

Variation in Seed Handling by Two Species of Forest Monkeys in Rwanda

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We examined temporal variability in the handling and dispersal of seeds by two sympatric species of monkeys, the arboreal blue monkey (*Cercopithecus mitis doggetti*) and the more terrestrial mountain monkey (*C. lhoesti*). Ten months of data on phenological patterns and foraging behavior, including details of seed handling based on scan sampling data, were combined with dung sample data to examine patterns of seed handling. The systematic scan sampling observations showed that blue monkeys and mountain monkeys alternated between acting predominately as seed droppers, seed predators, and seed defecators depending on fruit resource availability. All the mountain monkey dung samples examined contained intact seeds, and 94% of the blue monkey dung samples contained intact seeds. Both monkey species defecated a greater number of seeds per dung sample and larger-sized seeds than found elsewhere for *Cercopithecus* monkeys. We found a mean of 2.33 and 6.43 seeds >2 mm in blue and mountain monkey dung samples, respectively. The mountain monkeys dispersed relatively higher numbers of seeds and frequented open, disturbed forest, suggesting that terrestrial forest monkeys have been overlooked as potentially important seed dispersal agents. The variability in the ways seeds were handled was dependent on the array of available food resources and may suggest that the monkeys exert weak selective pressures on fruit traits. *Am. J. Primatol.* 45:83–101, 1998.

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INTRODUCTION

We studied the influence of temporal patterns of fruit abundance on seed handling in two sympatric species of forest monkeys, one arboreal and one terrestrial, in Nyungwe Forest Reserve, Rwanda. Conclusions from several recent studies assessing the role of African forest monkeys in seed dispersal are contradictory. For example, Gautier-Hion et al. [1985] and Sourd and Gautier-Hion

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[1986] found that forest monkeys are important agents of seed dispersal in Gabon. However, Wrangham et al. [1994] found that although forest monkeys defecate seeds in Kibale Forest, Uganda, they disperse low numbers and are believed to be less important seed dispersers than the larger-bodied chimpanzees. Rowell and Mitchell [1991] found no intact seeds larger than 2 mm in *Cercopithecus ascanius* and *C. mitis* dung in Kenya and concluded that African forest monkeys chew up and destroy most of the seeds they ingest. Furthermore, Gautier-Hion et al. [1993] showed that *Cercopithecus wolffi* in Zaire were important seed predators, especially on legumes; succulent fruits were a minor component of their diet.

Fruit-eating primates handle different fruits in different ways: chewing and ingesting seeds of some species, thus destroying them; swallowing pulp and seeds of other species and defecating the seeds later; and dropping other seed species from tree canopies after consuming the pulp [Corlett & Lucas, 1990]. Few studies, however, have examined these variations in seed-handling behaviors in relation to changes in fruit abundance [e.g., Estrada & Coates-Estrada, 1986; Davies, 1991; Gautier-Hion et al., 1993]. Such variation in seed handling will have an influence on the effectiveness of seed dispersal by these animals at a temporal scale and may help identify common patterns in the handling and dispersal of seeds among different forests.

Fruit-eating primates typically consume succulent, brightly colored fruits that contrast with the foliage [Terborgh, 1983; Gautier-Hion et al., 1985; Sourd & Gautier-Hion, 1986; Julliot, 1996] (although some studies have found that neotropical primates also eat green or brown fruits [Janson, 1983; Julliot, 1996]). Past studies have correlated fruit morphological characters (e.g., fruit color) with selection by particular frugivore dispersers [e.g., Van der Pijl, 1972; Snow, 1971; McKey, 1975]; these associations, or dispersal syndromes, have been taken to indicate coevolutionary relationships between certain plants and their dispersers. Because tightly coevolved plant-vertebrate dispersal systems are rare [Herrera, 1985], diffuse coevolution has been used to describe the selective pressures exerted between a group of disperser species and a group of plant species in a mutualistic relationship [Janzen, 1980; but see Lambert & Garber, 1998]. In general, such factors as dietary variability and lack of specificity between frugivore and plant species probably limit the potential for coevolution between fruit-producing plants and their dispersers [Chapman, 1995; Lambert & Garber, this issue].

Seed dispersal by animals is composed of a series of steps and includes removal and treatment of seeds by the animal, deposition of seeds, seed survival, regeneration, and recruitment. In this study we focus on components of the first step, the handling and dispersal of seeds out of tree canopies. The effectiveness of a particular dispersal agent must ultimately be evaluated by the contribution the disperser makes to the future reproduction of a plant [Schupp, 1993]. Effectiveness depends on aspects of the quantity of seed dispersal, such as the number of seeds moved away from parent trees, and aspects of the quality of seed dispersal, such as how the animal handles the seeds (e.g., whether the seed is digested, dropped from the parent canopy, or defecated) [Schupp, 1993]. Postdispersal seed fate will not be dealt with in this study.

Many primate species have been shown to disperse some seeds away from parent canopies [Lieberman et al., 1979; Estrada & Coates-Estrada, 1984; Gautier-Hion, 1984; Gautier-Hion et al., 1985; Garber, 1986; Chapman, 1989; Corlett & Lucas, 1990; Rowell & Mitchell, 1991; Wrangham et al., 1994]. Seeds defecated by primates have been found to maintain their germination ability [Lieberman et al., 1979; Estrada & Coates-Estrada, 1984; Garber, 1986; Idani, 1986; Chapman,

1989; Tutin, et al., 1991; Julliot, 1994], and in some cases germination rates are enhanced [Lieberman et al., 1979; Idani, 1986; Figueiredo, 1993; Wrangham et al., 1994]. African forest monkeys (*Cercopithecus* spp.) consume a wide array of fruit species, handle seeds in a variety of ways which facilitate the movement of seeds out of tree canopies, and travel through a variety of forest types [e.g., Rudran, 1978; Gautier-Hion, et al., 1981; Cords, 1986; Butynski, 1990; Kaplin et al., in press]. These factors lend support to the supposition that African forest monkeys may be important seed dispersers. As mentioned above, however, the results from studies looking at aspects of the quality and quantity of their seed dispersal activities are contradictory.

The purpose of this paper is to describe the handling and dispersal of seeds by two sympatric species of forest monkeys, the blue monkey (*Cercopithecus mitis doggetti*) and the mountain monkey (*C. lhoesti*), as it relates to phenological changes in fruit availability. This is the first study to evaluate the role in seed dispersal played by the terrestrial, relatively secretive forest monkey (*Cercopithecus lhoesti*). We combine data on 1) forest phenological patterns, 2) systematic observations of the monkeys' diet composition and seed-handling behaviors, and 3) dung samples. Data were collected during two periods of fieldwork totaling 10 months and included two dry seasons. The study provided an opportunity to compare fruit consumption and dispersal of seeds, here defined simply as the movement of seed away from the tree canopy, of a highly terrestrial species, the mountain monkey, with a more arboreal species, the blue monkey, across a temporal scale of fruit abundance. We found that as fruit resources varied, both monkey species alternated between acting predominately as seed defecators, seed droppers, or seed predators depending on the array of fruits available. This finding highlights the importance of considering forest phenological patterns in seed-handling and dispersal studies and suggests it is unlikely that these monkeys have selected for fruit characteristics in the tree species upon which they feed.

