

18 Plant–Animal Coevolution: Is it Thwarted by Spatial and Temporal Variation in Animal Foraging?

Colin A. Chapman^{1,2} and Lauren J. Chapman^{1,2}

¹Department of Zoology, University of Florida, Gainesville, FL 32611, USA;

²Wildlife Conservation Society, 185th Street and Southern Boulevard,
Bronx, New York, NY 10460, USA

Introduction

The last two decades have witnessed large changes in views on the evolution of seed-dispersal systems. Early theories generated straightforward, testable predictions based on several key assumptions (Snow, 1965; Howe and Estabrook, 1977; Howe, 1979). During the 1980s, there was a gradual accumulation of field studies that did not support these predictions or did so only in a very general way (Howe and Smallwood, 1982; Herrera, 1984, 1985; Howe, 1984). These developments coincided with the recognition that descriptions of tight coevolution, or at least mutual dependence of particular plants and dispersers, were anomalies that tended to involve either very large seeds and seed-dispersers (e.g. elephants, *Loxodonta africana*, and *Balanites wilsoniana* (Lieberman *et al.*, 1987; Chapman *et al.*, 1992); gorillas, *Gorilla gorilla*, and *Cola lizae* (Tutin *et al.*, 1991)) or island situations with depauperate disperser assemblages (e.g. *Lycopersicon esculentum* and Galapagos tortoises, *Testudo elephantopus* (Rick and Bowman, 1961; see also Temple, 1977)).

In 1985, Herrera provided a critical evaluation of early studies and their assumptions (see also Herrera, 1986). He concluded that coevolved plant–vertebrate seed-dispersal systems were, at best, very rare in nature. He suggested that numerous factors limit the potential for coevolution between plants and their animal dispersers. These factors include: inequality in the evolutionary lifespans of plant and animal taxa, difference in generation lengths of plants and their dispersers, extensive gene flow between plant populations, weak selective pressures on dispersers, ecological variables outside the control of the parent plant (e.g. the influence of other fruiting plants), unpredictability of germination sites, secondary dispersal and the lack of evolutionary plasticity (Wheelwright and Orians, 1982; Herrera, 1985, 1986, 1998; Fischer and Chapman, 1993; Chapman, 1995).

Foraging patterns of vertebrates can also constrain plant–animal coevolution. For example, Herrera (1985) emphasized that the identity of taxa dispersing a given plant species can change over relatively short distances. Because these different animal species will

probably handle seeds in different ways and individual plant species will be responding evolutionarily to the integrated selective pressures of all dispersers, the direction and intensity of the overall selection pressure will probably be inconsistent and weak.

Weak selection pressure can also result from changes in the behaviour of a single disperser species; a particular species might be a reliable disperser at one time or at one location, but not at a different time or location. For example, Gautier-Hion *et al.* (1993) studied the foraging behaviour of *Cercopithecus pogonias* and *Cercopithecus wolffi* in Gabon and the Democratic Republic of Congo and found that they were mainly seed-dispersers in Gabon and mainly seed predators in the Congo. Despite such examples and frequent claims in the seed-dispersal literature of substantial temporal variation in plant-vertebrate interactions (Herrera, 1982, 1984, 1998; Howe, 1983, 1993; Schupp, 1990; Jordano, 1992; Herrera *et al.*, 1998), there are few studies documenting variation across several years or across different spatial scales (but see Herrera, 1998).

We examine the degree to which the diets of red colobus (*Procolobus badius*), a seed predator, and redbtail monkey (*Cercopithecus ascanius*), a seed-disperser, vary over the following spatial and temporal scales: (i) groups of red colobus within Kibale National Park, Uganda, with overlapping home ranges; (ii) eight populations of red colobus and four populations of redbtail monkeys, each separated by approximately 15 km within or near Kibale; (iii) distantly separated populations within three primate genera across Africa; and (iv) annual variation among 4 years for a single red colobus group. For each scale, general diet data (e.g. % of the diet composed of fruit) are presented to illustrate the degree of dietary variability, and specific examples are provided to demonstrate how a given plant-animal interaction can change.

Study Animals

Red colobus monkeys are large-bodied (8.2 kg), diurnal primates, found in social groups of between 25 and 40 monkeys (Struhsaker, 1975). Groups usually contain at

least three adult males and many adult females; females are the dispersing sex. In all populations studied, young leaves are the most common food item. Fruits are also eaten on a seasonal basis. When red colobus eat fruits, the seeds are destroyed (no seeds have been found in 150 dung samples (T. Gillespie, Florida, 2000, personal communication)). During a single feeding bout, a large group of red colobus can dramatically reduce the number of fruits on a tree. Thus, they can be significant seed predators.

Redtail monkeys are small-bodied (3.6 kg) primates found in social groups that average 30–35 individuals and typically contain a single male (Struhsaker and Leland, 1979). Their diet is dominated by fruit and insects (Struhsaker and Leland, 1979). They can be significant seed-dispersers for some tree species, often processing fruits in their cheek pouches and spitting out seeds away from the parent tree (Chapman, 1995; Lambert, 1997).

Methods

We have studied red colobus and redbtail monkeys in Kibale National Park (766 km²; 0° 13'–0° 41' N and 30° 19'–30° 32' E) (Struhsaker, 1997; Chapman and Lambert, 1999) in western Uganda since 1994. Mean annual rainfall in the region (measured at Makerere University Biological Field Station) is 1778 mm (1990–1998). There is an elevational gradient from north to south, which reflects a north-to-south increase in temperature and decrease in rainfall.

