



Application of Protein-to-fiber Ratios to Predict Colobine Abundance on Different Spatial Scales

Colin A. Chapman,^{1,2,3} Lauren J. Chapman,^{1,2} Karen A. Bjorndal,¹ and Daphne A. Onderdonk¹

Received December 12, 2000; revised February 16, 2001; accepted April 24, 2001

*The biomass of arboreal folivorous primates in Africa and Asia is related to an index of mature leaf quality: the ratio of protein-to-fiber concentration. Investigations have considered variation in folivore biomass and forest composition among sites separated by hundreds or thousands of km. However, large variation in folivore abundance has been documented over much smaller spatial scales. We quantify the degree to which the average protein-to-fiber ratio of mature leaves of the 20 most abundant tree species predicts the biomass of western red colobus (*Ptilocolobus trephosceles*) and black-and-white colobus (*Colobus guereza*) over very small spatial scales. Four sites within Kibale National Park, Uganda, varied markedly in forest structure. Colobine biomass varied among sites from 191 to 2675 kg/km² and was related to the average protein-to-fiber ratio of mature leaves of the 20 most abundant tree species at each site. We examined the generality of the relationship between protein-to-fiber ratios and colobine abundance by adding our biomass and leaf chemistry values to previously published values to produce 9 comparable sites. At these locations, colobine biomass varied from 84 to 2675 kg/km² (mean biomass among sites = 910 kg/km²), and mean protein/fiber ratios varied from 0.167 to 0.577. Colobine biomass was related to the protein-to-fiber ratios of mature leaves ($R^2 = 0.616$, $P = 0.012$).*

KEY WORDS: population regulation; red colobus; black-and-white colobus; nutritional ecology; primate biomass; plant chemistry.

¹Department of Zoology, University of Florida, Gainesville, Florida 32611.

²Wildlife Conservation Society, 185th Street and Southern Boulevard, Bronx, NY 10460.

³To whom correspondence should be addressed; e-mail: cachment@zoo.ufl.edu.

INTRODUCTION

A fundamental issue in ecology is determining factors that regulate animal densities. A variety of potential factors have been proposed, including external ones, such as food resources, weather, predation, and disease, and internal conditions such as territoriality and aggressive behaviors (Andrewartha and Birch, 1954; Boutin, 1990; Krebs, 1978; Nicholson, 1934). The importance of understanding determinants of animal abundance has become increasingly vital as ecologists are asked to apply their knowledge to develop informed management plans for endangered or threatened species (Chapman and Peres, 2001). However, understanding and predicting factors that determine the abundance of particular species has proven extremely difficult.

Numerous studies of forest primates have revealed a high degree of intersite variation in density (Ganzhorn, 1992; Kay *et al.*, 1997; Oates *et al.*, 1990; Terborgh and van Schaik, 1987; Waterman *et al.*, 1988) on a variety of scales (Butynski, 1990; Chapman and Chapman, 1999), but there have been few direct tests of general hypotheses proposed to account for this variation. Notable exceptions are studies of folivorous primates. McKey (1978) proposed that year-round availability of digestible mature leaves, which are used by colobus when other more preferred foods are unavailable, limits the size of colobine populations (Milton, 1979). Thus, if easily digestible mature leaves are plentiful in an area during bottleneck periods when other more preferred foods are lacking, the site can support a relatively large population of colobines (Davies, 1994). By measuring overall mature leaf acceptability as the ratio of protein to fiber, several subsequent studies showed positive correlations between Asian and African colobine biomass and this index of leaf quality (Davies, 1994; Oates *et al.*, 1990; Waterman *et al.*, 1988). A similar relationship was found between the quality of leaves and the biomass of folivorous lemurs in Madagascar (Ganzhorn, 1992). Peres (1997) presented a similar argument to explain variation in primate density among 20 Amazonian sites, as did Emmons (1984) concerning Amazonian mammals. Milton (1979; Milton *et al.*, 1980) provided a physiological explanation for the importance of protein-to-fiber ratios. Each primate species has a protein threshold below which it cannot meet the protein required for bodily functions. If protein intake falls below this threshold, then the animal will suffer a negative nitrogen balance and eventually die. While there is substantial evidence that colobines can digest some fiber components, they cannot digest lignin (Waterman and Choo, 1981; Waterman and Kool, 1994). Increasing fiber content increases the amount of food ingested that the monkeys cannot digest and slows the rate of passage of digesta through the stomach as the efficiency of bacterial enzyme action is reduced, thus

reducing protein uptake (Milton, 1979; 1982; 1998). A number of studies of arboreal folivores have shown leaf selection to be strongly influenced by protein and fiber content, supporting the importance of protein and fiber levels in their diets (*Alouatta palliata*: Milton, 1979; 1998; *Presbytis johnii* (just selection for easily digestible material): Oates *et al.*, 1980, Waterman and Choo, 1981; *Presbytis rubicunda*: Davies *et al.*, 1988; *Colobus satanas*: McKey *et al.*, 1981; 10 out of 12 populations (8 species) of lemurs: Ganzhorn, 1992; *Procolobus badius*, *Colobus satanas*, and *Presbytis johnii* (just selection for easily digestible material): Waterman and Choo, 1981).

From investigations of the chemical constituents of mature leaves, it is apparent that folivores inhabiting forests separated by hundreds or thousands of km have access to food resources whose overall biochemical profiles differ (Cork, 1996; Cork and Foley, 1991; Waterman, 1986; Waterman and Choo, 1981; Waterman *et al.*, 1983; Waterman and Kool, 1994). For example, plants available to the colobines in Douala-Edéa Forest Reserve, Cameroon, invest more in quantitative defenses—digestion-inhibitors whose effects increase with increasing amounts—but less in nitrogen and qualitative defenses—toxic chemicals that will have an effect at much lower dose levels than quantitative defenses—than plants in Kibale National Park, Uganda, do (Gartlan *et al.*, 1980; McKey *et al.*, 1981).

Studies relating protein to fiber ratios and folivorous primate biomasses have only been made among areas separated by hundreds or thousands of km, yet primate densities can vary markedly over small spatial or temporal scales, e.g., within one forest (Butynski, 1990; Chapman and Chapman, 1999; Chapman and Fedigan, 1990) or within one site over time (Bronikowski and Altmann, 1996; Marsh, 1986; Struhsaker, 1976). Over a small spatial scale differences in plant communities or in many factors influencing investment in antifeedants, e.g., soil type, seasonality, deciduousness (Coley, 1983; Feeny, 1976; Janzen, 1975; Janzen and Waterman, 1984) should be smaller than among sites separated by hundreds or thousands of km.

Our objective was to determine if Milton's protein-to-fiber hypothesis could explain variation in the biomass of western red colobus (*Piliocolobus trephosceles*) and black-and-white colobus (*Colobus guereza*) among sites within the same forest. We first quantified variation in forest structure and red colobus diet among 4 sites in Kibale National Park, Uganda. Second, we quantified colobine biomass and related this to the average protein-to-fiber ratio of mature leaves of the 20 most abundant tree species at each site. Third, we assessed whether it was possible to improve the predictive power of this relationship by only including the average protein-to-fiber ratios of mature leaves from tree species actually eaten by red colobus. We also compared the protein-to-fiber ratios of the mature leaves of species eaten to species not eaten by red colobus. Finally, we examined the generality

and predictive power of the relationship between protein-to-fiber ratios and colobine abundance by combining our values with other published values.

METHODS

Study Sites

Kibale National Park (766 km²) is located in western Uganda (0 13'–0 41' N and 30 19'–30 32' E) near the foothills of the Ruwenzori Mountains (Chapman *et al.*, 1997; Skorupa, 1988; Struhsaker, 1975, 1997). We studied at four sites that are approximately 15 km apart from one another: (Sebatoli, Kanyawara (K-30 forestry department), Dura River, and Mainaro (Chapman *et al.*, 1997). Within Kibale, there is an elevational gradient from north to south, which corresponds to a southward increase in temperature and decrease in rainfall (Howard, 1991; Struhsaker, 1997; Table I). The northern most site, Sebatoli, is considered *Parinari* forest by foresters because the spreading crown of *Parinari excelsa* can be distinguished on aerial photographs. The canopy is dominated by trees of *Parinari excelsa*, *Carapa grandiflora*, *Olea welwitschii*, *Aningeria altissima*, *Strombosia schefleri*, and *Newtonia buchanani* (Osmaston, 1959). Kibale received National Park status in 1993. Before 1993, it was a Forest Reserve, gazetted in 1932, with the stated goal of providing sustained production of hardwood timber (Chapman and Chapman, 1997; Osmaston, 1959; Struhsaker 1997). As a result, the forest near Sebatoli was commercially logged in the late 1960s. We were unable to obtain information on the level of extraction. However, detailed quantification of stand structure suggests that the level of extraction was similar to or slightly lower than an area just to the south; K-15 forestry compartment (Chapman and Chapman, unpublished data), in which the harvest averaged 21 m³/ha or approximately 7.4 stems/ha (Skorupa, 1988; Struhsaker, 1997). Incidental damage in the K-15 forestry compartment was high, and it is estimated that approximately 50% of all trees were destroyed by logging and incidental damage (Chapman and Chapman, 1997; Skorupa, 1988). Kanyawara (K-30 forestry compartment) is a 282-ha area that has not been commercially harvested. However, before 1970, a few large stems (0.03 to 0.04 trees/ha) were removed by pitsawyers. This extremely low level of extraction seems to have had very little impact on the structure and composition of the forest (Skorupa, 1988; Struhsaker, 1997). At the Dura River, the forest is no longer considered a *Parinari* forest, as *P. excelsa* and the tree species associated with it are relatively rare. *Pterygota mildbraedii*, *Cola gigantea*, *Piptadeniastrum africanum*, and *Chrysophyllum albidum* are the dominant canopy species (Kingston, 1967). Further south at Mainaro, the

forest is dominated by *Cynometra alexandri* and affiliated species (Kingston, 1967). At both the Dura River and Mainaro sites, a few timber trees have been extracted by pitsawyers (approximately 0.1 trees/ha), but this activity has had little impact on the forest. Detailed enumeration of the tree communities in these areas is provided by Chapman *et al.* (1997).