METHODS

Study Area

Research was conducted in the Nyungwe Forest Reserve (2° 17' to 2° 50' S and 29° 07' to 29° 26' E), a 950 km² tropical montane rain forest in Rwanda. Daily temperatures varied little throughout the study period, with average maximum and minimum temperatures of 19.6°C and 10.9°C, respectively. Average annual rainfall was 1,744 mm. The main dry season occurs between July and August, with a short dry period in December and January. The study site was located between 2,100 to 2,700 m and included dense secondary forest with very dense understory, closed canopy forest, natural open areas of herbaceous vegetation, revegetating landslide areas, and gold-mined valleys.

Diet Composition and Seed-Handling Observations

We habituated one group of blue monkeys (*Cercopithecus mitis doggetti*) composed of 27 individuals and one group of mountain monkeys (*Cercopithecus lhoesti*) composed of 29 individuals between April 1990 and January 1991. The overlapping home ranges of both groups covered approximately 2 km² and were accessed by a dense trail system. We used scan sampling methods to collect data on the diet composition and seed-handling behaviors of the monkeys [Altmann, 1974; Martin & Bateson, 1986]. If the interval between samples is short relative to the

average duration of the behavior, this method provides a measure that approximates continuous sampling and yields an estimate of the proportion of time devoted to eating particular food items [Martin & Bateson, 1986].

Two different scan sampling methods were employed. We began using the frequency method [Struhsaker, 1975; Rudran, 1978; Butynski, 1990; Lawes, 1991]. We used a 10 min time interval every quarter hour to scan the groups and record food items eaten. This method may underestimate common items and overestimate uncommon ones.

We also employed instantaneous scan samples with a duration of 3 min in which an individual was scored only once during each scan. Observations of an individual were kept to a few seconds, and the first item consumed by each visible individual was scored. This method may overestimate common items and underestimate uncommon ones; it is, however, systematic in the duration of time allotted for observing and scoring individuals. Three of these 3 min scans were conducted every 15 min (12 scans/hour). The total of three scans every 15 minutes was comparable to the single 10 min scan period every 15 min from the first method.

Each group was followed from 0600–1800 h for 4–8 days per month, usually providing 12 h per day of observations. Efforts were made to observe as many group members as possible during each scan sample. Every 15 min the approximate center of the group was marked on a topographical trail map.

Items were defined as food items only if inserted into the mouth. Fruits eaten by the monkeys were categorized as 1) succulent pulp, 2) dry, fibrous pulp, or 3) pulpless. When fruits were eaten, we noted how the seeds were handled. To indicate the animals' effect on seeds, we regarded the monkeys as seed dispersers when they ate only the pulp and dispersed the seed by endo- or synzoochory. They were considered predators when they destroyed the seeds by chewing and digesting them; it was relatively easy to observe which seeds were eaten and destroyed because we heard and saw the animals crunching the seeds, and no identifiable pieces of the seed species were found in dung samples.

Data were collected from February 1991 through June 1991 using the 10 min frequency method time interval sampling and July 1991 through September 1991 and July 1992 to August 1992 using the 3 min instantaneous scan sampling method. No foraging data were collected on the mountain monkeys in June 1991. We collected data on the blue monkey group using both methods in July and August 1991 and used a two-way ANOVA applied to the data as ranks to determine if the two methods differ significantly in results [Conover, 1980]. We combined the 10 min and 3 min scan method data based on the outcome of this test (two-way ANOVA test, $r^2 = 0.79$, $P > 0.3550$) to determine overall diet composition of the blue monkey group for the period of the study. We combined the mountain monkey data based on these results also to determine overall diet composition during the study period. For all other analyses, scores were pooled within each sample month, and the proportions of items consumed were computed from these monthly totals for each monkey species.

Based on our observations of fruit and seed handling by the monkeys, we placed the scores for each fruit species eaten into one of three categories which described how the monkeys handled the seeds: seeds chewed and destroyed = seed predators; pulp removed and seeds dropped intact from the parent tree canopy = seed droppers; or seeds defecated intact = seed defecators. We then determined the proportion of all fruit and seed intake devoted to each category on a monthly basis. A fourth possibility exists for the handling of seeds by both monkey species: fruits could be stuffed into cheek pouches and carried out of the

parent canopy to be consumed later at a different substrate where the seeds would then be dropped. This method of seed handling was not quantified in this study due to the difficulty of observing cheek pouch use.

We present 10 months of data from 655 contact hours with the blue monkey group and 9 months for the mountain monkey from 574 contact hours; both data sets include two dry seasons. On average, four (± 2.99) blue monkey individuals and five (± 2.74) mountain monkey individuals were observed feeding per scan sample.

Seed Defecation Sampling

Dung samples were collected throughout the day as the monkey groups were followed except in June 1991, when no samples were collected for either species, and in February 1991, when no samples were collected for the mountain monkey. The occurrence of dung samples was not clumped in time or space during the follows. Sample sizes are low due to the opportunistic nature of the collection procedure and the dense vegetation of the study site, which made it difficult to locate fallen dung piles.

Samples were strained in a sieve with water, dried on filter paper, and examined under a microscope. The abundance of seeds less than 2 mm was ranked using relative scores: 1 = rare (1–10 seeds); 2 = few (11–20 seeds); 3 = common (20–40 seeds); 4 = abundant (40 to hundreds). Seeds greater than 2 mm were counted. We used 2 mm to separate large from small seeds because this size appears to be a natural separation for the animals between seeds that are swallowed intact and seeds that are dropped after the pulp is removed, based on our field observations. Two millimeters has also been used as a separation between large and small seeds by other researchers of *Cercopithecus* seed dispersal [Rowell & Mitchell, 1991; Wrangham et al., 1994], which will allow for comparisons with our results. Only intact seeds were included in the analyses. A seed reference collection was compiled to assist with species identification. Seed sizes were obtained by measuring the width or from published data [Troupin, 1982].

To increase our sample size, we collected all dung samples found that were known to be from *Cercopithecus* monkeys by walking through the study site during the last two months of the study (July and August 1992). These ad lib or opportunistic samples were not collected on days when the monkey groups were followed for data collection, and samples were collected only if it was certain they were from either *C. mitis* or *C. lhoesti*. These two species are the only guenons forming groups in this portion of the forest, although single *C. mona* and *C. ascanius* individuals have been observed with *C. mitis* groups in the area. Data from all ad lib samples were combined to determine mean number and mean size of seeds per sample.

