
Tree leaf chemical characters: selective pressures by folivorous primates and invertebrates

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Abstract

Plants have evolved a variety of chemical means to deter herbivory. Several studies have documented that secondary compounds are strong deterrents to certain herbivores, while others have demonstrated that some herbivores ingest large quantities of these compounds without exhibiting deleterious effects. This inconsistent response suggests that plants have evolved compounds to deter specific herbivores. Based on a study in Kibale National Park, Uganda, we explored how two major groups of herbivores, invertebrates and colobus monkeys, respond to chemical characteristics of leaves: protein, attractive from a nutritional perspective, and alkaloids, saponins and cyanogenic glycosides, which are all plant defences, deterring herbivory. The intensity that colobus monkeys fed on leaves of different tree species was determined by observations (1300 h), and invertebrate herbivory was indexed by collecting leaves from 20 species and digitizing tracings to quantifying invertebrate damage. Invertebrate damage to leaves varied among species (1.5–22.5%), but showed no relationship with saponin or protein content, or the presence or absence of alkaloids. Colobine foraging effort did not relate to the saponin and protein of leaf species, nor to the presence or absence of alkaloids. *Prunus africana*, the only species to test positive for cyanogenic glycosides, was fed on by colobus monkeys for 8.1% of their foraging time, but, as it occurred at low densities, it was the most preferred species. These results can be interpreted in different ways. First, it is possible that inactive compounds are retained because they increase the probability of producing new active compounds. Secondly, the indices used to evaluate compound effects may be inappropriate. For example, monkeys may only be able to tolerate a toxin to a specific threshold in a single feeding session, but our index

of foraging effort was averaged over the year. Thirdly, it may be that these compounds play an active role with organisms not considered (e.g. prevent fungal attack). Finally, these compounds may serve some unknown function and selection may operate for that purpose.

Key words: colobine monkeys, herbivory, nutritional ecology, plant chemistry, secondary compounds, toxins

Résumé

Les plantes ont développé des divers moyens de dissuasion contre les herbivores. Plusieurs études ont rapporté que des composés secondaires agissent comme une forte dissuasion pour certains herbivores, alors que d'autres ont démontré qu'il y a des herbivores qui peuvent ingérer les mêmes composés en grande quantité sans manifester des effets nuisibles. Cette réponse incohérente indique que les composés ont évolué pour dissuader des herbivores spécifiques. Basé sur une étude au parc national de Kibale en Uganda, nous avons enquêté comment deux groupes majeurs d'herbivores – invertébrés et singes colobus – réagissent aux caractéristiques chimiques des feuilles; la protéine, qui devrait être considérée sur une perspective nutritionnelle, et alcaloïdes, saponines et glycosides cyanogènes, qui sont tous des protections utilisées par la plante qui devait dissuader les herbivores.

Nous avons établi l'ampleur de la consommation de feuilles par les singes colobus à travers des observations (1300 hr), tandis que l'herbivorie des invertébrés fut indexé suite au recueil de 20 espèces de feuilles et la numérisation des traçages afin de quantifier les dégâts faits par les invertébrés. Les dégâts variaient selon l'espèce (1.5 à 22.5%), mais n'indiquaient aucun lien avec le contenu de saponines et protéines, ni la présence ou l'absence des alcaloïdes. A cet égard nous avons trouvés les mêmes résultats chez le fourrage des singes colobus. *Prunus Africana*, la seule espèce à contenir des glycosides cyanogènes, représentait 8,1% de l'alimentation des singes, mais – puis-

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qu'elle était rare – s'avérait l'espèce préférée. Ces résultats peuvent être interprétés de plusieurs façons. Premièrement, il est possible que les composés passifs soient retenus parce qu'ils augmentent la probabilité que la plante produise des nouveaux composés actifs. Deuxièmement, les indicateurs employés afin d'évaluer les effets des composés sont peut-être impropres. Par exemple, il se peut que le singe puisse tolérer une toxine jusqu'à un certain niveau lors d'une séance, alors que notre indice du niveau de fourrage fut moyenné sur l'année. Troisièmement, il est possible que les composés jouent contre des organismes que nous n'avons pas considérés ici, (par exemple, pour éviter une attaque fongique). Dernièrement, les composés peuvent avoir une fonction que nous ignorons et qui réagit sur la sélection.

