Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community

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Summary. Interactions between a large community of vertebrate frugivore-granivores (including 7 species of large canopy birds, 19 species of rodents, 7 species of ruminants, and 6 species of monkeys), and 122 fruit species they consume, were studied for a year in a tropical rainforest in Gabon.

The results show how morphological characters of fruits are involved in the choice and partitioning of the available fruit spectrum among consumer taxa. Despite an outstanding lack of specificity between fruit and consumer species, consideration of simple morphological traits of fruits reveals broad character syndromes associated with different consumer taxa. Competition between distantly related taxa that feed at the same height is far more important than has been previously supposed. The results also suggest how fruit characters could have evolved under consumer pressure as a result of consumer roles as dispersers or seed predators. Our analyses of dispersal syndromes show that fruit species partitioning occurs more between mammal taxa than between mammals and birds. There is thus a bird-monkey syndrome and a ruminant-rodent-elephant syndrome. The bird-monkey syndrome includes fruit species on which there is no pre-dispersal seed predation. These fruits (berries and drupes) are brightly colored, have a succulent pulp or arillate seeds, and no protective seed cover. The ruminant-rodent-elephant syndrome includes species for which there is pre-dispersal predation. These fruits (all drupes) are large, dull-colored, and have a dry fibrous flesh and well-protected seeds.

The study of interactions between fruit and vertebrate frugivores has made many advances in recent years, particularly for birds, but also for rodents, primates, bats and a few other mammals, and fish. Several studies have examined the relationships between a single plant species and a particular class of vertebrate frugivores (Leck 1969; Howe 1977, 1980; McDiarmid et al. 1977), or between a plant community and a species or guild of phylogenetically similar consumers (McClure 1966; Hladik and Hladik 1967, 1969; Alexandre 1978; Duplantier 1982).

Many characters have been interpreted as co-adapted features of plants that govern the choice of fruit species by animals. These include: color (Corner 1949; Turcek 1963; Van der Pijl 1969; Hallé 1974; Morden-Moore and Willson 1982; Willson and Thompson 1982; Stiles 1982; Willson and Melampy 1983; Cooper et al 1984); accessibility (Snow 1971; Denslow and Moermond 1982; Moermond and Denslow 1983); weight and profit margin (Diamond 1973; Howe and Vande Kerckhove 1979; Herrera 1981a; Moermond and Denslow 1983); palatibility and nutrient content of edible tissues (Morton 1973; Hladik 1981; Sorenson 1981, 1983; Herrera 1982); digestive capacities of consumers (Hladik 1981; Milton 1981); fruiting phenology and competition for dispersers (Snow 1965, 1971; Smythe 1970; Morton 1973; Howe and Estabrook 1977; Janzen 1978; Thompson 1981; Thompson and Willson 1979; Herrera 1981b; Sorenson 1981); and finally, disperser efficiency (Janzen 1971; McKey 1975; Fleming and Heithaus 1981). In addition, several reviews discuss many of the above factors (Corner 1949; Van der Pijl 1969; Janzen 1977; McKey 1975; Thompson 1982).

Janzen (1980) has defined the term coevolution and pointed out that demonstration of coadaptations between fruits and their consumers does not necessarily imply that coevolution has taken place. Wheelwright and Orians (1982) further define the fundamental differences between plant-animal interactions for pollen and seed dispersal: there may be tight coevolution between plants and their pollinators, but there seems to be little evolutionary specialization in the interactions between plants adapted for zoochory and frugivores. Plants without any possible control over the quality of dispersal of their seeds can still gain an advantage from multiple dispersers that simultaneously increase both the number of seeds dispersed and number of dispersal sites (see also Thompson 1982).

Lack of specialization among consumers should induce potential trophic competition among them. Consequently, plant-animal interactions cannot be understood without considering resource partitioning among consumers: adaptations observed between plants with zoochory and their consumers cannot be explained independently of those between different plant species on the one hand, and all of the frugivores on the other. As remarked by Fleming (1979), studies in the past have primarily focused on interactions within "ecotaxonomic guilds" rather than within "purely

trophically-based guilds" (Willis 1966; Terborgh and Diamond 1970; but see Bonaccorso et al. 1980).

Most studies in the current literature concern only "fleshy fruits" (drupes and berries), and use the circular reasoning that these fruits are automatically dispersed by zoochory, without necessarily observing the behavior of the animals towards the fruits. Even where all types of fruits have been considered, drupes with dry flesh have been classed with dry dehiscent pods or capsules (Knight and Siegfried 1983).

Many systems are complex, with seed predators also acting as dispersers (Janzen 1971; Smith 1975). Both frugivores and granivores should thus be included in community studies of fruit-animal interactions. Such studies of a whole trophically-related frugivore-granivore guild, are extremely difficult. A few attempts have been made, either as part of general studies of community structure (Harrison 1962; Gautier-Hion et al. 1980; Emmons et al. 1983), or focused on plant-animal interactions (Charles-Dominique et al. 1981; Janson 1983; Knight and Siegfried 1983).

The goal of the research we report here was to analyse interactions between a large community of vertebrate frugivore-granivores and the plant species they consume, with emphasis on the relationships between fruit morphology, nutrient content, and fruiting phenology of each plant species with respect to the individual roles of consumers as dispersers or seed predators. Throughout a year in the field, specialists on different taxa simultaneously studied frugivore-granivore diets. Botanists and zoologists combined forces to simultaneously observe both plant and animal species. Our study has two basic limitations: first, it did not include bats, despite their importances dispersers for a few plant species (frugivorous bats are much less important in Africa than in the Neotropics). Second, birds were only systematically observed for 6 months, and the considerable data on frugivorous diets collected prior to this project included no data on birds.

Our results show the relationships between kinds of fruits and kinds of consumers. We try to answer two questions: (1) how are morphological characters of fruits implicated in choice and partitioning of the available fruit spectrum by different consumer taxa? and (2) how can fruit characters evolve under consumer pressure as a result of the roles of consumers as dispersal agents or seed predators?

Materials and methods

Study area

The study was conducted during an annual cycle in 1981, on the plateau of M'passa, reserve of the IRET laboratory, Makokou, Gabon (0°34′N, 12°52′E, el. 500 m). The vegetation of the region is lowland evergreen rainforest, described elsewhere (Hallé 1964, 1965; Hallé and Le Thomas 1967, 1970; Hallé et al. 1967; Hladik and Hallé 1973, Florence and Hladik 1980). The study area is gridded with trails every 100 m and covers an area of about 2 km². Its fauna has been the subject of many ecological studies. Mean monthly temperatures range from 21° to 24° C. Rainfall is 1,755 mm (10-year av.) and divides the year into two rainy and two dry seasons.

Animal species studied

We studied intensively 39 species of frugivorous or granivorous vertebrates belonging to six categories (Appendix 1), including: 7 species of large canopy bird (hornbills and turacos); 8 species of small rodents (Muridae, Dendromuridae); 9 species of squirrels; 2 large rodents (gambian rat, brush-tailed porcupine); 7 species of ruminants; and 6 species of primates. The largest local species of the last two taxa (e.g. yellow-backed duiker and chimpanzee), as well as forest hogs, were too rare to be studied at our site and are thus excluded, although they would be important in an intact ecosystem.