Phenological Data Collection

We collected data on the phenological patterns of 25 fruit-producing species within the groups' home range on a monthly basis beginning in January 1991. This sample is a subset of a larger phenological study of 47 species [Sun et al., 1996], and represents 93% of the fruit and seed species in the blue monkey diet, and 70% of the fruit and seed species in the mountain monkey diet. The mean sample size was 11 individuals per species (SD = 3.87, range 4–22, n = 25). Individuals in the phenology sample were reproductively mature, were located throughout the home range, and were assumed to represent the phenology pat-

terns within the home ranges of the monkeys. All individual trees in the sample were marked with numbered aluminum tags, and species identifications were made with the assistance of Troupin [1982] and the herbarium at the Institute of Scientific and Technological Research, Rwanda.

Sampling took place over 2–3 days at the same time each month. The percentages of new leaves, flowering buds, flowers, and fruit in a given tree canopy were estimated. The estimates were assigned a score from 1–4: 0% of the canopy = 0, 1–25% = 1, 26–50% = 2, 51–75% = 3, and 76–100% = 4 [see Sun et al., 1996]. Fruit phenology patterns are presented in this paper as the monthly overall density of trees with a fruiting score of 1 or more, which is considered to be in that phenophase each month following van Schaik et al. [1993] as a representation of fruit abundance within the home range. Although tree density does not take into account between-species differences in the size distribution of trees and the intensity of phenological activities, density does take into account the relative abundance among tree species and improves the accuracy of depicting the abundance of plant resources [Chapman et al., 1994]. For a more fine-scale species specific-approach, we present the fruit phenology patterns individually of the five fruit and seed species most commonly eaten by both monkey species, again based on tree density.

Tree Abundance

We used a random stratified sampling method to determine fruit tree species' relative distribution and abundance within the home ranges. Sampling was conducted during the last 2 months of the study period when the maximum home range areas of the groups were known. Five to seven 0.1 ha plots were placed in each of 11 different forest types identified within the home ranges. A total of 52 plots was sampled, covering an area of 5.2 ha, or 4.6% of the home range. All trees with a diameter at breast height (DBH) ≥ 10 cm in each plot were identified to species, and their DBH was measured. Plant determinations were made with the assistance of Troupin [1982] and the herbarium at the Institute of Scientific and Technological Research, Rwanda. Each of the 11 different habitats was mapped on a topographic map and digitized to calculate relative areas. The density of each species found in the study site was then calculated from the sum of the tree density in each habitat multiplied by the proportion of each habitat in the study site. A total of 38 tree species were found in the plots; the 25 species included in the phenology sample were among these species.

RESULTS

Fruit Consumption and Seed Handling

Although the mountain monkeys ate almost half as much fruit as the blue monkeys (Table I), they handled the seeds of the fruits in their diet in similar proportions to the blue monkeys (Table II). Both species handled certain seed

TABLE I. Percentage of Items in the Diet of the Blue Monkey and Mountain Monkey (Numbers in Parentheses are Standard Deviations)

	Fruits	Seeds	Flowers	Inverts	Herbs	Other
Blue	48.00 (15.90)	9.34 (12.46)	6.36 (8.86)	24.19 (6.97)	3.30 (4.27)	8.81 (8.36)
Mountain	24.28 (9.85)	17.77 (11.69)	3.97 (3.27)	8.79 (8.47)	35.17 (10.19)	9.81 (8.00)

TABLE II. Fruit Consumption and Seed Handling by Blue and Mountain Monkeys

	Percent fruit in diet	Number of fruit spp. eaten	Percent succulent fruits	Number of spp. defecated ^a	Number of spp. dropped ^a	Number of spp. eaten
Blue	50%	34	69%	17 (50%)	21 (62%)	6 (18%)
Mountain	25%	31	74%	16 (52%)	17 (55%)	4 (13%)

^aOnly intact seeds included in the analyses.

species in more than one way (Table III); thus, the percentages may total to more than 100 in Table II. Of the 17 seed species defecated by the blue monkeys, two were also chewed and digested, and nine were also dropped from parent canopies or carried in cheek pouches. The mountain monkeys chewed and destroyed two of the seed species that they also defecated and dropped six seed species from the parent canopy that were also found to be defecated. Only two of the six seed species chewed and digested by the blue monkeys were from succulent fruits; the remainder were from dry fruits. Similarly, only one of the five seed species chewed and digested by the mountain monkeys was from a succulent fruit.

The greatest proportion of fruits consumed by both monkey species came from large canopy trees. Thirty-eight percent of the fruits eaten by the blue monkeys were from canopy trees, 21% were from understory trees, 15% were understory shrubs, and 24% were lianas. Thirty-four percent of the fruits eaten by the mountain monkeys were canopy trees, 24 percent were understory trees, 14 percent were understory shrubs, and 28% were lianas.

Seed Defecation

Both the mean rank of seeds less than 2 mm, and the average number of seeds greater than 2 mm, found in the dung samples were similar for both monkey species (Table IV). All the mountain monkey dung samples contained intact seeds, and 94% of the blue monkey dung samples contained intact seeds. As many as 42 seeds of a single species were found in one mountain monkey dung sample and a maximum of five seeds in the blue monkey dung sample. The largest seeds found in the dung were 6.8 mm from *Canthium* sp. lianas. The mean seed size for all tree species included in the entire phenology sample was 7.9 mm (SD = 7.06, median = 5.38 mm, range 0.5–30 mm, n = 47 species). We found crushed seeds of three different species in five samples (10%) of the blue monkey dung samples and one crushed seed species in only one of the mountain monkey dung samples.

The proportions of dung samples containing seeds of particular fruit species were also similar for both monkeys (Table III). Two species of fruit with seeds less than 2 mm (*Balthasarea schliebenii* and the fig, *Ficus oreodryadum*) were both found in more than 70% of the mountain monkey dung samples, and 66% and 84% respectively, of the blue monkey dung samples. A large canopy tree, *Harungana montana*, and an understory shrub (*Rubus* sp.) were the two species that differed the most when comparing seed defecation by the two monkey species: more blue monkey dung samples were found with the former seed species, and more mountain monkey dung samples were found with the latter species.