To determine the composition of the forest at each site, we conducted vegetation transects (200 m by 10 m): 12 at Kanyawara and 4 each at Dura River, Mainaro, and Sebatoli. In Kanyawara, transect location was within existing trail systems (Chapman and Chapman, 1997; Chapman *et al.*, 1999). At the Mainaro, Dura River, and Sebatoli there was no preexisting trail, and we established transects perpendicular to each other at 50-100-m intervals. This regime produced a total sampling area of 4.8 ha (2.4 ha at Kanyawara, and 0.8 ha at Dura River, Mainaro, and Sebatoli). We marked each tree >10 cm DBH (diameter at breast height) within 5 m of each side of the trail individually with a numbered aluminum tag and measured its DBH. This produced a sample of 2126 trees ($n = 1173$ at Kanyawara, 338 at Dura River, 293 at Mainaro, and 322 at Sebatoli).

Behavioral Observations

We observed the behavior of red colobus from July 1994 to June 1997 at Kanyawara (1592 hr), and from July 1996 to June 1997 at Sebatoli (248 hr), Dura River (116 hr), and Mainaro (117 hr), producing 2073 hours of observation. We used an observational method that approximates the methods used in several previous studies in Kibale (Butynski, 1990; Struhsaker, 1975; Waser, 1974). During each half-hour that the observer was with the group, 5 point samples were made of different individuals. If the animal was feeding, we recorded the species and the plant part: e.g., fruit, young leaf, and leaf petiole. We tried to avoid repeatedly sampling particularly conspicuous individuals by moving throughout the group when selecting subjects and by sampling subjects that were both in clear view and ones that were more hidden. Often the observer had to wait for several min to determine what a less observable subject was doing.

Abundance of Red Colobus and Black-and-white Colobus

We assessed the abundance of the two colobine species via the line-transect method (Chapman *et al.*, 2000; Chapman *et al.*, 1988; National Research Council, 1981; Plumptre and Reynolds, 1994; Whitesides *et al.*, 1988). Both species are large-bodied and diurnal: the subset of primates for

which the line-transect method is thought to be appropriate for estimating densities (National Research Council, 1981). However, the use of line transect censuses to estimate primate densities is difficult, particularly when species occur at low densities. Thus, density estimates should be viewed with caution. We initiated primate censuses along transects approximately 4 km long in June 1996 and collected data biweekly at Kanyawara ($n = 26$) and Dura ($n = 23$), and once a month at Sebatoli ($n = 14$) and Mainaro ($n = 10$). Rebel activity prevented us from sampling at Mainaro in January, February, and April of 1997. We conducted censuses between 0700 hr and 1400 hr at a speed of approximately 1 km/hr. Data collected includes primate species observed, time of observation, straight-line distance between the subject and observer (visually estimated), and mode of detection. At the beginning of the study, we trained together to estimate observer to subject distance. We assessed variation among observers in sighting estimates at the end of the study. While particular estimates could be inaccurate, overestimates of distances tended to be countered by underestimates.

A variety of methods have been proposed to estimate primate density via transect data, and considerable controversy exists regarding the accuracy of the different methods (Burnham *et al.*, 1980; Chapman *et al.*, 1988; Skorupa, 1988). Accordingly, we relied on empirical criteria to select the best method. Ghiglieri (1979, 1984), Struhsaker (National Research Council, 1981), and Skorupa (1988) concluded that a modified Kelker (1945) method produced the best empirical results for primates at Kibale. Following these recommendations, we pooled data from census areas where sighting distance did not differ (ANOVA) and plotted the distance at 10-m intervals. This permitted us to estimate the subject sighting distance for each species. We used a 50% cut-off rule to select the sighting distance. If X_i is the number of sightings in distance class i for a given species, the last distance considered was at the end of the first class such that X_{i+1}/X_i and X_{i+2}/X_i were both equal to ≤ 0.50 . We used the observer subject sighting distance, rather than perpendicular distance, because empirical data indicate that perpendicular distance underestimates transect width for forest dwelling primates (Chapman *et al.*, 1988; National Research Council, 1981; Struhsaker, 1997). Thus, we calculated the density of groups as the number of groups sighted within the truncated sighting distance divided by the area sampled (length of the census route times the truncated distance for subject sighting distance).

Obtaining reliable group counts of forest-dwelling primates is extremely difficult, because inactive individuals are often hard to locate and traveling ones often take different pathways. As a result, we made considerable effort to count groups in each area. Each month between July 1996 and May 1998 (22 mo), two observers spent 2 days at each site simply following groups and attempting to get counts. We rarely attempted counts when a group was

stationary; the best counts were obtained when a group was crossing a gap, such as the river (Dura, Sebatoli, and Mainaro) or a road (Kanyawara and Dura). We repeated counts of the same group to ensure accuracy. We identified groups either by recognizing individuals or by matching the group count to previous ones. In addition, we counted opportunistically when we were collecting behavioral data and groups were seen to cross a road or river. Skorupa (1988) found that red colobus groups in a logged area in Kibale occasionally divided into independent subgroups that could be separated by several hundred meters. We have observed similar patterns with a red colobus group in Kanyawara. As a result, we were concerned that counts of particular populations could be biased by considering subgroups to be groups. However, we did not observe group fission in any population other than the Kanyawara one, and we were able to determine that fissioning had occurred by noting individuals in the separate subgroups. Furthermore, the average maximum difference of counts of groups with recognizable individuals is small (mean difference among sites = 2.48, range = 1.0 to 4.3—excluding the group that fissioned).

To estimate the biomass of the colobines, we took adult male and female bodily masses from Struhsaker (1978). We used the composition of the groups as determined via the group counts to estimate biomass for each region. We estimated subadult and juvenile weights to be half that of adults.

Nutritional Analyses

We collected mature leaves of the 20 most abundant tree species (>10 cm DBH) at each site using a tree pruning pole to sever a tree limb. After collection, we sun-dried the leaves, stored them in sealed plastic bags, and transported them to the University of Florida. We ground dried samples in a Wiley mill to pass through a 1 mm mesh screen. We determined dry matter by drying a portion of each sample overnight at 105°C. We analyzed in samples duplicate and considered replicates for analyses acceptable if the relative error was <2%.

We assessed the protein (nitrogen) content of the plant parts via Kjeldahl procedures (Horwitz, 1970). Samples were digested using a modification of the aluminum block digestion procedure of Gallaher *et al.* (1975). The digestion mix contained 1.5 g of 9:1 K₂SO₄:CuSO₄, and digestion proceeded ≥4 h at 375°C in 6 ml of H₂SO₄ and 2 ml H₂O₂. We determined the nitrogen in the digestate by semiautomated colorimetry (Hambleton, 1977). Measuring total nitrogen provides an estimate of crude protein (protein levels = $N \times 6.25$; Maynard and Loosli, 1969). A better conversion factor for tropical foliage may be 4.3 (Conklin-Brittain *et al.*, 1999). However, we used

the 6.25 factor so that our results would be comparable to those of previous studies (Davies, 1994; Gartlan *et al.*, 1980; Oates *et al.*, 1990; Waterman *et al.*, 1988).

We measured fiber (ADF) via the methods outlined by van Soest (1963) and modified by Goering and van Soest (1970) and Robertson and van Soest (1980). ADF is a measure of cell wall cellulose and lignin, which are refractory components of fiber. ADF has a strong negative correlation with food selection by primates (Glander, 1982; Oates *et al.*, 1990). However, ADF is somewhat fermentable, while lignin is not (van Soest, 1982).

RESULTS

Forest Structure

Densities of many tree species differed markedly among sites (Table I). For example, 8 of the 10 most common trees at Mainaro did not occur at

Table I. Density of the 20 most abundant tree species at any of 4 study sites in Kibale National Park, Uganda (individuals per ha of trees >10 cm DBH). % of the total sample: the percentage of the total number of trees identified at each site that is included in the sample of the 20 most abundant tree species

Species	Kanyawara	Dura River	Mainaro	Sebatoli
<i>Uvariopsis congensis</i>	60.4	60.0	43.8	—
<i>Celtis durandii</i>	47.1	63.8	33.8	2.5
<i>Baphiopsis parviflora</i>	—	—	116.3	—
<i>Funtumia latifolia</i>	33.8	43.8	2.5	25.0
<i>Markhamia platycalyx</i>	50.0	8.8	1.3	38.8
<i>Chrysophyllum spp.</i>	2.6	47.5	21.2	8.8
<i>Bosqueia phoberos</i>	50.0	22.5	—	—
<i>Cynometra alexandri</i>	—	—	63.8	—
<i>Bequaertiodendron ob lanceolatum</i>	—	57.5	—	—
<i>Strombosia scheffleri</i>	12.5	2.5	—	36.3
<i>Diospyros abyssinica</i>	40.0	1.3	1.3	2.5
<i>Croton megalocarpus</i>	0.8	—	1.3	41.3
<i>Tabernaemontana sp.</i>	4.6	8.8	—	28.8
<i>Leptonychia mildbraedii</i>	35.4	—	—	—
<i>Celtis mildbraedii</i>	—	—	32.5	—
<i>Newtonia buchananii</i>	—	3.8	—	26.3
<i>Aningeria altissima</i>	1.7	2.5	—	23.8
<i>Pleiocarpa pycnantha</i>	1.3	13.8	2.5	6.3
<i>Chaetacme aristata</i>	17.1	3.8	1.3	—
<i>Xymalos monospora</i>	8.8	—	—	10.0
% of total sample	25.0%	24.2%	41.4%	30.0%
Rainfall (mm)	1778	1500	1394	1491
Elevation (m)	1500	1250	1200	1500

Sebatoli, while 7 of the 10 most common trees at Sebatoli were absent from Mainaro. *Baphiopsis parviflora* and *Cynometra alexandri* were the most abundant tree species at Mainaro, but were not at the other locations. *Bequaertiodendron oblanceolatum* was the third most common species at Dura River, but was not on transects at any other location. *Uvariopsis congensis*, which was very abundant at Kanyawara, Dura River, and Mainaro, was absent from Sebatoli. This suggests that there may be sufficient variation in forest composition and thus potentially in the protein and fiber content of the available mature leaves to test whether the protein-to-fiber ratios can predict colobus abundance. A complete description of the forests, including densities, average size, and phenology of each tree species, was given by Chapman *et al.* (1997) and Chapman and Chapman (2000).