Observations of diet were made over 4 complete years at one site and for 1 or 2 years at eight other sites, each separated by approximately 15 km within the same forest system. Behavioural observations of red colobus totalled 3355 h and of redbtail monkeys 587 h. During each half-hour that the observer was with the group, five point samples were made of different individuals. If the animal was feeding, the species and the plant part (e.g. fruit, young leaf, leaf petiole) were recorded. The percentage of time spent feeding on a particular plant species or part was calculated as the number of scans spent eating that item, divided by the total number of scans in which animals

were feeding. For detailed information on sampling methods, duration of sampling and locations, see Chapman *et al.* (1997, 2000). At each site, food availability was quantified with a series of 200 m by 10 m transects, monitored on a monthly basis to assess phenology (Chapman *et al.*, 1997, 1999).

Results

Spatial contrasts

Neighbouring groups

We quantified the diet of two groups of red colobus from May 1998 to June 1999. Group 1 (24 individuals) used an area of 26.4 ha, while Group 2 (48 individuals) used an area of 21.9 ha. Home-range overlap of these groups was 10.7 ha, which represented 41% of Group 1's home range and 49% of Group 2's home range. Group 2 spent 70% of its time in the area of overlap, whereas Group 1 spent 49% of its time in that area.

Despite this degree of overlap in home ranges, diets differed between the two groups

with respect of plant parts consumed (Fig. 18.1) and species exploited (Table 18.1). For example, there was a small grove of *Prunus africana* in the area of home-range overlap. Group 1 was a significant seed predator of *P. africana*, eating its seeds for 31% of the time they ate seeds, compared with 1.6% for Group 2. This difference occurred despite the fact that Group 2 spent 70% of its time in this area, while Group 1 spent only 49% of its time there.

Interdemic contrasts

Both species exhibited high variation among populations separated by approximately 15 km in both the plant parts and species consumed. For red colobus, the largest difference was found in the amount of time spent eating young leaves (38.2% maximum difference); however, the amount of time spent preying on seeds also varied among populations from 1.9% to 17.2% (Table 18.2).

The plant species most important to red colobus differed among populations (Table 18.3). Much of this variation reflected differences in forest composition among sites (Table 18.4; Chapman *et al.*, 1997). Some foods

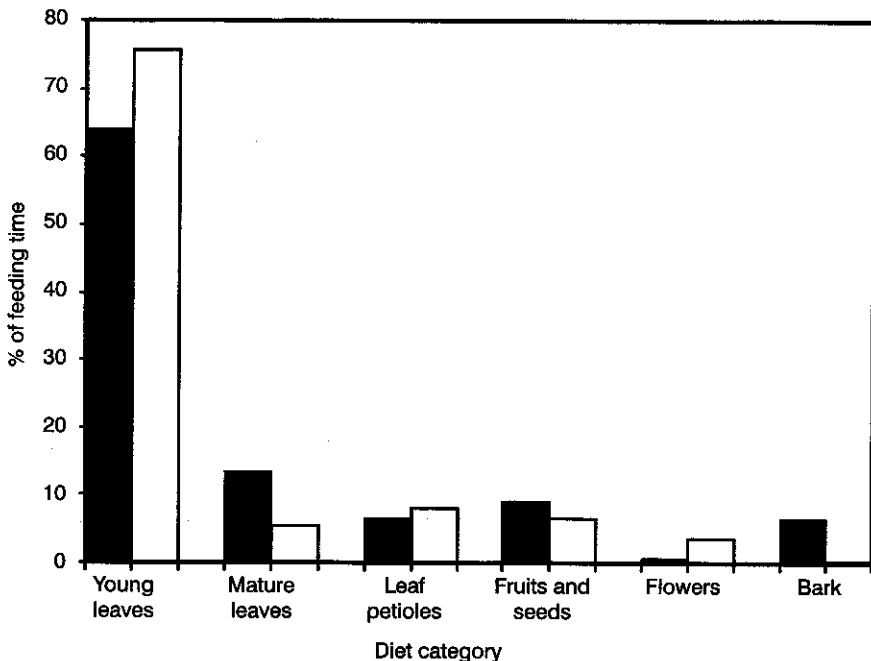


Fig. 18.1. The percentage of feeding time devoted to different plant parts by two neighbouring groups (solid bars vs. open bars) of red colobus monkeys (*Procolobus badius*) in Kibale National Park, Uganda.

Table 18.1. Density (trees ha⁻¹) and percentage of feeding time spent eating in 12 tree species used by two neighbouring groups of red colobus monkeys at the Kanyawara study area of Kibale National Park, Uganda.

Species	Family	Group 2		Group 1	
		Density %	Feeding time	Density %	Feeding time
<i>Albizzia grandibracteata</i>	Leguminosae	16	1.2	2	3.1
<i>Bosqueia phoberos</i>	Moraceae	45	7.8	34	4.1
<i>Celtis africana</i>	Ulmaceae	11	7.6	6	8.1
<i>Celtis durandii</i>	Ulmaceae	38	21.3	22	7.2
<i>Ficus exasperata</i>	Moraceae	8	2.1	4	0.5
<i>Funtumia latifolia</i>	Apocynaceae	35	8.2	25	8.9
<i>Markhamia platycalyx</i>	Bignoniaceae	32	9.0	16	3.2
<i>Milletia dura</i>	Leguminosae	9	1.3	1	0.6
<i>Olea welwitchii</i>	Oleaceae	4	0.9	2	2.2
<i>Parinari excelsa</i>	Rosaceae	2	6.7	2	8.1
<i>Dombeya mukole</i>	Sterculiaceae	2	7.5	1	2.3
<i>Prunus africana</i>	Rosaceae	1	4.1	3	17.2

Table 18.2. The percentage of scan samples in which red colobus were eating particular items at eight areas in or near Kibale National Park, Uganda. The values do not sum to 100% because of groups eating plant parts that are not listed below (e.g. pine needles).