The ad lib collection of *Cercopithecus* dung samples during July and August 1992 yielded 55 samples. All of these samples contained intact seeds; 51% (28 samples) contained intact seeds >2 mm. The mean number of large (>2 mm) seeds per sample was 16.86 (SD = 24.77, n = 28). This calculation is based on samples containing at least one large seed. The mean number of large seeds

TABLE III. Fruit Tree Parameters and Seed-Handling Behavior for Those Species Most Commonly Eaten

Species	Rel. Den./ha	Seed size (mm)	<i>C. mitis</i> seed-handling behavior	T of dung samples with seed	<i>C. lhoesti</i> seed-handling behavior	% of dung samples with seeds
Canopy trees						
<i>Canapa grandiflora</i>	5.11	30.00	Eat	—	Not eaten	—
<i>Magnustipula butayei</i>	—	25.00	Drop	—	Not eaten	—
<i>Parinari excelsa</i>	1.54	25.00	Drop	—	Not eaten	—
<i>Strombosia scheffleri</i>	3.98	18.30	Drop, eat	—	Eat ripe and unripe; drop—ripe	—
<i>Beilschmiedia troupini</i>	10.08	14.65	Eat—unripe; drop—ripe	—	Eat ripe and unripe; drop—ripe	—
<i>Chrysophyllum ruandense</i>	8.57	13.25	Eat—unripe; drop, defecate-ripe	2	Drop, defecate	2
<i>Syzygium parvifolium</i>	12.81	13.00	Drop	—	Drop	—
<i>Chrysophyllum gorungosanum</i>	0.03	10.40	Drop	—	Not eaten	—
<i>Ilex mitis</i>	0.64	5.00	Drop, defecate	2	Drop	—
<i>Ocotea michelsonii</i>	3.11	3.50	Drop	—	Drop	—
<i>Harungana montana</i>	0.02	2.00	Defecate	20	Defecate	2
<i>Balthasarea schliebenii</i>	1.48	1.50	Defecate	66	Defecate	79
Understory trees						
<i>Canthium melanophengos</i>	2.45	10.00	Drop, defecate	8	Drop, defecate	3.5
<i>Sericanthe leonardii</i>	0.45	8.65	Drop	—	Drop	—
<i>Rytiginea sp.</i>	0.62	5.12	Drop	—	Drop	—
<i>Rapanea melanophloeos</i>	0.29	4.40	Not eaten	—	Drop, defecate	?
<i>Macaranga neomilbraediana</i>	19.11	4.00	Eat	—	Eat	—
<i>Psychotria mahonii</i>	3.81	3.50	Drop, defecate	8	Drop, defecate	8
<i>Maesa lanceolata</i>	4.53	0.50	Defecate	2	Defecate	17
Understory shrubs						
<i>Alchornea hirtella</i>	—	8.00	Eat, defecate	2	Eat	0
<i>Galimiera coffeoides</i>	—	3.40	Defecate	4	Defecate	4
<i>Chassalia subochreatea</i>	—	3.00	Defecate	8	Defecate	10
<i>Tricalysia niamniamensis</i>	—	—	Drop, defecate	8	Defecate	?
<i>Rubus sp.</i>	—	—	Defecate	14	Defecate	66
Lianas						
<i>Canthium sp. A</i>	—	6.86	Drop, defecate	6	Drop, defecate	5
<i>Embellia libeniana</i>	—	4.36	Drop, defecate	16	Drop, defecate	20
<i>Embellia schimperii</i>	—	4.08	Drop, defecate	?	Drop, defecate	?
<i>Ficus oreodryadum</i>	6.77	1.00	Defecate	84	Defecate	76
<i>Canthium sp. B</i>	—	—	Drop, defecate	10	Drop, defecate	5

TABLE IV. Parameters of the Dung Samples Collected from Blue and Mountain Monkeys

	Number of samples	Mean number of samples/month (SD)	Mean number of different spp./sample (SD)	Mean rank ^a of seeds <2 mm/sample	Mean number ^a of seeds >2 mm/sample (SD)	Proportion of samples with seeds >2 mm
Blue	50	5.56 (2.59) N = 9	2.52 (1.08) range 0–5	2 (few)	2.33 (1.45)	30
Mountain	58	7.25 (2.73) N = 8	2.95 (0.88) range 1–5	2–3 (few–common)	6.43 (8.27)	40

^aMeans were calculated using samples containing at least one of a particular species.

from all ad lib dung samples was 8.58 (SD = 19.58, N = 55). We found as many as 105 large seeds of a single species in one dung sample. Forty-nine percent of the samples had fig seeds (*Ficus oreodryadum*) and 49% had *Balthasarea schliebenii* seeds (both <2 mm).

Fruit Phenology and Variability in Seed Handling

The availability of fruits consumed by the monkeys, expressed as the density of trees in fruit, varied temporally during the study period (Fig. 1). A fruiting trough occurred from January–March 1991 and in June–September 1992. Figure 2 shows the individual fruiting patterns of the five main fruit species consumed by the monkeys. During many months of the study, two or more succulent fruits consumed by the monkeys were available, in particular two species with single,

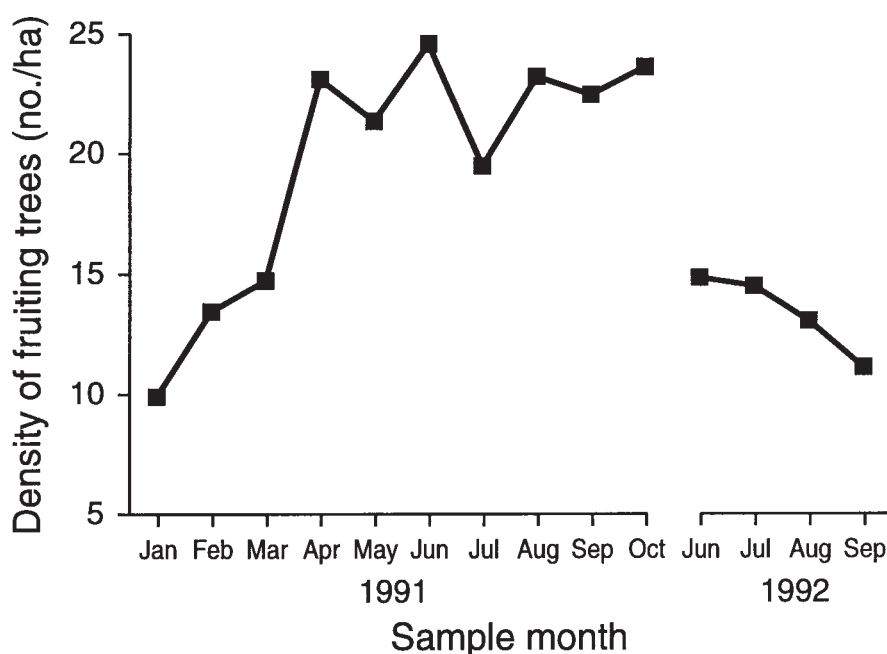


Fig. 1. Fruiting pattern of 25 plant species eaten by blue and mountain monkeys.