Red Colobus Diet

At all sites, red colobus ate young leaves more frequently than other plant parts; however, some populations relied heavily on fruit (typically unripe) or flowers, while others did not (Table II). This degree of dietary flexibility does not change our impression that red colobus are folivores, but it changes our impression of how much they rely on mature leaves or use flowers or fruit.

Red colobus populations also differed in the foraging effort devoted to specific species (Table III). In many cases this variation can be attributed to differences in the relative abundance of the tree species among different sites; however, in some cases other factors may be involved. For example, *Bosqueia phoberos* was very abundant at Kanyawara (50 individuals/km²; Table I), but the red colobus there rarely ate it (0.8% of their foraging time). In contrast, *Bosqueia phoberos* was about half as abundant at Mainaro (22.5 individuals/km²) as compared to Kanyawara, but the red colobus fed on it for 5.4% of total foraging time.

The percentage of time red colobus spent feeding on different tree species was not related to the protein-to-fiber ratio of their mature leaves

Table II. Dietary components from red colobus groups from 4 areas in Kibale National Park, Uganda. The components do not sum to 100% because of groups eating plant parts that are not listed below, e.g., the Kanyawara groups ate 3.0% pine needles

Location	Young leaves	Mature leaves	Leaf petiole	Fruit	Flowers	Bark
Sebatoli	72.4	7.4	7.1	6.4	3.3	2.0
Kanyawara	57.6	9.9	14.2	6.7	2.0	4.1
Dura River	65.1	4.6	8.7	13.9	6.2	0.0
Mainaro	57.5	16.2	1.8	10.8	7.2	3.6

Table III. Percentage of time red colobus spent feeding on species that averaged >1% of the foraging time across study 4 sites in Kibale National Park, Uganda

Species	Kanyawara	Sebatoli	Mainaro	Dura River
<i>Celtis durandii</i>	14.10	5.36	5.99	27.18
<i>Cynometra alexandri</i>	0.00	0.00	40.72	0.00
<i>Funtumia latifolia</i>	7.17	5.36	2.99	12.82
<i>Aningeria altissima</i>	0.82	8.67	0.00	14.87
<i>Strombosia scheffleri</i>	9.17	10.97	0.00	2.56
<i>Albizzia grandibracteata</i>	8.36	1.02	1.80	10.77
<i>Pygeum africanum</i>	12.97	5.87	2.40	0.00
<i>Celtis africana</i>	9.91	4.34	0.00	1.54
<i>Chrysophyllum spp.</i>	1.63	4.59	2.40	6.15
<i>Markhamia platycalyx</i>	9.20	3.06	0.00	1.03
<i>Bosqueia phoberos</i>	0.79	3.06	5.39	3.08
<i>Newtonia buchanani</i>	0.00	11.22	0.00	0.00
<i>Mimusops bagshawei</i>	0.40	0.77	5.39	4.62
<i>Parinari excelsa</i>	3.88	5.10	0.00	0.00
<i>Celtis zenkeri</i>	0.00	1.79	5.39	0.00
<i>Macaranga schweinfurthii</i>	1.27	4.85	0.60	0.00
<i>Croton megalocarpus</i>	0.00	4.85	0.60	0.00
<i>Cola gigantea</i>	0.00	0.00	0.00	5.13
<i>Milletia dura</i>	2.03	2.55	0.00	0.00
<i>Ficus brachylepis</i>	0.95	3.32	0.00	0.00
<i>Ficus mucoso</i>	0.00	0.00	4.20	0.00

(considering all species $r = 0.006$, $P = 0.478$, $n = 80$; only those species known to be eaten by red colobus, $r = -0.108$, $P = 0.253$, $n = 40$; percent foraging time arcsin square-root transformed; Table IV). These findings may relate to a number of different factors. 1) It may reflect the fact that the red colobus are typically eating young leaves from these species (Table II) and there could be a considerable discrepancy between the protein-to-fiber ratios of mature and young leaves among species. 2) Other chemical constituents of the leaves may strongly influence selection and outweigh any tendency to maximize protein intake, while minimizing fiber ingestion (Oates *et al.*, 1977; Waterman *et al.*, 1980). 3) As McKey (1978) suggested, a relationship between protein-to-fiber ratios and feeding time might only occur when red colobus are forced to feed on mature leaves because other, more preferred foods are unavailable.

Abundance of Red Colobus and Black-and-white Colobus

We conducted 73 census walks for a total of approximately 292 km (Kanyawara, $n = 26$; Dura, $n = 23$; Sebatoli, $n = 14$; Mainaro, $n = 10$). Red colobus and black-and-white colobus were present at all sites (Table V). The lowest density recorded for both species was at the undisturbed Dura River

Table IV. Description of the plant chemistry of mature leaves (expressed as % dry matter) from 4 sites in Kibale National Park, Uganda. Also, depicted is the percentage time that red colobus spent eating food items from these trees

Site	Species	Family	Protein	Fiber (ADF)	Protein/Fiber	% of foraging time
Kanyawara	<i>Bosqueia phoberos</i>	Moraceae	16.16	27.60	0.59	0.8
	<i>Cassipourea ruwensorens</i>	Rhizophoraceae	19.14	34.41	0.56	0.0
	<i>Celtis africana</i>	Ulmaceae	18.62	17.02	1.09	9.9
	<i>Celtis durandii</i>	Ulmaceae	25.72	25.64	1.00	14.1
	<i>Chaetacme aristata</i>	Ulmaceae	13.40	24.95	0.54	0.6
	<i>Diospyros abyssinica</i>	Ebenaceae	16.90	27.09	0.62	0.1
	<i>Dombeya mukole</i>	Sterculiaceae	19.61	32.93	0.60	3.5
	<i>Ficus exasperata</i>	Moraceae	20.11	26.05	0.77	0.3
	<i>Funtumia latifolia</i>	Apocynaceae	16.81	37.93	0.44	7.2
	<i>Ilex mitis</i>	Aquifoliaceae	16.58	32.21	0.51	0.0
	<i>Leptonychia mildbraedii</i>	Sterculiaceae	22.04	28.26	0.78	0.0
	<i>Markhamia platycalyx</i>	Oliaceae	13.85	42.51	0.33	0.0
	<i>Linociera johnsonii</i>	Bignoniaceae	16.30	50.47	0.32	9.2
	<i>Pancovia turbinata</i>	Sapindaceae	12.70	42.42	0.30	0.0
	<i>Prenna angolensis</i>	Verbenaceae	21.99	35.77	0.61	0.0
	<i>Strombosia scheffleri</i>	Oliaceae	18.49	41.31	0.45	9.2
	<i>Strychnos mitis</i>	Loganiaceae	11.36	34.99	0.32	0.0
	<i>Tabernaemontana holstii</i>	Apocynaceae	24.66	33.44	0.74	0.0
	<i>Teclaea nobilis</i>	Rutaceae	17.52	29.18	0.60	0.4
	<i>Uvariopsis congensis</i>	Annonaceae	18.55	31.70	0.59	0.0
	<i>Aphania senegalensis</i>	Sapindaceae	12.60	44.78	0.28	0.0
	<i>Bequeritodendron oblanceolatum</i>	Sapotaceae	11.87	46.85	0.25	2.1
	<i>Bosqueia phoberos</i>	Moraceae	13.70	30.72	0.45	3.1
<i>Celtis durandii</i>	Ulmaceae	17.47	21.13	0.83	27.2	
<i>Chaetacme aristata</i>	Ulmaceae	19.33	27.33	0.71	0.5	
<i>Chrysophyllum gorgosanum</i>	Sapotaceae	17.06	38.84	0.44	6.2	
<i>Cola gigantea</i>	Sterculiaceae	12.26	37.75	0.32	5.1	
<i>Dicyandra arborescens</i>	Rubiaceae	26.77	29.97	0.89	0.0	
<i>Funtumia latifolia</i>	Apocynaceae	16.81	37.93	0.44	7.2	
<i>Lovoa swynnertonii</i>	Meliaceae	13.25	30.93	0.43	0.0	
<i>Lynchodiscus cerospermus</i>	Sapindaceae	14.22	52.85	0.27	0.0	
Dura River						

Table IV. (Continued)

