

The Impact of Plant Secondary Compounds on Primate Feeding Behavior

KENNETH E. GLANDER

Department of Anthropology, Duke University, Durham, North Carolina 27706

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ABSTRACT The recent literature on plant secondary compounds and their influence on primate feeding behavior is reviewed. Many studies of nonhuman primates document the extreme selectivity that primates, particularly herbivorous species, demonstrate in their food choice. Until quite recently investigators interpreted this to mean that herbivorous primates were not food limited. This view has been challenged in the past 10 years by researchers concentrating on the primate-plant interaction. Chemical analyses have demonstrated that plant parts are of varying quality due to differences in nutrient and secondary compound content. The assumption that all leaves (or fruits, flowers, and insects) are potential foods of equal value to the primates eating them is refuted. The observed selectivity and preferences of primates for specific plant or insect species and parts are now viewed as strategies for dealing with the nutrient and secondary compound content variation in these foods.

The field of plant-herbivore interaction is a rapidly expanding one that includes the phytochemical relationship between plants and herbivores. It has long been acknowledged that plants and insects profoundly influenced each others' evolutionary courses, but only recently have the biological and ecological roles of plant-produced secondary compounds been recognized.

Stahl (1888) was the first to suggest that plants use chemical defenses in addition to the more familiar morphological and mechanical means of protecting themselves. Despite this early observation, plant produced chemicals were considered nothing more than waste products of plant metabolism until Fraenkel (1959) again suggested a defensive function for these compounds. Since then impressive evidence, which demonstrates that plants do use secondary compounds for defensive purposes, has accumulated (Ehrlich and Raven, 1965; Feeny, 1968; Janzen, 1969; Rhoades and Cates, 1976; Rosenthal and Janzen, 1979; and included references). Mothes (1976) went so far to suggest that secondary substances may be primarily defensive in nature and are neither essential nor of any physiological importance to the plants that produce them. He stated that the loss of these chemicals does not reduce the plant's viability.

PRIMARY VERSUS SECONDARY COMPOUNDS

The term "secondary compounds" is difficult to define, but Mothes (1980) suggests that its origin may be found in a lecture given by Albrecht Kossel in 1891 and published in *Archiv für Physiologie* (1891:181), in which he said:

Just as microscope research has succeeded in stripping the cell of its non-essential accessories and in separating its casing and the reserves stored in it from the actual life-carriers, so now chemistry must attempt to separate those compounds which are present, without exception, in a protoplasm capable of developing, and to recognize the substances which are either incidental or not absolutely necessary for life. Finding and describing those atom complexes to which life is bound comprises the most important basis for the investigation of life processes. I propose calling *these essential components of the cell primary components, and those which are not found in every cell capable of developing, secondary*. To decide whether a substance belongs to the primary or secondary components is extremely difficult in certain cases (Mothes, 1980:3, my emphasis).

It is indeed difficult to define secondary compounds since a compound may have a primary role in one species and a secondary role in another. However, in most of the modern literature primary compounds generally are defined as those required for basic metabolism and all others are secondary compounds, just as Kossel suggested in 1891.

It is important to point out that the terms "toxin, toxic, or poisonous" and "secondary compound(s)" should not be used interchangeably. They are not synonyms. Janzen (1979:335) states that "toxicity is not an intrinsic property of any naturally occurring molecule, and secondary compounds are no exception." He gives the example of the allyl glucosinolate in cruciferous plants that is very toxic to black swallowtail larvae (*Papilio polyxenes*), only moderately toxic to southern armyworm larvae (*Spodoptera eridania*), and completely harmless to cabbage butterfly larvae (*Pieris rapae*). A secondary compound (canavanine) actually may be used as a nitrogen source by the larvae of the bruchid beetle, *Caryedes brasiliensis* (Rosenthal et al., 1978), while it is very lethal at exactly the same concentration to the larvae of the bruchid beetle, *Callosobruchus maculatus* (Janzen et al., 1977). It should be clear from these examples that the words toxic, toxin, and poisonous cannot be substituted universally for secondary compounds.

These results point out the problems in generalizing. The fact that a secondary compound is harmless or even beneficial to one or more herbivores does not permit the conclusion that it has lost its defensive function for the plant. In the same manner, the ingestion by some herbivores of plant material containing secondary compounds cannot be interpreted to mean that all herbivores can ingest that plant material. Exactly these conclusions have been reached by some investigators studying primate-plant relationships. Since plant secondary compounds are ubiquitous, it is highly probable that they influence primate food choice. There is, however, no a priori reason to assume this impact is either negative or positive, or that either is mutually exclusive. The challenge lies in determining how the system works. The cost in time and money is likely to be high since the interaction is very complex; nevertheless, this should not cause anyone to ignore what must be considered as a major question in primate feeding behavior.

DISTRIBUTION OF SECONDARY COMPOUNDS

The total number of plant secondary compounds can only be guessed, but Swain (1977) is of the opinion that the more than 10,000 presently known secondary metabolites represent only the tip of the iceberg. He predicts that the total number of all plant secondary compounds may equal the 400,000 known plant species.

Rhoades and Cates (1976) list (with included references) the following plant produced secondary compounds that have been shown to have either a negative impact on herbivore fitness (increased mortality, lowered growth rates, or fecundity) or to have a deterrent effect on herbivore feeding activity: alkaloids, pyrethrins, rotenoids, long-chain unsaturated isobutylamides, cyanogenic glycosides, phytoecdysones, juvenile hormone analogues, cardenolides, saponins, sesquiterpene lactones, nonprotein amino acids,

mustard oil glycosides, isothiocyanates, oxalates, protoanemonin, hypericin, fluoro-fatty acids, seleno-amino acids, 6-methoxybenzoxazoline, gossypol, condensed tannin, phenolic resin, phenoloxidase, and proteinase inhibitors.

Most of the above pertain to insects, but some of these compounds certainly serve the plants as defenses against vertebrate herbivores. For example, terpene and phenolic resins present in the adventitious shoots of paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), and green alder (*Alnus crispa*) were experimentally shown to be repellent to snowshoe hares (*Lepus americanus*) (Bryant, 1981). Cyanogenic glycosides deter voles from feeding on *Lotus corniculatus* and rabbits from grazing on *Trifolium repens* (Cooper-Driver and Swain, 1976). The consumption of twigs of ponderosa pine (*Pinus ponderosa*) by tassel-eared squirrels (*Sciurus aberti*) is inversely correlated with the concentration of alpha-pinene (Farentinos et al., 1981).

