

FRUIT CHOICE AND SEED DISSEMINATION BY BIRDS AND MAMMALS IN THE EVERGREEN FORESTS OF UPLAND MALAWI

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The study of interactions between fruit and their vertebrate consumers has generated a great deal of interest in recent decades. Most authors have investigated the habits of single bird or mammal species (e.g. Phillips, 1926, 1927, 1928 ; Frith, 1957 ; Snow, 1962 ; Gautier-Hion, 1971 ; Alexandre, 1978) or the assemblages of species — mainly birds — attracted to the fruits of particular trees (e.g. Land, 1963 ; Willis, 1966 ; Leck, 1969 ; Howe, 1977, 1981 ; Bronstein & Hoffmann, 1987). Studies of the fruit-eating behaviour of phylogenetically-related groups of consumers are fewer (e.g. Snow & Snow, 1971 ; Crome, 1975 ; Gautier-Hion, 1980 ; Beehler, 1983) and those dealing with a whole class of vertebrates such as birds are evidently rare (Frost, 1980 — incompletely published ; Herrera, 1984 ; Wheelwright *et al.* 1984). Noteworthy is the work by Gautier-Hion *et al.*, (1985a) who analysed fruit choice in a large community of mammals (bats excepted) and seven large canopy bird species in a Gabon rain forest.

Early models of plant-frugivore interactions have stressed the distinction between specialized, obligate frugivores that feed on, and disperse efficiently, high-quality fruits (with low and extended fruit production), and the unspecialized, opportunist feeders that take less nutritious fruits (with scattered, shorter seasons) (McKey, 1975 ; Howe & Estabrook, 1977 ; Snow, 1981). However, subsequent field work has largely failed to confirm these original predictions on diet specialization and dispersal quality ; most studies of birds have, instead, emphasized the tremendous diversity of frugivores at fruiting trees, even with high-reward fruits (e.g. McDiamird *et al.*, 1977 ; Frost, 1980 ; Wheelwright *et al.*, 1984 ; other references in Wheelwright & Orians, 1982, p. 403). Non-obligate, « opportunist » fruit-eaters may be better seed disseminators than obligate frugivores (Pratt & Stiles, 1983). McKey's (1975) theory on diet specialization and dispersal quality has also been criticized strongly on theoretical grounds (Wheelwright & Orians, 1982 ; Howe, 1984 ; Herrera, 1985 ; Wheelwright, *in press*) : plants have little or no control over the quality of dispersal of their seeds, and finely-tuned coevolved interactions between plants and their seed dispersers are expected to be at best very rare in nature (Wheelwright & Orians, 1982). Rather, diffuse coevolution between groups of species is more likely to occur (Janzen, 1980) and can explain the broad co-adaptations observed between fruits and their consumers (van der Pijl, 1969). Recent examples are the

discoveries of broad fruit character syndromes associated with different consumer taxa in Gabon (Gautier-Hion *et al.*, 1985a), and in Peru (Janson, 1983). Co-adapted features of fruits that influence the choice of fruit species by animals include colour (e.g. Turcek, 1963 ; Wheelwright & Janson, 1985), size (limited in birds by gape width : Wheelwright, 1985a), fruit structure (e.g. Gautier-Hion *et al.*, 1985 ; Pratt & Stiles, 1985) and accessibility (Snow, 1971 ; Moermond & Denslow, 1983).

The present study examines the interactions between fruit plants in the upland evergreen forests of Malawi and their consumers — mostly birds, also a few mammals including a *Cercopithecus* monkey. It analyses the extent of trophic competition (versus specialization) between species, and consumer choice as it relates to fruit characters (type, size and colour). The likelihood of coevolutionary trends between fruiting seasons and frugivores is investigated. Finally, from data on seed transit (based partly on the literature), I discuss the potential role of various consumers as seed disseminators, particularly with regard to plants that are endemic to the Afromontane Region (White, 1983a), i.e. with scattered distribution on isolated mountains. As seed predators can also act as dispersers (e.g. van der Pijl, 1969), they are included in this account.

MATERIALS AND METHODS

Study area and methods

Malawi is a country of diverse, mountainous relief, with just over 40 areas of evergreen forest isolated from each other on hills and plateaux (Fig. 1). Most of them are small (from a few to several hundred ha in size, rarely more) and situated at high altitudes — mainly 1 600-2 400 m north of 14 N, 1 200-2 300 m in the south. The main chorological categories of tree species are Afromontane endemics (i.e. confined to the Afromontane Region, White, 1983a) and near-endemics (predominantly Afromontane). There are few lowland forests (at 600-1 100 m).

The flora of the evergreen forests was described in part by Chapman & White (1970) ; more complete accounts have been prepared, for the Nyika Plateau in the north (Dowsett-Lemaire, 1985a) and elsewhere (Dowsett-Lemaire, 1988 and *in prep.*).

The main study area is the southwestern Nyika Plateau, with 550 ha of forest on either side of the Zambia-Malawi international border, at 1 950-2 200 m alt. Monthly censuses of fruiting trees and miscellaneous observations on frugivores were carried out for a total of 16 months (between October 1980 and June 1983). Visitation rates of frugivores to fruit trees varied extensively between tree species, from 0/10 hours (e.g. *Pittosporum viridiflorum*) to sometimes over 100/hour in popular trees such as *Polyscias fulva*. In a few cases, I attempted to make quantitative assessments of the numbers of fruits taken by different species at a particular tree, but results were too incomplete for analysis. A major problem was the varying flight distance of different bird species : a close watch prevented the shier non-passerines from feeding while a more distant watch (possible only for the crowns of some canopy trees visible from prominent sites outside forest) led to smaller birds being overlooked. As a result, data on fruit consumption cannot be presented quantitatively.

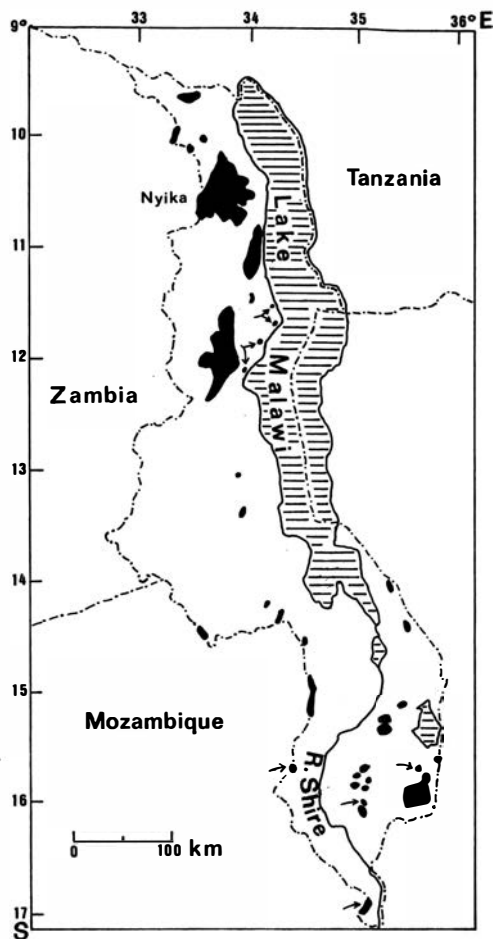


Figure 1. — Map of Malawi showing the main study site (Nyika Plateau) and other areas of evergreen forest on hills and high plateaux. The few localities of lowland forest are indicated with arrows.