Site	Species	Family	Protein	Fiber (ADF)	Protein/Fiber	% of foraging time
Mainaro	<i>Markhamia platycalyx</i>	Bignoniaceae	16.30	50.47	0.32	9.2
	<i>Mimusops bagshawei</i>	Sapotaceae	14.42	40.97	0.35	4.6
	<i>Monodora myristica</i>	Annonaceae	13.86	37.03	0.37	0.0
	<i>Newtonia buchanani</i>	Leguminosae	17.70	38.46	0.46	0.0
	<i>Plectocarpa pycnantha</i>	Apocynaceae	15.49	35.63	0.43	0.0
	<i>Prenna angolensis</i>	Verbenaceae	21.28	39.59	0.54	0.0
	<i>Pseudospondias microcarpa</i>	Anacardiaceae	12.91	36.14	0.36	0.0
	<i>Tabernaemontana holstii</i>	Apocynaceae	17.18	33.52	0.51	0.0
	<i>Uvariopsis congestis</i>	Annonaceae	19.38	34.92	0.55	0.0
	<i>Aphania senegalensis</i>	Sapindaceae	12.31	45.45	0.27	5.3
	<i>Baphiopsis parviflora</i>	Leguminosae	20.09	42.19	0.48	0.0
	<i>Celtis durandii</i>	Ulmaceae	24.02	24.66	0.97	6.0
	<i>Celtis mildbraedii</i>	Ulmaceae	23.51	30.84	0.76	0.0
	<i>Chaetacme aristata</i>	Ulmaceae	12.20	20.13	0.61	1.2
	<i>Chrysophyllum gorganosanum</i>	Sapotaceae	17.49	38.51	0.45	2.4
	<i>Cynometra alexandri</i>	Leguminosae	15.12	51.31	0.29	40.7
	<i>Dicyandra arborecens</i>	Rubiaceae	27.05	27.93	0.97	0.0
	<i>Diospyros abyssinica</i>	Ebenaceae	16.86	27.76	0.61	3.0
	<i>Ficus exasperata</i>	Moraceae	21.80	26.42	0.82	0.0
	<i>Ficus mucosa</i>	Moraceae	17.32	31.93	0.54	4.2
	<i>Funtumia latifolia</i>	Apocynaceae	15.69	25.76	0.61	3.0
	<i>Harrisonia abyssinica</i>	Simaroubaceae	16.74	28.70	0.58	0.0
	<i>Markhamia platycalyx</i>	Bignoniaceae	16.53	47.32	0.35	0.0
	<i>Monodora myristica</i>	Annonaceae	15.51	33.37	0.46	0.0
	<i>Plectocarpa pycnantha</i>	Apocynaceae	15.04	33.58	0.45	0.0

Sebatoli									
	<i>Polyscias fulva</i>	Araliaceae	14.57	30.50	0.48	0.0			
	<i>Premna angolensis</i>	Verbenaceae	21.74	31.50	0.69	1.2			
	<i>Turraea robusta</i>	Meliaceae	21.18	25.09	0.84	0.0			
	<i>Uvaritopsis congensis</i>	Annonaceae	19.03	32.13	0.59	0.0			
	<i>Alangium chinense</i>	Alangiaceae	22.84	22.33	1.02	0.3			
	<i>Aningeria altissima</i>	Sapotaceae	16.80	41.47	0.40	8.7			
	<i>Blighia unijugata</i>	Sapindaceae	15.03	35.60	0.42	0.5			
	<i>Chrysophyllum gorganosanum</i>	Sapotaceae	16.90	44.39	0.38	4.6			
	<i>Cordia abyssinica</i>	Boraginaceae	12.95	46.50	0.28	0.0			
	<i>Croton macrostachyus</i>	Euphorbiaceae	29.01	29.63	0.98	2.4			
	<i>Croton megalocarpus</i>	Euphorbiaceae	22.76	35.58	0.64	2.4			
	<i>Ehretia cymosa</i>	Boraginaceae	14.38	26.89	0.53	0.0			
	<i>Funtumia latifolia</i>	Poeynaceae	12.93	29.35	0.44	5.4			
	<i>Ilex mitis</i>	Aquifoliaceae	18.92	33.57	0.56	0.0			
	<i>Linociera johnsonii</i>	Oleaceae	12.59	43.78	0.29	0.0			
	<i>Markhamia platcalyx</i>	Bignoniaceae	15.35	50.65	0.30	3.1			
	<i>Mimusops bagshawei</i>	Sapotaceae	11.24	39.42	0.29	0.8			
	<i>Myrianthus arboreus</i>	Moraceae	12.49	43.05	0.29	0.0			
	<i>Necobotonia macrocalyx</i>	Euphorbiaceae	17.46	37.76	0.46	0.0			
	<i>Newtonia buchanani</i>	Leguminosae	11.31	40.90	0.28	11.2			
	<i>Plectocarpa pycnantha</i>	Poeynaceae	12.03	34.93	0.34	0.0			
	<i>Srombosia scheffleri</i>	Oleaceae	20.25	33.94	0.60	11.0			
	<i>Tabernaemontana holstii</i>	Poeynaceae	19.37	28.83	0.67	0.0			
	<i>Turraeanthus africanus</i>	Meliaceae	21.86	37.66	0.58	0.0			

Table V. Descriptions of the colobine populations in 4 areas of Kibale National Park, Uganda. Density estimates for the monkeys are from line transect surveys (groups/km²), and group size and composition data are from group counts at each site (the numbers of groups counted are in parentheses)

Species	Sebatoli	Kanyawara	Dura	Mainaro
No of km walked	50.4	120.6	95.1	39
No of groups seen				
<i>C. guereza</i>	9	12	5	12
<i>P. trephosceles</i>	35	51	6	27
Group density				
<i>C. guereza</i>	2.05	2.00	0.79	3.85
<i>P. trephosceles</i>	6.53	5.50	0.53	10.25
Average group size				
<i>C. guereza</i>	5.9 (7)	9.2 (14)	9 (17)	10.1 (12)
<i>P. trephosceles</i>	14.2 (5)	40 (15)	34 (14)	30.5 (5)
Individuals per km ²				
<i>C. guereza</i>	12.1	18.4	7.1	38.9
<i>P. trephosceles</i>	92.7	220.0	18.0	312.6
Biomass (kg/km ²)				
<i>C. guereza</i>	79	361	48	253
<i>P. trephosceles</i>	590	1370	146	2422

site. Group size also varied between sites (black-and-white colobus mean = 8.6, range 5.9–10.1; red colobus mean 29.7, range 14.2–40).

To provide a context to view the variation we documented in red colobus density, we obtained data from a number of studies that report red colobus group density. These studies illustrate more variation in red colobus density within Kibale than has been documented among other geographically remote sites in Africa (Fig. 1). We do not present an analysis for black-and-white colobus because there are few studies that report density estimates in comparable forested habitats.

Protein/Fiber Ratios and Biomass

There was a marginally significant difference in the protein-to-fiber ratios among sites ($F = 2.237$, $P = 0.091$, $n = 80$; mean protein to fiber ratio - Sebatoli = 0.488, Kanyawara = 0.588, Dura River = 0.461, Mainaro = 0.592). However, variation in the protein-to-fiber ratios among tree species was considerable (range = 0.25 to 1.09). For some tree species, protein-to-fiber ratios varied little among sites, while for other species they showed a great deal of intersite variation (Table IV). We used a paired t-test (paired by species) to contrast protein-to-fiber ratios among pairs of sites. Mainaro has a higher average protein-to-fiber ratio than Sebatoli ($t = 3.78$, $P = 0.032$, $n = 4$ species) and Dura River ($t = 2.34$, $P = 0.041$, $n = 11$ species) and a

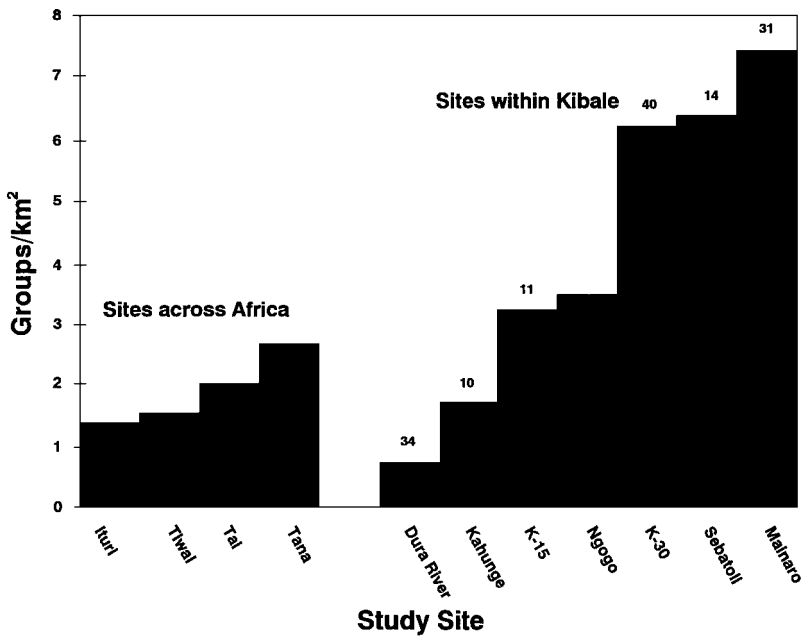


Fig. 1. The density of red colobus groups at 7 sites in or near Kibale (this study and Chapman and Chapman, 1999) and at 4 other African sites: Ituri Forest, Democratic Republic of the Congo (Thomas, 1991); Tiwai Island, Sierra Leone (Oates *et al.*, 1990); Tai National Park, Côte d'Ivoire (Galat and Galat-Luong, 1985), and Tana River, Kenya (Marsh, 1986). Data are expressed as groups/km² to facilitate comparisons with sites outside of Kibale; however, in Kibale, mean group size is indicated for each population above each bar.

marginally higher ratio than Kanyawara ($t = 2.00$, $P = 0.086$, $n = 8$ species). Other comparisons did not reveal significant differences (Dura River to Kanyawara $t = 1.37$, $P = 0.214$, $n = 8$ species; Dura River to Sebatoli $t = 0.909$, $P = 0.398$, $n = 7$ species; Kanyawara to Sebatoli ($t = 0.36$, $P = 0.735$, $n = 6$ species).

The difficulty in testing the generality of the relationship between protein-to-fiber ratios and colobine abundance is primarily logistical: censusing arboreal primates is difficult and should be done over many months, and determining the protein and fiber content for 20 species at each site is time-consuming. We are therefore limited in the strength of our test because we only have 4 sites. However, with this limitation in mind, colobine biomass appears to be related to the average protein-to-fiber ratio of the 20 most abundant tree species at each site (Fig. 2).