Introduction

Plants have evolved a variety of structural and chemical means to deter herbivory (Rosenthal & Janzen, 1978; Cork & Foley, 1991). In fact, it is hypothesized that the radiation of angiosperms was facilitated by their extraordinary chemical versatility (Kubitzki & Gottlieb, 1984). Several studies have documented that secondary compounds are strong deterrents to certain herbivores (Coley, 1983; Bryant *et al.*, 1992; Feeny, 1992), while other studies have demonstrated that some herbivores ingest large quantities of secondary compounds without exhibiting apparent deleterious effects (Cork & Foley, 1991; Waterman & Kool, 1994; Chapman & Chapman, 2002). This inconsistent response suggests that compounds may have been evolved to deter specific herbivores and raises the intriguing question as to their effects on different taxa of herbivores (reviewed by Feeny, 1992).

Some of the earliest Devonian fossils of vascular plants (approximately 400 Ma) show evidence of invertebrate herbivory and there is a more or less continuous fossil record of plant/invertebrate interactions (Chaloner, Scott & Stephenson, 1991). This record illustrates when different types of invertebrate foraging strategies evolved, and clearly illustrates a long and intense history of interaction. Presently, mammals are the second major group of herbivores. For tropical canopy trees, the mammals having the most significant impact on tree fitness through herbivory are the leaf-eating monkeys. In Africa and Asia, these are the colobine monkeys. In contrast to invertebrates, the duration of the interaction between colobine monkeys and plants is relatively short. The earliest

well-known colobine (*Mesopithecus pentelicus*) was recovered from Miocene sites in Europe dating to approximately 8.5 Ma, and colobines probably did not reach Africa until the Pliocene (Delson, 1994).

Attempting to understand if certain classes of secondary compounds have evolved to deter specific herbivores is complex (Foley & McArthur, 1994). The long period of interactions between invertebrates and plants might lead one to speculate that most chemical characteristics found in plants today are a result of evolution occurring during this long history of interaction. However, colobine monkey foraging can result in nearly a total loss of a tree's leaf crop, so the strength of the selective pressure they exert may be high. It may be that some compounds are acting on the symbiotic microorganisms that are responsible for cellulose digestion in the invertebrate and colobine monkey's guts and not directly on the invertebrates or monkeys. Thus, these compounds could be effective at deterring herbivory from both groups. It may be that the coevolutionary relationship is very specific and that specific compounds are only effective at deterring herbivory of certain species within these groups (i.e. particular compounds only affect specific invertebrates or colobine species). Available data argue against this, as nutrient requirements of a variety of invertebrates are similar (Feeny, 1992). Alternatively, plant-herbivore interactions could represent very diffuse coevolution, or there could be selection for diversity rather than specificity (Jones & Firn, 1991). Under this later scenario, only plants with a diversity of compounds would be well defended because only high diversity confers a reasonable probability of producing active compounds. Inactive compounds are retained because they increase the probability of producing new active compounds (Jones & Firn, 1991; Firn & Jones, 2000). This implies that the relationship between specific chemical compounds of a plant and efficiency of its defence may be weak.

Given this controversy, the objective of this study was to explore how two groups of herbivores, invertebrates and colobine monkeys, respond to chemical characteristics of a diverse suite of tree species. We examined how protein, a nutritionally attractive component, and three classes of secondary compounds (alkaloids, saponins, and cyanogenic glycosides), assumed to act as plant defences, relate to the diet choice of these two groups of herbivores in Kibale National Park, Uganda.

Within Kibale there are two colobine monkeys: red colobus (*Piliocolobus tephrosceles*) and black-and-white colobus (*Colobus guereza*). Both species are arboreal

folivores that possess a specialized ruminant-like digestive system with a sacculated stomach, where bacteria digest cellulose (Struhsaker, 1975; Bauchop, 1978; Chivers, 1994; Kay & Davies, 1994; Milton, 1998). Milton (1979) proposed that the protein to fibre ratio was a good predictor of leaf choice. By measuring overall mature leaf acceptability as the ratio of protein to fibre, several subsequent studies have found positive correlations between colobine biomass and this index of leaf quality at local (Chapman & Chapman, 2002; Chapman *et al.*, 2004) and regional scales (Waterman *et al.*, 1988; Oates *et al.*, 1990; Davies, 1994). As a result, we consider the effects of the protein content of the leaves on colobine leaf selection.