TOXIC VERSUS DIGESTIBILITY-REDUCING

These two terms are often used interchangeably. Toxins have lower molecular weights than digestibility-reducing substances, are present and active in smaller amounts, and to be effective, must leave the stomach, enter the target cell, and disrupt the metabolism of the cell (Rhoades and Cates, 1976). Herbivores have the ability to detoxify toxins by a combination of metabolism and excretion. Specialist herbivores particularly have evolved very effective detoxification systems against toxins found in their host plants (Rhoades and Cates, 1976). In fact, some specialist insect herbivores use secondary substances in their host plants to locate the plant, while some sequester the plant's secondary chemicals for their own defensive purposes (Rhoades and Cates, 1976).

Digestibility-reducing substances have properties very different from toxins. Since they do not need to cross cell membranes, they can be of various sizes and chemical nature. The only requirement is that they disrupt digestion (Rhoades and Cates, 1976). The known protein digestibility-reducing substances are of two types. The first class is hydrolyzable and condensed tannins (Rhoades and Cates, 1976). These bind peptide groups making them unavailable to the digestive process (Feeny, 1976) and inhibit starch (Feeny, 1970) and cellulose (Rhoades and Cates, 1976) digestion. Hydrolyzable tannins can be easily broken down and thus they are less of a deterrent to predators, while condensed tannins are extremely resistant to attack. There is only one known organism that can degrade condensed tannins (*Penicillium adametzi*) (Swain, 1979).

The second type of protein digestibility-reducing substances inhibits proteolytic enzymes (Rhoades and Cates, 1976; Ryan, 1979). They function by binding to the enzymes that split peptide bonds of proteins, preventing them from breaking down proteins (Ryan, 1979). Fortunately for humans, proteinase inhibitors can be denatured quite easily by heating to 100°C (Rhoades and Cates, 1976).

SPECIALIST VERSUS GENERALIST

Basically there are two feeding strategies that can be adapted by herbivores faced with plant secondary metabolites: either become a specialist and feed on only one or a few food species, or become a generalist and feed on a wide variety of plant species (Cody, 1974). Specialists such as the koala (*Phascolarctos cinereus*), which feeds only on *Eucalyptus* (and in some case favors only one eucalyptus species, *E. viminalis*, Eberhard, 1978) have to deal with only one or a few secondary compounds. Generalists, on the other hand, are faced with a wide variety of different chemicals. It is impossible for them to maintain detoxification systems for all of these chemicals. Therefore, generalists reduce the number of chemicals or the amount of any one chemical that they must deal with by selecting plants or plant parts that contain little or no chemical protection or by ingesting small amounts of several foods. They cannot eat all of the plants available because their detoxification systems cannot possibly handle all of the many secondary compounds that plants use.

SECONDARY COMPOUNDS AND INSECTS

Plants evolved secondary compounds as a defensive measure against insect predation (Fraenkel, 1959). In turn, insects evolved methods of handling the new plant chemicals and thus were able to maintain their association with their host plants (coevolution) (Ehrlich and Raven, 1965). This is an evolutionary arms race in which the plants must spend energy to constantly change their chemical defenses and in which the insects must devote some of their energy to locating and detoxifying these chemicals (Feeny, 1975). The fact that some plant secondary chemicals are also toxic or serve as a deterrent to vertebrate herbivores is accidental, although the value to the plant may be increased with the added protection against these predators that appeared later in evolutionary time.

SECONDARY COMPOUNDS AND PRIMATES

The arms race that exists between insects and plants has major implications for plant-eating primates. Plants provide food for the majority of nonhuman primate species, in many cases their only food. Humans also rely on plants for a considerable amount of their food. Every part of the plant may be eaten, but leaves constitute the bulk of vegetable food for nonhuman primates. Since the evolutionary survival of the plants is primarily due to their own defensive strategies and since, as indicated above, there are excellent reasons for suspecting that this defense has a considerable chemical component, it should be apparent that plant secondary compounds are of great significance in understanding primate-plant interactions. Janzen (1979:332) makes it very personal for the human primate when he states that "herbivores are responsible for the caffeine in your morning coffee, the tannin to make leather shoes, and synthetic pesticides in the environment." He could have mentioned the many spices used for flavoring foods, quinine used for the treatment of malaria, and many other medicinals obtained from plants (see Morton, 1977).

Diet composition and food selection (by plant part and species) are important items in ecological studies of nonhuman primates. If one accepts that plants are fully capable of protecting themselves, and most primatologists can be tentatively placed in this group, the new horizon in primate ecological studies should be in viewing plants as complex organisms with chemical defenses and not simply unending food vendors for hungry primates. Plant parts ingested by primates are more than just convenient packets of nutrients. Plants cannot run away so they defend themselves. In fact, plants may be able to run away in time if not space. Some plants apparently have the ability to change their chemical defenses in response to herbivore attack (Carroll and Hoffman, 1980). The response time ranges from 40 minutes to several years. Thus, feeding becomes a tracking problem for herbivorous primates.

Plants can and do defend themselves. To survive, nonhuman primates must deal with this fact. In order to understand primate survival and adaptation, primatologists must place more emphasis on the primate-plant interaction. For example, do the chemical defenses that plants have evolved to protect themselves from insect herbivores affect primate herbivores, and if so, how and to what extent? If these chemicals do not affect primates, why not?

Listings of the plant species a particular primate eats may be useful for comparing different species or the same species in different habitats, but such lists will not answer the above or similar questions. Modern primate field work has moved beyond simple descriptive studies and has become more complex and time consuming, but it is absolutely essential if primate-plant interactions are to be understood. Part of the complex problem is determining the chemical composition (nutrients and secondary compounds) of both the plants that are eaten and those that are not eaten. The data that are available for insect-plant interactions clearly document that secondary compounds negatively or positively affect insect feeding. However, since insects are very different from primates, we cannot simply assume that primates will be affected because insects are affected. Ultimately, to understand primate feeding behavior, the primate-plant relationship must be documented in a manner similar to that done for insects and plants.