On average, red colobus were only observed feeding on half of the 20 most abundant trees at each site (range among sites 45–55%). Feeding

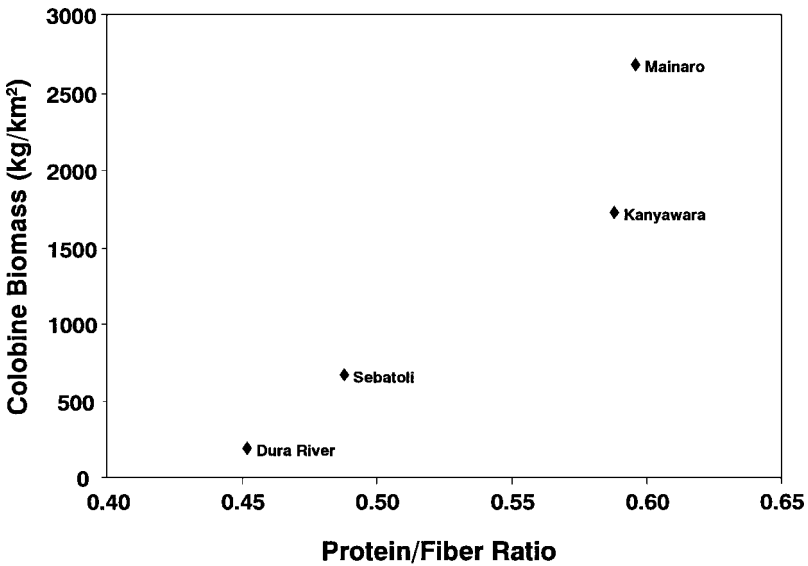


Fig. 2. The relationship between the average protein-to-fiber ratio of the leaves from the 20 most abundant tree species at 4 sites in Kibale National Park, Uganda, and the biomass of red colobus and black-and-white colobus there.

on items from these tree species constituted an average of 58.8% of their feeding time (Sebatoli, 50.4%, Kanyawara 55.3%, Dura River 62.6, Mainaro 67.0%). The mean protein-to-fiber ratios of the trees on which red colobus fed (0.55) did not differ significantly from those that they did not eat (0.52, $t = 0.696$, $df = 78$, $P = 0.489$). It is therefore not surprising that the average protein-to-fiber ratio of only species eaten by the red colobus did not seem to improve the predictive power of the test for either red colobus biomass or total colobine biomass (Fig. 3a,b).

Predictive Power of the Relationship between Protein to Fiber Ratios and Colobine Abundance

Colobine biomass and leaf chemistry have been quantified at 9 sites, which facilitates examination of the predictive power of the relationship between protein-to-fiber ratios and colobine abundance. Oates *et al.* (1990) presented 6 sites, and we have an additional 4 sites; however, Kanyawara is in two of the data sets. For Kanyawara, we took the mean of the previous values provided by Struhsaker and Waterman (Oates *et al.*, 1990) and our new values. If a range of biomass values was given for a site, we used the mean of the range in the regression.

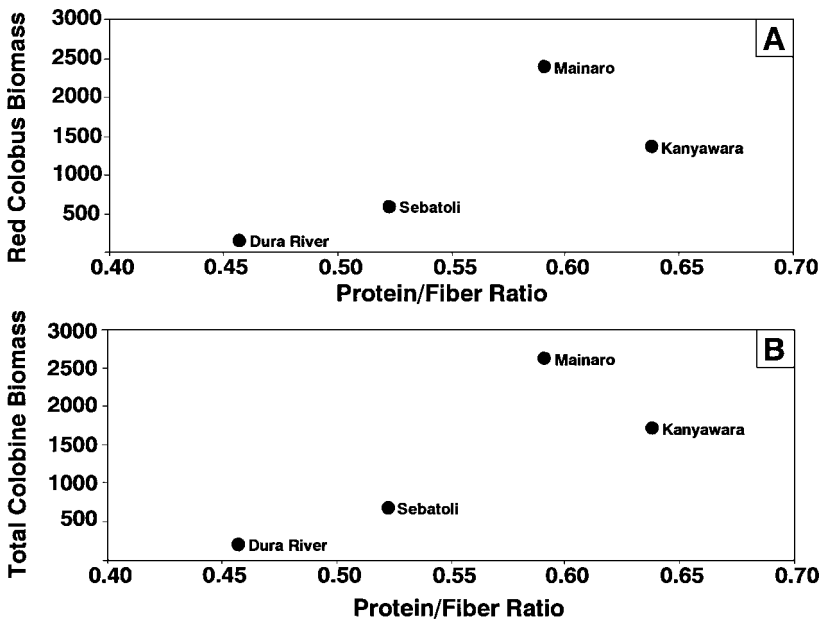


Fig. 3. (A) The relationship between the average protein-to-fiber ratio of the leaves from the tree species that red colobus ate at 4 sites in Kibale National Park, Uganda, and the biomass of red colobus there. (B) The relationship between the average protein-to-fiber ratio of the leaves from the tree species that red colobus ate at 4 sites in Kibale National Park, Uganda, and the biomass of red colobus and black-and-white colobus there.

Colobine biomass varied from 84 kg/km² at Sepilok, Malaysia, to 2675 kg/km² at Mainaro (mean biomass across sites = 910 kg/km²). The protein/fiber ratios in these studies showed a similar degree of variation (mean = 0.306, range 0.167–0.577). Colobine biomass at the 9 sites could be predicted from the protein-to-fiber ratios of the mature leaves ($R^2 = 0.616$, $P = 0.012$; Fig. 4). This relationship is also significant via a nonparametric approach ($r_s = 0.800$, $P = 0.01$).

DISCUSSION

Generality in the Colobine Protein/Fiber Model

Our data suggest that colobine biomass within Kibale National Park can be predicted by the protein-to-fiber ratio of mature leaves in their environment. Digestible mature leaves that are rich in protein have been suggested

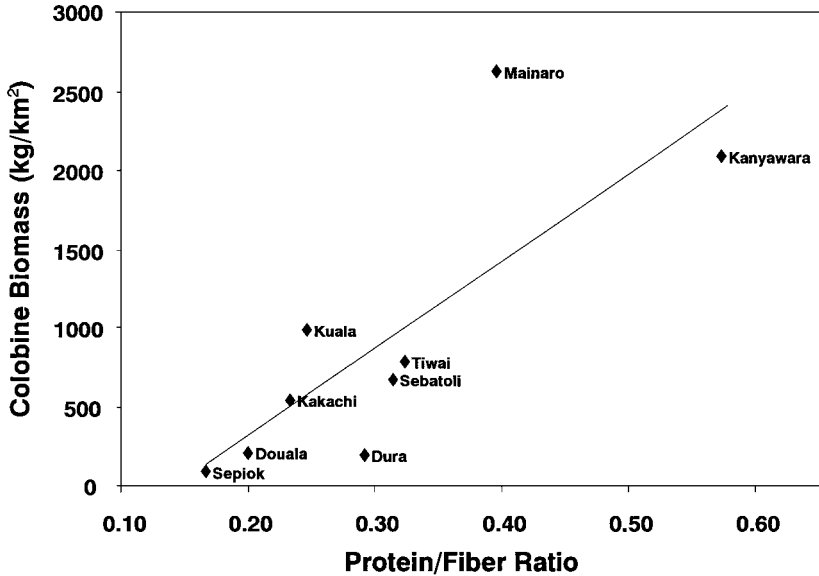


Fig. 4. The relationship between mature leaf chemistry and colobine biomass at rain forest sites in Africa and Asia. Chemical values are weighted mean percentages of dry mass, standardized to the basal area of species to account for different proportions of the flora being sampled at each site. The weighted values were calculated from $\Sigma (P_i + X_i) / \Sigma P_i$ in which P_i is the proportion of the basal area contributed by species i and X_i is the chemical measure for species i . This figure is standardized to 100%. Excluding the four new sites from Kibale, all chemical and biomass data are from Oates *et al.* (1990).

to maintain colobine biomass when other more preferred foods are unavailable (Davies *et al.*, 1999; McKey, 1978; Oates *et al.*, 1990). This study adds to our previous understanding of determinants of colobine biomass by documenting that this relationship holds when comparisons are made both among sites scattered across the continent and among populations within a single forest. Given the inaccuracies associated with estimating primate densities, the means of collecting mature leaves (by basal area—Oates *et al.*, 1990, density—this study, or haphazardly—Ganzhorn, 1992), and the fact that many of the colobine species depend on mature leaves of lianas to support them through periods of food scarcity and that liana density is not quantified (Bennett and Davies, 1994; *Colobus polykomas* Dasilva, 1994; *Presbytis rubicunda* Davies, 1991; Davies *et al.*, 1988), it is surprising that 62% of the variance in colobine abundance among the 9 sites can be explained by this relationship. Furthermore, the whole notion that protein-to-fiber ratio could predict colobus biomass assumes that all populations experience a seasonal shortage of preferred foods and must fall

back to eating mature leaves; some populations may not experience this shortage.

The strength of this relationship is more surprising when one considers the many factors that could cause these populations not to be at equilibrium. If some populations were not at carrying capacity because disease or predation had temporarily reduced their numbers, then food availability and quality should not correlate with primate density, when in fact food may typically regulate primate numbers. Factors such as disease (Anderson and May, 1979; Freeland, 1977; Scott, 1988) and predation (Boinski and Chapman, 1995; Boinski *et al.*, 2000; Isbell, 1994) strongly influence primate populations. For example, yellow fever caused in a major population decrease of howlers on Barro Colorado Island, Panama between 1933 and 1951 (Collias and Southwick, 1952). Similarly, predators can dramatically decrease primate numbers. For example, Isbell (1990) documented a substantial increase in the rate of predation by leopards on vervets (*Chlorocebus aethiops*) in Amboseli National Park, Kenya. Between 1977 and 1986, the average vervet predation rate was $\geq 11\%$. This rate increased to $\geq 45\%$ in 1987, possibly because of an increase in the leopard population. Despite such documented examples of disease and predation influencing primate populations, none of the colobine populations examined to date deviated greatly from what would be predicted by protein-to-fiber ratios.