Location	Young leaves	Mature leaves	Leaf petiole	Fruit/seeds	Flowers	Bark
Sebatoli	72.4	7.4	7.1	6.4	3.3	2.0
K-15	69.8	2.6	5.8	17.2	2.3	0.3
Mikana	87.0	2.0	4.2	3.0	2.2	0.0
K-30	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
Nkuruba	67.3	18.4	2.8	1.9	2.3	6.4
Kahunge	48.8	21.0	0.0	3.1	22.7	2.7
Largest difference	38.2	19.0	14.2	15.3	20.7	6.4

important to particular populations were not present at other sites. The Kahunge group represents a striking example. These monkeys fed on *Acacia kirkii* 92% of the time, and this tree species was only found at this site. Similarly, *Cynometra alexandri* was eaten by the Mainaro population for 41% of that group's feeding time, and was only found at this site. In contrast, some of the observed differences could not be attributed to availability. For example, *Celtis africana* was eaten at six of the seven sites where it was found and was not eaten at Mainaro, despite the fact that it was common there. A dramatic example of interdemographic variation in seed predation concerns red colobus feeding on the seeds of *Celtis durandii*. The K15 group ate *C. durandii* seeds for 15.4%

of its foraging time. In contrast, the Mainaro group was never recording eating *C. durandii* seeds and yet the density of this tree was very similar at the two sites (K15 = 33.0 trees ha⁻¹, Mainaro = 33.8 trees ha⁻¹).

The time redtail monkeys spent feeding on different plant parts varied among sites (Fig. 18.2). For example, the animals at Kanyawara ate fruit for only 35.7% of their feeding time, while those at Mainaro ate fruit for 59.7% of their feeding time (Fig. 18.2). The amount of time redtail monkeys spent eating from particular plant species also varied among areas (Table 18.5). In some cases, the variation could be related to plant density, while in other cases there was no apparent relationship (Table 18.5). For example, *Mimusops bagshawei*

Table 18.3. The percentage of red colobus feeding time involving the top five most frequently eaten plant species (underlined) at each of eight sites in Kibale National Park, Uganda, and the corresponding use at the other sites. Species are listed in order of their overall frequency of use at all sites. Only four plant species were eaten at Kahunge, and two species tied for the fifth at Sebatioli.

Species	Sebatioli	K15	Mikana	K30	Dura	Mainaro	Nkuruba	Kahunge
<i>Acacia hockii</i>	-	-	-	-	-	-	-	91.9
<i>Celtis durandii</i>	5.4	23.6	19.0	10.4	27.2	6.0	-	-
<i>Celtis africana</i>	4.3	12.2	13.7	9.9	1.5	-	19.1	-
<i>Albizia grandibracteata</i>	1	4.1	3.6	8.4	10.8	1.8	14.6	0.68
<i>Prunus africana</i>	5.9	1.7	3.2	13.0	-	2.4	16.3	-
<i>Cynometra alexandri</i>	-	-	-	-	-	40.7	-	-
<i>Funtumia latifolia</i>	5.4	8.1	3.1	7.2	12.8	3.0	-	-
<i>Aningeria altissima</i>	8.7	8.7	0.3	0.9	14.9	-	-	-
<i>Markhamia platycalyx</i>	3.1	10.2	6.1	9.2	1	-	0.9	-
<i>Mimusops bagshawei</i>	0.8	-	-	0.4	4.6	5.4	16.1	-
<i>Strombosia scheffleri</i>	10.9	0.9	-	9.2	2.7	-	-	-
<i>Dombeya mokole</i>	-	4.1	5.2	3.5	-	-	12.8	-
<i>Olea welwitschii</i>	5.1	1.5	13.5	3.9	-	-	0.2	-
<i>Bosqueia phoberos</i>	3.1	-	2.9	0.8	3.1	5.4	0.9	-
<i>Newtonia buchananii</i>	11.2	-	0.4	-	-	-	-	-
<i>Parinari excelsa</i>	-	-	5.3	0.1	-	-	-	-
<i>Celtis zenkeri</i>	-	-	-	-	-	5.4	-	-
<i>Cola gigantea</i>	-	-	-	-	5.1	-	-	-
<i>Sapium ellipticum</i>	1.3	-	-	0.1	-	0.6	-	0.68
<i>Bridelia micrantha</i>	-	-	-	1.63	-	-	-	0.68

Table 18.4. The density (individuals ha⁻¹) of preferred red colobus food trees (top five most eaten species at any of the sites) found at seven sites in or near Kibale National Park, Uganda. The superscripts indicate the ranking of the five most commonly eaten species for sites where behavioural data were collected (if a superscript number is given twice, the species were tied). Densities of trees are not available for the Nkurúba and Mikana sites.

Species	Family	Sebatoli	K15	K30	Dura	Mainaro	Kahunge
<i>Celtis durandii</i>	Ulmaceae	2.5 ⁵	33.0 ¹	47.1 ²	63.8 ¹	33.8 ²	–
<i>Funtumia latifolia</i>	Apocynaceae	25.0 ⁵	27.0 ⁵	33.8	43.8 ³	2.5	–
<i>Markhamia platycalyx</i>	Bignoniaceae	38.8	43.0 ³	50.0 ⁴	8.8	1.3	–
<i>Bosqueia phoberos</i>	Moraceae	–	–	50.0	22.5	1.3 ⁴	–
<i>Cynometra alexandri</i>	Leguminosae	–	–	–	–	63.8 ¹	–
<i>Strombosia scheffleri</i>	Oleaceae	36.3 ²	1.0	12.5 ⁵	2.5	–	–
<i>Newtonia buchananii</i>	Leguminosae	26.3 ¹	1.0	–	3.8	–	–
<i>Aningeria altissima</i>	Sapotaceae	23.8 ³	2.0 ⁴	1.7	2.5 ²	–	–
<i>Mimusops bagshawei</i>	Sapotaceae	6.3	1.0	3.3	7.5	– ⁴	–
<i>Acacia kirkii</i>	Leguminosae	–	–	–	–	–	20.0 ¹
<i>Celtis africana</i>	Ulmaceae	–	7.0 ²	4.2 ³	–	1.3 ⁵	–
<i>Albizia grandibracteata</i>	Leguminosae	–	–	1.3	1.3 ⁴	–	10.0 ²
<i>Blighia</i> sp.	Sapindaceae	7.5	2.0	0.8	1.3	–	–
<i>Cola gigantea</i>	Sterculiaceae	–	–	–	6.3 ⁵	–	–
<i>Prunus africana</i>	Rosaceae	2.5 ⁴	–	– ¹	–	–	–
<i>Sapium ellipticum</i>	Euphorbiaceae	2.5	–	–	–	–	2.0 ²
Total density		171.3	117.0	204.0	164.0	102.7	32.0
Cumulative dbh		9496	2759	5548	6708	4747	1765.0