Many invertebrates are sensitive to levels of dietary nitrogen and/or protein (Slansky & Feeny, 1977; Mattson, 1980; Wint, 1981; Feeny, 1992), and this has led to a number of studies examining the effects of proteinases on invertebrate herbivory (Wolfson, 1991). As the protein content of leaf material can influence rates of invertebrate growth and reproduction (Feeny, 1992), its importance seems apparent.

Effects of secondary compounds on invertebrate herbivory are widely documented (Feeny, 1992). Given their small size and relatively short lifespan, invertebrates are more amenable to experimental research than mammals. Despite this, there is still controversy over the degree to which specific secondary compounds deter invertebrate herbivory and the evolution of this system is still contentious (Rosenthal & Berenbaum, 1992). Unfortunately, the role of secondary plant compounds in colobine digestion is not well known. The gut flora of these animals may enable them to detoxify some toxins (Oates, Waterman & Choo, 1980; Waterman, 1984; Waterman *et al.*, 1988). For example, McKey *et al.* (1981) found that black colobus (*Colobus satanas*) can consume appreciable quantities of the alkaloid-rich leaves of *Rauvolfia vomitoria* that would be lethal to non-adapted folivores. Chapman & Chapman (2002) recently documented that there was no evidence that colobines avoid plants with high total phenolic or tannin levels. However, Waterman *et al.* (1988) and Kay & Davies (1994) suggest that colobines avoid eating the foliage of certain plant families because they contain compounds that kill bacteria and would lower the efficiency of their gut flora.

Many alkaloids are bitter-tasting and perhaps play a role as a feeding deterrent or damage the microbial community of an animal's stomach (Harborne, 1993; Roberts & Wink, 1998). A number of studies have shown that alkaloids act directly and reduce invertebrate feeding and hence growth

(Feeny, 1992). For both colobus monkeys and most invertebrates (with the exception of cockroaches and higher termites), the digestion of most leaf material is typically mediated by symbiotic microorganisms that reside in the hindgut (Martin, 1991; Waterman, 1993). Thus, alkaloids may have the ability to disrupt the activity of the microorganisms found in the guts of both of these animal groups.

Saponins are surfactants, and have a 'soap-like' foam-forming property in aqueous solutions. In mammals, they have the ability to haemolyse red blood cells when injected, irritate the digestive tract, inhibit proteases, cause bloating and can serve as a steroid hormone precursor (Phillips-Conroy, 1986). These compounds are bitter-tasting, and are found in plants of over 70 families. To our knowledge, the role of saponins in colobine diet selection has not been investigated. Saponins can inhibit invertebrate proteases and complex with sterols, thereby preventing their absorption (Slansky, 1992). Given the importance of proteins in invertebrate growth and reproduction (Feeny, 1992), it is reasonable to expect saponins to be a general deterrent to invertebrate herbivory.

Cyanogenic glycosides are capable of releasing toxic hydrogen cyanide. Their role in determining herbivory is questionable (Seigler, 1991; Jones, 1998), but studies have shown that some invertebrates are capable of differentiating between acyanogenic and cyanogenic phenotypes of the same plant species (Berenbaum & Zangerl, 1992).

Materials and methods

Study system

Kibale National Park (795 km²) is located in western Uganda (0°13'–0°41'N and 30°19'–30°32'E) near the foothills of the Ruwenzori Mountains (Struhsaker, 1975, 1997; Chapman *et al.*, 1997; Chapman & Lambert, 2000). Mean annual rainfall in the region is 1741 mm (1990–2003). Rainfall is bimodal, with two rainy seasons generally occurring from March to May and September to November. Behavioural observations were made in the K-30 forestry compartment near Makerere University Biological Field Station. The biomass of red colobus (*P. tephrosceles*) and black-and-white colobus (*C. guereza*) in Kibale is estimated to be 1116 kg km⁻² (Chapman *et al.*, 2000; Chapman & Lambert, 2000). While these animals typically forage in a number of different trees in a day during short foraging bouts, on a number of occasions, we

have seen a deciduous tree that is initiating leaf flush to be almost completely denuded in a single day. Tree species nomenclature follows the most recent citation for a given species in Hamilton (1991), Katende, Birnie & Tengnäs (1995), or Polhill (1952).