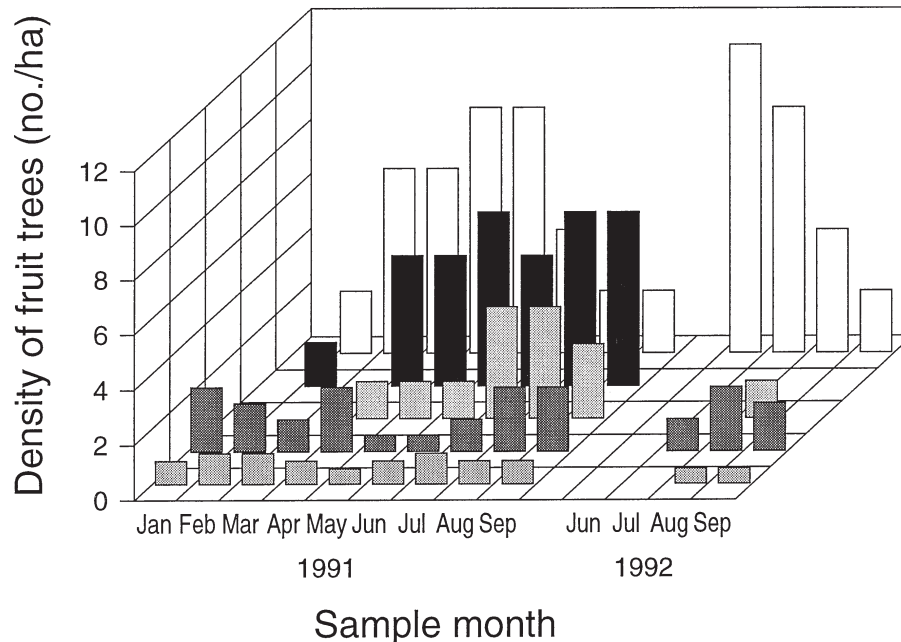


Fig. 2. Fruiting patterns of the five tree species most commonly eaten by the blue and mountain monkeys. Medium grey bars, *Balthasarea schleibonii*; dark grey bars, *Ficus oreodryadum*; light grey bars, *Chrysophyllum rwandense*; solid bars, *Beilschmiedia troupinii*; clear bars, *Macaranga neomildbraediana*.

large-sized seeds, *Beilschmiedia troupinii*, and *Chrysophyllum rwandense*. When these two species were available, they composed a large proportion of the blue monkey diet and, to a lesser extent, the mountain monkey diet (Fig. 3).

During the fruiting troughs (February–March, 1991 and July–August, 1992), these large-seeded fleshy fruits were not available to the monkeys, but certain small-seeded species were fruiting (Fig. 2). *Ficus oreodryadum*, a strangler fig, and *Balthasarea schleibonii*, a large canopy tree, were fruiting at low densities nearly every month of the study, including the periods of low fruit availability (Fig. 2). Both of these species have succulent fruits with numerous small seeds. *Macaranga neomildbraediana*, a dry fruit, was also available during every month of the study.

Blue monkeys and mountain monkeys were seed predators most often during periods of low fruit availability (Fig. 4). We found a negative correlation between fruit abundance and overall seed consumption (based on scan sampling data for diet composition) in both species, although not significant for the mountain monkey (blue: $r_s = -0.709$, $P = .01$, $n = 10$; mountain: $r_s = -0.53$, $P > 0.50$, $n = 9$). The proportions of fruit and seeds in the diet were negatively correlated in both species, although again not significant in the mountain monkey (blue: $r_s = -0.794$, $P = .01$, $n = 10$; mountain: $r_s = -0.517$, $P > 0.50$, $n = 9$).

A single tree species, *Macaranga neomildbraediana*, contributed the most to the seed component of the diets of both monkey species. *M. neomildbraediana* seeds composed 35.25% of the blue monkey diet in July 1992 and 25.36% in August 1992, a period of low fruit availability; seeds of this species were virtually ignored during other months of the study (Fig. 3). During the same two month period, *M. neomildbraediana* seeds composed nearly 35% of the mountain monkey diet (Fig. 3). Seeds of an understory shrub with dry fruits (Euphorbiaceae: *Alchornea hirtella*) contributed to most of the seed consumption by the mountain