Most species were followed by radio tracking. Diets were compiled by direct observation, including 24-h watches from hides at fruit trees; analysis of stomach contents collected outside the reserve; and feeding tests in captivity (murid rodents only). Data from previous years on diets of the same populations (Gautier-Hion 1971, 1977, 1978, 1980 for monkeys; Emmons 1981 for squirrels; Duplantier 1982 for murid rodents; Dubost in press for ruminants) were included in the list of fruit species eaten. We also collected fruits and seeds from piles of elephant dung. Because we did not have an adequate year-round sample of elephant diets, we include the data mainly for the sake of comparison. For analysis we pool the data on diet for each of the six zoological groups (plus elephants) and analyse it only at the group level.

Plant species studied

One hundred and twenty-two plant species whose mature fruits are consumed by one or more of the frugivores studied are included in our analysis. We consider only mature fruits. We collected fruit on 6 km of trails 70 cm wide, cleaned every 2 weeks, to record phenology and species present. Secondary and understory vegetation was poorly represented in our samples. Appendix 2 lists the characteristics of plant species in our sample, their consumers, and the effects of the latter upon their seeds.

Fruits were weighed fresh, measured, and described from a consumer's viewpoint, without regard to the botanical origin of fruit parts. When the fruit was an apocarp, each mericarp was described as the edible item or "fruit" (e.g. Xylopia spp.), likewise for a false fruit (e.g. Nauclea sp.). Each fruit was described with regard to characters liable to facilitate or hinder consumption of the disseminule as a whole, or the seed. These characters included size, resistance to opening, kind of flesh, and attractive or defensive displays. We retained the following seven parameters and their 25 variables for analysis. Table 1 summarizes the representation of each character within the whole fruit sample.

1. Color: the external color of the fruit, except in the case of mericarps that roll back to expose bright internal colors at maturity (e.g. Xylopia), or in the case of fruits decorated with colored structures ("fruit flags", Stiles 1982), where we refer to the latter colors. For multicolored fruits, we arbitrarily chose to consider only the color of the external surface. For statistical analysis multicolored fruits are treated separately, as an additional variable.

2. Protective coat: the resistance presented by the outer barrier that prevents access to the flesh. (a) There is no

Table 1. Frequency distribution of the 122 fruit species according to the different parameters considered

Fruit color	Yellow	Orange	Red	Violet	Brown	Green
$n = 122$	27	12	26	11	29	17

Fruit weight, g	<5		5–50		>50	
$n = 116$	51		43		32	

Fruit protection	dehiscent	indehisc., thin husk	indehisc., thick husk
$n = 122$	38	70	14

Type of flesh	juicy soft	juicy fibrous	dry fibrous	aril	fleshless
$n = 122$	42	31	12	20	17

Seed protection	absent	present
$n = 121$	79	42

N° of seeds	01–02	03–05	10–50
$n = 121$	51	49	21

Seed weight, g	<0.5	0.5–2.5	>2.5
$n = 118$	34	47	37

Table 2. Coefficient of community between each pair of consumers (can varys from 0 to 1). BI = birds; SR = small rodents; SQ = squirrels; LR = large rodents; RU = ruminants; MO = monkeys. For the number of fruit species eaten by each group, see Appendix 2

	SR	SQ	LR	RU	MO
BI	0.32	0.32	0.27	0.30	0.42
	SR	0.33	0.35	0.37	0.38
		SQ	0.39	0.36	0.36
			LR	0.43	0.33
				RU	0.42

Each table was analysed by multifactorial analysis. This seeks to extract, from a cloud of more-or-less dependent points in an n-dimensional space, the independant orthogonal axes with maximum inertia that account for most of the variance in a smaller space than that occupied by the initial points (Benzecri 1973; Fénelon 1981). In the analysis dealing with consumers, data on elephants were treated as an additional variable; they were not included in the search for axes, but projected *a posteriori* into the factorial space.

The existence of a fruit-choice on the basis of our chosen characters was tested with χ^2, by comparing the partitioning of each class of each character in the sample of fruits eaten, and those not eaten, by each consumer group.

barrier in the case of dehiscent fruits; (b) there is a thin skin that can be cut with a fingernail (as in a cherry); or (c) there is a thickened wall (as in an orange).

3. Type of edible tissue: (a) there is one of four types of flesh defined by decreasing water content and increasing fiber content – juicy soft pulp (as in a cherry); juicy fibrous pulp (as in a mango, either berries or drupes); dry soft aril (dehiscent fruits with arillate seeds); dry fibrous pulp (like a walnut husk, all these are drupes); (b) there is no flesh, only the seed is edible (dehiscent fruits with non-arillate seeds).

4. Seed protection: (a) there is no protection; (b) the seed coat can be opened with a fingernail (as an apple seed); (c) the seed coat is lignified or there is a true stone.

5. Seed number: the three classes of seed number are defined in Table 1.
6. Fruit and 7. seed weights: the three weight classes are defined in Table 1. We retained only the size character of weight: length, width, and depth were strongly correlated and gave a less integral measure.

Statistical treatment

To test for association between fruit parameters we erected a symmetrical 2 × 2 contingency table of dimensions 25 × 25 with the 25 variables of the 7 parameters: where $F(i, j)$ is the number of times that a fruit with character i also has character j.

The correlation between fruit characters and consumer groups was tested with a 25 × 6 contingency table, where $C(i, j)$ is the frequency of character i in the diet of consumer j. Each consumer can be thought of in a 25-dimensional fruit-character space, or each fruit character in a 6-dimensional consumer space.

Results

Frugivore diets and resource partitioning

The sample of 122 plant species in 41 families represents about 60% of the known fruits in the diets of the ruminants considered and about 80% to 90% in those of the other groups (dubious identifications were excluded). Of the fruit species sampled, over 8% are eaten by all frugivore groups, and almost 50% are used in common by at least half of them.

The coefficient of community between consumer groups varies from 0.27 to 0.43 (Table 2). We remark that the fruit-species overlap in diet within groups of arboreal or terrestrial consumers is of the same order as that between groups. Moreover, overlap between phylogenetically close groups is no more than that between distant groups.

Association between fruit characters

Before looking at how animal diets are distributed on the range of fruits, we need to know how the individual fruit characters are interrelated within fruit species.

The 1–2–3 factorial space of the analysis accounts for 55% of the total inertia. Contributing most to the first axis (28% of the total inertia) are: kind of flesh (29%), dehiscence (23%), fruit weight (16%), and seed protection and weight (14% and 11%). The color red contributes weakly but is well represented.

The second axis (17% of the total inertia) is chiefly composed of protective coat of indehiscent fruit (27%) and seed number (26%). Type of flesh (44%) and color (38%) make up most of the third axis (10% of the inertia).