Indices of invertebrate and primate foraging effort

The intensity that the two species of colobine monkeys fed on the leaves of different tree species was determined by direct observations. Behavioural observations were made on two groups of red colobus (24 and 48 members) and two groups of black-and-white colobus groups (nine and twelve members) during dawn to dusk observations for 5 days each month from August 1998 until June 1999, producing approximately 800 h of observations for red colobus and 500 h for black-and-white colobus. We have fewer observations on black-and-white colobus because at times many members of a group would be obscured from the observer's sight by dense vegetation. Each group had recognizable individuals allowing verification of group identity. We used an observational method similar to the

methods used in a number of previous studies in Kibale (Struhsaker, 1975; Butynski, 1990). During each half-hour, the observer was with the group, five-point samples were made of different individuals. If the animal was feeding, the species and plant part (e.g. young leaf, leaf petiole) were recorded. We made an effort to avoid repeatedly sampling particularly conspicuous animals by moving throughout the group when selecting subjects and by sampling animals that were both in clear view and those that were more hidden. Often, the observer had to wait a number of minutes to determine what a less observable animal was doing. These behavioural observations were conducted by Lauren Chapman, Colin Chapman, and a team of three Ugandan field assistants. The field assistants have worked with us since 1990 and knew the tree species, the observational technique and monkey age classes prior to the start of the project.

Invertebrate herbivory was indexed by collecting leaves and quantifying invertebrate foraging damage, for four trees for each of 20 species. Trees found on the edge or in a treefall gap were excluded. Two small branches from the mid-canopy or lower canopy were cut down with a tree-

Table 1 The density (individuals >10 cm DBH ha⁻¹), invertebrate damage (see text), % foraging by black-and-white (*Colobus guereza*) and red colobus (*Piliocolobus tephrosceles*), and leaf chemistry for 20 species of trees evaluated in Kibale National Park, Uganda. Alkaloids and cyanogenic glycosides are present (1) or absent (0) tests

Species	Density (tree ha ⁻¹)	% Leaf remaining	Colobus foraging	Crude protein %	Alkaloids	Cyanogenic glycosides	Saponins (300 s)	Saponins (1800 s)
<i>Bosqueia phoberos</i>	50.0	97	6.05	15.67	0	0	28.75	24.50
<i>Celtis africana</i>	4.2	96	10.48	22.22	0	0	12.33	9.33
<i>Celtis durandii</i>	47.1	98	24.63	28.19	0	0	19.25	16.50
<i>Chaetacme aristata</i>	17.1	96	0.25	19.68	0	0	11.50	9.75
<i>Chrysophyllum sp.</i>	2.6	92	1.75	19.53	0	0	13.25	11.00
<i>Diospyros abyssinica</i>	40.0	97	1.00	23.34	1	0	29.50	21.00
<i>Erythrina abyssinica</i>	0.4	98	0.20	26.86	1	0	21.50	20.25
<i>Funtumia latifolia</i>	33.8	91	5.83	17.24	1	0	16.50	13.50
<i>Markhamia platycalyx</i>	50.0	91	7.15	25.68	0	0	24.00	22.75
<i>Mimusops bagshawei</i>	3.3	95	0.65	14.00	0	0	10.75	9.25
<i>Neoboutonia macrocalyx</i>	1.3	94	0.08	21.47	0	0	14.75	13.00
<i>Olea welwitschii</i>	3.3	93	2.33	14.56	1	0	11.00	9.00
<i>Parinari excelsa</i>	2.9	97	4.4	12.87	0	0	20.50	16.75
<i>Polyscias fulva</i>	0.8	95	0.18	16.43	0	0	30.00	28.50
<i>Premna angolensis</i>	4.6	92	0.33	25.96	1	0	20.00	17.75
<i>Prunus africana</i>	0.4	92	8.18	15.97	1	1	19.50	16.00
<i>Spathodea campamulata</i>	0.8	97	0.08	16.29	0	0	16.25	14.00
<i>Strombosia scheffleri</i>	12.5	78	5.48	20.50	0	0	16.25	14.25
<i>Strychnos mitis</i>	7.5	98	0.20	14.80	1	0	18.00	14.00
<i>Uvariopsis congensis</i>	60.4	97	0.05	24.75	1	0	10.75	10.25

pruning pole. So as not to bias selection to leaves with certain characteristics, we selected every third leaf on the branch until 20 leaves were collected. Leaves were traced onto paper in the field and holes or damage caused by invertebrates were noted. Additional leaves were collected for nutritional analyses (see below). Digital images of the tracings were made and the area of the whole leaf was determined using Scion Image[®] software (Scion Corporation, Frederick, MD, USA). Edge areas that were removed by invertebrate foraging were estimated and included in the estimate of whole leaf areas. Removed edges and holes were summed and the percent area of the leaf damaged was calculated.