For another 18 months (between September 1982 and June 1984) visits were paid to all the important forested areas in Malawi; several forests in the north were revisited in October–November 1986. Field work involved broad floristic and faunistic research, and observations on frugivores were obtained as opportunities arose during bird and plant surveys.

Plant species studied

All species of plants studied and others mentioned in the text are listed with authors' names in systematic family order in Appendix 1. Nomenclature follows Palgrave (1981) except for some recent changes advised by F. White (University of Oxford) and staff at the Herbarium of Kew. Most trees and climbers in upland forest in Malawi have fleshy fruits. For instance, of 127 trees and large lianas

recorded on the SW Nyika, 14 are wind-dispersed (11 %), five have pods (4 %), six woody capsules (5 %) and 102 (80 %) have fleshy fruits.

The type, size (transverse diameter) and colour categories of 134 fruit species are summarized in Table I — excluding the small dry diaspores of species used by seed-eaters only, and full details are given for 128 individual species in Table V. The distinction between berry and drupe is maintained in the absence of a more appropriate ecological classification; unlike drupes, berries do not have an extra seed protection coat, but most of them (with the exception of the mistletoes, Loranthaceae and Viscaceae) do have hard seed coats. Berries are usually multi-seeded and drupes single-seeded. Some of the capsules are fleshy before splitting and are ecologically close to drupes (*Clutia abyssinica*, *Macaranga* spp.). Some drupes are generally eaten before they are fully mature: only a very few fruits of *Olea africana*, *O. capensis* and *Jasminum abyssinicum* are left to turn purple; those of *Rauvolfia caffra* (red when mature) were also seen to be eaten when soft and green. The colour of such fruits was categorized as green. The ripe fruits of *Ekebergia capensis* were not seen to turn red — as observed elsewhere in the range.

Overall, the main fruit types are berries (including infructescences) and drupes, of which there are about equal proportions, and the main colours are red and purple/black. On average, berries are larger than drupes (Table II, the difference is significant with $\chi^2 = 22.48$, $P < 0.001$). The largest drupes are 40 mm in diameter (*Parinari* spp.), whereas berries reach 200-250 mm (*Tabernaemontana stapfiana*, *Treculia africana*).

Fruits of eight important large trees were collected for nutrient analysis, but results could be obtained for only three species.

Fruiting phenology

The main rains in Malawi fall in the summer months from November to April (Dowsett-Lemaire, 1985a). A few plant species fruit aseasonally (*Clutia abyssinica*, *Ficus* spp., *Viscum shirensis*); figs *Ficus* spp. show inter-tree asynchrony

TABLE I

Frequency distribution of 134 fruit species according to type, size (transverse diameter) and colour.

B = berry (including figs and infructescences); D = drupe or drupelet; A = aril (including fleshy receptacle in *Podocarpus*); C = capsule; C + A = capsules containing arils but usually eaten whole (slightly fleshy). Green includes greenish-yellow, and red includes reddish-brown.

Fruit type					Size (mm)			
B	D	A	C	C + A	3-9	10-19	20-29	30-250
56	58	9	8	3	69	35	14	16
Green	Yellow	Orange	Red	Purple/black	Blue	Brown	White	
21	14	17	38	29	1	12	2	

TABLE II

Distribution of size classes in berries and drupes.

	n	Transverse diameter in mm			
		3-9	10-19	20-29	30-250
Berry	56	16	16	10	14
Drupe	58	39	14	3	2

TABLE III

Fruiting seasonality of forest plant species (n = 75).

Data on complete fruiting seasons come mostly from northern Malawi, especially the Nyika Plateau.

	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Total species in fruit	21	20	14	11	6	6	10	20	34	33	29	24

(cf. Janzen, 1979). With these exceptions (excluded from Table III), fruiting of most species is highly seasonal and shows a peak in September-November and a trough in March-July. Many of the larger trees, however, do not fruit every year (Dowsett-Lemaire, 1985a).

Animal species studied

Bird nomenclature follows Dowsett & Forbes-Watson (in press); mammal names are those of Ansell (1978) and Ansell & Dowsett (1988).

Observations on fruit-eating animals involve 48 bird and 10 mammal species. The only well-studied mammal is the blue monkey *Cercopithecus albogularis* (perhaps conspecific with *C. mitis*). The better-known birds are mainly those studied on the SW Nyika Plateau (Dowsett-Lemaire, 1983a): for example the diet of *Andropadus tephrolaemus* and *Tauraco schalowi* common in the Nyika forests is more completely known than that of their congeners *A. milanjensis* and *T. livingstonii* encountered in other forests. Table IV gives the weight (as indication of size, data from R.J. Dowsett, *pers. comm.*) and gape size of 15 bird species with at least 12 specific fruit-eating records, and summarizes briefly their status in the Malawi forests. Gape width was measured on museum specimens, with

samples of three to 12 individuals per species. The main breeding season of forest frugivorous birds is September-November (Dowsett & Dowsett-Lemaire, 1984) during the peak of fruit production (Table III). For further details of bird distribution in the country, see Benson & Benson (1977).

TABLE IV

Weight, gape breadth and status of 14 fruit-eating birds and one seed-eater (Aplopelia). Afromontane (near-) endemics are asterisked.