Controversy over the Colobine-Protein/Fiber Model

While the predictive power of the protein/fiber ratios seem clear, there is controversy surrounding why it can predict colobine biomass. Little information is available to determine rigorously the nutritional requirements of primates in the wild (Oftedal, 1991). The relationship that we found between colobine biomass and the protein-to-fiber ratio of mature leaves suggests that the monkeys are close to a protein threshold below which they cannot meet the protein required for bodily functions, at least on a seasonal basis. However, primates have relatively low protein requirements (Oftedal, 1991). Oftedal (1991) calculated that even a primate population that had low protein digestibility due to effects of tannins would require only 7–11% protein on a dry matter basis for growth and maintenance, and only 14% for reproduction. However, impact of tannins on digestibility is not well understood. They may have positive or negative effects on the acquisition of proteins, and there is evidence that some animals have mechanisms to prevent ingested tannins from acting in a deleterious manner (Mole and Waterman, 1985; Waterman and Kool, 1994). Since the leaves eaten by primates average 12–16% protein (Calvert, 1985; Glander, 1982), Oftedal concludes that it is

unlikely that protein deficiency will be a problem for most primates, except for lactating females eating a diet high in tannins. With respect to colobines, protein demand might be even lower, since blood urea can be recycled by secreting it into saliva or diffusing it across the wall of the foregut. This nitrogen source can be used by microbes for protein synthesis, and they are, in turn, digested in the small intestine (Kay and Davies, 1994). Furthermore, the microbial metabolism involved in the fermentation system of colobine monkeys presumably entails synthesis of essential amino acids, so they are likely not deficient with respect to any particular amino acid (van Soest, 1982).

Dasilva (1992, 1994) found no relationship between the food items selected by *Colobus polykomos* and their protein content, even though the leaves they selected were from rare lianas and had more protein and less fiber than tree leaves, and they were calorically high. During the wet season, there is an absence of good sources of energy, and there is evidence that *Colobus polykomos* are not able to meet their energy needs then. This suggests that these monkeys might be limited by the availability of suitable energy-rich foods.

The estimates of requirements and Dasilva's (1992; 1994) findings seem to run counter to the observation that colobine biomass can be predicted by the protein-to-fiber ratios in the mature leaves. Such discrepancies may reflect several factors. First, the correlation between protein-to-fiber ratios and colobine biomass may not represent a causal relationship; protein-to-fiber concentrations may correlate with other leaf constituents that drive the relationship, e.g., energy. Second, we may not adequately understand the protein requirements of primates in the wild. For example, the impact of tannins and other protein digestion inhibitors on protein digestibility is poorly understood, and they may have mechanisms that prevent tannins from binding with protein (Foley and McArthur, 1994; Robbins *et al.*, 1987). Furthermore, the costs to protein uptake of ingesting other secondary compounds, like cyanogenic compounds, are not resolved (Jones, 1998). Finally, it may be that current methods of calculating protein in chemically complex leaves are inappropriate. Crude protein concentrations are usually calculated by measuring total nitrogen and assuming that total protein contains 16% nitrogen (protein levels = $N \times 6.25$; Maynard and Loosli, 1969). However, plants contain a number of non-protein compounds that contain nitrogen, e.g., alkaloids. Milton and Dintzis (1981) suggested that it may be appropriate to multiply total nitrogen by 4.4, rather than 6.25 for leaves of tropical plants; Izhaki (1993) suggested 4.05; Levey *et al.* (2000) suggested 5.64 and Conklin-Brittain *et al.* (1999) suggested 4.3. To understand why there is a relationship between protein-to-fiber ratios of leaves and colobine biomass, more research on the factors underlying colobine food selection and nutritional requirements is critical.

The study of colobines in Kibale illustrates the need to consider not only the abundance of food resources but also their quality when attempting to understand determinants of colobine abundance or when testing behavioral ecological models that require assessment of food availability. By contrasting 6 sites in Kibale, we showed that the density of important red colobus food trees varied among sites from 32 to 204 trees/ha, and red colobus density ranged from 0.70 to 7.41 groups/km². Among sites, red colobus density was related to the cumulative DBH of important food trees, when one apparently anomalous site, the Dura River, was excluded. Based on Struhsaker's (pers. comm.) descriptions of an epidemic that killed male red colobus in the early 1980s in Kibale, we suggested that this population had been reduced below carrying capacity by disease (Chapman and Chapman, 1999). However, a consideration of the protein-to-fiber ratio at the Dura River suggests that food is abundant, but of low quality.

Studies of Asian colobine populations showed positive correlations between population density and biomass and legume biomass (Davies, 1994; Davies *et al.*, 1988; Waterman *et al.*, 1988). Waterman and Kool (1994) suggested that legumes with nitrogen-fixing root symbionts were a good source of amino acids. Nitrogen can also be translated into toxins such as non-protein amino acids. Building on these findings, Maisels *et al.* (1994) and Maisels and Gautier-Hion (1994) suggested that soil quality can influence plant community composition: on poor soils, legumes will be abundant, and colobine populations in such areas would rely heavily on leguminous seeds. Accordingly, forests with an abundance of legumes will be optimal habitats for colobines (Davies *et al.*, 1999). Contrasting sites where colobine biomass and legume abundance data were available, Davies *et al.* (1999) pointed out that an abundance of legumes does not necessarily lead to an abundance of colobines. Our data supports Davies *et al.* (1999) and suggest that there is no relationship between colobine biomass and legume abundance. While Mainaro had the greatest colobine abundance and percentage of the stems that are legumes (20.9%), Kanyawara with the second highest colobine biomass had the smallest percentage of legumes (1.0%; Dura River = 2.2%, Sebatoli = 8.4%). While, legumes are an important component of the diet of many populations, it seems that one cannot predict colobine biomass based on their abundance.

Several factors should be considered when attempting to understand and to predict variation in primate abundance: zoogeography, disease, predation, food availability, seasonal cycles of food availability, habitat heterogeneity, plant chemistry, and human disturbance (Oates *et al.*, 1990). Finding single factor explanations for consistent causes of complex biological phenomena, like determinants of colobine abundance, is unlikely. Instead, several elegant long-term studies have highlighted the importance of searching

for multifactoral explanations. For example, based on a 68-month study of howlers (*Alouatta palliata*) and a parasitic bot fly (*Alouattomyia baeri*), Milton (1996) concluded that the annual pattern of howler mortality results from a combination of effects, including age, physical condition, and larval burden of the parasitized individual, which becomes critical when the population experiences dietary stress. Gulland (1992) provided a similar example with Soay sheep (*Ovis aries*).

Application of the Colobine-Protein/Fiber Model

Throughout the tropical world, <5% of rain forests are legally protected from human exploitation (Oates, 1996; Redford, 1992). Furthermore, many tropical species are locally endemic or are rare and patchily distributed (Richards, 1996; Struhsaker, 1975). Such restricted distributions predispose many tropical forest species to increased risk of extinction, simply because their range may not fall within a protected area (Terborgh, 1992). Consequently, national parks and reserves, even if effectively protected, will fail to conserve many species. As a result, the conservation of many tropical species will depend on the capacity of disturbed forests to support their populations (Struhsaker, 1997). With respect to primates, it is widely recognized that the most significant factor endangering primate populations is habitat modification (Chapman *et al.*, 1999; Chapman and Onderdonk, 1998; Mittermeier and Cheney, 1987); the bushmeat trade is also seriously impacting many populations (Fa *et al.*, 1995; Oates, 1996). For forest-dwelling primates, such modifications range from forest clearing for agriculture, to selective logging, or to simply harvesting non-timber forest products (Chapman and Peres, 2001).

Sound conservation and management policies could be implemented if there were evidence that one form of extraction had a less deleterious impact on primate abundance than others. For example, if trees that were important to the colobines could be left standing in selective logging operations or if loggers could use directional felling to reduce impact to important food trees, for species that are negatively impacted by logging their population decline might be less or the speed of population recovery might be improved. Our results indicate that tree species that should be targeted for such treatment should have mature leaves with a high protein-to-fiber ratios. Furthermore, the trees should be relatively abundant and ones frequently eaten by colobus. In Kibale, such a tree would be *Celtis durandii*. Its mature leaves have one of the highest protein-to-fiber ratios among the species that we examined (mean of 3 sites = 0.94). It is a relatively common tree (mean density among sites is 36.8 individuals/ha), and both red colobus (15.7% of their feeding

time) and black-and-white colobus (Oates, 1977) feed heavily on the species during many months of the year (Baranga, 1982, 1983). Understanding the factors that influence primate populations and how different species respond to different types of disturbance will provide information useful in planning informed management programs.

ACKNOWLEDGMENTS

Funding for this research was provided by the Wildlife Conservation Society and National Science Foundation (grant number SBR-9617664, SBR-990899). Permission to conduct this research was given by the Office of the President, Uganda, the National Council for Science and Technology, the Uganda Wildlife Authority, and the Ugandan Forest Department. We thank J. Kasenene, John Paul, April Randle, J. Mickle, and A. Katende for help with difficult tree identifications, Tom Gillespie and Sophia Balcomb for help with the census work, Matt Burgess, Alan Bolten, and Peter Eliazar for help with nutritional analysis, and John Oates, Joanna Lambert and the anonymous referees for helpful comments on the manuscript.

REFERENCES

- Anderson, R. M., and May, R. M. (1979). Population biology of infectious diseases. *Nature* 271: 361–366.
- Andrewartha, H. G., and Birch, L. C. (1954). *The Distribution and Abundance of Animals*, University of Chicago Press, Chicago.
- Baranga, D. (1982). Nutrient composition and food preferences of colobus monkeys in Kibale Forest, Uganda. *Afr. J. Ecol.* 20: 113–121.
- Baranga, D. (1983). Changes in chemical composition of food parts in the diet of colobus monkeys. *Ecology* 64: 668–673.
- Bennett, E. L., and Davies, A. G. (1994). The ecology of Asian colobines. In Davies, A. G., and Oates, J. F. (eds.), *Colobine Monkeys: Their Ecology, Behaviour and Evolution*, Cambridge University Press, Cambridge, pp. 129–171.
- Boinski, S., and Chapman, C. A. (1995). Predation in primates: Where we are and what next? *Evol. Anthropol.* 4: 1–3.
- Boinski, S., Treves, A., and Chapman, C. A. (2000). A critical evaluation of the influence of predators on primates: Effects on group movement. In Boinski, S., and Garber, P. (eds.), *On the Move: How and Why Animals Travel in Groups*, University of Chicago Press, Chicago, pp. 43–72.
- Boutin, S. (1990). Food supplementation experiments with terrestrial vertebrates: Patterns, problems and the future. *Can. J. Zool.* 68: 203–220.
- Bronikowski, A. M., and Altmann, J. (1996). Foraging in a variable environment: Weather patterns and the behavioral ecology of baboons. *Behav. Ecol. Sociobiol.* 39: 11–25.
- Burnham, K. P., Anderson, D. R., and Laake, J. L. (1980). Estimation of density from line-transect sampling of biological populations. *Wildl. Monogr.* 72: 1–202.
- Butynski, T. M. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. *Ecol. Monogr.* 60: 1–26.