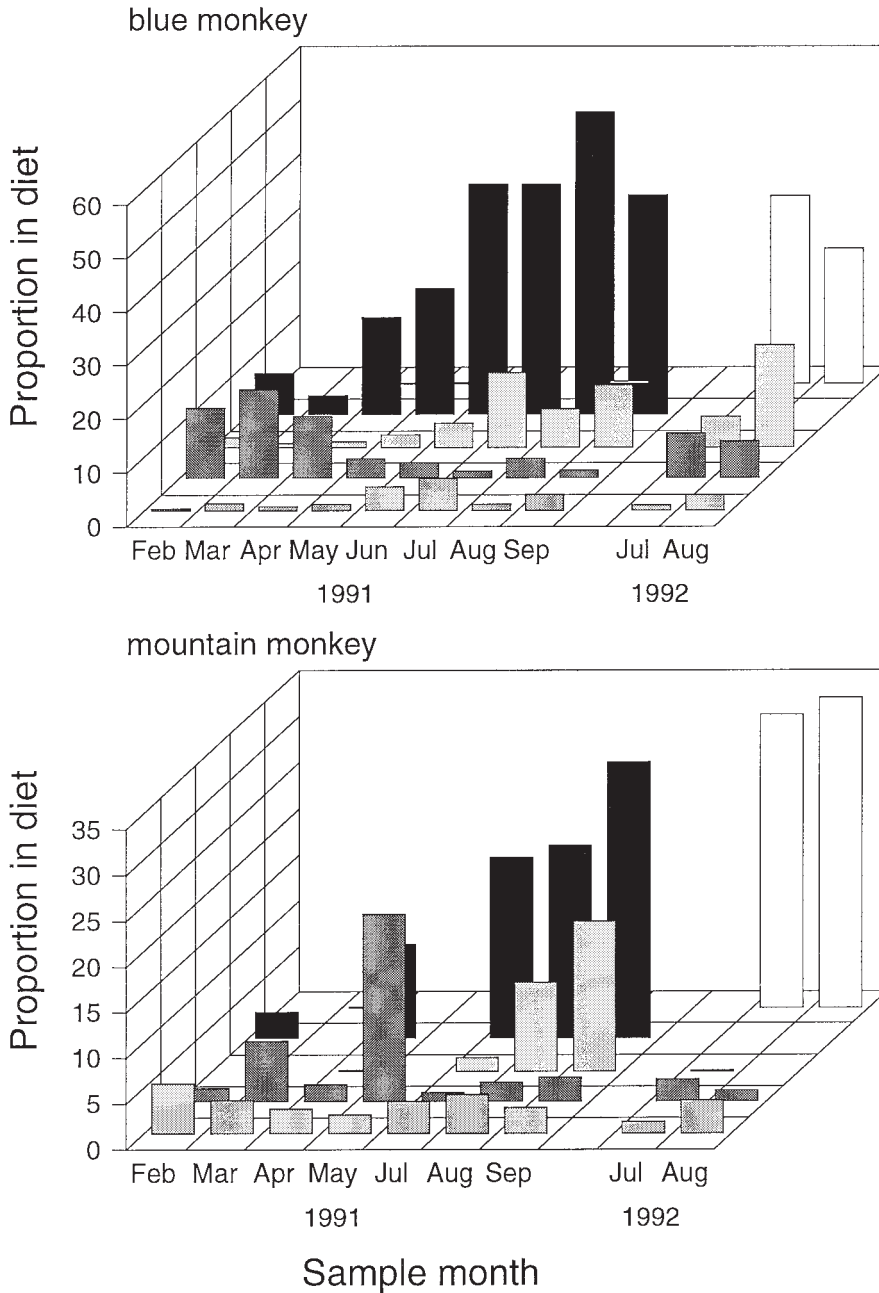


Fig. 3. Monthly proportions of the principle fruits and seeds in the diet of the blue and mountain monkey. Medium grey bars, *Balthasarea schleibonii*; dark grey bars, *Ficus oreodryadum*; light grey bars, *Chrysophyllum rwandense*; solid bars, *Beilschmiedia troupinii*; clear bars, *Macaranga neomildbraediana*.

monkeys outside of July and August 1992. Fruit density and the proportion of *M. neomildbraediana* seeds consumed were not correlated in the blue monkey diet ($r_s = -0.081$, $P > 0.50$, $n = 10$) and were negatively correlated in the mountain monkey diet ($r_s = -0.683$, $0.01 < P < .05$, $n = 9$).

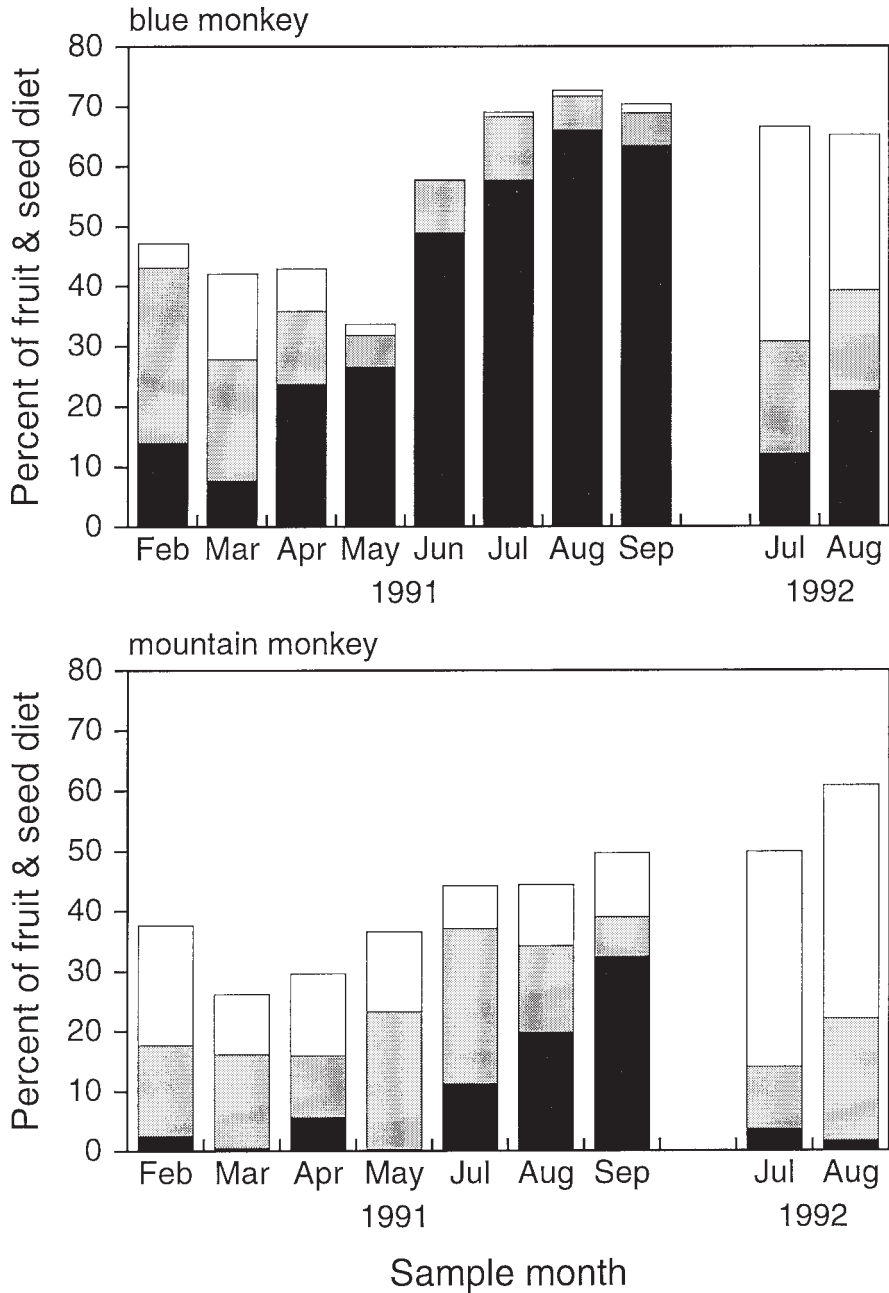


Fig. 4. Monthly percentages of the fruit diet with seeds handled in the following different ways by the monkeys: solid bars, seed droppers; grey bars, seed defecators; open bars, seed predators.

The monkeys alternated between acting predominately as seed predators, seed defecators, or seed droppers during the course of the study. There were significant differences in the proportions of fruit in the blue monkey diet with seeds either dropped, digested (= seed predation), or defecated each month based

on diet composition (Kruskal-Wallis, $H = 10.23$, $P = 0.006$, $df = 2$, $n = 10$) (Fig. 4). These differences were not significant for the mountain monkey (Kruskal-Wallis, $H = 5.4$, $P = 0.067$, $df = 2$, $n = 9$) (Fig. 4). The blue monkeys consumed more fruits containing seeds that were dropped from tree canopies than the mountain monkeys based on diet composition (Mann-Whitney U, $W = 71.00$, $P = 0.007$, $df = 1$, $n = 9$) (Fig. 4), but there was no difference between the two monkey species in the dietary proportions of fruit with seeds that were defecated (Mann-Whitney U, $W = 33.00$, $P = 0.50$, $df = 1$, $n = 9$).

Both monkey species dispersed some seed species consistently through time: seeds of *Ficus oreodryadum* and *Balthasarea schliebenii* were found in dung samples throughout the study period (Fig. 5). These seed species were found in every mountain monkey dung sample examined and in all but three of the blue monkey samples. The frequency of occurrence of other seed species, particularly large-sized seed species, was much more variable. This may in part be due to the small sample sizes but also reflects the fruiting pattern at the study site.