Species	Weight (g)	Gape breadth (mm)	Status
Columbidae :			
<i>Columba arquatrix</i> *	366	ca 13	Largely a breeding migrant ; also wanders
<i>Treron australis</i>	252	ca 13	A woodland bird, seasonal visitor to forest
<i>Aplopelia larvata</i> *	152	12-13.5	Mostly resident ; a few winter wanderers to lower altitudes
Musophagidae :			
<i>Tauraco schalowi</i>	290	12-13	Common resident west of Rift
<i>T. livingstonii</i>	290	12-13	Replaces <i>T. schalowi</i> east of Rift
Bucerotidae :			
<i>Bycanistes brevis</i>	1 200	40-49	Localized ; one population consists largely of breeding migrants
<i>B. bucinator</i>	680	36-43	More widespread than last, with little overlap
Capitonidae :			
<i>Pogoniulus leucomystax</i> *	12	ca 8	Mostly resident
Pycnonotidae :			
<i>Andropadus milanjensis</i> *	40	10-11	Mostly resident 1 100-2 000 m
<i>A. tephrolaemus</i> *	37	10-11	Commonest bulbul, 1 500-2 450 m ; a few winter wanderers to lower altitudes
<i>Pycnonotus barbatus</i>	35	10-11	Common on forest edges
Sylviidae :			
<i>Sylvia borin</i>	19	7.5-9	Palearctic migrant
Sturnidae :			
<i>Onychognathus walleri</i> *	90	ca 14	Resident with local wanderings
<i>Cinnyricinclus leucogaster</i>	42	12-13	Breeding migrant
Zosteropidae :			
<i>Zosterops senegalensis</i>	11	6-7	Common resident

RESULTS

The list of plant species whose fruits are eaten by the better-known 15 bird and two mammal species is given in Table V, with details of fruit characters and fruiting months. Fruit-eating records (of fewer than 10 plant species) of another 33 birds and eight mammals appear in Appendix 2. These include species that eat fruit only occasionally, are rare residents or visitors to forest, or have very secretive habits (e.g. the babbler *Alcippe abyssinica*, the thrushes *Turdus gurneyi*, *T. olivaceus*, most mammals). Nutrient values of the pulp of nine fruit species are presented in Table VI.

The proportions of obligate frugivores and mixed feeders

Of the 15 bird species considered in Table V, the seed-eating dove (*Aplopelia larvata*) also eats invertebrate food. The two pigeons (*Columba arquatrix*, *Treron australis*) and the two turacos (*Tauraco livingstonii*, *T. schalowi*) are obligate frugivores (the latter also, but rarely, take leaf and flower buds). The two hornbills (*Bycanistes brevis*, *B. bucinator*) are essentially frugivorous but take insects occasionally. The small barbet *Pogoniulus leucomystax* regularly hawks for insects and takes a mixture of insects and fruit to its young. The remaining species (seven passerines) are all mixed insect-fruit eaters. In one starling, *Onychognathus walleri* (Dowsett-Lemaire, 1983b), and in the white-eye *Zosterops senegalensis* insects are more important than fruit. Of the less well documented birds in Appendix 2, all 14 fruit-eating passerines are known to eat at least some insects, as do also some (at least) of the seed-eaters, e.g. *Cryptospiza reichenovii*.

Blue monkeys *Cercopithecus albogularis* have a mixed diet in which fruits appear predominant. Squirrels *Paraxerus lucifer* favour several large seeds, but eat the pulp of other species.

Ecological overlap and segregation in birds and monkeys

There is wide variation in the overlap of fruit diets between different bird species pairs (Table VII). So far the two pigeons (*Columba arquatrix*, *Treron australis*) are known to share only one fruit item. *Columba arquatrix* appears highly selective: the fruits eaten fall mainly into two categories, woody capsules rich in fibre (Table VI) and oily drupes (of Araliaceae, Cornaceae, Myricaceae, Oleaceae etc...). It ignores figs. The distribution and abundance of breeding birds is correlated to that of *Afrocrania volkensii* and *Olea capensis* (*pers. obs.*); on the Nyika returning migrants usually arrive in August, when *Afrocrania* fruits begin to ripen, but in years when the Oleaceae *Chionanthus battiscombei* fruits (as in 1980 and 1983, from May-June) large flocks returned two months earlier to feed on these drupes. In December, with the end of the Oleaceae fruiting season (*Olea capensis*, *Jasminum abyssinicum*), and of other popular fruit crops (*Myrica salicifolia*, *Polyscias fulva*), most *C. arquatrix* leave the country.

By contrast, *Treron australis* prefers figs and sweet-fleshed fruits (e.g. *Syzygium* spp., *Cassine aethiopica*, Table VI); its diet of forest fruits is restricted by the timing (in the summer rains) of its annual post-breeding visits to Afromontane forests.

The two closely-related turacos (*Tauraco livingstonii*, *T. schalowi*) overlap widely in fruit diet, but are completely separated geographically, replacing each other on either side of the Rift valley. The two large hornbills (*Bycanistes* spp.) share at least 71 % of their fruits; their diets are still incompletely known, but they seem especially fond of figs and are numerous in only a few forests where fig trees are well represented. They are largely allopatric in Malawi. Despite year-round availability of figs, the population of *B. brevis* in the Misuku hills (extreme north of the country) migrates out of the area every year from December-January, and further diet studies are needed to explain this.

Figs are also important for two barbets (*Stactolaema leucotis*, *S. olivacea*: Appendix 2), and *S. olivacea* is restricted to two forests (Misuku, Thyolo) where fig crops are plentiful.

TABLE V

List of plant species whose fruits are eaten by birds and mammals with at least 10 species records each ;
where seeds only are taken, records are indicated by s.

Plant species that are Afromontane endemics or near-endemics are asterisked. Fruit type : A = aril, B = berry, C = capsule, D = drupe (see also Table I). Size given is diameter (of round fruit) or length × greatest breadth. Colours are : G = green, Y = yellow, O = orange, R = red, Pi = pink, P = purple, Bk = black, Bl = blue, Br = brown, W = white. Fruiting season is in () when only partly known. Bird species are *Columba arquatrix* (Ca), *Aplopelia larvata* (Al), *Treron australis* (Ta), *Tauraco livingstonii* (Tl), *T. schalowi* (Ts), *Bycanistes brevis* (Bb), *B. bucinator* (Bu), *Pogoniulus leucomystax* (Pl), *Andropadus milanjensis* (Am), *A. tephrolaemus* (At), *Pycnonotus barbatus* (Pb), *Sylvia borin* (Sb), *Onychognathus walleri* (Ow), *Cimniricinclus leucogaster* (Cl), *Zosterops senegalensis* (Zs); mammals are *Cercopithecus albogularis* (Cal) and *Paraxerus lucifer* (Plu.). Records from other observers are in ()^a.