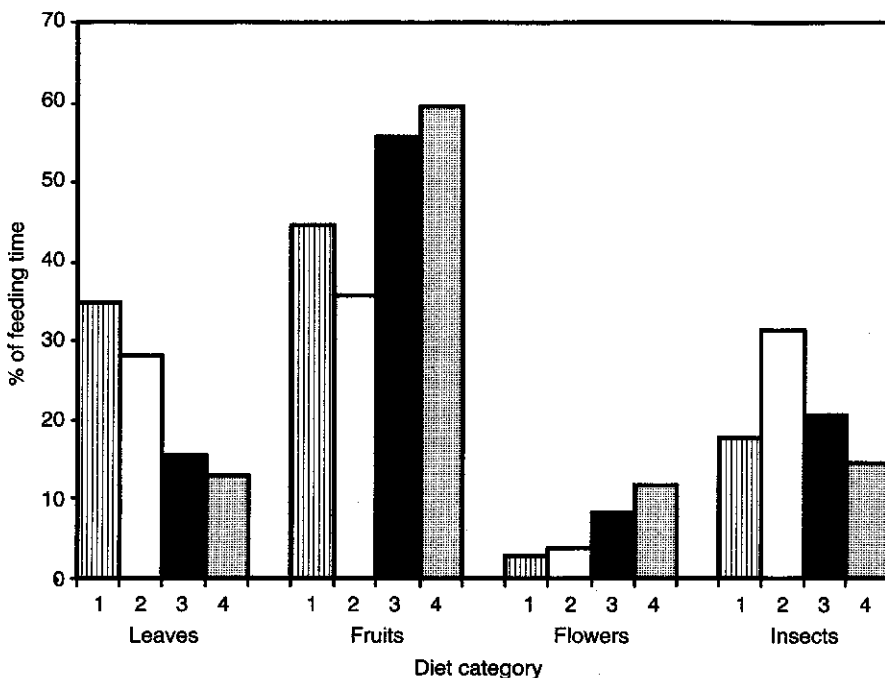


Fig. 18.2. The percentage of feeding time devoted to different plant parts by redtail monkeys (*Cercopithecus ascanius*) from four different populations (1, Sebatoli; 2, Kanyawara; 3, Dura; 4, Mainaro) in Kibale National Park, Uganda.

is a canopy-level or emergent tree with a drupe that averages 1.7 cm in length and contains an oval-shaped, 1.1 cm seed. Redtail monkeys are important dispersers of these seeds (Lambert, 1997). *Mimusops bagshawei* fruits were eaten at Kanyawara (1.8% of annual diet and 32% of the diet in the month when it fruited) and at Dura River (4.5% of total annual diet and 57% of the diet in the months it was available), but the redtail monkeys at Sebatoli were never observed to eat this fruit. At Dura River, *M. bagshawei* is relatively rare (< 1.3 trees ha^{-1}); it is more common at Kanyawara (3.3 trees ha^{-1}), but its availability is greatest at Sebatoli (6.3 trees ha^{-1}), where it was not eaten. Monthly monitoring of tree phenology indicates that the magnitude and duration of *M. bagshawei*'s fruiting was similar at all sites (Chapman *et al.*, 1999).

Distantly separated populations

Most study sites that provide detailed data on primate diets are widely separated. Thus, if one wants to compare widely separated sites, one first needs to find plant and animal species that occur over a wide area. While it is generally true that tropical trees do not have wide distributions, Africa is a bit of an exception in that many of the tree species range very widely and some are found in all major tropical-forest blocks (Richards, 1996). We take advantage of this and first contrast two sites where both diet data and plant lists are available. Subsequently, we contrast the published descriptions of diet of different populations or subspecies of red colobus (*P. badius*), different species of black-and-white colobus (*Colobus* spp.) and members of the 'Cephus' group of cercopithecine monkeys, which includes the redtail monkey. This 'Cephus' group is comprised of six closely related species that probably diverged from a common ancestor during recent isolation events associated with glaciation. Since species within these groups have recently diverged, it seems reasonable to expect that they might have similar dietary needs and consume similar foods.

First, to examine large-scale variation in primate seed dispersal and predation, we contrast the primate and tree communities from Kibale and Lopé, Gabon. The Lopé Reserve

(5000 km^2 ; $0^\circ 10' \text{S}$, $11^\circ 35' \text{E}$) in central Gabon is similar to Kibale in several ways. Both areas receive similar levels of rainfall (Lopé = 1548 mm (Tutin *et al.*, 1997b); Kibale = 1778 mm (C.A. Chapman and L.J. Chapman, unpublished data)) and have similar seasonal cycles and temperature regimes. Lists of trees > 10 cm diameter at breast height (dbh) are available for both sites (Tutin *et al.*, 1991; Chapman *et al.*, 1999). While these lists are not totally comparable (e.g. the sampling areas differ, and Kibale's list does not include opportunistic collections), they do provide a general indication of similarity in the tree communities.