DISCUSSION

Several factors must be considered in the evaluation of an animal as an agent of seed dispersal, including the numbers of seeds dispersed and the fate of the dispersed seeds. The blue monkeys and the mountain monkeys in this study dispersed a mean of 2.33 and 6.43 large seeds (>2 mm), respectively, per dung sample, with each sample containing a mean of 2.5 and 2.9 seed species, respectively. For some plant species, the monkeys disperse seeds continuously through time, and for other species the occurrence of seeds in the dung is much more variable. Dung samples from blue monkeys ($n = 25$) and mountain monkeys ($n = 50$) that were allowed to lie protected and watered in boxes of forest soil have shown that 80% and 73% of the seed species, respectively, were able to germinate [B. Kaplin, unpublished data]. Although these sample sizes are small and we made no attempt to compare germination rates with seeds not handled by the monkeys, the results show that at least some seed species are viable after passage through the digestive tracts of blue and mountain monkeys. We have no quantified data on the fate of seeds dispersed; the evaluation of the effectiveness of monkeys as seed dispersers is not complete without such data.

The mountain monkeys and blue monkeys dispersed equivalent numbers of seeds per dung pile even though the blue monkeys consumed twice as much fruit as the mountain monkeys. The potential role of terrestrial monkeys as seed dispersers was previously unreported; these monkeys may be important seed-dispersal agents, particularly because they frequently use disturbed forest sites for foraging [B. Kaplin, unpublished data]. Their movements between closed canopy and open, disturbed forest may facilitate the transport of seeds into a variety of forest sites. However, as indicated in this work, these monkeys also serve as seed predators. Future studies will need to evaluate the role of mountain monkeys in the dispersal of seeds into disturbed forest.

Although our dung sample sizes are small due to the difficulty of finding them during animal follows, the data suggest that both blue and mountain monkeys defecated a greater number of seeds per dung sample and in particular more large-sized seeds (>2 mm) than found elsewhere for *Cercopithecus* species. Wrangham et al. [1994] found a mean of only 0.37 seeds per frugivorous monkey dung in the Kibale Forest, Uganda, and determined that forest monkeys play a relatively unimportant role in seed dispersal dynamics in tropical forests compared with larger-bodied apes. Rowell and Mitchell [1991] called *Cercopithecus*

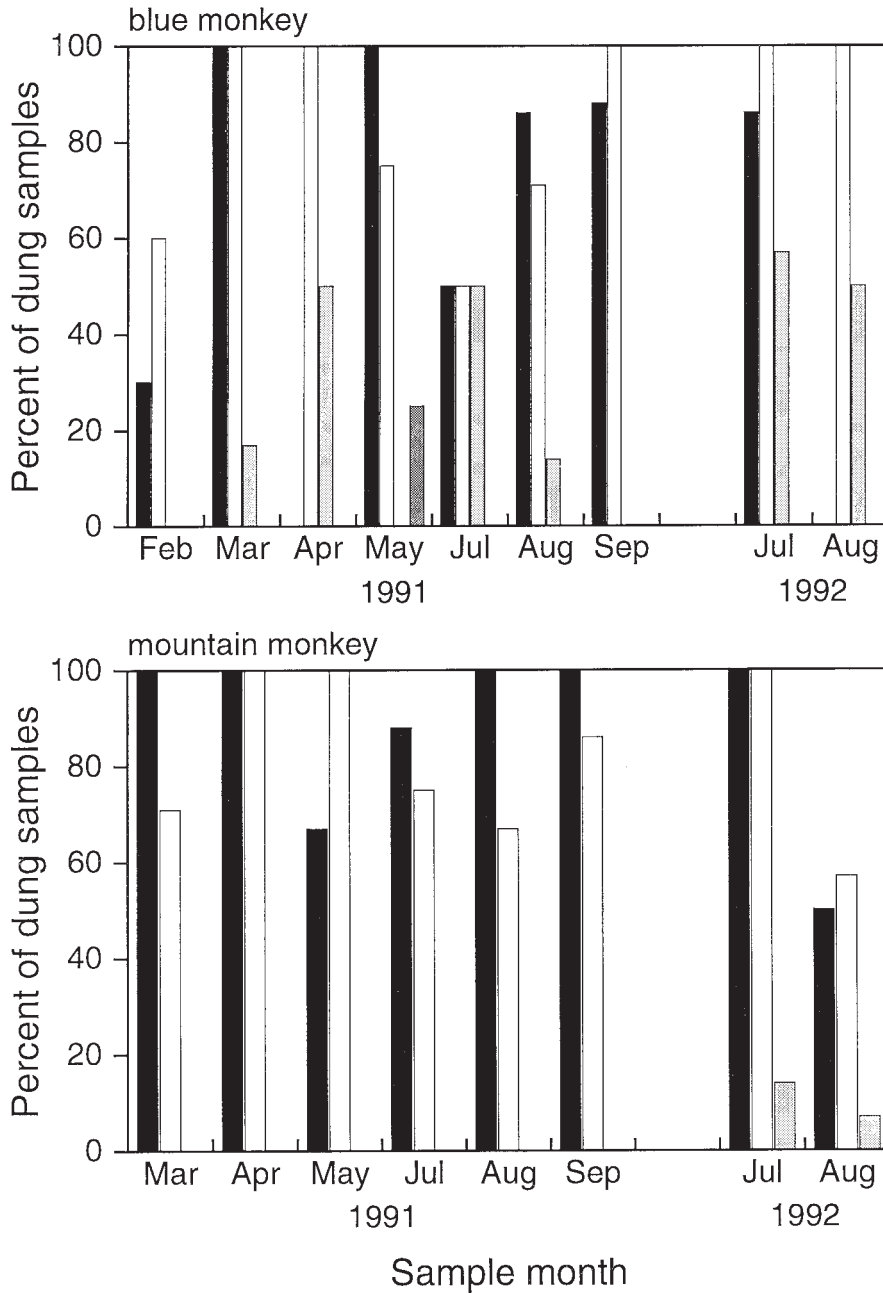


Fig. 5. Monthly percentages of dung samples containing the most commonly found small-sized (<2 mm) seeds. Open bars, *Ficus oreodryadum*; solid bars, *Balthasarea schleibonii*, light grey bars, *Harungana montana*; dark grey bars, *Ilex mitis*.

monkeys fruit thieves because they were found to chew and destroy most of the seeds they ingested in Kakamega Forest, Kenya. They speculated that this occurred because African forest monkeys have a high proportion of leaves in the diet and thus must spend more time chewing. About 30% of the dung we exam-

ined from each monkey species contained seeds greater than 2 mm. Mountain monkeys, which consumed more vegetation than blue monkeys, might be expected to crush most of the seeds they ingest, according to Rowell and Mitchell [1991]; this hypothesis was not supported by our observations.