To select the twenty species for which we quantified invertebrate damage and leaf chemical properties, we included species that varied with respect to importance in the colobine diets. Preferences were calculated as the foraging effort devoted to a particular species divided by its density. Foraging effort was quantified as number of scans in which the animals were recorded eating from that tree divided by the total number of foraging scans. Tree density was calculated in 26 permanent vegetation plots (200 m × 10 m) with the location of plots being selected at random from within the existing trail system. This provided a total sampling area of 5.4 ha and involved identification of 2111 trees. Each tree with a diameter at breast height (DBH) ≥ 10 cm within 5 m of each side of the trail was identified and measured (DBH). We made a list of all species found in the vegetation plots, ranked them based on their preference to colobus monkeys and selected every third species on this list until twenty were selected (Table 1).

Nutritional analyses

After collection, leaves were dried, stored in sealed plastic bags, and transported to the University of Florida. Dried samples were ground to pass through a 1-mm-mesh screen in a mill. Dry matter was determined by drying a portion of each sample overnight at 105°C. Samples were analysed in duplicate, and replicates for analyses were considered acceptable if the relative error was <2%.

The protein (nitrogen) content of the leaves was assessed using Kjeldahl procedures (Horowitz, 1970; Gallaher, Weldon & Futral, 1975). The presence of alkaloids was tested using a spot test with Dragendorff's reagent (Waterman, 1993). The quantity of saponins present in a sample was indexed using the Froth test (H.H.S. Fong,

M. Tin-Wa, N. R. Farnsworth, unpublished guide) using a 300-s and a 30-min criterion. The presence or absence of hydrogen cyanide was determined by the Feigler–Anger test (Feigler & Anger, 1966; Glander *et al.*, 1989; see Chapman & Chapman, 2002 for a more detailed description of the nutritional analysis).

Statistical analyses

To provide an estimate of the amount of invertebrate damage for a leaf species, we averaged the twenty leaves per tree and the four trees, to obtain a species average. An index of colobus foraging pressure was calculated as the average percentage of scans that the two species spent eating from each of the twenty species. We used simple linear regression to predict the amount of invertebrate damage or colobine foraging effort based on the saponins and the protein content of the leaves. As the density of the tree species may influence the likelihood of it being fed upon (i.e. more common trees are eaten more frequently because they are encountered more often), we performed a multiple regression and partialled out the effect of tree density. Variables were log-transformed to normalize the data and stabilize the variance. Saponin contents estimated with the 300-s and 30-min criteria were very similar ($r = .975$, $P = <0.001$), thus we report saponins using only the 30-min criteria. We determined whether the presence or absence of alkaloids were significant predictors of invertebrate damage and colobine foraging effort using logistic regression. As cyanogenic glycosides were found in only one of the twenty species, no statistical evaluation was made.

Results

The amount of invertebrate damage to leaves varied among species. The percentage of the leaf area remaining (i.e. not removed by invertebrates) averaged 94.2% across species, ranging from 77.5% (*Strombosia scheffleri*) to 98.5% (*Strychnos mitis*). Excluding *S. scheffleri*, which was heavily damaged, most other species had relatively little damage (range 2–9%). By design, the variation in the amount of time that the two colobus monkeys fed on the different species was greater than that of the invertebrates. It ranged from *Uvariopsis congensis*, which a black-and-white colobus monkey was seen to eat on one occasion, to *Celtis durandii*, which both colobine species fed on intensively (21.2% of all foraging scans).

No relationship existed between the average amount of invertebrate damage and either the saponin content ($r = 0.042$, $P = 0.859$, $n = 20$) or protein content ($r = -0.065$, $P = 0.787$). In these regressions, *S. scheffleri* was a significant outlier ($P < 0.01$); however, excluding it from the analysis lead to the same conclusions (saponin: $r = 0.048$, $P = 0.846$; protein $r = -0.024$, $P = 0.921$, $n = 19$). A multiple regression including tree density was also not significant for saponins ($R^2 = 0.006$, $P = 0.959$), or protein ($R^2 = 0.006$, $P = 0.949$). Similarly, we were unable to predict the presence or absence of alkaloids in the leaves based on the amount of invertebrate damage that each species received ($P = 0.667$), and incorporating density into the logistic regression did not improve the predictive power ($P = 0.872$). Surprisingly, *Prunus africana*, the only species to test positive for cyanogenic glycosides, ranked fifth in invertebrate damage.