Thirteen per cent of the tree species found at Kibale ($n = 109$ tree species) also occurred at Lopé. The list of tree species at Lopé ($n = 258$) was greater than at Kibale; thus a smaller percentage of that flora was shared with Kibale (5.4%). Of the 14 plant species found at both sites, differences in use were documented. At Kibale, *C. ascanius* used *Spathodea campanulata* and *Symphonia globulifera*, while these plant species were not used by *Cercopithecus cephus* at Lopé. In contrast, *C. cephus* at Lopé ate *Irvingia gabonensis* and *Myrianthus arboreus*, while *C. ascanius* at Kibale ignored these species. There were also differences in the use of specific plant parts between closely related species at the two sites (Table 18.6). For example, *Colobus guereza* was rarely seen to prey on unripe seeds, while *Colobus satanus* did so regularly.

Kibale's primate biomass is eight times that of Lopé (total biomass Kibale = 2710 kg km^{-2} , Lopé = 319 kg km^{-2} ; frugivore biomass Kibale = 634 kg km^{-2} , Lopé = 228 kg km^{-2} , folivore biomass Kibale = 2077 kg km^{-2} , Lopé = 91 kg km^{-2} (Table 18.6)). Such differences in the biomasses of dispersers and seed predators is likely to translate into differences in plant-taxa exploitation between sites.

Secondly, to examine large-scale variation in primate seed dispersal and predation in a more general way, we obtained diet data from 32 studies that used similar behavioural methods to collect feeding data (Table 18.7). Some populations of red colobus monkeys are primarily seed predators (the maximum % of time spent eating seeds was 54.4%), while others rarely eat seeds (5.6%) (Table 18.7). Different species of black-and-white colobus varied even

Table 18.5. The density of trees > 10 cm dbh and the percentage of time spent feeding by redtail monkeys on these trees at four sites in Kibale National Park, Uganda. Listed are those species that the redtail monkeys used for > 1% of their foraging effort at any site. The plant parts eaten for each tree species are listed in order of importance in their diet.

Species	Family	Part	Kanyawara (K30)				Sebatoli				Mainaro				Dura River	
			% Foraging	Density	% Foraging	Density	% Foraging	Density	% Foraging	Density	% Foraging	Density	% Foraging	Density	% Foraging	Density
<i>Celtis durandii</i>	Ulmaceae	UF/RF/YL/LB	14.84	47.1	4.82	2.50	29.37	33.80	29.79	63.80						
<i>Chrysophyllum gorganusanum</i>	Sapotaceae	RF/RL/UF/YL/SD	0.47	2.6	12.53	8.80	15.84	21.20	5.05	47.50						
<i>Celtis africana</i>	Ulmaceae	YL/UF/RF/FL	7.66	4.2	4.34	0.00	1.65	1.30	0.00	0.00						
<i>Bosqueia phoberos</i>	Moraceae	YL/RF/UF	3.89	50.0	1.93	0.00	0.00	0.00	5.92	22.50						
<i>Teclea nobilis</i>	Rutaceae	RF/FL/YL/UF	7.07	17.1	0.00	0.00	1.32	0.00	2.26	0.00						
<i>Diospyros abyssinica</i>	Ebenaceae	RF/UF/YL/FL	7.42	40.0	1.93	2.50	0.99	1.30	0.00	0.00						
<i>Prunus africana</i>	Rosaceae	YL/RF/LB/BA	2.47	0.0	7.23	2.50	0.00	0.00	0.00	0.00						
<i>Warbugia stuhlmanni</i>	Canellaceae	RF/UF/YL/FL	0.00	0.0	0.00	0.00	7.92	0.00	0.52	0.00						
<i>Croton</i> sp.	Euphorbiaceae	RF/UF/FL/YL/BA	0.00	0.8	8.19	41.30	0.00	1.30	0.00	0.00						
<i>Uvariopsis congensis</i>	Annonaceae	RF/UF	1.06	60.4	0.00	0.00	3.96	43.80	2.79	60.00						
<i>Maesa lanofolata</i>	Myrsinaceae	RF	1.65	0.0	6.02	0.00	0.00	0.00	0.00	0.00						
<i>Albizia grandbracteata</i>	Leguminosae	YL	0.94	1.3	4.58	0.00	0.00	0.00	1.05	1.30						
<i>Bequeriobdendron oblanceolatum</i>	Sapotaceae	YL/RF	0.00	0.0	0.00	0.00	0.00	0.00	6.27	57.50						
<i>Mimusops bagshawei</i>	Sapotaceae	RF/UF/YL/FL	1.18	3.3	0.00	6.30	0.33	0.00	4.53	0.00						
<i>Ficus exasperata</i>	Moraceae	RF/YL/UF	1.65	3.8	2.17	2.50	1.98	1.30	0.00	0.00						
<i>Cynometra alexandri</i>	Leguminosae	FL/YL	0.00	0.0	0.00	0.00	4.29	63.80	0.00	0.00						
<i>Celtis mildbraedii</i>	Ulmaceae	RF/YL/UF	0.00	0.0	0.00	0.00	4.29	32.50	0.00	0.00						
<i>Ficus natalensis</i>	Moraceae	RF	0.00	0.4	0.00	0.00	0.00	0.00	3.83	0.00						