The work of Glander (Glander, 1975a, 1975b, 1978a, 1978b, 1979, 1980, 1981; Rockwood and Glander, 1979), the Hladiks (A. Hladik, 1978; C.M. Hladik, 1977a, 1977b, 1978), McKey and associates (McKey, 1974, 1978, 1979; McKey et al., 1978; Waterman et al., 1980; Gartlan et al., 1980), Milton and associates (Milton, 1977, 1978a, 1978b, 1979, 1980, 1981a, 1981b; Milton, et al., 1979, 1980; Nagy and Milton, 1979a, 1979b), Oates and associates (Oates, 1977, 1978; Oates et al., 1977, 1980), and Wrangham and Waterman (1981) has taken this direction, trying to evaluate the impact of plant secondary compounds on primate food selection. In all cases this was done by comparing observed feeding behavior with the results of chemical analyses. Several other investigators have reported analyses of nutrient content and/or may have speculated that secondary compounds affect primate feeding, but they have not analyzed secondary metabolites (Brazo Lloret, 1978; Brazo Lloret et al., in press; Coelho et al., 1976a, 1976b, 1977; Curtin and Chivers, 1978; Estrada, 1981; Estrada et al., 1978; Gaulin, 1977; Goodall, 1977; Hausfater and Bearce, 1976; Hladik and Hladik, 1969; Hladik et al., 1971; Kawai, 1979; Smith, 1977). Their work, therefore, will not be included in this discussion of the impact of plant secondary compounds on primate feeding behavior. In so doing, I make no evaluation of their worth, but simply include (to the best of my knowledge) only work documenting the impact or lack of impact of plant secondary chemicals on primate feeding.

After comparing results of chemical analyses and primate feeding behavior, C.M. Hladik and Milton concluded that nutrients are the most important factor in determining primate food choice. However, both suggested that plant secondary compounds may influence primate feeding behavior. Glander, McKey, Oates, and Wrangham and Waterman all found a negative correlation between the presence of certain secondary compounds and primate feeding behavior. They concluded that there is a dynamic and complex relationship between secondary compounds and nutrients that hinges on the type of defensive compound present, the amount of nutrient present, and the digestive system of the primate. While each of the above researchers have their favorite hypotheses about primate feeding behavior, none suggests that only one factor is responsible for the observed selectivity in primate feeding. All would surely agree that the complex nature of the primate-plant relationship is just beginning to be unraveled.

SECONDARY COMPOUNDS AND HERBIVOROUS PRIMATES

Schaller (1963) was probably the first to consider that plant properties can affect food choice of primates. He reported that gorillas (*Gorilla gorilla*) ignored all but 29 kinds of plants available to them in their habitat, but offered no explanation for why they should show this selectivity. He noted that many of the food plants were bitter or in other ways unpleasant to his taste, but did not know if the gorillas experienced similar sensations.

Glander (1975a, 1975b, 1978a) reported that mantled howling monkeys (*Alouatta palliata*) in Costa Rica did not feed equally on all available tree species, but were extremely selective both within and between tree species. The howlers avoided mature leaves of most of the common tree species, ate mature leaves of only certain individual trees, never ate mature leaves of other individuals of the same species even though they were immediately adjacent, ingested only new leaves and never mature leaves of certain tree species, ate only the petiole or pulvinus but dropped untouched the leaf blades of certain tree species, preferred new leaves, fruits, and flowers to mature leaves, and ingested the pedicel of *Anacardium excelsum* fruits but never ingested the fruits. (Basilisk lizards, *Basiliscus basiliscus*, demonstrated the same selectivity when feeding on *Anacardium* fruits dropped by foraging howlers; Glander, 1979.)

Glander (1975a, 1975b) first suggested that this feeding selectivity of the howlers may be the direct result of the presence of secondary compounds produced by the trees to protect themselves from predators. He also suggested that the presence of these chemicals eliminated many tree parts as potential food for howlers; i.e., what appeared to the observer to be food (leaves) was not in fact food because the howlers were not able to handle all of the secondary compounds present or that the secondary compounds reduced nutrient availability.

This hypothesis was very different from the suggestions in the literature that food for howlers was no problem (Altmann, 1959; Baldwin and Baldwin, 1972; Carpenter, 1934; Chivers, 1969; Hladik and Hladik, 1969; Hladik et al., 1971). It was also the converse of the suggestions of Altmann (1959) that the home range of howlers contained far more food than they could use, of Chivers (1969) that food in tropical forests was widely and evenly distributed, and of Hladik and Hladik (1969) that, based on the available food, the territory of a group of Barro Colorado howlers could support three times as many animals as were present. In 1976 and 1977 Coelho et al. (1976a, 1976b, 1977) suggested that howlers at Tikal were not food limited. They hypothesized that the food available and its nutrient content should be able to support many more howlers than they actually found at Tikal. Milton (1977, 1980), on the other hand, presented evidence that nutritional quality restricted the availability of food for Barro Colorado Island howlers, thereby resulting in lower population density than might be expected.

In order to test the hypothesis that plant secondary compounds affected howling monkey feeding behavior, Glander (1981) subjected samples of both food and nonfood items of howlers to chemical analyses to determine the presence or absence of alkaloids and phenolics as well as to quantify the amount of total protein, 16 amino acids, fiber, ash, and water. The results demonstrated seasonal and intraspecific variability in secondary compound content. [More recent results (Glander, unpublished data) indicate variability within the canopy of a single tree.] Tannins and alkaloids were found in a tree's leaves during one season but not another, and their presence or absence was not necessarily consistent from year to year. A comparison of the chemical results with the howler feeding pattern clearly indicated that they were avoiding plant material containing certain secondary compounds (potential toxic or digestibility-reducing compounds), yet were selecting material of highest nutritive value. Howlers were observed to ingest leaves from a tree that did not contain alkaloids or tannins (or if tannin was present it was the hydrolyzable kind). They were observed not to eat the leaves from an adjacent tree containing alkaloids or condensed tannins. Similarly, the new leaves and petioles of certain tree species that were eaten did not contain alkaloids or condensed tannins, while the uneaten mature leaves of the same species contained either one or both. It was clear that the howlers were very selective within a tree species, utilizing only those individual trees whose leaves had little or no secondary chemicals and the highest nutrient content. For example, during one 12-month period they ate mature leaves from only 6 of 19 *Bursera simarouba* and 12 of 149 *Gliricidia sepium*. They avoided leaves with condensed tannin, low total protein, and unbalanced amino acids (Glander, 1981). Chemically, the leaves they ate were very different from those they avoided, yet they were all from the same tree species.