Plant species	Fruit		Fruiting months	Bird (15)	and mammal (2) species																	
	type	size(mm)			colour	Ca ^c	Al	Ta	Tl	Ts	Bb	Bu	Pl	Am	At	Pb	Sb	Ow	Cl	Zs	Cal	Plu
Large trees (15-30 m) of canopy and forest edges:																						
<u><i>Afrocrania volkensii</i>*</u>	D	9-12x6	P-Bk	VIII-XI	x		x	x				x	x	x		x	x			x		
<u><i>Allophylus abyssinicus</i>*</u>	D	9x8	R	X-XI					x					x		x	x	x	x			
<u><i>Aningeria adolfi-friedericii</i>*</u>	B	35-40x30	Br	IX-XII																x	s	
<u><i>Anthocleista grandiflora</i></u>	B	25x20	G-Br	(IX)			x															
<u><i>Bersama abyssinica</i></u>	A	11x8	R+Y	VI-XI									x			x						
<u><i>Blighia unijugata</i></u>	A	13x7	Y	(XII)						x												
<u><i>Bridelia brideliifolia</i>*</u>	D	10x7	P-Bk	IX-X					x	x			x	x	x		x	x	x	x		
<u><i>B. micrantha</i></u>	D	8-10x6	P-Bk	IX-X				x	x	x			x	x			x	x			x	
<u><i>Casearia battiscombei</i>*</u>	C+A	18x12	Y	IX-X	x				x													
<u><i>Celtis africana</i></u>	D	6	R	XII-III					x					x			x				x	
<u><i>C. gomphophylla</i></u>	D	8-10x6	Y	(I-II)									x									
<u><i>Chrysophyllum gorungosanum</i>*</u>	B	30-35	Br	VIII-XII		s															x	s
<u><i>Cola greenwayi</i>*</u>	B	14-15	Br	XII-II		s		x	x												x	s
<u><i>Croton macrostachyus</i>*</u>	C	12-14x10	R-Br	VII-X	x	s									s							x
<u><i>C. sylvaticus</i></u>	C	10	R-Br	(II-III)	x	s																

Plant species	Fruit		Fruiting months	Bird (15) and mammal (2) species																	
	type	size(mm)		colour	Ca ^o	Al	Ta	Tl	Ts	Eb	Bu	Pl	Am	At	Pb	Sb	Ow	Cl	Zs	Cal	Flu
<u>Ilea africana</u>	D	12x9	G(P)	IX-XI					x												x
<u>O. capensis*</u>	D	18-22x12	G(P)	IX-XI	x	s			x												x
<u>Olinia rochetiana*</u>	D	6-7	Y-R	III-IV					x				x								x
<u>Parinari excelsa</u>	D	40	Br	XI-II																	x s
<u>Pittosporum viridiflorum*</u>	C+A	5-8	O	VIII-IX																	(x)
<u>Podocarpus latifolius*</u>	A	25	R	IX-X	x				x				x			x					x
<u>Polyscias fulva*</u>	D	4-5	P-Bk	VIII-XII	x	s			x		x	x	x	x	x	x	x	x	x	x	x
<u>Prunus africana*</u>	D	9-10x7	P	VIII-XI					x					x	x		x				x
<u>Rapanea melanophloeos*</u>	D	6	P-Bk	XII-IV				x	x					x							x
<u>Rauvolfia caffra</u>	D	14-15	G(R)	(I-III)				x	x	x					x						x
<u>Sapium ellipticum</u>	D	8-9x7	P	(I,V)					x						x						
<u>Schefflera umbellifera*</u>	D	8	P-Bk	(IX-X)	x				x					x							
<u>Scolopia stolzii*</u>	B	15-20	Y	(I)																	(x)
<u>Syzygium cordatum</u>	B	13-15x12	P	I-III				x	x	(x)	x			x	x						x
<u>S. guineense</u> subsp. <u>afromontanum*</u>	B	20-30	P	XII-II	?	s	x		x	(x)	x			x	x						x x
<u>Trema orientalis</u>	D	3-5	P-Bk	(III)					x	x					x	x					x
<u>Trichilia dregeana</u>	A	15x10	R	(II-III)												x					
Medium-sized trees (8-18 m)																					
of the understorey:																					
<u>Aphloia theiformis*</u>	B	9-12x7-10	W	XI-XII	?	s			x				x	x		x	x			x	x
<u>Aulacocalyx diervilloides*</u>	B	8	P	(X)										x							
<u>Bequaertiodendron natalense</u>	B	20x14	Br	(X-XI)					x	x											
<u>Cassine aethiopica</u>	D	15-20	R	IX-II			s	x		x											x
<u>Chionanthus battiscombei*</u>	D	25-28x20	P	V-VII	x				x	x											
<u>Ehretia cymosa</u>	D	10	P	(XI)					x	x											
<u>Garcinia kingensis*</u>	B	30x25	G	XI-II			s			x											x x
<u>Halleria lucida*</u>	B	15x12	P	I-III						x					x						

Plant species	Fruit			Fruiting months	Bird (15) and mammal (2) species																
	type	size(mm)	colour		Ca ^c	Al	Ta	Tl	Ts	Bb	Bu	Pl	Am	At	Pb	Sb	Ow	Cl	Zs	Cal	Plu
Small trees/shrubs (≤ 8 m) of the forest edge:																					
<u>Clerodendrum quadrangulatum*</u>	D	8	P	IV-V																	x
<u>Clusia abyssinica*</u>	C	6	G-Y	any																	x
<u>Maytenus heterophylla</u>	A	6	O-R	VIII-IX																	x
<u>Ochna stolzii*</u>	D	8x6	Bk	II								x									x
<u>Osyris lanceolata</u>	D	8-10	R	(IX)						x											x
<u>Rhamnus prinoides*</u>	D	4-6	R	X-II																	x
<u>Rhus longipes</u>	D	6-7	O	IX-XI						x				x	x	x				x	
<u>Rubus ellipticus</u>	D	8-10	O	IX-X																	(x)
<u>Rytigynia denodonta*</u>	D	5	P	II-III																	x
Woodland trees near forest edges:																					
<u>Ficus ingens</u>	B	10-13	Pi	(XI)						x											x
<u>F. sycamorus</u>	B	20-30	Y-Br	any						x											x
<u>Parinari curatellifolia</u>	D	30-40	Br	(XII-I)																	x
<u>Uapaca kirkiana</u>	D	25-30	O	(VIII-X)																	x
<u>U. nitida</u>	D	15-18	Y	(XI)																	
<u>U. sansibarica</u>	D	15-20	O	(IX-XI)																	x

^a Additional data on *Tauraco livingstonii* from Edwards (1982), *T. schalowi* from Fr. Tréguier (*pers. comm.*), *Bycanistes brevis* from I. Bampton (*pers. com.*), *B. bucinator* from S. Fischer (*pers. comm.*), *Cercopithecus albogularis* from Darwin (1984).

^b Size of fruit given for *Ureia hypselodendron* is that of clustered drupelets, as eaten by birds.

^c Single *Columba arquatrix* were flushed from heavily-fruited *Aphloia* and *Syzygium guineense*, but fruit consumption was not confirmed.

TABLE VI

Composition of the pulp of some fruit species.