The differences in seed defecation rates among the sites may be due to the plasticity of the *Cercopithecus* monkey feeding behavior [Gautier-Hion et al., 1993], differing phenological patterns and fruit availability, and plant species composition at the respective sites. Dietary flexibility, or the ability to make switches in diet composition, has been shown for a number of primate species [Chapman & Chapman, 1990]. Primates may turn to certain items as fallback foods during periods of food shortage; these dietary changes in turn may influence rates of seed dispersal and seed predation. For example, the level of seed predation pressure by primates in Gabon at any time depends on community-wide effects such as availability of succulent fruits [Tutin et al., 1996]. Work by Gautier-Hion et al. [1993] identified differences in seasonal diets within the same population that probably influence seed dispersal patterns as well as differences between the diets of closely related monkeys: *Cercopithecus pogonius* in Gabon dispersed the seeds of succulent fruits, while *C. wolfi* in Zaire were mainly seed predators. The density and number of fleshy fruits was lower at the Zaire site, and *C. wolfi* could be considered either seed predators, leaf eaters, or aril eaters depending on the season.

In our study, both monkey species alternated between acting predominately as seed predators, seed droppers, or seed defecators. Variability in how seeds were handled and the proportions of large or small seeds in dung were related to phenological patterns and the changing availability of food sources for the animals. This finding emphasizes the important influence of plant species composition and the temporal context of variability in fruit abundance on rates of seed dispersal, especially when attempting to extrapolate results to other sites.

The treatment a seed receives by a frugivore has a great influence on the likelihood that the seed will survive to become a reproductive individual. *Cercopithecus* monkeys tend to drop seeds greater than about 10 mm of large succulent fruits out of parent canopies after removing the pulp. The importance of seeds dropped by monkeys is only just beginning to receive attention. Chapman and Chapman [1996] found a positive relationship between the proportion of the fruit crop removed from parent canopies and both seed disappearance and seedling survival under the parent canopy of some species, suggesting that some species have seeds that can both disperse away from the parents and recruit under or nearby the parent canopies as a reproductive strategy. This is particularly interesting given that tropical tree species have been shown to have aggregated distributions [e.g., Ashton, 1969; Hubbell, 1979; Fleming & Heithaus, 1981].

In our study, seed dropping was the predominate mode of seed handling in certain months, and those tree species in Nyungwe Forest with seeds handled in this manner appear to have aggregated distributions (e.g., *Beilschmiedia troupinii* and *Chrysophyllum rwardense* [B. Kaplin, unpublished data]). We found that 63% (n = 73) and 35% (n = 14) of the seeds of the two main species dropped by the blue monkeys (*Beilschmiedia troupinii* and *Chrysophyllum rwardense*, respectively) were viable after being dropped [Kaplin et al., in press], and 22% (n = 54) and 21% (n = 78) of the *Beilschmiedia troupinii* and *Chrysophyllum rwardense* seeds, respectively, were viable after being dropped by the mountain monkey [B. Kaplin, unpublished data]. As hypothesized by Chapman and Chapman [1996], certain tree species with fruits that are dropped beneath parent canopies may have been selected to recruit under or near the parent; seed germination, seed-

ling survivorship, and recruitment must be assessed and combined with observations on the effectiveness of other dispersers to better understand this relationship.

All *Cercopithecus* monkeys have cheek pouches used to hold fruits which are often consumed elsewhere [Corlett & Lucas, 1990; Rowell & Mitchell, 1991; B. A. Kaplin, personal observation]. Seeds transported in cheek pouches can be carried about 30–50 m from the parent tree, and up to 100 m, before being discarded [Rowell & Mitchell, 1991]. Many of the fruits with large seeds (greater than about 10 mm) are not only dropped from parent canopies but also are stuffed into cheek pouches. The importance of dropped seeds and seeds carried in cheek pouches to plant reproduction needs to be examined.

Various authors have suggested that the traits of certain fruits belong to dispersal syndromes that have been selected by the primates that disperse them [e.g., Gautier-Hion, et al., 1985; Julliot, 1994]. However, numerous factors may place constraints on the likelihood for coevolution between plants and their animal dispersers [Howe, 1984; Herrera, 1985; Howe & Westley, 1988; Charles-Dominique, 1993; Chapman, 1995]. Selective pressures exerted by dispersers on plants depend not only on the dispersers but on the characteristics of coexisting plant species [Herrera, 1985]. Selection pressure on fruit traits will be weak if primates have flexible diets and are inconsistent or unreliable dispersers [Chapman, 1995; Lambert & Garber, 1998]. Results from our study suggest that blue and mountain monkeys have flexible diets with consequences for the reliability of their seed dispersal behavior. Not only did the monkeys in this study alternate between consuming pulp or seeds during the study, but we found variations in how certain seed species were handled: some seed species were either defecated intact or crushed and digested. It may be, as Janzen [1971] noted, that when an animal is regularly the seed dispersal agent and seed predator for the same plant species, seed predation is simply the cost of reliable dispersal. The flexible diets of *Cercopithecus* monkeys in response to variability in fruit abundance have been shown at a number of sites [Gautier-Hion, 1980; Beeson, 1989; Gautier-Hion et al., 1993; Kaplin et al., in press]; this behavior may result in weak selective pressure on fruit traits [Lambert & Garber, 1998].

The fate of dispersed seeds must be assessed to understand the impact of *Cercopithecus* monkey feeding behavior on plant reproduction. Data presented here show that variability is an important component of the seed dispersal system of *Cercopithecus* monkeys. Although the monkeys have the capacity to disperse large numbers of seeds, the future of these seeds following deposition and the relative effectiveness of dispersal by *Cercopithecus* monkeys compared to dispersal by other animals is an open area of study.

CONCLUSIONS

1. The blue monkeys and mountain monkeys defecated a mean of 2.52 and 2.95 different seed species per dung pile, respectively (intact seeds only).
2. A mean of 2.33 seeds greater than 2 mm were found in blue monkey dung and a mean of 6.43 seeds greater than 2 mm in mountain monkey dung, which are greater numbers than reported elsewhere for African forest monkeys.
3. Some seeds were defecated in relatively large quantities consistently through time, while other seed species showed much greater variability in their frequency of occurrence in dung samples.
4. Despite the finding that the mountain monkeys consumed half as much fruit as the blue monkeys, they dispersed equivalent numbers of large-sized seeds (>2 mm) in their dung.

5. Both the blue and the mountain monkeys alternated between acting predominantly as seed predators, seed droppers, or seed dispersers during the course of the study; this variability depended on the array of fruit resources available to them at any time.

6. Some seed species were both dispersed and destroyed (digested) by the monkeys, thus generating contrasting consequences for plant reproductive fitness.

7. Because of their dietary flexibility and their responses to temporally fluctuating resources, their roles as seed dispersers vary in time and space.

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