Surprisingly, when leaves were compared without regard to whether or not the howlers ate them (i.e., a random sample of both new and mature leaves), there were few nutritive differences between all mature and new leaves (Glander, 1981). Significant differences occurred only when the howlers' feeding behavior was considered. Mature leaves that were eaten contained more of all amino acids except isoleucine, more total protein, and less crude fiber than those not eaten (all statistically significant differences). There were no nutritive differences between the ingested mature leaves and the new leaves that were eaten except for the expected difference in water content (i.e., the howlers were selecting mature leaves with young leaf characteristics). In other words, the howlers were not selecting leaves based on whether or not they were mature or young, but on their secondary compound content as well as on their nutrient content. Similarly, the howlers were selecting mature leaves with very low fiber content. There was no significant difference in fiber content between mature and young leaves that were eaten by the monkeys. This was further supported by the fact that the digestibility coefficient of total protein for ingested mature leaves was significantly higher than for mature leaves not eaten.

Glander (1978b) also reported that howlers drank from arboreal water sources only during the wet season and did not drink at all during the five-month dry season. Three factors were hypothesized: (1) young leaves, which made up a significantly greater part of the dry season diet, had significantly greater water content; (2) there was reduced

intake of plant secondary compounds in the dry season diet; and (3) there was an increased need for water during the wet season to flush secondary compounds out of the monkeys' systems. The latter hypothesis remains to be tested, but Glander (1981) found that new leaves had more water and less secondary compounds (both statistically significant).

Beyond affecting feeding and drinking behavior, secondary compounds may account for facultative birth spacing and differential infant mortality in howlers (Glander, 1980). Experimental evidence that mammals respond to chemical cues in their food is now available and observational data on rodents and marsupials suggests that they may utilize chemical cues from their plant foods to time their reproductive efforts (Berger et al., 1981; Sanders et al., 1981). Howlers may be using chemicals in their food in a similar fashion to produce offspring at the optimal time for maximal survival of the young during some years. This hypothesis remains to be tested, but howler infant survivorship was different in different years (Glander, 1980).

In summary, Glander (1981:250-251) believes that howler feeding behavior is affected by the complex interaction of plant secondary compounds, nutrient content, and digestibility:

Plant secondary compounds certainly influenced food choice but were not the only factors involved in the selectivity of the howlers. Several other factors, such as the nutrient content of the plant material as well as its digestibility, must be considered. All of these factors interact, either decreasing or increasing the value of an item.

C.M. Hladik (1977a) found large amounts of alkaloids in the fruits of *Strychnos potatorum* eaten by *Presbytis entellus* in Sri Lanka and suggested that the bacterial flora of their stomach protected the grey langurs from the potential toxins by detoxifying these chemicals. He then suggested: "As a protective device against primate leaf-predators, the secondary substances of plants would not be efficient" (C.M. Hladik, 1977a:351). Hladik feels that the small amounts of nutrients present in some plant species offer better protection from predators by encouraging the predators to eat foliage with higher levels of nutrients. For example, "The selection of the natural food substances by different primate species can be related to their content in primary nutrients (soluble carbohydrates, lipids, and proteins)" (C.M. Hladik, 1978:389). However, he continues by pointing out that allelochemicals such as tannins, alkaloids, saponins, and glycosides are present in leaves and other plant parts and may serve as repellents or toxic agents against folivorous primates. Hladik gives the example of a young gorilla feeding on liana leaves, which tested negative, while avoiding leaves that tested positive, indicating the possible presence of alkaloids. Hladik notes that nontoxic allelochemicals may serve to help primates find their preferred foods.

The Hladiks (A. Hladik, 1978; C.M. Hladik, 1977b) found alkaloids in about 15% of the plant species present in chimpanzee (*Pan troglodytes*) habitats in Gabon. Since the chimpanzees ate 38 of the tested plants (6 of which contained alkaloids), C.M. Hladik (1977b) concluded that alkaloids are either not toxic or are not sufficiently concentrated to be toxic in plants.

C.M. Hladik favors the idea that the primary compound content of plants has more impact on primate food choice than secondary compounds.

The secondary compounds have a secondary role in most of the cases on which we have collected precise data. . . . the monkeys only need to avoid a few toxic plant species; the rest of their strategy is to balance their diet with different amino acids if they do not have a bacterial flora to synthesize those essential nutrients, or to detoxify the rare harmful allelochemicals (C.M. Hladik, 1978:390).

McKey et al. (1978) reported that black colobus (*Colobus satanus*) in the Douala-Eden Reserve, Cameroon, avoided the mature leaves of all and the new leaves of most of the common tree species, while feeding selectively on leaves from relatively rare tree species and colonizing plant species. Chemical analyses documented that mature leaves of the common tree species at the Douala-Eden site contained very high concentrations of phenolics, twice as high as mature leaves from common tree species at the Kibale site

in Uganda. Further, new leaves from the abundant tree species at Uganda were significantly lower in total phenolic content than those from Cameroon. Digestibility comparisons of leaves from the two sites demonstrated that digestibility was negatively correlated with the phenolic content and with the content of condensed tannins. The greater concentrations of condensed tannins and total phenolics bound more protein and interfered more with the digestibility, possibly due to the inactivation of microbial enzymes by tannins (Waterman et al., 1980). Thus most of the Douala-Eden leaves were unsuitable as food for the black colobus. With their higher concentration of phenolics, mature leaves from Douala-Eden provided only one-half the net energy value of leaves from Kibale, even though the gross energy content of the Douala-Eden leaves was significantly higher than that of the Kibale leaves. It may be significant that, unlike other colobus monkeys, the black colobus of the Douala-Eden Reserve fed extensively on seeds that contained lower levels of phenolic compounds than leaves at this site. Although the seeds contained lower concentrations of phenolics, they contained other secondary compounds, i.e., strychnine and other highly toxic indole alkaloids (McKey, 1978). McKey proposed that the colobus consumed seeds with high levels of toxic secondary chemicals and ignored mature leaves with the same chemicals because the reward of nutrients in the seeds was much higher than in the same weight of leaves. Thus, the seeds were not toxic while the leaves were, although both contained the same chemicals. The low nutrient content resulted in the leaves being toxic.