<i>Linociera johnsonii</i>	Oleaceae	FL/YL	5.4	0.96	8.80	2.64	0.00	0.00	0.00
<i>Markhamia platycalyx</i>	Bignoniaceae	FL/LP/YL	50.0	1.45	38.80	0.00	0.59	0.00	0.00
<i>Stychnos mitis</i>	Loganiaceae	RF/TL/FL/UF	7.5	0.48	0.00	1.32	0.82	0.00	1.05
<i>Olea welwitschii</i>	Oleaceae	YL	3.3	0.00	0.00	0.00	2.00	0.00	0.00
<i>Bridelia micrantha</i>	Euphorbiaceae	RF/LB	0.0	1.45	0.00	0.00	0.82	0.00	1.30
<i>Funtumia latifolia</i>	Apocynaceae	RF/FL/YL/UF	33.8	0.72	2.50	0.00	0.12	0.00	0.00
<i>Ficus sansibarica</i>	Moraceae	RF	0.0	0.72	0.00	0.00	1.06	0.00	43.80
<i>Monodora myrsitica</i>	Annonaceae	FL	0.4	0.00	0.00	0.00	0.00	0.00	0.00
<i>Fagara angolensis</i>	Rutaceae	YL/FL	0.0	1.69	0.00	0.00	0.00	0.00	1.74
<i>Pseudospondias microcarpa</i>	Anacardiaceae	YL	1.7	0.48	0.00	0.00	0.12	0.00	0.00
<i>Lovoa swynnertonii</i>	Meliaceae	FL	0.8	0.00	3.80	0.00	0.00	0.00	3.80
<i>Balanites wilsoniana</i>	Balanitaceae	FL/RF/YL	1.7	1.20	0.00	0.33	0.00	0.00	3.80
<i>Newtonia buchanani</i>	Leguminosae	YL	0.0	1.45	26.30	0.00	0.00	0.00	1.30
<i>Chaetacme aristata</i>	Ulmaceae	RF	17.1	0.00	0.00	0.00	0.35	0.00	3.80
<i>Casearia</i> sp.	Flacourtiaceae	RF/UF	1.3	0.00	0.00	0.00	0.00	0.00	3.80
<i>Spathodea campanulata</i>	Bignoniaceae	FL	0.8	0.00	0.00	0.00	0.00	0.00	0.00
<i>Dombeya mukole</i>	Sterculiaceae	YL/FL	9.2	0.00	0.00	0.00	1.18	0.00	1.30

dbh, diameter at breast height; RF, ripe fruit; UF, unripe fruit; YL, young leaves; FL, flower; LB, leaf bud; BA, bark; SD, seed.

more dramatically in the extent to which they were seed predators: populations are reported to eat seeds from 0% to 60.1% of their feeding time. The amount of time that different populations of monkeys within the 'Cephus' group ate fruit varied from 35.7% to 81.3%.

Temporal contrasts

Annual variation

Data on the diet of the same groups of red colobus were collected in 1994, 1995, 1996 and 1998. These data reveal considerable

interannual variation in dietary components (Fig. 18.3). For example, in 1994 red colobus spent 55.8% of their feeding time eating young leaves and in 1998 they spent 75.8% of their feeding time doing so. Much of this interannual variation probably reflects interannual differences in food availability. Chapman *et al.* (1999) examined the phenology of 3793 trees from 104 species at two sites over 76 months and found marked variation among years in phenology for several species. However, some of the red colobus variation in diet is clearly not a function of availability (Table 18.8). For example, *C. durandii* fruits were available to red colobus every year, but

Table 18.6. Descriptions of the primate community found at Kibale, Uganda and Lopé, Gabon (annual rainfall = mm, biomass = kg km⁻², density = individuals km⁻²).

	Density	Biomass	Leaves	Ripe fruit	Unripe fruit/seed	Insects
Kibale National Park, Uganda*						
<i>Perodicticus potto</i>	17.7	1.9				
<i>Galagoides thomasi</i>						
+ <i>Galago matschiei</i>	79.5	12.6				
<i>Lophocebus albigena</i>	9.2	60	5	59	3	26
<i>Papio anubis</i>	—	—	—	—	—	—
<i>Cercopithecus ascanius</i>	140	328	16	44	15	22
<i>Cercopithecus mitis</i>	41.8	133	21	45	13	20
<i>Cercopithecus lhoesti</i>	8	13				
<i>Cercopithecus aethiops</i>	rare	rare				
<i>Procolobus badius</i>	300	1760	75	6	16	3
<i>Colobus guereza</i>	58.1	317	76	13	2	0
<i>Pan troglodytes</i>	2.5	85	8	80	0	0
						(12% THV)

Total density, ~ 656.8; total biomass, 2710; frugivore biomass, 633.5; folivore biomass, 2077.

Lopé Reserve, Gabon†

<i>Cercopithecus nictitans</i>	19.2	62.8				
<i>Cercopithecus pogonias</i>	4.6	10.1				
<i>Cercopithecus cephus</i>	5.1	10.2	11	49	5	35
<i>Lophocebus albigena</i>	8.1	33.7	30	36	4	28
<i>Colobus satanas</i>	10.8	90.7	4	60	26	—
<i>Gorilla gorilla</i>	0.6	45.3				
<i>Pan troglodytes</i>	0.6	22.5		—		
<i>Mandrillus sphinx</i>	3.8	43.9				

Total biomass, 318.6; frugivore biomass, 227.9; folivore biomass, 90.7.

*Struhsaker (1975, 1978, 1980), Struhsaker and Leland (1979), Chapman and Wrangham (1993), Weisenseal *et al.* (1993), Chapman *et al.* (1995), Chapman (unpublished data).

†Primate density, mean of five neighbouring sites from, White (1994a, b), diet data for *L. albigena* from Ham (1994), diet data for *C. satanas* from Harrison (1986).

red colobus feeding time on this species varied from 1.3% in 1994 to 7.3% in 1995.