Species	Water (%)	Pulp constituents (% of dry weight)					Locality	Source
		ash	lipid	protein	fibre ^a	CHO ^b		
<i>Bridelia micrantha</i>	84	1.9	0.6	5.1	10.1	(82)	S. Africa	Frost (1980)
<i>Cassine aethiopica</i>	?	4.5	1.2	3.3	14.3	(77)	S. Africa	Viljoen (1983)
<i>Croton macrostachyus</i>	0	1.0	2.1	7.8	40-45	?	Malawi	C.M. Herrera
<i>Ekebergia capensis</i>	75	6.3	8.6	21.6	9.8	(54)	S. Africa	Frost (1980)
<i>Ficus lutea</i> ^c	85	7.9	3.3	4.6	21.7	(62)	S. Africa	Frost (1980)
<i>F. thonningii</i> ^c	86	5.3	5.2	5.0	18.3	(66)	S. Africa	Frost (1980, <i>in litt.</i>)
<i>Neoboutonia macrocalyx</i>	0	0.3	0.8	7.3	61-78	?	Malawi	C.M. Herrera
<i>Syzygium cordatum</i>	86	5.6	1.4	4.2	10.6	(78)	S. Africa	A.S. Wehmeyer (<i>in litt.</i>)
<i>S. guineense</i>	87	2.3	2.4	4.8	21-37	?	Malawi	C.M. Herrera

^a The two values for fibre come from the use of two methods, that of acid detergent (lower figure) and that of neutral detergent (higher figure).

^b These figures represent residues and may be too high (A.S. Wehmeyer, *in litt.*).

^c *Ficus lutea* is considered synonymous with *F. vogelii* (name used by Frost, 1980) and *F. thonningii* with *F. natalensis* (ditto).

TABLE VII

*Overlap in fruit diet between species pairs,
expressed as proportion (%) of the smaller diet in common.*

Ca = *Columba arquatrix*, Ta = *Treron australis*, Tl = *Tauraco livingstonii*, Ts = *T. schalowi*,
Bb = *Bycanistes brevis*, Bu = *B. bucinator*, Pl = *Pogoniulus leucomystax*, Am = *Andropadus*
milanjensis, At = *A. tephrolaemus*, Pb = *Pycnonotus barbatus*, Sb = *Sylvia borin*,
Ow = *Onychognathus walleri*, Cl = *Cinnyricinclus leucogaster*, Zs = *Zosterops senegalensis*,
Cal = *Cercopithecus albogularis*.

	Ta	Tl	Ts	Bb	Bu	Pl	Am	At	Pb	Sb	Ow	Cl	Zs	Cal
Ca	6	21	62	0	7	15	19	37	25	25	25	31	19	56
	Ta	21	62	40	50	0	19	37	31	0	6	15	6	50
		Tl	79	29	21	0	29	43	29	8	21	29	14	64
			Ts	73	71	38	44	52	86	50	82	100	81	66
				Bb	71	8	27	33	40	0	20	23	13	66
					Bu	8	21	29	43	8	14	15	14	79
						Pl	23	46	23	17	15	23	31	23
							Am	76	32	33	47	54	37	40
								At	64	83	88	85	94	51
									Pb	42	53	69	62	55
										Sb	33	33	75	50
											Ow	69	56	71
												Cl	62	77
													Zs	62

The bulbul *Andropadus milanjensis* shares at least 76 % of its fruit diet with its congener *A. tephrolaemus*; these are only partly separated in altitudinal (Table IV) and geographical distribution. A strong overlap of diet is recorded also between bird species that are not phylogenetically close, as between several passerines (*Pycnonotus barbatus*, *Onychognathus walleri*, *Cinnyricinclus leucogaster*, *Zosterops senegalensis*) and *Tauraco schalowi*. Fruits in common are small fleshy species taken in and near the canopy (Table V). Similarly, a migrant warbler (*Sylvia borin*), two starlings (*Onychognathus walleri*, *Cinnyricinclus leucogaster*) and the white-eye *Zosterops senegalensis* share most of their fruits with the bulbul *Andropadus tephrolaemus*.

The tinkerbird *Pogoniulus leucomystax* shares little with other species; it rarely takes fruit other than mistletoe berries, which are consumed in large

numbers and all year round. By contrast, I have only one sighting of a tinkerbird eating a capsule of *Maytenus acuminata*, and two of an individual consuming *Polyscias* drupes, though consumption of *Ochna* spp. and *Macaranga* spp. appears more regular. The distribution of the tinkerbirds in the Nyika forest patches is explained by the availability of mistletoes (Dowsett-Lemaire, 1982) : they are resident in forests with 4-5 species (providing fruits most of the year), but only seasonal visitors to nearby patches with two species fruiting part of the year. Similarly their distribution elsewhere in the Malawi montane forests is correlated to the presence of at least 4-6 mistletoe species (*pers. obs.*). Surprisingly, mistletoe berries are almost ignored by other bird species, records of *Tauraco schalowi* and *Pycnonotus barbatus* at *Viscum shirensense*, and of *Bycanistes brevis* at *Englerina inaequilatera* being isolated sightings.

Overall, there is a greater diversity of frugivorous birds in the upper strata of the forest : data from the better-known Nyika sample show an average of 4.8 bird species feeding in larger trees (≥ 15 m, $n = 29$) against 1.8 in small trees (≤ 8 m, $n = 20$; $t = 2.05$, $P < 0.05$), while the few trees in the mid-stratum ($n = 8$) attract an average of 3.0 bird species. Some of the large non-passerines (pigeons and hornbills) rarely descend below the mid-stratum. *Tauraco schalowi* is not a strong flier and escapes usually by hopping-running along branches : it frequently feeds in the mid-stratum and occasionally lower. On the SW Nyika, the bulbul *Andropadus tephrolaemus* (elsewhere also *A. milanjensis*) is the most regular consumer of understorey fruit.

Monkeys *Cercopithecus albogularis* share many of their fruits with birds (Table VII). Altogether 42 of 47 fruit species are taken in common (two for seeds only by the parrot *Poicephalus robustus* : Appendix 2). Of the five remaining species, two (*Pittosporum viridiflorum*, *Scolopia stolzii*) have the characters of bird fruit (Table V) and should be expected to be taken by birds. Thus the overlap is almost complete.

Fruit characters and consumer choice

Table VIII summarizes fruit choice of the main bird species and monkeys according to fruit type, size and colour.

Size is obviously a limiting factor in fruit consumption by birds except for some very soft fruits of which fragments can be taken (e.g. figs). Overall, the smaller the fruit, the greater the number of bird species attracted to it : the small, oily drupes of *Myrica salicifolia* (5 mm) attract as many as 10 bird species on the Nyika alone (Table V and Appendix 2). The oily drupes of *Polyscias fulva* (4-5 mm) are eaten by up to 16 species, and the fleshy capsules of *Macaranga capensis* (6-8 mm) by 14 species. The small-sized fig *Ficus thonningii* (10 mm) is eaten by 19 bird species. Data from the Nyika (with the exclusion of mistletoes) show a highly significant inverse correlation between fruit diameter and the number of bird consumers ($r = -0.84$, 65 d.f., $P < 0.001$).