The majority of potential food items (leaves of the common tree species) in the habitat of the black colobus of Douala-Eden were, in fact, not food, because of the digestibility-reducing compounds of the leaves that protect the trees from herbivores. As McKey (1978) indicated, the trees could not afford to lose a leaf crop because the nutrient content of the soil was very low.

McKey (1978) also suggested that not only do plant secondary compounds affect colobine feeding behavior, but that these chemicals were primarily responsible for the evolution of foregut fermentation as a means of processing foods containing toxic compounds. This view challenges the long-held idea that ruminant digestion evolved to process foods containing high levels of structural carbohydrates.

In summary, McKey proposes that soil poor in nutrients forces trees to increase the secondary compound content of their leaves in order to protect against loss to herbivores. Primates in these locations avoid these leaves and concentrate on other tree parts. Thus,

Since the soils of the Cameroon site have much lower contents of plant nutrients, there has been selection for greater investment in chemical defense in the vegetation of this site, because the loss of a leaf entails a greater cost to the plant than if it were growing in a site richer in nutrients. The resultant lower quality of leaves in this site as food for herbivores may have led evolutionarily to the black colobus' dependence on seeds rather than leaves, and to the observed greater selectivity in leaf-feeding by black colobus (McKey, 1978:436).

Milton (1977, 1980) collected data on the feeding behavior of the mantled howling monkeys (*Alouatta palliata*) of Barro Colorado Island, Panama, in order to test the expectations that the howlers would select food with a high nutritional quality, select a balanced diet, and select foods in order to minimize the intake of digestibility reducing compounds and/or potential toxins. Her results demonstrated that the howlers were not selecting food from the most common tree species. The top 10 food species accounted for 64% of the total feeding time, but accounted for only 12% of the total trees present in the sample plots. The howlers overwhelmingly preferred young leaves to mature leaves, and were not deterred from obtaining these leaves by sharp thorns, biting ants, presumably caustic sap, or sticky exudates. The strong preference for young leaves was indicated by the fact that the howlers ate young leaves from all but two species of the top 10 food species, but ate mature leaves of only two species from the same list. Milton (1978a) suggested that this preference for young leaves may be because new leaves provide a higher return of energy per unit weight.

The following hypotheses were suggested by Milton (1979) and chemical analyses were carried out in order to determine which nutritional and/or other chemical factors might influence the observed food choices:

1. Young leaves contain more protein than mature leaves, or contain more available protein (after the effects of digestibility-reducing secondary compounds).
2. Young leaves contain less fiber than mature leaves, which would make them more digestible and would also imply that howlers could eat more of them within a given period of time (i.e., the limit on the intake of young leaves would be higher).
3. Young leaves contain less toxins than mature leaves . . .
4. Young leaves contain more nonstructural carbohydrates than mature leaves, particularly simple sugars which are rapidly digested.
5. More than one of the above factors determine the preference of howlers for young leaves (Milton, 1979:365).

The results demonstrated that young leaves had significantly more protein, less fiber content, more total phenolics, and less nonstructural carbohydrates content than mature leaves (Milton, 1979). The howlers ate mostly the leaves with higher protein content and lower cell wall content, but the higher total phenolics did not stop them from eating young leaves. Based on these chemical results and behavioral data, Milton (1979) concluded that protein content and fiber content were factors that influence howler leaf choice, and that total phenolics and nonstructural carbohydrates were not generally influential factors:

The results on total phenolics suggest that, at least in some species, young leaves have higher contents of toxins, as proposed by Rhoades and Cates (1976); but without analyses to identify particular compounds and their effects on howlers, any conclusions on "toxins" are highly speculative. The results on condensed tannins are even more difficult to interpret (Milton, 1979:373).

Milton also suggested that such compounds may not in themselves influence howlers to choose or avoid young leaves, but may affect food selection by forcing howlers to eat from five or six different species each day in order to avoid ingesting too much of a particular toxin. She further noted that the howlers avoided both the young and mature leaves of certain tree species, an observation which suggests that they may have been avoiding certain secondary compounds.

Based on foraging behavior of howler and spider (*Ateles geoffroyi*) monkeys, Milton (1981b) hypothesized that the temporal and spatial predictability patterns of plant foods may have served to stimulate mental development in primates. She also considered similar factors that might have been involved in the mental development of hominids, and in the process provided a possible ecological and environmental base for the evolution of hominid mental capacities.

In summary, Milton believes that howlers on Barro Colorado Island are living on narrow nitrogen and energy balance margins and must be very selective in their leaf-eating in order to maintain these balances. She stresses food quality over secondary compounds as the primary factor influencing primate food choice. She also makes the important and critical point that food quality may be a limiting factor for herbivorous primates, a factor that is not apparent to investigators:

Since smaller herbivores may require higher quality foods (such as young leaves, fruits, and flowers), and since these foods may be very patchy in space and time, such animals may be subject to food limits that are not immediately apparent to researchers. . . . Of the content factors, the protein:fiber ratio may be the most important in determining the preference of many herbivores for young leaves (Milton, 1979:374-375).

Oates (1977) reported that black and white colobus (*Colobus guereza*) in the Kibale Forest Reserve of Western Uganda were very selective in their choice of food. They selected food from the relatively rare tree species and avoided the common tree species. More than two-thirds of the diet came from five tree species with one, *Celtis durandii*, being the most important food source. The guerezas preferred young leaves even though they were never as abundant as mature leaves. Chemical analyses of food and nonfood

items clearly demonstrated that the preferred foods of the black and white colobus contained low amounts of tannins (Oates et al., 1977). Young leaves of *C. durandii* contained less than 25% of the amount of tannin found in mature leaves of this species. In addition to having less tannin, the young leaves of *C. durandii* had up to twice as much crude protein and less than three-quarters as much lignin. Mature leaves of *Trema orientalis* contained extremely high concentrations of tannins and were never eaten by guerezas although the red colobus (*C. badius*) did occasionally eat these leaves. Oates (1977) suggested that plant secondary compounds need not always be deleterious (e.g., leaves high in tannin may be eaten to counteract bloat and to help detoxify alkaloids that they precipitate). This hypothesis remains to be tested.