Discussion

The examination of the diet of the red colobus, a seed predator, and the redtail monkey, a seed-disperser, across different spatial and temporal scales demonstrates considerable variation among plant parts and species consumed. It seems likely that this variation will lead to spatial and temporal variation in selection pressures associated with the interaction between these monkeys and specific plant species. This variation may constrain coevolution of the participants (Herrera, 1988; Horvitz and Schemske, 1990; Jordano, 1993). This interpretation is open to debate, however. It is possible, although we regard it

as unlikely, that successful recruitment at any particular site is very episodic and that these animals play a consistent role at these times. Regardless, the variation we describe will induce stochasticity in the number and species composition of recruiting seedlings.

Unfortunately, studies of a sufficiently long duration to document the temporal variability in frugivore behaviour are extremely rare (Herrera, 1998). Similarly, few studies document frugivore foraging and seed dispersal over a spatial scale where the same species of plants and animals are probably interacting, but where variation in frugivore foraging behaviour occurs (Chapman and Chapman, 1999). On the practical side, this shortcoming highlights the importance of long-term studies of frugivore-plant interactions across a range of spatial scales (Herrera, 1985, 1998; Jordano, 1993; Wilson and Whelan, 1993). The

Table 18.7. Percentage of feeding time devoted to different plant parts by red colobus, black-and-white colobus and redtail monkeys or 'Cephus' group from a variety of sites across Africa.

Red colobus* (<i>Procolobus badius</i>)	Young leaves	Mature leaves	Seeds	Flowers	Other
<i>P.b. tholloni</i> (1)	54.3	6.4	37.9	1.4	
<i>P.b. badius</i> (2)	31.7	20.2	31.2	16.1	
<i>P.b. rufomitrat</i> a (3)	52.4	11.5	25.0	6.2	4.9
<i>P.b. temminckii</i> (4)	41.5	6.5	54.4	8.7	7.4
<i>P.b. temminckii</i> (5)	34.9	11.8	44.5	8.7	2.9
<i>P.b. tephrosceles</i> (6)	34.8	44.1	11.3	6.8	2.9
<i>P.b. tephrosceles</i> (7)	50.6	23.1	5.6	11.8	†
<i>P.b. kirkii</i> (8)	46.7	14.6 [‡]	31.7	10.6	2.3
<i>P.b. kirkii</i> (8)	53.4	11.9 [§]	31.2	5.4	1.3
<i>P.b. tephrosceles</i> (9)	46.8–87.1	2.0–21.0	1.9–17.2	2.0–22.7	
Black-and-white colobus*	Young leaves	Mature leaves	Seeds	Flowers	Other
<i>C. angolensis</i> (10)	21.2	6.4	66.7	5.9	
<i>C. angolensis</i> (11)	67.9		32.1		
<i>C. angolensis</i> (12)	24.9	38.9			
<i>C. polykomos</i> (13)	29.9	26.7	36.5	2.7	4.7
<i>C. satanas</i> (14)	23.0	19.0	58.0		
<i>C. satanas</i> (15)	23.0	3.0	64.2	5.3	4.4
<i>C. guereza</i> (16)	23.7	29.1	36.9	0.5	8.1
<i>C. guereza</i> (17)	29.7	28.0	46.6	2.9	14.5
<i>C. guereza</i> (18)	33.1	19.8	45.6	7.7	2.1
<i>C. guereza</i> (19)	36.9	24.8	37.6	8.9	2.6
<i>C. guereza</i> (20)	61.7	12.4	13.6	2.1	10.2
<i>C. guereza</i> (21)	80.1	5.8	9.8	0.1	4.2
<i>C. guereza</i> (22)	85.6	3.7	7.3	2.3	0.8

(Contd.)

Table 18.7. Continued.

Redtail monkeys (<i>Cercopithecus</i>) 'Cephus' group	Young leaves	Mature leaves	Fruit pulp	Flowers	Insects	Seeds
<i>C. ascanius</i> (23)	6.8	0.4	61.3	2.0	25.1	0.4
<i>C. ascanius</i> (24)	10.9	3.3	43.6	15.3	21.8	0.1
<i>C. ascanius</i> (25)	34.7	0.0	44.6	2.7	17.6	
<i>C. ascanius</i> (26)	27.8	0.4	35.7	3.7	31.2	
<i>C. ascanius</i> (27)	15.0	0.4	55.6	8.2	20.6	
<i>C. ascanius</i> (28)	12.2	0.7	59.7	11.6	14.5	
<i>C. cephus</i> (29)	6.1		81.3	—	12.6	
<i>C. cephus</i> (30)	11.4		67.0	5.7	9.1	6.8
<i>C. cephus</i> (31)	4.0		49.0	6.0	35.0	5.0

(1) Democratic Republic of Congo: Maisels *et al.* (1994); (2) Sierra Leone: Davies *et al.* (1999); (3) Kenya: Marsh (1981); (4) Senegal: Gatinois (1977); (5) Gambia: Davies (1994); (6) Tanzania: Clutton-Brock (1975, 1977); (7) Uganda: Struhsaker (1975); (8) Mturi 1993 two groups in the same area: Mturi (1993); (9) range of populations: this study, (10) Democratic Republic of Congo: Maisels *et al.* (1994); (11) Kenya: Moreno-Black and Maples (1977); (12) Rwanda: Fimbel *et al.* (unpublished data); (13) Sierra Leone: Dasilva (1992, 1994); (14) Cameroon: McKey *et al.* (1981), McKey and Waterman (1982); (15) Gabon: Harrison and Hladik (1986); (16) Kakamega, Kenya: Fashing (1999); (17) Ituri Forest, Democratic Republic of Congo: Bocian (1997); (18) Budongo, Uganda (logged area): Plumptre and Reynolds (unpublished data); (19) Budongo, Uganda (unlogged area): Plumptre and Reynolds (unpublished data); (20) Kibale, Uganda: Oates (1977), Struhsaker and Oates (1975); (21) Kibale, Uganda: this study (Group 1); (22) Kibale, Uganda: this study (Group 2); (23) Kakamega, Kenya: Cords (1986); (24) Kibale, Uganda (young leaves and leaf buds combined): Struhsaker (1978); (25) Kibale at Sebatoli, Uganda (young leaves, buds and petioles combined): this study; (26) Kibale at Kanyawara, Uganda (young leaves, buds and petioles combined): this study; (27) Kibale at Dura River, Uganda: this study; (28) Kibale at Mainaro, Uganda: this study; (29) Makokou, Gabon (all leaves assumed to be young): Gautier-Hion *et al.* (1980); (30) Lopé (continuous forest), Gabon (all leaves assumed to be young): Tutin *et al.* (1997a); (31) Lopé (forest fragment), Gabon (all leaves assumed to be young): Tutin (1999), Tutin *et al.* (1997b).