Within 1-2 mm there is good agreement between gape width (Table IV) and upper size limit of fruits swallowed whole in all bird species except the pigeons and turacos. These have a gape breadth of *ca* 13 mm with the bill closed, but their flexible mandible tissues allow them to swallow fruit up to the size of 20-25 mm (*Columba arquatrix*) and 30 mm (*Treron australis*, *Tauraco* spp.). These and other

TABLE VIII

Summary of fruit selection in bird and mammal species with records of a least 16 fruit species eaten.

n = total number of fruit species recorded ; fruit types (A = aril, B = berry, C = capsule, D = drupe) as defined in Table I and text ; size is fruit breadth (transverse diameter), number of larger fruits eaten piecemeal is in () ; colours are G = green (including greenish-yellow), Y = yellow, O = orange, R = red (and reddish-brown), P = purple/black, Bl = blue, Br = brown, W = white.

Animal species	n	Fruit type					Size (mm)					Colour							
		B	D	A	C	C+A	range	3-9	10-19	20-29	30+	G	Y	O	R	P	Bl	Br	W
<u>Columba arquatrix</u>	16	-	9	1	5	1	4-25	6	8	2	-	4	1	-	4	5	-	2	-
<u>Treron australis</u>	16	9	7	-	-	-	6-30	2	7	4	3	3	3	-	3	5	-	2	-
<u>Tauraco</u> spp. ^a	60	21	35	1	1	2	3-30	28	21	9	2	11	5	6	15	20	-	2	1
<u>Bycanistes</u> spp. ^b	19	11	7	1	-	-	4-50	5	5	4	4(1)	5	4	1	3	5	-	1	-
<u>Andropadus</u> spp. ^c	71	20	42	4	3	2	3-15	53	14	(3)	(1)	5	4	10	23	26	1	-	2
<u>Pycnonotus barbatus</u>	21	7	12	-	2	-	3-15	15	3	(2)	(1)	4	2	3	1	10	-	1	-
<u>Onychognathus walleri</u>	16	4	9	2	1	-	4-15	14	1	(1)	-	1	3	1	4	6	-	-	1
<u>Zosterops senegalensis</u>	16	3	12	-	1	-	3-10	15	(1)	-	-	2	2	3	3	5	-	-	1
<u>Cercopithecus albogularis</u>	47	18	24	1	3	1	4-100	20	14	4	9	12	7	3	7	12	-	5	1
Total fruit sample	134	56	58	9	8	3	3-250	69	35	14	16	21	14	17	38	29	1	12	2

^aTauraco schalowi alone provides 57 species records.

^bBoth hornbills are treated together as diets largely overlap (Tables 5 and 7).

^cAndropadus tephrolaemus alone provides 63 species records.

broad-gaped species (*Bycanistes* spp.) eat a wide range of fruit sizes (Table VIII). The size of seeds swallowed by the dove *Aplopelia larvata* ranges from 1 mm (*Ficus thonningii*) to 20 × 10 mm (*Chrysophyllum*), which requires no distortion of the gape.

Monkeys *Cercopithecus albogularis* have manipulative abilities that do not set an upper size limit ; it is noticeable however that most of the fruits eaten are small, apparently a reflection of the fruit diameter distribution of the plant community (Table VIII).

Berries and drupes are equally abundant fleshy fruits, but berries are on average larger (see above, Tables I and II). Small-gaped passerines eat relatively more drupes than berries, presumably a consequence of the generally smaller size of drupes. *Columba arquatrix*, however, has not yet been recorded to eat berries in Malawi, which cannot be explained by size alone : the drupes consumed are all noticeably oily and assumed to be rich in nutrients (cf. the analyses of Cornaceae by Herrera, 1981, of Oleaceae by Jordano & Herrera, 1981, and Araliaceae by Snow, 1981). It may be that drupes are often richer in lipids and proteins than berries, but more nutrient analyses are needed to investigate this possibility. There are examples of drupes poor in fats (e.g. *Bridelia* and *Cassine*, Table VII).

Red and purple/black are the most frequent colours of the fruit sample, and are usually the two most important colours of fruits eaten by birds. Green is not uncommon in fruits chosen by monkeys, and some green fruits are eaten by all bird species, especially the turacos. Green is the colour of several ripe *Ficus* spp. (Table V) and of the popular capsules of *Macaranga* spp. Oleaceae drupes are taken usually when green and soft, before they turn fully mature (and purple). In addition some birds, especially the bulbul *Andropadus tephrolaemus*, often eat unripe (green) fruits from about a month before the ripening time (e.g. *Afrocrania*, *Ilex mitis*, *Maesa lanceolata*, *Polyscias fulva*) ; whereas blue monkeys frequently take unripe fruits at an earlier stage, from the time they are just formed (e.g. of *Maesa*, *Olinia rochetiana*, *Polyscias*).

Fruiting seasons and frugivory

Most trees and climbers fruit for periods of two to four months (Table V). One might expect an increase in the number of frugivore species with the length of the fruiting season. This is not confirmed : even after excluding small trees/shrubs (≤ 8 m) which are usually exploited by one or two understory birds, no correlation is found between the number of fruiting months and the number of consumers (there is an average of 5.4 frugivores for 17 2-month fruiting plants, 5.2 for 14 3-month fruiting plants and 4.7 for 15 4-month fruiting plants). Examples of popular, small-sized fruits can be found equally in species with short seasons (e.g. *Myrica salicifolia* fruits for six weeks and attracts 10 birds and a monkey) and with long seasons (e.g. *Polyscias fulva* fruits for five months and has 17 consumers). Some of the longest-fruiting plants are Rubiaceae trees of the understory with low fruit production (*Chassalia parvifolia* for six months, *Psychotria zombamontana* for eight months) and with just one main fruit consumer, the bulbul *Andropadus tephrolaemus*.

Fruits with high pre-dispersal predation are predicted to have irregular and massive crops in order to minimize predation (Janzen, 1969). On the Nyika *Aningeria adolfi-friedericii* fruited massively at the end of 1979 and again at the end of 1982. However *Parinari excelsa*, equally popular with seed-eating squirrels

(*Paraxerus lucifer*, *Helioscurus mutabilis*) and parrots (*Poicephalus robustus*), fruits every year from November to February, i.e. at highly predictable times. Individual trees of *Chrysophyllum gorungosanum* fruit every two years (August-December) but not all synchronously, thus some trees are in fruit every year.