The guerezas frequently came to the ground and fed on herbs growing in pools and consumed clay from certain spots (Oates, 1978). In order to investigate this unusual behavior, analyses were done on samples of the aquatic plants and clay, and compared to results of dry-land items and soil. The swamp plants had a higher concentration of sodium, iron, manganese, and zinc than the dry-land plants. Since tree leaves are relatively low in sodium and high in potassium, Oates suggested that the unbalanced ratio of these two chemicals may make it advantageous for the guerezas to select plants high in sodium rather than trying to obtain the necessary sodium by increasing leaf consumption. He also suggested that clay (kaolins) was ingested not as a mineral supplement but to adsorb plant toxins or to adjust the pH of the forestomach.

Oates et al. (1980) documented that leaf-monkeys (*Presbytis johnii*) of South India exhibited considerable selectivity in what they ate. Despite the fact that mature foliage was the most available potential food throughout the year, mature leaves made up only 27% of the Nilgiri langur's yearly diet, and more than 80% of this came from only four tree species, which did not include the most abundant tree species in the forest. The langurs further showed a preference for young leaves, flowers, and fruits. In two cases the monkeys ate only the petioles and dropped the leaf blades. Chemical analyses were done on 16 of the most important tree species in order to determine the basis for this selectivity and to test the hypothesis that the digestibility and toxicity of the foliage affected the monkey's food choices. Mature leaves that were ingested contained lower fiber and total tannin content than those not eaten, but since the langurs ate some leaves with very high concentrations of condensed tannins their presence alone apparently did not prevent feeding. There was no correlation between alkaloid content and selection. Oates et al. (1980) suggested that the microflora of the colobine forestomach can detoxify alkaloids. The selection of petioles was attributed to their high concentration of sap. The authors felt that fiber content was a more reliable predictor of *P. johnii* food choice than crude protein, secondary compounds, minerals, or digestibility. Failure to find a correlation between condensed tannin concentrations and food choice in this study differs from the results of Glander (1981), McKey et al. (1978), Oates et al. (1977) (different species), and Wrangham and Waterman (1981). All found a negative correlation between food ingestion and the presence of condensed tannin. This difference emphasizes the danger of extrapolating from one primate species to another even when they are in the same subfamily. One monkey's poison may thus be another's main course.

In summary, Oates believes that colobus are faced with a diet that is high in cellulose content, contains secondary compounds and lacks essential nutrients. To combat these factors, colobus have evolved fermentation and choose only certain plant material:

... The guereza diet is monotonous and dominated by large leaf-blades. ... the diet will have a high cellulose content and therefore be relatively indigestible for a mammal. ... Although both stomach bacteria and its own microsomal system provide a detoxification capacity to a ruminant-type mammal, it will be advantageous for the animal to select a diet with a minimal toxic component. ... Guerezas might be expected to adopt strategies to counteract dietary mineral deficiencies, such as the feeding on aquatic vegetation observed at Kanyawara (Oates, 1977:312-313).

Wrangham and Waterman (1981) reported that vervets (*Cercopithecus aethiops*) were never observed to eat mature leaves from either *Acacia tortilis* or *A. xanthophloea* even though they were plentiful. Immature leaves, seeds, fruits, and flowers of both species

were eaten. Gum from *A. xanthophloea* and the clear but not the reddish-brown gum from *A. tortilis* was consumed. The vervets preferred products of *A. tortilis*. Chemical analyses for phenolics demonstrated that for the four plant parts (immature leaves, seeds, fruits, flowers) vervet preference was never for the *Acacia* species in which total phenolics or condensed tannin levels were highest. Similarly, condensed tannin was almost absent from the sought after *A. xanthophloea* gum and present in very high levels in the avoided reddish-brown gum of *A. tortilis*. Wrangham and Waterman suggested that the avoidance of mature leaves was likely related to the higher amount of indigestible fiber they contained rather than tannin levels.

Combining the results for nutrients and secondary compounds can be very informative in interpreting the vervet preference for *A. xanthophloea* over *A. tortilis* gum. The gum of *A. xanthophloea* is high in soluble carbohydrates, while *A. tortilis* is almost devoid of this element (Hausfater and Bearce, 1976). *A. tortilis* gum is highly proteinaceous (Anderson and Bell, 1974), but the presence of large amounts of tannin in *A. tortilis* gum is likely to counteract any gain because of its protein content (Wrangham and Waterman, 1981).

In summary, Wrangham and Waterman believe that because of the relatively simple system they studied (four plant parts of related species), confounding variables present in other more complex systems have been greatly diminished. Therefore, their comparisons between feeding behavior and food secondary compound content is less subject to challenges:

Whatever the ultimate causes of selectivity by vervets eating *Acacia* parts, differential food availability and quality clearly have important consequences. . . . The quality of the diet thus has important long-term consequences for the behavioral ecology and population dynamics of vervet monkeys in Amboseli (Wrangham and Waterman, 1981:730).

SECONDARY COMPOUNDS AND INSECTIVOROUS PRIMATES

The inclusion of primates that eat insects in a discussion of plant secondary compounds may perhaps be questioned. Nevertheless, insects are the reason plants evolved secondary compounds, which means that insects must deal with these chemicals in order to survive. Some insects have developed the ability to sequester plant secondary compounds of their host plants. For example, certain aposematic butterflies are able to store secondary compounds such as the cardiac glycosides found in milkweeds (*Asclepias*) and oleander (*Nerium*) (Rothschild, 1972). Polyphagous insects may store two or more unrelated toxins. Once stored, the plant chemicals act as a deterrent to potential predators by rendering the insect distasteful and unacceptable to its predators (Jones, 1932; Brower et al., 1968). It is definitely to the insect's advantage to advertise its distastefulness by being brightly colored (aposematic) in order to warn potential predators (Rothschild, 1975). Nontoxic insects trade on this protection by mimicking the bright colors and shapes of toxic insects. Thus, food eaten by insects serves not only as a source of nutrients but also as a means of protection from predators. If birds can learn to avoid aposematic insects (Brower and Brower, 1964; Roeske et al., 1976), primates should be able to do the same.