*For the colobine monkeys some studies listed fruit and seeds separately. Based on the fact that no seeds have been found in 270 *C. guereza* and *P. badius* fecal samples (T. Gillespie, Florida, 2000, personal communication), we assume that, when the colobines ingest fruit pulp, they are also ingesting the seeds and are acting as seed predators.

†10.4% leaves of unknown age.

‡Includes 7.3 on leaf stalks.

§Includes 5.6 on leaf stalks.

||Young and mature leaves.

investigations that have examined spatial and temporal variation in plant–animal interactions typically suggest that a single year's study at one site of how a particular frugivore disperses the seed of a specific plant may at best provide a snapshot of the interaction and at worst present a serious distortion or an erroneous picture (Herrera, 1998).

Studies such as this one and several that have preceded it (Herrera, 1985, 1998; Jordano, 1993) suggest that there is still much to be learned if we are to make advances in understanding the evolution of fruit

morphology using ecological evidence, or in identifying important processes determining how seed dispersal contributes to the distribution of adult trees. These studies also stress the need to identify novel systems or approaches that can be used to identify selective pressures acting on fruit morphology and to determine how seed dispersal patterns influence the distribution of seedlings and, subsequently, adult trees. It is clear that 10+ year studies at a number of spatially separated sites will continue to be constrained by field logistics and time.

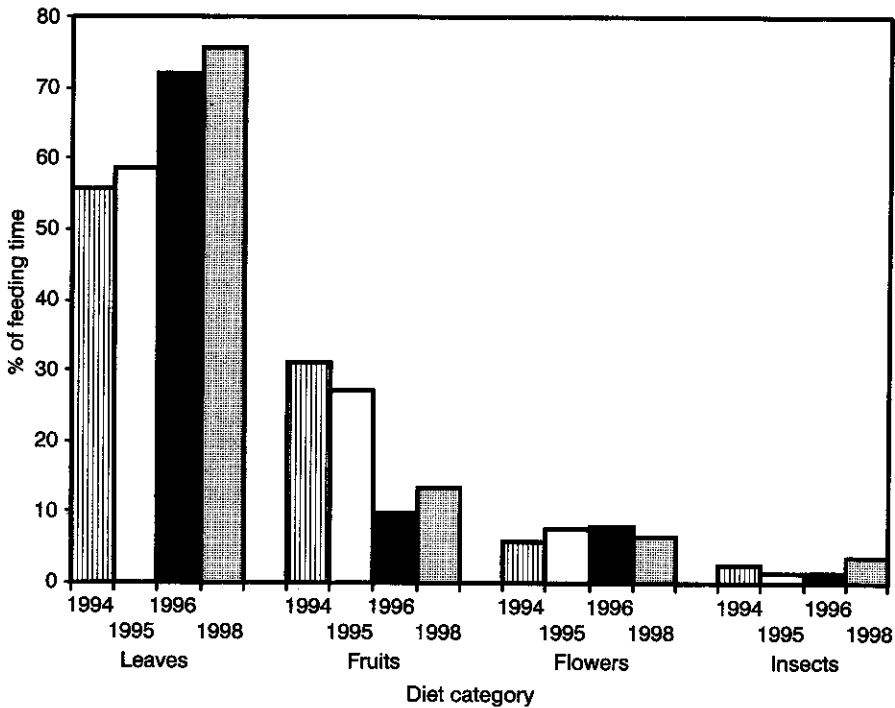


Fig. 18.3. The percentage of feeding time devoted to different plant parts by one group of red colobus monkeys (*Procolobus badius*) in Kibale National Park, Uganda, over 4 years.

Table 18.8. The percentage of time spent feeding from the five most important food species in the diet of the red colobus in K30 in each of the years of study (underlined) and the percentage of time eating these species in years when they were not in the top five.

Species	Family	1994	1995	1996	1998
<i>Celtis durandii</i>	<i>Ulmaceae</i>	11.8	<u>16.3</u>	<u>17.2</u>	<u>21.3</u>
<i>Strombosia schlefferi</i>	<i>Olacaceae</i>	9.5	<u>8.0</u>	<u>10.6</u>	<u>10.2</u>
<i>Prunus africana</i>	<i>Rosaceae</i>	<u>16.4</u>	<u>11.6</u>	4.5	4.1
<i>Markhamia platycalyx</i>	<i>Bignonaceae</i>	9.3	<u>10.5</u>	6.3	<u>9.0</u>
<i>Celtis africana</i>	<i>Ulmaceae</i>	<u>12.2</u>	<u>8.1</u>	<u>6.1</u>	7.5
<i>Albizia grandibracteata</i>	<i>Leguminosae</i>	<u>10.5</u>	4.2	<u>9.6</u>	1.2
<i>Dombeya mukole</i>	<i>Sterculiaceae</i>	1.7	5.0	<u>6.6</u>	<u>6.8</u>
<i>Bosqueia phoberos</i>	<i>Moraceae</i>	–	1.0	2.9	7.8

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