- Calvert, J. J. (1985). Food selection of western gorillas (*G. g. gorilla*) in relation to food chemistry. *Oecologia* 65: 236–246.
- Chapman, C. A., Balcomb, S. R., Gillespie, T., Skorupa, J., Struhsaker, T. T. (2000). Long-term effects of logging on African primate communities: A 28 year comparison from Kibale National Park, Uganda. *Conserv. Biol.* 14: 207–217.
- Chapman, C. A., and Chapman, L. J. (1997). Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. *Biotropica* 29: 396–412.
- Chapman, C. A., and Chapman, L. J. (1999). Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates* 40: 215–232.
- Chapman, C. A., and Chapman, L. J. (2000). Constraints on group size in red colobus and red-tailed guenons: Examining the generality of the ecological constraints model. *Int. J. Primatol.* 21: 565–585.
- Chapman, C. A., Chapman, L. J., Wrangham, R., Isabirye-Basuta, G., and Ben-David, K. (1997). Spatial and temporal variability in the structure of a tropical forest. *Afr. J. Ecol.* 35: 287–302.
- Chapman, C. A., and Fedigan, L. M. (1990). Dietary differences between neighboring cebus monkey groups: Local tradition or responses to food availability? *Folia Primatol.* 54: 177–186.
- Chapman, C. A., Fedigan, L. M., and Fedigan, L. (1988). A comparison of transect methods of estimating population densities of Costa Rican primates. *Brenesia* 30: 67–80.
- Chapman, C. A., Gautier-Hion, A., Oates, J. F., and Onderdonk, D. A. (1999). African primate communities: Determinants of structure and threats to survival. In Fleagle, J. G., Janson, C. H., and Reed, K. (eds), *Primate Communities*, Cambridge University Press, Cambridge, pp. 1–37.
- Chapman, C. A., and Onderdonk, D. A. (1998). Forests without primates: Primate/plant codependency. *Amer. J. Primatol.* 45: 127–141.
- Chapman, C. A., and Peres, C. (2001). Primate conservation in the new millennium: The role of scientists. *Evol. Anthropol.* 10: 16–33.
- Chapman, C. A., Wrangham, R. W., Chapman, L. J., Kennard, D. K., and Zanne, A. E. (1999). Fruit and flower phenology at two sites in Kibale National Park, Uganda. *J. Trop. Ecol.* 15: 189–211.
- Coley, P. D. (1983). Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.* 53: 209–233.
- Collias, N., and Southwick, C. (1952). A field study of population density and social organization in howling monkeys. *Proc. Amer. Phil. Soc.* 96: 143–156.
- Conklin-Brittain, N. L., Dierenfeld, E. S., Wrangham, R. W., Norconk, M., and Silver, S. C. (1999). Chemical protein analysis: A comparison of Kjeldahl crude protein and total ninhydrin protein using wild, tropical vegetation. *J. Chem. Ecol.* 25: 2601–2622.
- Cork, S. J. (1996). Optimal digestive strategies for arboreal herbivorous mammals in contrasting forest types: Why koalas and colobines are different. *Austral. J. Ecol.* 21: 10–20.
- Cork, S. J., and Foley, W. J. (1991). Digestive and metabolic strategies of arboreal mammalian folivores in relation to chemical defenses in temperate and tropical forests. In Palo, R. T., and Robbins, C. T. (eds.), *Plant Defenses Against Mammalian Herbivory*, CRC Press, Boca Raton, pp. 133–166.
- Dasilva, G. L. (1992). The western black-and-white colobus as a low-energy strategists: Activity budget, energy expenditure and energy intake. *J. Anim. Ecol.* 61: 79–91.
- Dasilva, G. L. (1994). Diet of *Colobus polykomos* on Tiwai Island: Selection of food in relation to its seasonal abundance and nutritional quality. *Int. J. Primatol.* 15: 1–26.
- Davies, A. G. (1991). Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in dipterocarp forest of Northern Borneo. *Int. J. Primatol.* 12: 119–143.
- Davies, A. G. (1994). Colobine populations. In Davies, A. G., and Oates, J. F. (eds.), *Colobine Monkeys: Their Ecology, Behaviour and Evolution*, Cambridge University Press, Cambridge, pp. 285–310.
- Davies, A. G., Bennett, E. L., and Waterman, P. G. (1988). Food selection by two South-East Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. *Biol. J. Linn. Soc.* 34: 33–56.

- Davies, A. G., Oates, J. F., and Dasilva, G. L. (1999). Patterns of frugivory in three West African colobine monkeys. *Int. J. Primatol.* 20: 327–357.
- Emmons, L. H. (1984). Geographic variation in densities and diversities of non-flying mammals in Amazonia. *Biotropica* 16: 210–222.
- Fa, J. E., Juste, J., del Val, J. P., and Castroviejo, J. (1995). Impact of market hunting on mammal species in Equatorial Guinea. *Conserv Biol* 9: 1107–1115.
- Feeny, P. (1976). Plant apparency and chemical defense. In Wallace, J., and Mansell, R. L. (eds.), *Biochemical Interactions Between Plants and Insects. Recent advances in Phytochemistry*, Plenum Press, New York, pp. 1–40.
- Foley, W. J., and McArthur, C. (1994). The effects and costs of allelochemicals for mammalian herbivores: An ecological perspective. In Chivers, D. J., and Langer, P. (eds.), *The Digestive System in Mammals: Food, Form and Function*, Cambridge University Press, Cambridge, pp. 370–391.
- Freeland, W. (1977). *The Dynamics of Primate Parasites*. Ph.D. Dissertation, University of Michigan, Ann Arbor.
- Galat, G., and Galat-Luong, A. (1985). La communauté de primates diurnes de la forêt de Taï, Côte d'Ivoire. *Revue d'Ecologie (Terre et Vie)* 40: 3–32.
- Gallaher, R. N., Weldon, C. O., and Futral, J. G. (1975). An aluminum block digester for plant and soil analysis. *Soil Sci. Soc. Amer. Proc.* 39: 803–806.
- Ganzhorn, J. U. (1992). Leaf chemistry and the biomass of folivorous primates in tropical forests: Test of a hypothesis. *Oecologia* 91: 540–547.
- Gartlan, J. S., McKey, D. B., Waterman, P. G., Mbi, C. N., and Struhsaker, T. T. (1980). A comparative study of the phytochemistry of two African rain forests. *Biochem. Syst. Ecol.* 8: 401–422.
- Ghiglieri, M. P. (1979). *The Socioecology of Chimpanzees in Kibale Forest, Uganda*. Ph.D. Dissertation, University of California, Davis.
- Ghiglieri, M. P. (1984). *The Chimpanzees of Kibale Forest*, Columbia University Press, New York.
- Glander, K. E. (1982). The impact of plant secondary compounds on primate feeding behaviour. *Yearbook of Physical Anthropology* 25: 1–18.
- Goering, H. K., and van Soest, P. J. (1970). Forage fiber analysis. Agricultural Handbook No. 379, Agricultural Research Service, U.S. Dept. of Agriculture.
- Gulland, F. M. D. (1992). The role of nematode parasites in Soay sheep (*Ovis aries* L.) mortality during a population crash. *Parasitology* 105: 493–503.
- Hambleton, L. G. (1977). Semiautomated method for simultaneous determination of phosphorus, calcium, and crude protein in animal feeds. *Journal of the Association of Official Agricultural Chemists* 60: 845–852.
- Horowitz, W. (ed). (1970). Official methods of analysis of the Association of Official Analytical Chemists 11th edn, AOAC Washington, DC.
- Howard, P. C. (1991). *Nature Conservation in Uganda's Tropical Forest Reserves*. IUCN, Gland, Switzerland.
- Isbell, L. (1990). Sudden short-term increase in mortality of vervet monkeys (*Cercopithecus aethiops*) due to leopard predation in Amboseli National Park, Kenya. *Amer. J. Primatol.* 21: 41–52.
- Isbell, L. A. (1994). Predation on primates: Ecological patterns and evolutionary consequences. *Evol. Anthropol.* 3: 61–71.
- Izhaki, I. (1993). Influence of nonprotein nitrogen on estimation of protein from total nitrogen in fleshy fruits. *J. Chem. Ecol.* 19: 2605–2515.
- Janzen, D. H. (1975). *The Ecology of Plants in the Tropics*, Edward Arnold, London.
- Janzen, D. H., and Waterman, P. G. (1984). A seasonal census of phenolics, fibre and alkaloids in foliage of forest trees in Costa Rica: Some factors influencing their distribution and relation to host selection by Sphingidae and Saturniidae. *Biol. J. Linn. Soc.* 21: 439–454.
- Jones, D. A. (1998). Why are so many food plants cyanogenic? *Phytochemistry* 47: 155–162.
- Kay, R. F., and Davies, G. (1994). Digestive physiology. In Davies A. G., and Oates, J. F. (eds.), *Colobine Monkeys*, Cambridge University Press, Cambridge, pp. 229–249.