The ability of some insects to utilize plant secondary compounds for defensive purposes means that insectivorous primates are faced with a problem familiar to herbivorous primates; i.e., all that appears to be food is in fact not food. Or stated in another way, dealing with the secondary compounds found in their insect prey must be considered an expense to insectivorous primates just as energy expended to acquire any food is a cost. In some cases, the cost outweighs the benefits (just as for herbivorous primates), and an insect that appears to the observer to be acceptable food is in fact not because of the sequestered secondary compounds. Insect-eating primates then should have evolved the ability to make these cost/benefit decisions. This is not a case of one insect being toxic and another nontoxic, since the amount of chemical that would be contained by several insects is unlikely to be poisonous to any insectivorous primates. Rather, this is an example of increased fitness; fitness in the sense of getting a greater return per unit of expended energy since it takes energy to find and catch the insect as well as to deal with any plant secondary chemicals that the insect contains. Thus, other things

being equal, the advantage comes in finding and catching the insect with little or no sequestered secondary compounds. It also is possible that at times of lowered insect availability, primates may be forced to eat the lower quality insects and thereby have their overall fitness reduced.

Primates are frequently observed to eat only a part of an insect and discard the remainder. In light of the above, it is possible that primates use the bright colors of aposematic insects to locate them and, warned by their coloration, discard the part of the insect that contains the sequestered chemicals. Such behavior would fit the strategy outlined above and could be selected for.

Since the first primates were insectivorous (Kay and Cartmill, 1977) it is likely that they evolved detoxification mechanisms for the sequestered secondary compounds of their insect prey. The insects obtained these secondary compounds from the local plants. Therefore, the insectivorous primates, with their specialized detoxification systems, may have been preadapted to eventually evolve as herbivores and feed on the same plants for which they already had the means of detoxifying the contained secondary compounds.

SECONDARY COMPOUNDS AND NECTAR- AND GUM-EATING PRIMATES

Several primate species have been reported to ingest nectar (Oppenheimer, 1968; Sussman, 1979; Sussman and Raven, 1978) or gum (Hausfater and Bearce, 1976; Moynihan, 1976). Many primates eat flowers (Curtin and Chivers, 1978; Freese, 1977; Glander, 1975a; Milton, 1977, 1980; Oates et al., 1977, 1980; Richard, 1978; Wrangham and Waterman, 1981; and others). Since these are plant products, they may also present the problem of secondary compounds (McKey, 1979). Some nectar and pollen contains alkaloids, nonprotein amino acids, and glycosides (Baker and Baker, 1975; Pryce-Jones, 1944), and gum from certain plant species contains large amounts of tannin (Wrangham and Waterman, 1981). In the later case, primates avoided the gum containing tannin. Thus, researchers studying primates feeding on nectar, gum, and flowers must also consider the impact of plant secondary compounds in addition to the nutrient content of these plant foods.

SECONDARY COMPOUNDS AND HUMANS

Almost everyone is familiar with cyanide, quinine, morphine, cocaine, caffeine, and nicotine. All are plant derived secondary compounds and all affect humans. Most cyanide poisonings are accidental, but many people are exposed daily to low concentrations of cyanogenic compounds (HCN) in the foods they eat. Cyanogenic compounds are found in at least 800 plant species (Seigler, 1977). Seigler reported that cassava flour in Nigeria may have 35 mg of HCN in 750 gm. Humans can detoxify fairly large amounts of HCN, but chronic intake may cause neurological damage (Seigler, 1977). Quinine, morphine, and cocaine have medicinal uses (Morton, 1977). Newspapers carry frequent headlines on the negative effects of caffeine in coffee and chocolate, and nicotine in cigarettes. Tea and wine (both contain tannin) have been linked to esophageal cancer (Morton, 1979). Morton also indicated that the protein in milk added to tea binds the tannin and prevents its effects on the mucous membranes.

Of course, the effects of plant produced secondary compounds are not all negative nor have their benefits been only recently recognized. Many human populations use plant chemicals as medicines, yet folk medicine cures and treatments are often dismissed as folklore. Many have proven to be effective, e.g., *Combretum mucronatum* expels Guinea worms, while herbs of the Loganiaceae family have antidiabetic properties (Ayesnu, 1978). The first recorded use of plants in the treatment of cancer was 1500 B.C. (Cordell, 1978).

The details of all cases of plant secondary compounds and their effect on humans are beyond the scope of this review. Rather, several documented instances of the ubiquitous nature of plant chemicals and their influence on modern humans as well as on our evolutionary history will be discussed.

The family Solanaceae contains the important human foods: potato, tomato, eggplant, and pepper, but also contains the highly poisonous nightshade, henbane, and tobacco. Even though considered an important food crop, the common potato (*Solanum tuber-*

osum L.) contains the toxic alkaloids alpha-solanine and alpha-chaconine, the phenolic compounds chlorogenic and caffeic acids, and the coumarins scopolin, umbelliferone, and coumarin (Chaube and Swinyard, 1976). Chaube and Swinyard state that chlorogenic and caffeic acids are present in many human foods, but their toxicity is unknown. However, alpha-solanine and coumarin are proven human toxins. The alkaloids are present in concentrated form not only in green potatoes, sprouts, and blossoms, but also are present in lesser amounts in the tubers. Cooking probably destroys or reduces the toxins in the tubers, but there are documented cases of human deaths from green potato soup with sprouts (Chaube and Swinyard, 1976).

The ubiquitous presence of secondary compounds has necessitated the development of specialized means of treating or preparing many of the foods utilized by modern humans as well as our ancestors. Clay eaten with acorns may act as an adsorbant of tannin (Hladik and Gueguen, 1974). The staple food Manioc (*Manihot* sp.) is known to be toxic if not properly prepared (Berlin and Berlin, 1977). Cyanogenic glucosides in the root can cause neuropathologies (Osuntokun, 1973, as cited by Berlin and Berlin, 1977). A majority of the domestic plant assemblage identified at a village in the Bolivian highlands, dated to 1200–1000 B.C., contained significant levels of toxins in the untreated condition (Browman, 1981). The potato species that grows best at these high altitudes contains high levels of alpha-solanine in addition to a proteolytic inhibitor. Some of the other foods contain high levels of saponin, oxalates, cyanogenic glycosides, and hydrocyanic acid (Browman, in press).

It should be apparent that proper cooking or preparation of foods is important, but cooking is no guarantee that the secondary compounds have been destroyed or that the processed foods are safe. Parsnip (*Pastinaca sativa*) roots contain toxic psoralens that are not destroyed by cooking (Ivie et al., 1981). Similarly, even though they are processed, coffee and chocolate still contain secondary compounds that affect humans. We may only be beginning to understand the effects that our food and its contained secondary compounds may be having on us. In most cases the effects are not immediate, but any instance of lowered fitness is important, particularly for our early ancestors who were primarily plant eaters without the benefits of fire. Leopold and Ardrey (1972) suggested that early humans were food-limited because of toxins. Based on the effect that plant secondary compounds have on nonhuman primate feeding, the idea that our ancestors were limited in their choices of food is reasonable.