These results reveal three main associations. First, between dehiscence, weight, fiber content, and seed protec-
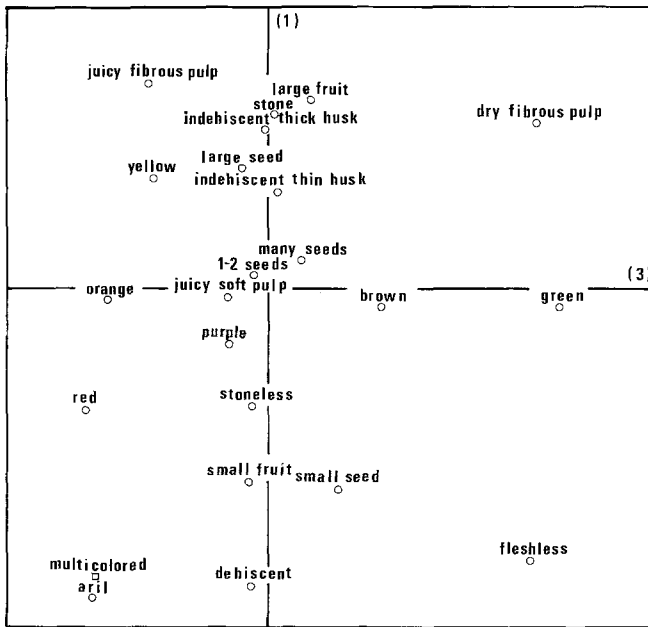
Fig. 1. Factorial plane 1–3 of the multifactorial analysis showing contingencies among the different characters of fruits (*white circle*: active variable; *white square*: supplementary variable)

Fig. 2. Factorial plane 1–2 of the multifactorial analysis showing the interrelationships among the six group of consumers and the fruit characters (*white circle*: active variable for fruit; *black circle*: active variable for consumers; *white square*: supplementary variable for fruit; *black square*: supplementary variable for consumer

tion: that is, the heaviest indehiscent fruits have a tendency to have fibrous flesh and well-protected seeds; and dehiscent fruits have a tendency to be lighter, with small, unprotected seeds, and many are red. Second, between protection of indehiscent fruit and seed number: indehiscent fruits with a thickened pericarp tend to have many seeds. Third, between kind of flesh and color of fruit: very juicy fruits and arillate fruits are brightly colored; dry fleshy fruits and dehiscent fruits with non-arillate seeds tend to be dull-colored. Figure 1 diagrams the 1–3 factorial plane of fruit characters.

Fruit characters and consumer taxa

We can now analyse the overall interactions between consumer groups and fruit characters (Fig. 2). The 1–2 factorial plane of the analysis accounts for 83% of the total inertia. Note that the fruit characters are differently arranged compared to Fig. 1. Contributing most to the first axis (52% of the total inertia) are again fruit weight (34%) and seed weight and kind of flesh (17% each). Seed protection, the colors red and purple, and dehiscence contribute weakly but are well represented.

The second axis (21% of the total inertia) is mostly due to color and type of flesh (42% each).

Consumer groups are arranged chiefly around: (1) the parameter of *fruit weight*, where the first axis separates birds (44%) from large rodents (40%) – On this axis ruminants contribute weakly but are closest to large rodents, while small rodents are closer to birds; and (2) around the parameter of *color*, where monkeys (48%) diverge from squirrels (45%).

A comparison of the results of the two multifactorial analyses shows whether or not consumers are exercising a choice among fruit types within the constraints of the more-or-less strong and complex associations between the fruit characters themselves. Thus pericarp thickness of in-
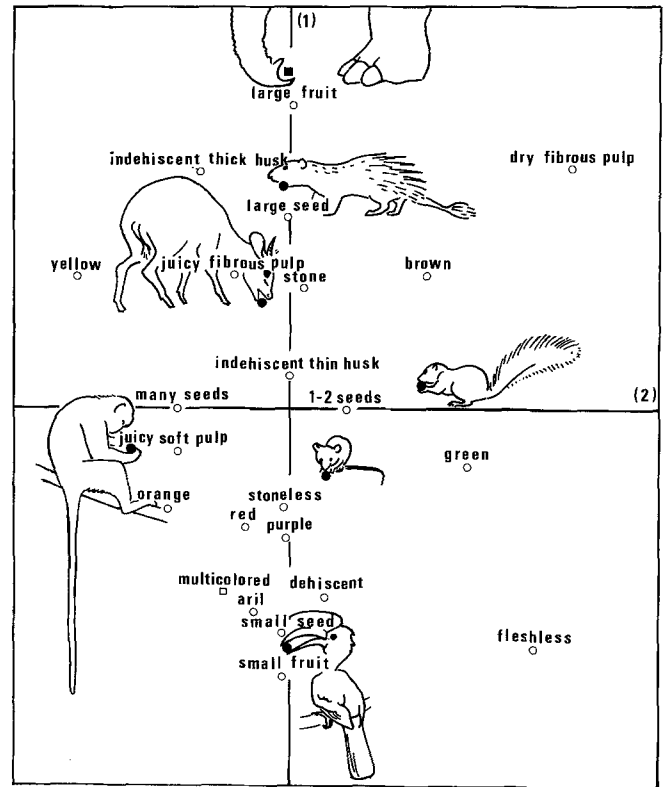
dehiscent fruits and seed number, which in the first analysis contribute to the second axis, drop out of the second analysis. This means that they have little influence on the consumer spectrum (even if fruit protection plays a role in choice by birds, see below). In contrast, weight, color, and the kind of edible tissue account for a much larger part of the inertia when consumers are added to the analysis, suggesting that animals exert a direct or indirect choice based on these criteria.

We now can test which fruit characters are significantly involved in choice of fruits by each consumer group (Table 3). Birds choose fruits by color, weight, and outer protection, as well as by type of flesh. All of these characters are statistically correlated. Small rodents do not significantly select fruits according to our parameters. Squirrels choose fibrous fruits with one or two seeds. Large rodents choose large fruits with large seeds, well-protected seeds, and fibrous flesh. These characters are also statistically associated. Like squirrels, large rodents choose fruits with few seeds. Ruminants choose fruits only by weight. Finally, monkeys select fruits by color, kind of flesh, and weight.