Most plant species fruit at the end of the dry season and in the early rains (Table III). Even among closely-related plants there is no clear evidence that flowering and fruiting seasons tend to be separated, with reduced competition between pollinators and dispersers (cf. Snow, 1965; Smythe, 1970). The examples where this occurs are few: the two *Croton* species, the two *Macaranga* in part, and the three distinct subspecies of *Bersama abyssinica* (Dowsett-Lemaire, 1985a). Segregation of flowering and fruiting does not take place in several species pairs (*Allophylus*, *Bridelia*, *Celtis*, *Olea*, *Parinari*, *Syzygium*) which often occur alongside each other. The two *Syzygium* not infrequently hybridise (*pers. obs.*) and dispersal agents are largely shared. In figs *Ficus* spp., fecundation by species-specific trap-lining wasps (Janzen, 1979; Bronstein, 1987) has favoured inter-tree asynchrony; thus some individuals of each species are in fruit at any time of year, and naturally trees of different species are often found in fruit simultaneously (contrary to the erroneous predictions of McKey, 1975, p. 177).

Fruit handling and seed transit

Birds swallow fruit whole more or less up to the limit of their gape width (see above). Some large soft fruits are eaten piecemeal, either with seeds (*Ficus* spp.), or the flesh only (e.g. of *Syzygium* spp. by bulbuls and thrushes *Turdus olivaceus*, of *Podocarpus latifolius* by *Onychognathus walleri*). Occasionally the skin is peeled off and dropped before the fruit is swallowed, as is the case with the hairy pericarp of *Dendrophthoe pendens* and *Phragmenthera usuiensis* (by *Pogoniulus leucomystax*) and of *Cyphostemma masukuense* (by *Andropadus milanjensis*), but also the smooth red skin of some *Tapinanthus* mistletoes (*P. leucomystax*).

Seed regurgitation in birds has been observed regularly in only one species, the tinkerbird *P. leucomystax*: the sticky (viscin-covered) seeds of mistletoe berries are rubbed off onto branches within a few minutes of ingestion, and germinate quickly (some certainly within a day or two). Seeds are deposited usually near the fruit source, sometimes on the host plant; in the breeding season some seeds of *Englerina inaequilatera* (which are white and conspicuous) are « wasted » by being stuck in circles around the rim of occupied nest-holes, on dead wood. Fruits are fed whole to nestlings and rejected seeds are often carried away by the parents, thus favouring dissemination.

Regurgitation of some large seeds (*Ekebergia capensis*, *Uapaca kirkiana*) in the vicinity of the fruit source has been observed in *Bycanistes* hornbills. With *Ekebergia*, *B. brevis* swallowed several fruits then regurgitated seeds from the fruit tree or in neighbouring trees (within 50 m) before flying off. Smaller seeds are presumably defecated; one interesting exception is the mistletoe *Englerina inaequilatera*: in *B. brevis* the sticky seeds were seen to be rubbed off the bill by lateral wiping against branches (I. Bampton, *pers. comm.*).

There are several instances of apparently undamaged seeds defecated in bird bags (after mistnet capture) by *Andropadus* bulbuls, *Sylvia* warblers and *Zosterops*. Both *Sylvia borin* and *S. atricapilla* have been found to defecate directly below fruiting trees of *Polyscias fulva*, but that is the only tree species where they linger. *Tauraco schalowi* takes fruits to its nestlings from sources 50-200 m away,

and seeds are dropped below the nest. The starlings *Onychognathus walleri* (Dowsett-Lemaire, 1983b) and *Cinnyricinclus leucogaster* have feeding ranges of several km²; whole fruits are fed to nestlings and faecal sacs containing seeds are dropped by the adults at distances which may be 100 m to over 1 km from the fruit source.

The handling methods of *Cercopithecus albogularis* depend on the size and type of fruit. All succulent fruits up to 12-13 mm in length or diameter are swallowed whole; the flesh of larger fruits is usually sucked off and the seeds spat or dropped to the ground (many below the parent tree), except in the small-seeded berries of *Ficus* and *Landolphia* where the seeds are swallowed. The woody capsules of *Croton* and *Neoboutonia* are munched in such a way that the seeds are likely to be damaged.

Squirrels are mostly seed predators, but disseminate seeds in some cases. They often transport fruits to eat them away from the parent tree, and may drop parts of multi-seeded fruit with intact seeds (seen in *Chrysophyllum gorungosanum*, *Landolphia buchananii*).

Undamaged seeds of *Olea capensis* and *Syzygium guineense* were found in faeces of bushpig *Potamochoerus porcus*.

DISCUSSION

The importance of obligate frugivorous birds in Africa

Only a minority of frugivorous birds are exclusively so, and all of them are large non-passerines. This observation concurs with data obtained by Frost (1980) in a frugivorous community in Natal, South Africa — there only four of 35 bird species feed (almost) entirely on fruit. No African passerine has so far been documented to be an obligate frugivore, but there are some elsewhere in the tropics (e.g. some Cotingidae in the Neotropics: Snow, 1981).

There is an odd record of a crop of *Columba arquatrix* containing caterpillars (Roberts, 1924), which I consider likely to be an error. This statement is repeated uncritically in recent handbooks (Rowan, 1983; Morel *et al.*, 1986). In his world survey of tropical frugivorous birds, Snow (1981) excludes African Columbidae from the families of legitimate frugivores, as he assumes (wrongly, see below) that they are seed predators.

Frugivores' diets and resource partitioning in birds and monkeys

There is a wide dietary overlap between most birds and between birds and *Cercopithecus albogularis*. In birds, this takes place equally between phylogenetically close and more distant species. Competition is reduced in some cases by (partial) allopatry (*Bycanistes* spp., *Tauraco* spp.). It is greatest in the upper strata of the forest, with few species (mostly bulbuls) exploiting the lower storey: a similar situation was found in a Costa Rican forest (Wheelwright *et al.*, 1984).

In Gabon, Gautier-Hion *et al.* (1985a) have analysed the diets of seven large bird species (four Bucerotidae, three Musophagidae) and of monkeys (Cercopithecinae): it appears from data in their Appendix 2 that 75% of the fruit species eaten by these birds are shared with the monkeys. If all bird diets are

combined in Malawi, this proportion is over 90 %. The low figures of overlap given by Fleming (1979) for some Neotropical birds and monkeys may be the result of incomplete field data.

One pigeon and a tinkerbird, however, are rather selective frugivores, and their diets show reduced overlap with other birds'. *Columba arquatrix* prefers oily drupes and fibrous capsules and apparently ignores the figs and sweet-fleshed fruits favoured by *Treron australis*. Dietary overlap should also be restricted by the different seasons spent by these pigeons in Afromontane forests (*C. arquatrix* mostly from June or August to December, and *T. australis* from November or January to March). Naturally the diet of these species is only incompletely known: for example the fruits taken by the few *C. arquatrix* remaining in January-May are largely unidentified — most of these pigeons were seen flying over forest, not in fruit trees. The poor fruiting of some species (e.g. crops of *Ocotea usambarensis* aborted to a large extent) leaves the question of their main consumers unanswered; whereas *C. arquatrix* is reported to feed on *Ocotea* spp. elsewhere (Phillips, 1927; Benson, 1960), in Malawi only some mammals were seen to take the (often galled) fruits.