The actual impact plant secondary compounds have had on our evolutionary past remains unknown. But, the possibility that plant secondary compounds did affect our evolutionary history has been significantly strengthened by recent experimental evidence demonstrating that mammals respond to naturally occurring chemicals in their plant food (Berger et al., 1981). Prior to the use of fire, our ancestors were exposed to the full impact of the secondary compounds in their food. Thus, the potential for major population consequences existed because of the effect these ingested secondary compounds may have had on fitness and the age at first reproduction. Initially the effect probably was unsuspected, but with increasing awareness our ancestors could have chosen specific effects by ingesting certain foods. For example, the modern Aguaruna Jivaro regularly use plant products as: (1) contraceptives, (2) menses prohibitors, (3) abortives, (4) aphrodisiacs, and (5) enhancers (Berlin, 1977). The major plants used are genipa, *Genipa americana* (contraceptive, permanent sterility); ginger, *Zingiber officinale* (contraceptive, fertility returns when stopped); and yam bean, *Pachyrrhizus tuberosus* (abortive, very effective and can be poisonous to user if too much is used). The Jivaro administer these by enemas, but these and others may also be effective if ingested. For example, some species of yams (*Dioscorea*) contain diosgenin which is widely used in the preparation of birth-control drugs (Ayensu, 1978). Ayensu also lists 21 plant species used as abortifacients in West Africa.

CONCLUSION

Investigation of plant phytochemicals and their impact on primates is less than 10 years old despite the accumulation of more than 20 years of evidence that plants and insects have profoundly affected each others' evolutionary courses. Insects are the reason that plants evolved chemical defenses. In turn, insects evolved counter strategies

of dealing with these chemicals. The first primates were insectivorous, but plant material soon became their primary food. Plants already had their chemical defenses in place because of the insects' selective pressure long before primates evolved. To exploit plants as food, the primates had to adapt to this functioning relationship by developing their own strategies for handling plant secondary compounds. These strategies range from becoming a specialist with a specialized detoxification system to becoming a generalist and carefully selecting the highest quality items or only eating small amounts of many different species. Small amounts of a potential toxin are more easily and less expensively detoxified (Freeland and Janzen, 1974). Oates (1977) has suggested that diet diversification is a method of coping with the greater concentration of potential toxins and digestibility-reducing compounds present in a mature forest and leads to larger home ranges.

Plant secondary compounds do not affect all primates equally, and there is no a priori reason to expect primates to respond to all secondary compounds in a universal way. It is reasonable to expect that some primates will be deterred, while others may not be affected by the same substance. In some instances the secondary compounds may actually attract the animals by serving as feeding cues. None of these results refutes the hypothesis that secondary compounds influence primate food choice. The fact that one or more primate species ingests foods containing secondary compounds is not sufficient to suggest that secondary compounds do not serve as deterrents to other primates. For example, langurs eating fruits containing strychnine does not mean that strychnine or other secondary compounds are not effective against primates. Langurs have ruminant-like digestive systems and therefore can detoxify this potential toxin. Primates without this kind of digestion can not eat strychnine, and langurs may not be able to eat something that would disrupt their carefully balanced digestive system. Other examples of apparent failure of plant secondary metabolites (e.g., phenolics) may be in reality good examples of a specialist primate that has evolved an efficient detoxification system for specific chemicals.

Neither nutrients nor secondary compounds can be considered as the only factor influencing primate feeding behavior because each affects the other. Some secondary compounds make some nutrients unavailable, and large amounts of some nutrients make some secondary compounds less effective as deterrents to herbivores. For example, leaves or seeds containing large amounts of protein may be ingested even though they contain very toxic chemicals (McKey, 1978). The primates can afford the risk of the toxin because of the net gain, even after discounting the negative effects of the toxin. Of course this is only true if the primate does not die from the toxin. Few primates die directly from the effects of ingested secondary compounds of either the toxic or digestibility-reducing kind. Glander (1981) has suggested that they seldom die because they sample unfamiliar items by taking only a few bites of the new item. Such small amounts are unlikely to contain enough toxin to kill. If the new item causes discomfort, they do not go back for more; if it causes no discomfort, they return and gradually increase their feeding time over several weeks.

An inadequate amount and balance of nutrients obviously leads to reduced fitness. Secondary compounds also interfere with nutrient availability or result in greater cost for detoxification. Understanding the interaction of nutrients and secondary compounds is vital to understanding primate feeding behavior. If no high quality foods are available and a primate is forced to eat low quality foods, it is theoretically possible for that primate to be ingesting what appear to be sufficient quantities of food but still be starving because the quality of the food is lowered by secondary compounds.

Even though data demonstrating the impact of plant secondary compounds on nutrient availability are not yet available for primates, experiments on other animals are informative. Steers fed high tannin sorghum gained 16.3% less weight and were 19.6% less efficient in digestion than those fed low tannin sorghum (Bertrand and Lutrick, 1971). Similarly, humans eating low tannin beans (*Phaseolus vulgaris*) showed twice the weight gain than those eating high tannin beans (Morton, 1979). The difference in both instances is not a nutrient difference, but one in the availability of nutrients that are present. The higher tannin content reduced the available nutrients. The expected primate feeding pattern should be to avoid plant species or parts containing a

higher secondary compound content. This is in fact what Glander (1981), McKey (1978), Oates et al. (1977), and Wrangham and Waterman (1981) documented. However, it may actually be advantageous, in some instances, to ingest foods that have lower amounts of protein or other nutrients because they have less secondary compounds than those with high nutrient content (Glander, 1981). On the other hand, the presence of specific amino acids (Glander, 1981) or large amounts of certain nutrients (McKey, 1978) may favor the ingestion of those plant parts despite the presence of toxins or digestibility-reducing chemicals. The net return is greater than eating some other plant material (Glander, 1981; McKey, 1978).

The work on primate-plant relationships has just begun and it is clear that the impact of plant secondary compounds on primate feeding is complex. However, to ignore their documented effect because of this complexity avoids the issue. Secondary compounds exist and affect primate feeding negatively and positively. Continued documentation of these effects and experimental feeding manipulations are the next logical step.

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