The amount of time that the two colobus species spent feeding on the leaves of the species was independent of the saponin ($r = 0.092$, $P = 0.699$) and protein content of the leaves ($r = -0.024$, $P = 0.919$). A multiple regression including tree density was not significant for saponins ($R^2 = 0.104$, $P = 0.392$), or protein ($R^2 = 0.112$, $P = 0.365$). The presence or absence of alkaloids could not be predicted by colobus monkey foraging effort ($P = 0.701$), and this relationship was not improved by incorporating density ($P = 0.419$). The only species to test positive for cyanogenic glycosides, *P. africana*, was fed on for 8.1% of colobus foraging time, but as it occurred at a low density, it was the most preferred species of the 20 examined.

There was no correlation among species between the amount of invertebrate damage and colobus monkey foraging effort ($r = -0.288$, $P = 0.218$ all species $n = 20$; $r = 0.239$, $P = 0.326$, excluding *S. scheffleri* $n = 19$).

Discussion

Invertebrate and colobus monkey foraging effort among the 20 selected tree species could not be predicted from any of the leaf chemical characteristics we considered. These results can be interpreted in a number of different ways. First, they provide support for the idea put forward by Jones & Firn (1991) that only plants with a diversity of compounds will be well defended, because only high diversity confers a reasonable probability of producing active compounds. Inactive compounds are retained, not eliminated, because they increase the probability of producing new active compounds. This implies that the rela-

tionship between specific chemical compounds of a plant and its overall degree of defence will likely be weak, at best or as we documented non-existent.

Secondly, the indices we used to evaluate the effect of the compounds may be inappropriate. For example, colobus monkeys may only be able to tolerate a plant toxin to a specific threshold in a single feeding session. Thus, in a single day, the presence of that plant toxin may limit the damage from these herbivores. This action is not demonstrated by our index that quantified the foraging effort over a number of days. This threshold effect is less likely to influence many invertebrate herbivores, as they are less mobile and cannot easily switch among trees. The importance of considering time scale when evaluating the effect of a plant compound on an herbivore is potentially illustrated with respect to our evaluation of the importance of protein. We demonstrated that colobus monkeys do not appear to select foods high in protein (see also DaSilva, 1992, 1994 who found no relationship between the food items selected by *Colobus polykomos* and their protein content). Thus, when considering the importance of protein to colobus monkeys, the time scale is critical: on a day-to-day basis or when groups are not stressed (Chapman & Chapman, 2002) they may not select high-protein foods, but when preferred foods are scarce, high-protein, low-fibre leaves can maintain their numbers.

Third, these compounds may be inactive now but were active in the past, may be inactive against the organisms considered, or they may be inactive but facilitate the persistence of a pathway that via mutation can produce active compounds (Jones & Firn, 1991). In Kibale, it is clear that colobus monkeys and invertebrates are major consumers, but other organisms also play roles. For example, redtail monkeys (*Cercopithecus ascanius*) consume a significant amount of leaves during some times of the year, and their consumption could be curtailed by these compounds. Similarly, it may be that these compounds operate at specific times in the trees life history (e.g. at the early seedling stage), but continue to be produced at all life history stages. Freeland, Calcott & Anderson (1995) demonstrated that mice whose food contained saponins exhibited weight loss. It may be that saponins function to deter rodent foraging at the seedling stage, when mortality is often the greatest (Chapman, 1995).

Finally, these compounds may serve some unknown function and selection may be acting to promote that function. This is suggested by the fact that one of the most preferred trees, *Prunus africana*, was the species with the

highest levels of cyanogenic glycosides. There is evidence that the red colobus might be eating this plant for its medicinal qualities; extracts from this plant have been shown to inhibit parasite larval development and the bark of this species is used by the Batoro people of Western Uganda as a treatment for parasitic infections (T. Gillespie, unpublished data).

This study joins the ranks of many that have illustrated the complexity of understanding the evolution of plant chemical ecology. There are many potential chemicals that influence diet selection, there are unforeseen associative effects, and unknown adaptations by the animals to avoid deleterious effects of particular chemicals. Furthermore, we are only now beginning to understand the constraints on the coevolutionary relationships between plants and animals (Herrera, 1985). It is our hope that field observations will serve as a guide from refining the chemical analysis to address more questions (Feeny, 1992).

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