Combined with those in Fig. 2, the above results (Table 3) allow us to describe the major overall fruit syndromes that are characteristically chosen by consumer groups. In the system we have studied, we can say that: (1) "*bird fruits*" are small, red or purple, and without seed protection; they are are often dehiscent with arillate seeds; (2) "*small rodent fruits*" are variable; with a slight tendency only to be small; (3) "*squirrel fruits*" are dull-colored, with dry fibrous flesh and few seeds; their weight is unimportant;

Table 3. Significant choice parameters of fruit for the six animal groups. $+ = P < 0.05$; $++ = P < 0.01$; $+++ = P < 0.001$; blanks indicate no significant choice

Parameters	Birds	S. rodents	Squirrels	L. rodents	Ruminants	Monkeys
Fruit color	+ violet, red					+++ orang, red, yel
Fruit weight, g	+++ <5			+ >50, >5	+ >50, >5	+ 5–50
Fruit protection	+ dehiscent thin husk			+ indehiscent		
Type of flesh	+ arils		+ dry fibrous pulp	++ dry, juicy fibrous		+++ aril, succulent pulp
Seed protection				+ present		
N° of seeds			+ 01–02	+ 01–02		
Seed weight, g	+ <0.5			+ >2.5		+ 0.5–2.5

(4) "*large rodent fruits*" are fibrous, large, and have few, well-protected seeds; (5) "*ruminant fruits*" are chiefly characterized by their heavy weight and they are rarely red or purple. Because of their relative frequency in the sample (Table 1), fleshy fruits (66%) and brown and yellow fruits (66%) are the most often eaten; (6) "*elephant fruits*" are large; and (7) "*monkey fruits*" are brightly colored, generally weigh 5–50 g, and are either dehiscent with arillate seeds, or are succulent fleshy fruits.

Consumer action on seeds

It is not always easy to define the effect of a frugivore on the future of the seeds of fruit that it eats, both because of problems of observation and because a consumer may have several effects whose relative importance can vary. Only if the fate of seeds is followed through germination can the relative dispersal contributions of members of a trophic guild be measured.

For 88 of the 122 fruit species in our analysis, we could evaluate the basic roles of the consumer groups (Appendix 2). We defined three consumer categories: (1) *dispersers*, that disperse intact seeds by either endozoochory or synzoochory; (2) *neutral consumers*, that leave the seed intact under the parent plant; (3) *predators*, that destroy the seed, whether the remains are spat out, eliminated in feces, or rotted whole in a food hoard.

Birds and monkeys disperse seeds of most of the fruits they eat (Table 4). Dispersal seems mostly endozoochorous in turacos and hornbills. Because they choose small fruits, most seeds are swallowed. Our observations indicate that passage through their weak gizzards does not destroy the seeds.

Dispersal by monkeys is endozoochorous for small-seeded fruits. For others the dispersal mode depends on the degree of attachment of the flesh to the seed. The more strongly attached, the more probable that the monkey will swallow both flesh and seed (e.g. *Cissus dinklagei* or various Apocynaceae). When the soft flesh is free from the seed, the latter is often spat out. This usually happens at some distance from the parent tree because the monkeys fill their cheek-pouches and move to another place to eat the con-

Table 4. Number of fruit species whose seeds are dispersed, not dispersed, or predated by the different groups of consumers (see Appendix 2)

Groups	Dispersers	Neutral consumers	Predators
Birds	32	0	4
Small rodents	14	0	51
Squirrels	7	0	34
Large rodents	12	4	28
Ruminants	13	8	37
Monkeys	59	10	3

tents. When the seed is very easily separated from the fruit (e.g. *Polyalthia suaveolens*), it may be spat out under the parent tree. Finally, depending on the relative sizes of monkey and fruit species, the seed may or may not be swallowed with an aril. *Cercocebus albigena* (8 kg) thus swallows seeds of Myristicaceae without first detaching the aril, while *Cercopithecus* species (3–6 kg) spat out most seeds and swallow only arils, after carrying away a full cheek-load of arillate seeds.

Almost all other consumers are seed-predators, including most terrestrial species (Table 4), particularly squirrels and small rodents, which are chiefly granivores that eat only the flesh of a few fleshy fruits with many tiny seeds (e.g. *Ficus* spp. and *Musanga cecropioides*). For the latter, they are dispersers (as are almost all consumers), but for the most part they tear off and spit out the fibrous flesh that surrounds nuts and eat only the seeds. The small gape of small rodents prevents them from eating very large fruits unless the husk has first been removed by another agent, such as a ruminant, or has rotted off. Dispersal by these rodents lies mainly in their food hoarding behaviors (including seeds inevitably dropped in transit).

Squirrels store fruits temporarily for use within a few days by wedging them in crevices, or else bury them for longer storage. We have no information on the germination success of any of these seeds. Squirrels, like monkeys, also transport fruits to eat them away from the parent tree, and often drop partially eaten multiseeded fruits with intact seeds remaining.

Table 5. List of fruit parameters which significantly differ between the two fruit species categories. $***=P<0.001$; $**=P<0.01$; $*=P<0.05$

Fruit species categories	No seed predation before dispersal	Seed predation before dispersal
$N=$	65	29
Fruit color***	yellow, orange, red, violet	brown, green
Fruit weight**	<50 g	>50 g
Type of flesh***	succulent pulp, arils	dry fibrous pulp, fleshless
Seed protection*	absent or weak	strong

Small rodents take seeds to eat them in sheltered "dining rooms"; there are many of these, most often under the crown of the fruit tree. Few transported seeds escape total destruction (parts of seeds can sometimes germinate).

Of the large rodents, the Gambian rat hoards large numbers of certain fruits in its deep burrows: most are completely destroyed; only the hardest nuts last significantly and twice these were seen to germinate (*Detarium macrocarpum*).

The brush-tailed porcupine has a clearer disperser role. It carries fruits to eat them under the shelter of fallen logs, sometimes dozens of meters from the source. Many seeds can accumulate, some of them intact (notably Myristicaceae); however, we have not yet seen these germinate.

Ruminants normally eat entire fruits: husk, flesh and seed are destroyed by chewing. Nonetheless, a few observations in the field and experiments in captivity show that for a few medium-sized fruits with hard nuts (e.g. *Antrocaryon klaineanum*) ruminants may spat out seeds during rumination. This always occurs away from the fruit source. When fruits have seeds that are too large, the role of ruminants is neutral, as the husk is chewed off and the nuts are left where found (e.g. *Detarium macrocarpum*). It is thus likely that the size of seeds dispersed increases with the size of the ruminant consumer: the larger the animal, the greater the number of fruit species it disperses.

Elephants are certainly one of the major terrestrial dispersers and some plant species may primarily depend on them for dispersal. Piles of old elephant dung are commonly covered with vigorous seedlings that have sprouted from seeds that have passed through the animal, complete with fertilizer. Some huge fruits for which elephants would seem the only possible dispersers could conceivably also be eaten by the largest primates – apes and mandrills (e.g. *Picralima nitida* or *Strychnos aculeata*).

Fruit characters and disperser activity

As suggested by Janzen (1969) we can divide fruit into two classes according to whether or not we have observed seed predation before dispersal (Appendix 2). On this basis, we find a significant difference between the two classes with regard to our fruit characters. The classes differ in color, weight, seed protection, and kind of flesh (Table 5). Fruits with no pre-dispersal predation are generally brightly colored, with a juicy flesh or arillate seed. They tend to be

small and lack a hard nut. Fruits with pre-dispersal seed predation are generally dull-colored, with fibrous flesh and a well-protected seed, or are dehiscent without any edible flesh. Neither seed number, thickness of the outer covering, nor seed size differ significantly between the two classes.

