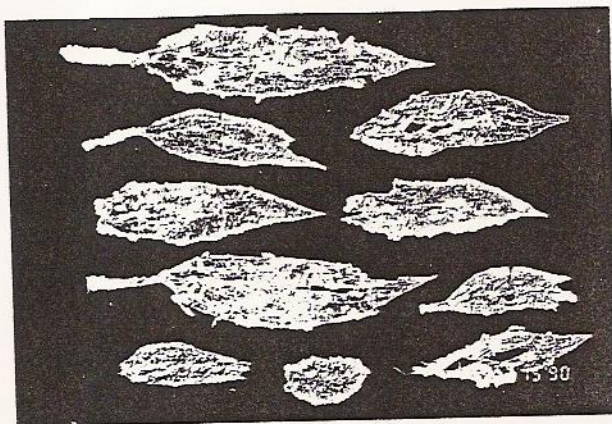
Humans also rely on plants for a considerable amount of their food. The secondary compounds of plants have major implications for our ancestors and for ourselves.

Our early hominid ancestors, who were primarily plant-eaters and did not have the benefits of fire, were faced with the same problems as those faced by non-human primates. It has even been suggested that the numbers of early humans were limited by food availability because of plant toxins. Before the use of fire for cooking, which may have come relatively late in human evolution, early humans were exposed to the full impact of plant secondary compounds. These ingested secondary compounds may have had important effects on general fitness and even on the age of reproduction. For example, some species of yams (*Dioscorea*) contain diosgenin, which is widely used in birth-control drugs. Initially, such effects were probably unsuspected, but with increasing awareness our ancestors could have chosen specific effects by ingesting certain foods. The modern Aguaruna Jivaro of Peru regularly use natural plant products as contraceptives, suppressors of menstruation, abortifacients, aphrodisiacs and reproductive enhancers.



Some plant secondary compounds, such as caffeine, nicotine, quinine and tannin, are actively sought by humans. Carbonated water with quinine in it is mixed with gin and imbibed. The quality of tea and wine is determined in part by the amount of tannin present. The drinking of tea and wine has been linked to oesophageal cancer, but if milk is added to tea it binds the tannin and prevents its harmful effects. No similar protection is known for wine.

Special ways of treating or preparing many of the foods used by modern humans are required because of plant secondary compounds. For example, clay is often eaten with acorns to absorb tannin and manioc (*Manihot*) must be soaked because it contains cyanogenic glucosides that can cause nerve disorders. Even the common potato (*Solanum tuberosum*) contains the toxic α -solanine and α -chaconine as well as coumarin and must be cooked to make it safe to eat. However, cooking is no guarantee that the toxins have been destroyed or that processed foods are safe. The tubers of parsnips (*Pastinaca sativa*) contain toxic psoralens that are not destroyed in cooking, though these are not in dangerous quantities. Similarly, even though they are processed, coffee, chocolate and tobacco still contain the potentially poisonous caffeine and nicotine, yet we ingest them daily.



Chimpanzees and baboons – and probably other primates as well – eat plants with known medicinal properties. Chimpanzees, for example, make special foraging trips at dawn to eat young leaves of *Aspilia plurisetta* (left), a member of the sunflower family and a popular African herbal remedy. The leaves contain a potent antibiotic, which is also effective against parasitic worms. Normally, a chimpanzee stuffs leaves into its mouth as fast as it can pull them off the branches, and chews them quickly before swallowing them. It adopts quite a different method for *Aspilia* leaves. It chooses each bristly leaf carefully and then rolls it around its mouth slowly before swallowing it whole. Chimpanzees select and eat the leaves of *Commelina*, another herb with pharmacological properties, in a similar way. The leaves pass through the chimpanzee's gut undigested and appear in the dung whole, presumably having released medicinal chemicals on the way (above).

Cyanide, morphine and cocaine are all plant secondary compounds that affect humans. Most cyanide poisonings are accidental, but many people are exposed daily to low concentrations of cyanogenic compounds in foods such as nuts. Humans can detoxify fairly large amounts of such compounds, but chronic intake may cause damage to the nervous system. Morphine and cocaine can have positive effects on humans when used as medicines or negative ones when abused. And any food eaten to excess can be poisonous – for example, vitamin A found in liver and in carrots. There is a possible example of this in the human evolutionary record of 1.7 million years ago. Pathological changes in a *Homo erectus* skeleton (KNM-ER 1808) found at Koobi Fora in Kenya are consistent with chronic hypervitaminosis A that could have been caused by the individual eating the livers of carnivores or honeybee broods, both of which contain large amounts of vitamin A.

The impact of plant poisons on our evolutionary past remains unknown, but modern humans continue to suffer in the battle with such compounds. An understanding of how our close relatives have dealt with this problem may assist our own survival.

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See also 'Body size and energy requirements' (p. 41), 'Diets and guts' (p. 60) and 'Human diet and subsistence' (p. 69)