- Kay, R. F., Madden, R. H., van Schaik, C., and Higdon, D. (1997). Primate species richness is determined by plant productivity: Implications for conservation. *Proc. Natl. Acad. Sci.* 94: 13023–13027.
- Kelker, G. H. (1945). *Measurement and Interpretation of Forces that Determine Populations of Managed Deer*, Ph.D. Dissertation, University of Michigan, Ann Arbor.
- Kingston, B. (1967). Working plan for Kibale and Itwara Central Forest Reserves. Uganda Forest Department, Entebbe, Uganda.
- Krebs, C. J. (1978). A review of the Chitty hypothesis of population regulation. *Can. J. Zool.* 56: 2463–2480.
- Levey, D. J., Bissell, H. A., and O'Keefe, S. F. (2000). Conversion of nitrogen to protein and amino acids in wild fruits. *J. Chem. Ecol.* 26: 1749–1763.
- Maisels, F., and Gautier-Hion, A. (1994). Why are Caesalpinioideae so important for monkeys in hydromorphic rainforests of the Zaire Basin? In Sprent, J. I., and McKey, D. (eds.), *Advances in Legume Systematics 5: The Nitrogen Factor*, Royal Botanical Gardens, Kew, England. pp. 189–204.
- Maisels, F., Gautier-Hion, A., Gautier, J.-P. (1994). Diets of two sympatric colobines in Zaire: More evidence on seed-eating in forests on poor soils. *Int. J. Primatol.* 15: 681–701.
- Marsh, C. W. (1986). A resurvey of Tana primates and their forest habitat. *Primate Conserv.* 7: 72–81.
- Maynard, A. B., and Loosli, J. K. (1969). *Animal Nutrition*. McGraw-Hill, New York.
- McKey, D. B. (1978). Soils, vegetation, and seed-eating by black colobus monkeys. In Montgomery, G. G. (ed.), *The Ecology of Arboreal Folivores*, Smithsonian Institution Press, Washington, DC, pp. 423–437.
- McKey, D. B., Gartlan, J. S., Waterman, P. G., and Choo, C. M. (1981). Food selection by black colobus monkeys (*Colobus satanas*) in relation to plant chemistry. *Biol. J. Linn. Soc.* 16: 115–146.
- Milton, K. (1979). Factors influencing leaf choice by howler monkeys: A test of some hypotheses of food selection by generalist herbivores. *Am. Nat.* 114: 363–378.
- Milton, K. (1982). Dietary quality and demographic regulation in a howler monkey population. In Leigh, E. G., Rand, A. S., and Windsor, D. M. (eds.), *The Ecology of a Tropical Forest*. Smithsonian Institution Press, Washington, DC, pp. 273–289.
- Milton, K. (1996). Effects of bot fly (*Alouattomyia baeri*) parasitism on a free-ranging howler (*Alouatta palliata*) population in Panama. *J. Zool. (London)* 239: 39–63.
- Milton, K. (1998). Physiological ecology of howlers (*Alouatta*): Energetic and digestive considerations and comparison with the Colobinae. *Int. J. Primatol.* 19: 513–547.
- Milton, K., and Dintzis, F. R. (1981). Nitrogen-to-protein conversion factors for tropical plant samples. *Biotropica* 12: 177–181.
- Milton, K., van Soest, P. J., and Robertson, J. B. (1980). Digestive efficiencies of wild howler monkeys. *Physiol. Zool.* 53: 402–409.
- Mittermeier, R. A., and Cheney, D. L. (1987). Conservation of primates and their habitats. In Smuts, B. B., Cheney, D. L., Seyfarth, R., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*, Chicago University Press, Chicago, pp. 477–490.
- Mole, S., and Waterman, P. G. (1985). Stimulatory effects of tannins and cholic acid on tryptic hydrolysis of proteins: Ecological implications. *J. Chem. Ecol.* 11: 1323–1332.
- National Research Council. (1981). *Techniques for the Study of Primate Population Ecology*, National Academy Press, Washington, DC.
- Nicholson, A. J. (1933). The balance of animal populations. *J. Anim. Ecol.* 2: 132–178.
- Oates, J. F. (1977). The guereza and its food. In Clutton-Brock, T. H. (ed.), *Primate Ecology: Studies of Feeding and Ranging Behaviour of Lemurs, Monkeys and Apes*, Academic Press, London, pp. 276–322.
- Oates, J. F. (1996). Habitat alteration, hunting, and the conservation of folivorous primates in African forests. *Austral. J. Ecol.* 21: 1–9.
- Oates, J. F., Swain, T., and Zantovska, J. (1977). Secondary compounds and food selection by colobus monkeys. *Biochem. Syst. Ecol.* 5: 317–321.

- Oates, J. F., Waterman, P. G., and Choo, G. M. (1980). Food selection by the south Indian leaf-monkey, *Presbytis johnii*, in relation to leaf chemistry. *Oecologia* 45: 45–56.
- Oates, J. F., Whitesides, G. H., Davies, A. G., Waterman, P. G., Green, S. M., Dasilva, G. L., and Mole, S. (1990). Determinants of variation in tropical forest primate biomass: New evidence from West Africa. *Ecology* 71: 328–343.
- Oftedal, O. T. (1991). The nutritional consequences of foraging in primates: The relationship of nutrient intakes to nutrient requirements. *Phil. Trans. R. Soc. Lond. B* 334: 161–170.
- Osmaston, H. A. (1959). *Working Plan for the Kibale and Itwara Forests*. Uganda Forest Department, Entebbe, 60 p.
- Peres, C. A. (1997). Effects of habitat quality and hunting pressure on arboreal folivore densities in neotropical forests: A case study of howler monkeys (*Alouatta spp.*). *Folia Primatol.* 22: 137–154.
- Plumptre, A. J., and Reynolds, V. (1994). The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. *J. Appl. Ecol.* 31: 631–641.
- Redford, K. H. (1992). The empty forest. *Bioscience* 42: 412–422.
- Richards, P. W. (1996). *The Tropical Rain Forest*, 2nd edn, Cambridge University Press, Cambridge, England.
- Robbins, C. T., Mole, S., Hagerman, A. E., and Hanley, T. A. (1987). Role of tannins in defending plants against ruminants: Reduction in dry matter digestion? *Ecology* 68: 1606–1615.
- Robertson, J. B., and van Soest, P. J. (1980). The detergent system of analysis and its application to human foods. In James, W. P. T., and Theander, O. (eds.), *The Analysis of Dietary Fiber in Foods*, Marcel Dekker Inc, New York, pp. 123–158.
- Scott, M. E. (1988). The impact of infection and disease on animal populations: Implications for conservation biology. *Conserv. Biol.* 2: 40–56.
- Skorupa, J. P. (1988). *The Effect of Selective Timber Harvesting on Rain-forest Primates in Kibale Forest, Uganda*. Ph.D. Dissertation, University of California, Davis.
- van Soest, P. J. (1963). Use of detergents in the analysis of fibrous feeds: II A rapid method for the determination of fiber and lignin. *J. Assoc. of Official Agricultural Chemists* 46: 829–835.
- van Soest, P. J. (1982). *Nutritional Ecology of the Ruminant*, O & E Books, Inc. Corvallis.
- Struhsaker, T. T. (1975). *The Red Colobus Monkey*, University of Chicago Press, Chicago.
- Struhsaker, T. T. (1976). A further decline in numbers of Amboseli vervet monkeys. *Biotropica* 8: 211–214.
- Struhsaker, T. T. (1978). Food habits of five monkey species in the Kibale Forest, Uganda. In Chivers, D. J., and Herbert, J. (eds.), *Recent Advances in Primatology*, Academic Press, New York, pp. 225–248.
- Struhsaker, T. T. (1997). *Ecology of an African Rain Forest: Logging in Kibale and the Conflict Between Conservation and Exploitation*, University Presses of Florida, Gainesville.
- Terborgh, J. (1992). *Diversity and the Tropical Rain Forest*, Scientific American Library, New York.
- Terborgh, J., and van Schaik, C. P. (1987). Convergence vs. nonconvergence in primate communities. In Gee, J. H. R., and Giller, P. S. (eds.), *Organization of Communities, Past and Present*, Blackwell Scientific Publications, Oxford, pp. 205–226.
- Thomas, S. C. (1991). Population densities and patterns of habitat use among anthropoid primates of the Ituri Forest, Zaire. *Biotropica* 23: 68–83.
- Waser, P. M. (1974). Inter-group interactions in a forest monkey the mangabey *Cercocebus albigena*. Ph.D. Dissertation, Rockefeller University, New York.
- Waterman, P. G. (1986). A phytochemist in the African rain forest. *Phytochemistry* 25: 3–17.
- Waterman, P. G., and Choo, G. M. (1981). The effects of digestibility-reducing compounds in leaves on feed selection of some Colobinae. *Malaysian Applied Biology* 10: 147–162.
- Waterman, P. G., Choo, G. M., Vedder, A. L., and Watts, D. (1983). Digestibility, digestion inhibitors and nutrients of herbaceous foliage and green stems from an African montane flora and comparison with other tropical flora. *Oecologia* 60: 244–249.

- Waterman, P. G., Mbi, C. N., McKey, D. B., and Gartlan, J. S. (1980). African rainforest vegetation and rumen microbes: Phenolic compounds and nutrients as correlates of digestibility. *Oecologia* 47: 22–33.
- Waterman, P. G., and Kool, K. M. (1994). Colobine food selection and plant chemistry. In Davies A. G., and Oates, J. F. (eds.), *Colobine Monkeys*, Cambridge University Press, Cambridge, pp. 251–284.
- Waterman, P. G., Ross, J. A. M., Bennett, E. L., and Davies, A. G. (1988). A comparison of the floristics and leaf chemistry of the tree flora in two Malaysian rain forest and the influence of leaf chemistry on populations of colobine monkeys in the Old World. *Biol. J. Linn. Soc.* 34: 1–32.
- Whitesides, G. H., Oates, J. F., Green, M. S., and Kluberanz, R. P. (1988). Estimating primate densities from transects in a West African rain forest: A comparison of techniques. *J. Anim. Ecol.* 57: 345–367.