Discussion

Consumer dietary overlap and competition

The modes of fruit-species partitioning within a group of trophically-related consumers simultaneously involve both individual species constraints related to metabolic needs, digestive physiology, and ingestion and manipulative capacities, and an interplay of interspecific relations of competition and mutualism between combinations of consumers and resources.

We showed that there is major overlap in the fruit diets of members of the community studied, even between taxonomically distant groups. The degrees of overlap we found exceed those calculated by Fleming (1979) from data in the literature. Fleming calculates a coefficient of community at the level of fruit genera of 0.13 between three cebid primates on Barro Colorado Island and Trinidad birds, while the Colombian spider monkey eats 7 genera of 22 in common with the same birds. Calculated on the fruit species level, the minimum community coefficients observed in Gabon were 0.27 (birds/large rodents) and 0.30 (birds/ruminants) while the maximum values reach 0.42 (birds/monkeys; ruminants/monkeys) and 0.43 (large rodents/ruminants).

Competition between distantly related taxa, often considered weak (Fleming 1979) or as a "past competition" (Smith in Fleming 1979) is, therefore, potentially far more important than has been supposed. Furthermore, earlier studies of phylogenetically related species in our study area (Emmons 1981; Gautier-Hion 1980; Duplantier 1982; Sourd 1983; Dubost in press) show that interspecific overlap is high: of 100 plant species identified in the diets of *Cercopithecus* species, at least 70% are used in common by all four species.

Fruit characters and consumer choice

These results confirm an outstanding lack of specificity between fruit and consumer species as noted by several authors (e.g. Gautier-Hion et al. 1980: Wheelwright and Orians 1982; Howe and Smallwood 1982). Despite this lack of specificity, consideration of simple morphological traits of fruits reveals broad character syndromes associated with consumption by different taxa of vertebrate frugivore-granivores whether considered as either consumers or as dispersers and predators.

Other studies of dispersal syndromes have usually distinguished bird-dispersed plants from mammal- or monkey-dispersed fruits. Our study shows that partitioning occurs rather within the mammals than between birds and mammals and that there is a greater trophic difference based upon foraging patterns (foraging levels, daily metabolic needs...) than upon phylogenetic affinities. There is thus a bird-monkey syndrome and a ruminant-rodent syndrome. Likewise, the diets of large rodents are closer to those of ruminants than to those of other rodents. (We must note

·that we have only considered the largest birds which are the most likely to compete with monkeys.)

Fruit species and their arboreal dispersers

In the system we studied, the arboreal frugivores, birds and monkeys (and probably bats) are selective consumers and essential dispersers. Because they are the best placed for making first choice of available fruits (understory is an insignificant fruit source; unpublished data), we might expect them to exert a primary selection pressure on plant species. All fruits whose seeds they disperse offer a resource to reward their mutualist dispersers (Thompson 1982): either a sugar-rich flesh with few fibers, or an aril rich in lipid and protein. They have also developed bright color displays; some very complex for arillate seeds (f.e. *Trichillia gilgiana*: purple dehiscent capsule, shiny black seeds, bright orange arils). These fruits show no tendency to develop physically protected seeds.

Fruit choice by birds.

Birds choose fruits which differ from those of the total sample by weight, color, and type of flesh, all parameters which have been found to be associated.

Color alone doubtless has an essential role in fruit discrimination by these diurnal frugivores with good color vision. The choice by turacos and hornbills of purple-black, followed by red, supports previously reported bird preferences. The notable attraction of red was observed by Corner (1949) and shown experimentally by Turcek (1963) for temperate birds, whose preference order was red, black, blue. In tropical moist forest in Peru, "bird fruits" are red, black, white, blue, and purple (although relatively few species were actually seen eaten by birds, Janson 1983); and in South Africa, birds prefer black, followed by orange, then red (Knight and Siegfried 1983); while in French Guiana, they choose purple-black (Charles-Dominique et al. 1981). In all habitats, fleshy green fruits are avoided and are for the most part "bat fruits" (Fleming 1979; Charles-Dominique et al. 1981 and pers.obs.). Turcek (1963) showed experimentally that some birds avoided yellow, orange and green.

The choice by birds of purple-black and/or red thus seems universal and correlates with their good discrimination of red wavelengths. Willson and Melampy (1983) showed experimentally that the combination red-black, often found in arillate seeds, was particularly attractive to temperate birds. The attractiveness of highly nutritive arils to turacos and hornbills in Gabon has been similarly observed for toucans in the Neotropics (Skutch in McKey 1975; Sabatier 1983) and hornbills in the Camerouns (McKey 1975). In Central America, the role of birds in dispersal of the arillate seeds of Myristicaceae has been particularly well documented (Howe and Vande Kerckhove 1981). In Gabon, hornbills are equally important dispersers.

In his sample of fleshy fruits of a peruvian forest, Janson (1983) found that red, black, white, blue, and purple fruits ("bird fruits") tend to lack a thickened pericarp. This association did not clearly appear in our sample (Fig. 1) but it is evident that birds (other than parrots) lack the physical capacity to attack heavily protected fruits (Fig. 2). On the other hand, results from Gabon (this study), Peru (Janson 1983), and French Guiana (Sabatier 1983) show an association between small size and the colors red and purple. These two colors are the most selected by turacos and hornbills

in Gabon for which the size of items swallowed is limited by throat size and mandibulation capacities.

Fruit choice by monkeys.

Like birds, monkeys are attracted by the red and multicolored displays and are important consumers of arils and effective dispersers of arillate seeds plant species (Gautier-Hion 1984). For these latter and especially for Myristicaceae, they are in direct competition with hornbills which are far from being "specialized dispersers" (McKey 1975). Similar competition for arils of *Virola* (Myristicaceae) between spider monkeys and toucans has been reported in French Guiana (Sabatier 1983). Monkeys are also attracted by orange and yellow fruit which characterize mainly the succulent fleshy fruit (Fig. 2).

Janson (1983) and Knight and Siegfried (1983) consider "mammal fruits" to be yellow, orange or green, and larger than "bird fruits". Knight and Siegfried moreover add that mammals avoid red, but do not specify the sample of mammals considered and data on actual consumption are unclear. In the system we studied, monkeys clearly avoid green and brown fruits but not red ones. Their strong canines and advanced manipulative abilities allow them to attack very thick pericarps.

Recently Terborgh (1983) reported that five primates in Peru tended to choose yellow, orange, and red fruits. Snodderly (1979) in contrast notes a preference by *Callicebus torquatus* for green and brown fruits while spider monkeys in French Guiana take green (immature) *Virola* (Sabatier 1983).

Fruit species and their predators

In predator-dispersers, color does not seem to influence fruit choice, even when the animals are diurnal and have color vision (squirrels, Jacobs 1978, and several duikers). We remark that many fruits lose their bright colors and turn brown after falling on the ground where terrestrial mammals feed on them. In contrast to the hypothesis of Cooper et al. (in press), even arboreal squirrels do not seem to choose more colorful fruits that contrast with the foliage than do terrestrial squirrels.

Squirrels are mainly granivorous and choose dry fibrous fruits with few seeds. The flesh is not a basis of choice; it is usually spat out. They differ from large rodents chiefly in that they do not select fruits by weight, although the largest squirrel species can eat very large fruits because of their excellent manipulative ability.

Small rodents, with small energy requirements and small home ranges and movements (i.e. there may not be many fruit species to choose from in their area) do not seem to select fruits on the basis on the fruit characters analysed here. These granivores feed on all types of fruit and may choose more narrowly on the basis of individual items rather than species.

Large rodents are more clearly selective: they choose large, fibrous fruits with one or two large seeds. Their strong jaw musculature and teeth allow them to open well-protected seeds that yield a large reward. The trophic role of large rodents puts them more in competition with ruminants than with other rodents. This can be seen in a number of other ecological characteristics (Emmons 1983; Roussilhon and Emmons, unpublished data). A major difference is that where ruminants eat whole fruit, the rodents are mainly seedeaters.

Finally ruminants appear to eat all types of fruit except very small ones. This can be related to their energy requirements. Given the strong association between fruit weight and fiber content, choice of large fruits gives ruminants necessary bulk for their digesta.

The selective pressures exerted by the above predator-dispersers seem to have led mainly to thickening the shell protecting the seeds. The thicker the shell, the higher the chances of seed survival, either because harder nuts are spat out (by ruminants) or because they are swallowed and pass intact through the gut (by elephants and the largest ruminants), or because they cannot be opened efficiently (by small murid rodents and squirrels), or resist rotting in rodent food hoards.

Seed size and number do not appear to have been much modified, considering the array of species eaten by the most destructive vertebrate predators (rodents and ruminants). These results support hypotheses proposed by Smith (1975), who distinguished variables independent of consumer influence, such as amount of reserves within a seed, from consumer-influenced variables such as seed protection. The situation may not be so simple, however: nutshell thickness may influence survival independantly of consumer action, for example retarding rotting during dormancy. On the other hand, seed reserves can influence predation pressures. Thus large rodents who choose large, few-seeded fruits may select for polymorphism in seed number, as the presence of an extra seed may increase chances of survival (Smith 1975). The same is true for small rodents which often break off their meals before finishing a fruit; if they leave the fruit after having eaten one seed, others can survive.

The development of a hard nut in large, indehiscent fruits is associated with a fibrous mesocarp. In drupes, the development of such a mesocarp cannot be easily explained by selection by food-hoarding rodents, for which the mesocarp is simply a barrier to be removed. It is more likely to be selected for by elephants and larger ruminants, both of which are effective dispersers of large seeds and for which the fibrous flesh is a useful nutrient. The characters of such drupes recall those of some South America fruit species which, according to Janzen and Martin (1982) would have evolved under pressure of large mammals now extinct (but we note that several of their listed "megafaunal fruits" are in fact bat-dispersed; Emmons, unpublished data). We also cannot reject the hypothesis that a dry fibrous flesh confers some advantage to germination.

Fruit transport

Janzen (1971) proposed two hypotheses to explain why arboreal animals transport fruits instead of feeding at the fruit source: (1) the fruit tree provides inadequate supports and (2) the tree is a focal point for predators. The predator avoidance model, also discussed by Howe (1979) seems reasonable to account for fruit transport in Gabon by large birds, monkeys and squirrels in the canopy and also by terrestrial rodents. Transport is the rule from large emergents with open foliage. Hornbills, passing into a *Pycnanthus angolensis* (Myristicaceae) rapidly gather several fruits in their beaks and immediately fly to a neighboring dense foliage tree. Likewise, monkeys avidly fill their cheek pouches before retiring to an area of dense foliage in order to eat. In contrast, in middle story trees hornbills, turacos and monkeys may or may not remain and feed in the fruit

tree. Risk of predation by birds of prey (notably by the crowned hawk-eagle) is reduced in dense vegetation.

Large fruiting trees may also serve as focal points for terrestrial predators: remnants of brush-tailed porcupines capture by leopards have been found several times under large fruiting *Drypetes gowweileri*, under which porcupines congregate to feed.

Results

Several basic plant strategies can be demonstrated in our plant sample. First, species that have developed an extra resource for arboreal consumers and associated color displays have thin walls around their seeds: these fruit are either juicy, sugar-rich berries or drupes (e.g. Apocynaceae; Anacardiaceae) or are dehiscent fruits with arillate seeds (Myristicaceae, Meliaceae). Most of these fruit species are dispersed by canopy birds and monkeys. However, some species of small juicy fruits with thin pericarp and many tiny seeds are eaten by most frugivorous and granivorous vertebrates. Because of their tiny seeds, all consumers disperse them by endozoochory, with essentially no predation. Examples include many Moraceae and Rubiaceae ("generalized fruits", McKey 1975).

Another syndrome includes fruits with a resource of dry, fibrous flesh, with well-protected large seeds. These are large fruits (Irvingiaceae, Pandaceae, Olacaceae) primarily dispersed by ruminants and elephants, and secondarily by rodents. With the latter, the costs are particularly high: analysis of burrow contents of *Praomys tulbergi minor* showed that of 1880 hoarded nuts, 85% of seeds had been eaten, 13.3% were rotten, and only 1.7% were intact. No germination was seen. These are like the results of Calahane (in Janzen 1971) that gray and fox squirrels recovered 415 of 419 buried nuts.

To these zoochorous fruits can be added mechanically dispersed dehiscent dry pods and capsules, with non-arillate seeds that are not physically (but probably chemically) protected (e.g. Euphorbiaceae, Cesalpinoid legumes). Many of these are eaten by vertebrate predators that may accidentally disperse a few seeds: we found little seeds of *Croton oligandrum* capsules intact in elephant dung and bird gizzards, just as legume seeds may occasionally emerge intact from the guts of ruminants. These "accidental" methods of dispersal are probably of little importance to the plant.

Even if, as argued by Howe and Smallwood (1982), definitions of dispersal syndromes should not substitute for field studies of the dispersal process, our analysis lets look to the related phenomena of: (1) the organization of trophic niches in the community and (2) the coadaptive tendencies between the plants and animals in the system.

Testable predictions can be generated that can be easily transposed to other community types for comparative purposes. Sabatier (1983) has similarly proposed a classification of fruit from French Guiana, based upon morphological traits without regard to botanical structure. More such methodological research is needed, especially with regard to features relevant to actual (and not theoretical) consumers.

Appendix 1

List of animal species studied

In each family, species are listed by increasing weight; (*n*) = number of stomach contents analysed; *A* = arboreal; *T* = terrestrial; *A T* = arboreal-terrestrial; *D* = diurnal; *N* = nocturnal; *D N* = diurnal-nocturnal

Birds – mean weight range: 250–1,900 g
  Bucerotidae: *Tockus fasciatus* (*n* = 1), A, D; *Bycanistes fistulator* (*n* = 1), A, D; *B. albotibialis* (*n* = 2), 1, D; *Ceratogymna atrata* (*n* = 2), A, D
  Musophagidae: *Tauraco persa* (*n* = 5), A, D; *T. macrorhyncus* (*n* = 6), A, D; *Corytheola cristata* (*n* = 2), A, D
Small Rodents – mean weight range: 20–78 g
  Muridae: *Hylomyscus stella* (*n* = 73), AT, N; *H. fumosus* (*n* =

12), T, N; *Praomys tulbergi minor* (*n* = 30), T, N; *Thamnomys rutilans* (*n* = 5), A, N; *Hybomys univittatus* (*n* = 51), T, D; *Stochomys longicaudatus* (*n* = 14), A, N; *Malacomys longipes* (*n* = 24), T, N
  Dendromuridae: *Deomys ferrugineus* (*n* = 29), T, N
Squirrels – mean weight range: 16.5–690 g
  Sciuridae: *Myosciurus pumilio* (*n* = 3), A, D; *Aethosciurus poenis* (*n* = 8), A, D; *Funisciurus isabella* (*n* = 14), AT, D; *Heliosciurus rufobrachium* (*n* = 15), A, D; *Epixerus ebii* (*n* = 4), T, D; *Protoxerus stangeri* (*n* = 13), A, D
Large Rodents – mean weight range: 1,250–3,650 g
  Cricetidae: *Cricetomys eminii* (*n* = 10), T, N
  Hystricidae: *Atherurus africanus* (*n* = 13), T, N
Ruminants – mean weight range: 4,900–68,000 g
  Tragulidae: *Hyemoschus aquaticus* (*n* = 50), T, N
  Bovidae: *Cephalophus monticola* (*n* = 30), T, D; *C. leucogaster* (*n* = 15), T, D; *C. nigrifons* (*n* = 11), T, D; *C. callipygus* (*n* = 30), T, D; *C. dorsalis* (*n* = 24), T, N; *C. sylvicultor* (*n* = 6), T, DN
Monkeys – mean weight range/ 1,250–7,800 g
  Cercopithecidae: *Miopithecus talapoin* (*n* = 9), A, D; *Cercopithecus cephus* (*n* = 62), A, D; *C. pogonias* (*n* = 51), A, D; *C. nictitans* (*n* = 100), A, D; *C. neglectus* (*n* = 9), AT, D; *Cercocebus albigena* (*n* = 18), A, D

Appendix 2.

List of plant species whose fruit are eaten by the vertebrate community
Life forms: EP = epiphyte; HE = herbs; LI = liana; SH = arborescent shrub (< 7 m); ST = small tree (7–15 m); MT = middle-sized tree (15–30 m); TT = tall tree (> 30 m)
Types of fruit: BE = berries; CA = capsules; DR = drupes; PO = pods; SY = all syncarpic forms; WF = winged fruit or seed
Consumers: BI = birds; SR = small rodents; SQ = squirrels; LR = large rodents; RU = ruminants; MO = monkeys; EL = elephant
Types of consumption: d = disperser; n = neutral consumer; p = predator; + = unknown

Plant species	Life Form	Fruit Type	BI	SR	SQ	LR	RU	MO	EL
Agavaceae									
Dracaena arborea (Willd.) Link.	MT	BE	d	+		+	+		
Anacardiaceae									
Antrocaryon klaineanum Pierre	TT	DR		p		p	d,n	d	d
Antrocaryon nannanii de Wild.	TT	DR					+		
Pseudospondia longifolia Engl.	MT	DR	+	p	p	p	d,n	d	d
Sorindeia nitidula Engl.	ST	DR			p	p		d	
Trichoscypha acuminata Engl.	ST	DR			+	+	p	d,n	
Trichoscypha arborea (A. Chev.) A. Chev.	TT	DR			+	+		d,n	
Tricoscypha cf. *mannii* Hook. f.	MT	DR	+					d,n	
Tricoscypha sp. 1	ST	DR		+	+		+	d,n	
Annonaceae									
Anonidium mannii (Oliv.) Engl. and Diels	MT	SY	+			p	p	d	d
Hexalobus crispiflorus A. Rich.	MT	SY		p				d	d
Monanthotaxis schweinfurthii (Engl. and Diels) Verdcourt	LI	SY						+	
Pachypodanthium sp. 1	MT	SY	d	p			p	d	
Polyalthia suaveolens Engl. and Diels	MT	BE	d	p	p	n,p	p	d,n	d
Uvaria klaineana Engl. and Diels	LI	BE		p			p	d	
Uvariopsis solheidii (De Wild.) Robyns and Ghesq.	ST	BE		+	+				
Xylopia aethiopica (Dunal) A.Rich.	MT	SY	d	d,p	p	+	p	d	
Xylopia gilbertii Boutique	MT	SY	d	d,p				d	
Xylopia hypolampra Mildbr.	TT	SY	d		p		p	d	
Xylopia quintasii Engl.	MT	SY	d					d	
Xylopia staudtii Engl. and Diels	MT	SY	d	d,p			p	d	
Xylopia sp. 1	MT	SY		d,p				d	
Apocynaceae									
Cylindropsis parvifolia Pierre	LI	BE	p	p			p	d	
Dictyophleba stipulosa (S. Moore and Wernh.) Pichon	LI	BE	p	p			p	d	
Landolphia owariensis P. Beauv.	LI	BE					+	d	
Picralima nitida (Stapf) Th. and Dur.	ST	BE		d,p		d,p			d
Apocynaceae sp. 1	LI	BE						d	

Appendix 2 (continued)

Plant species	Life Form	Fruit Type	Consumers						
			BI	SR	SQ	LR	RU	MO	EL
Burseraceae									
Canarium schweinfurthii Engl.	TT	DR	+	+	+		+	+	
Dacryodes buettneri (Engl.) Lam.	TT	DR	d	p		p	p	d	
Dacryodes klaineana (Pierre) Lam.	MT	DR	d					d	
Dacryodes normandii Aubrév. and Pellegr.	MT	DR	d			p			d
Santiria trimera (Oliv.) Aubrév.	MT	DR		p	p	+	+	d	
Caesalpiniaceae									
Crudia gabonensis Pierre ex De Wild.	TT	PO		d,p					d,p
Detarium macrocarpum Harms	TT	DR		p		d,p	n		d
Dialium dinklagei Harms	MT	PO			p		p	d,p	
Griffonia physocarpa Baill.	LI	PO	p	p			p		
Scorodophloeus zenkeri Harms	MT	PO					p		
Chrysobalanaceae									
Parinari excelsa Sabine	TT	DR			+	+			
Connaraceae									
Castanola paradoxa (Gilg) Schelleb.	LI	PO		+				+	
Cnestis sp. 1	LI	PO		p			p	d	
Convolvulaceae									
Neuropeltis acuminata (P. Beauv.) Benth.	LI	WF		p					
Dichapetalaceae									
Dichapetalum integripetalum Engl.	LI	DR					p	d	
Dichapetalum monbuttense Engl.	LI	DR				p		d	
Ebenaceae									
Diospyros crassiflora Hiern	MT	BE					+		
Euphorbiaceae									
Alchornea floribunda Muell. Arg.	SH	CA		+			p		
Croton oligandrus Pierre	MT	CA	d,p	p	d,p				d
Drypetes gossweileri S.Moore	TT	DR		p		p			d
Drypetes spinosodentata (Pax) Hutch.	MT	DR				p		d	
Macaranga barteri Muell. Arg.	SH	CA	d,p		p			p	
Plagiostyles africana (Muell. Arg.) Prain	MT	DR					p	d	
Uapaca paludosa Aubr. and Leandri	MT	DR	+	p	p	d	p	d	d
Flacourtiaceae									
Caloncoba welwitschii (Oliv.) Gilg	SH	CA						d	
Campostylus mannii (Oliv.) Gilg	ST	DR		p				d	
Lindackeria dentata (Oliv.) Gilg	SH	CA		p				d	
Guttiferaceae									
Allanblackia klainei Pierre	MT	DR				+	+		+
Mammea africana Sabine	TT	BE			p	+	p	d	d
Pentadesma butyracea Sabine	MT	DR				+	+		
Symphonia globulifera L.f.	MT	DR	+				+	d	
Hippocrateaceae									
Salacia sp. 1	SH	BE	+	+		+	+	+	
Icacinaceae									
Lavigeria macrocarpa (Oliv.) Pierre	LI	DR				+			
Irvingiaceae									
Irvingia gabonensis Baill.	MT	DR					d,n	n	d
Klainedoxa gabonensis Pierre	TT	DR		d,p	p	n	n	n	d
Klainedoxa sp. 1	TT	DR		d,p	p	n	n		

Appendix 2 (continued)

Plant species	Life Form	Fruit Type	Consumers						
			BI	SR	SQ	LR	RU	MO	EL
Lauraceae									
Beilschmiedia fulva Rob. and Wilcz.	MT	DR	d			p	p		d
Lecythidaceae									
Petersianthus macrocarpus (P. Beauv.) Liben	MT	WF	p	d,p	p				
Linaceae									
Hugonia planchonii Hook. f.	LI	CA					d		
Hugonia platysepala Welw. ex Oliv.	LI	CA	d				d	d	
Hugonia spicata Oliv.	LI	CA	d	d,p			d	d	
Loganiaceae									
Strychnos aculeata Solered	LI	BE		p	p	p			d
Loranthaceae									
Viscum sp. 1	EP	BE	+					+	
Maranthaceae									
Hypselodelphis violacea (Ridl.) M.-Redh.	HE	CA		p				p	
Sarcophrynium schweinfurthianum M.-Redh.	HE	BE		+					
Meliaceae									
Guarea glomerulata Harms	SH	CA		+					
Lovoa trichilioides Harms	TT	CA	d						
Trichillia gilgiana Harms	MT	CA	d	p	p	p	p	d	
Trichillia prieureana A. Juss.	MT	CA	d					d	
Trichillia sp. 1	TT	CA	d	p	p			d	
Mimosaceae									
Entada gigas Fawcett and Rendle	LI	PO			p				
Parkia bicolor A. Chev.	TT	PO					+		
Pentaclethra eetveldeana De Wild and Th. Dur.	MT	PO			p		p		
Pentaclethra macrophylla Benth.	MT	PO				p			
Piptadeniastrum africanum Brenan	TT	PO	+	p			p		
Moraceae									
Ficus craterostoma Warb.	EP	SY	d	d				d	d
Ficus cf. *lingua* Warb.	EP	SY	d				d		
Ficus wildemaniana Warb.	EP	SY	d	d	d	d	d	d	d
Musanga cecropioides R. Br.	MT	SY	d		d	d	d	d	
Myrianthus arboreus P. Beauv.	ST	SY					p	d	d
Myristicaceae									
Coelocaryon preussii Warb.	MT	DR	d	d,p	d,p	d,p	p	d	
Pycnanthus angolensis (Welw.) Exell	TT	DR	d		d,p	d,p	p	d	d
Scyphocephalium ochocoa Warb.	TT	DR			p	p	p	n	
Staudtia gabonensis Warb.	TT	DR	d	d,p	d,p	d,p	p	d	
Ochnaceae									
Lophira alata Banks ex Gaertn.	TT	WF		+	+		+		
Olacaceae									
Coula edulis Baill.	MT	DR		p	p	p	n		d
Diogoa zenkeri (Engl.) Exell and Mendonça	ST	DR			p		p		
Heisteria parvifolia Sm.	ST	DR	d	d,p	p	p	p	d	d
Ongokea gore (Hua) Pierre	TT	DR		p		d,p	d,n		
Strombosia grandifolia Hook. f.	ST	DR	d	p	p	d,p	p	d	
Strombosiopsis tetrandra (Engl.) Engl	MT	DR	+	p	+	+		n	d
Pandaceae									
Panda oleosa Pierre	MT	DR		p	d,p	d,n,p	n		d

Appendix 2 (continued)

Plant species	Life Form	Fruit Type	Consumers						
			BI	SR	SQ	LR	RU	MO	EL
Passifloraceae									
Paropsia grewioides Welw. ex Mast.	ST	CA		p					
Rhizophoraceae									
Anopyxis klaineana (Pierre) Engl.	TT	CA					p		
Rubiaceae									
Massularia acuminata (G. Don) Bullock ex Hoyle	SH	BE		+					
Mussaenda sp. 1	LI	BE		+				+	
Nauclea diderrichii (De Wild.) Merr.	TT	SY		d,p		d,p	+	d	
Tarenna sp. 1	SH	BE		+					
Samydaceae									
Casearia barteri Mast.	MT	CA				p		d	
Sapindaceae									
Allophylus sp. 1	SH	DR	+					+	
Blighia welwitschii (Hiern.) Radkl	TT	CA	d	p	p		+		
Chytranthus gillettii De Wild.	SH	BE						d	
Pancovia pedicellaris Radkl. and Gilg	SH	BE				p	p	d	
Sapotaceae									
Baillonella toxisperma Pierre	TT	BE		+		+			
Gambeya beguei Aubrév. Pellegr.	MT	BE		p		+	d		d
Gambeya boukokoensis Aubrév. and Pellegr.	MT	BE					d		d
Gambeya lacourtiana (De Wild.) Aubrév. and Pellegr.	TT	BE		p		+	d	d,n	d
Synsepalum longecuneatum De Wild.	ST	BE			p			d	
Sterculiaceae									
Sterculia tragacantha Lindl.	MT	PO	d						
Tiliaceae									
Duboscia macrocarpa Bocq.	MT	DR						p	d
Grewia coriacea Mast.	MT	DR	+	p	p			d	
Urticaceae									
Urera cameroonensis Wedd.	LI	BE	+						
Verbenaceae									
Vitex sp. 1	ST	DR		+					
Violaceae									
Rinorea sp. 1	ST	CA		p					
Vitaceae									
Cissus dinklagei Gilg. and Brandt	LI	DR	d	p	p	p	p	d	

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