In South Africa, *C. arquatrix* appears to have a more diverse diet than in Malawi (Phillips, 1927; Rowan, 1983), showing some overlap with that of *T. australis* (Rowan, 1983). Olives *Olea capensis*, however, remain one of its favourite fruits (Phillips, 1927; *pers. obs.*) and figs are taken on only rare occasions (C.J. Vernon, *in litt.*; W.R.J. Dean, *pers. comm.*) whereas the latter are among the fruits most often sought by *T. australis* (Rowan, 1983).

The tinkerbird *Pogoniulus leucomystax* stands out as a highly selective fruit consumer, specializing on Loranthaceae and Viscaceae berries. The attraction of mistletoe berries for *Pogoniulus* barbets is reported for several species of this African genus (Godschalk, 1983). *P. chrysoconus* has been studied extensively in the Transvaal, South Africa, and shown to be by far the main consumer and disperser of mistletoe berries, other birds being only incidental consumers (Godschalk, 1985). In a Natal coastal forest, two *Pogoniulus* species are the only consumers of the mistletoe *Erianthemum dregei* (Frost, 1980); one of them, *P. bilineatus*, eats many other fruit species and may not be as closely associated with mistletoes as *P. leucomystax* obviously is. Limited observations on fruits eaten in Malawi by *P. bilineatus* (Appendix 2) support Frost's data. Indeed this species is present in several forests in Malawi noticeably poor in mistletoes (with the exception of one *Viscum*) and from which *P. leucomystax* is absent.

Fruit characters and choice by birds and monkeys

Results show that forest birds in Malawi and the monkey *Cercopithecus albogularis* eat mostly small, brightly-coloured, fleshy and unprotected fruits. This is in accordance with the bird-monkey syndrome described by Gautier-Hion *et al.* (1985a) for a forest in Gabon, except that among fruit types the proportion of arillate seeds in the Malawi forests is much smaller. Knight & Siegfried (1983), with a South African sample, provide the only other African study of fruit characters (type, size and colour) as they relate to dispersers (birds versus mammals). However their conclusions are of limited use as the source of their data is unclear, based partly on assumptions, and the birds and mammals considered are not stated. For size, Knight & Siegfried use fruit length and not

transverse diameter, but as birds swallow large fruits lengthwise, only the breadth is relevant in a study of size as limiting factor.

Leighton & Leighton (1983) in Borneo, Terborgh & Diamond (1970) and Pratt & Stiles (1985) in New Guinea have stressed the importance of fruit diameter in structuring birds' diets. P.G.H. Frost (*in litt.*, 1982) remarked that « fruit size rather than fruit quality appears to be the major determinant of the number of species exploiting a fruit crop », but his data from Natal (South Africa) remain largely unpublished. The most thorough study to date of the relationship between fruit diameter and bird consumers is that of Wheelwright (1985a) in a Costa Rican forest. His main conclusions are verified in the Malawi sample, i.e. (1) small-fruited plant species draw significantly more species of birds than large-fruited ones ; (2) large-gaped birds feed commonly on small fruits. Consequently, small-fruited plants attract potentially more seed disseminators than those with large fruits.

The main bird-fruit colours in this study are purple/black and red. Turacos and hornbills in Gabon (Gautier-Hion *et al.*, 1985a) similarly prefer purple/black, followed by red ; and bird fruits in Costa Rica and Peru are most commonly black, then red, or combinations of red and black (Wheelwright & Janson, 1985). In temperate birds the preference order is red then black (Turcek, 1963). That fleshy green fruits are avoided, as in Gabon (Gautier-Hion *et al.*, 1985a) and southern Africa (Knight & Siegfried, 1983, perhaps an assumption) is far from being the case in Malawi, where some of the most popular fruits are green (*Macaranga* spp., *Ficus* spp.) and Oleaceae drupes are eaten when soft but still green. Fruits taken by *Cercopithecus albogularis* are of a wide range of colours, and brown and (especially) green are not ignored, though monkeys of the same subfamily in Gabon clearly avoid them (Gautier-Hion *et al.*, 1985a).

Co-adaptation between fruiting phenology and frugivores ?

Observations on fruiting phenology in relation to frugivores can be summed up as follows : (1) fruiting of almost all plant species is highly seasonal and of short duration (2-4 months), with a marked trough in the late rains and early winter that apparently forces some obligate frugivores (most *Columba arquatrix*, some *Bycanistes brevis*) to migrate out of the study area ; (2) there is no correlation between the length of the fruiting seasons in trees with 2- to 4-month seasons and the number of frugivorous species attending ; (3) zoochorous plant species may have annual, biannual or multiannual cycles, with or without fruiting synchrony among individuals of the same species (Nyika sample analysed in Dowsett-Lemaire, 1985a) ; (4) fruit species with high pre-dispersal predation produce massive crops, but at predictable times (with one possible exception in *Aningeria*) ; (5) there is no temporal segregation of fruiting in most congeneric fruit trees. These facts do not overall suggest an evolutionary influence of consumers on the timing of fruiting. Gautier-Hion *et al.* (1985b) arrive at the same conclusion in an extensive study of fruiting phenology of forest plants in Gabon. In a Costa Rican forest, Wheelwright (1985b) found that fruiting seasons of 23 lauraceous species were aggregated, despite evident competition for seed dispersers. More ample and critical discussion of the topic can be found in those two papers.

A case of close plant-disperser association

Coevolution between plant and animal dispersers is constrained for several reasons (Howe, 1984 ; Herrera, 1985 ; Wheelwright, *in press*). These include : weak selection (e.g. because of the diversity of dispersers, of dispersers' diets, and other types of interactions diluting the seed dispersal interaction) ; inconsistent selection in space and time (geographical variability of animals' diets, temporal variability of fruit crops) ; unpredictability of favourable germination sites ; intrinsic, genetic features limiting evolutionary responses (such as generation times, much longer in plants than in animals).

These constraints apply generally to the type of fruit-frugivore interactions observed in this study, except for the close mutualism existing between the tinkerbird *Pogoniulus leucomystax* and Loranthaceae/Viscaceae berries. *P. leucomystax* is by far the main consumer of these berries and, reciprocally, the bird eats few other fruit species and then infrequently. It is present only in those forests with at least 4-6 mistletoe species providing fruit all year round. The viscous seeds are regurgitated and rubbed off onto branches where the parasitic plants germinate and develop quickly. Indeed, life-cycles of birds and plants in this case appear rather similar : plants of *Erianthemum degrei* in Natal flower within a year of germination (P.G.H. Frost, *pers. comm.*), and those of *Viscum capense* in the Cape fruit within 18 months (R.S. Knight, *pers. comm.*). Tropical birds the size of tinkerbirds start breeding at the age of one or two years (e.g. Dowsett-Lemaire, 1985b). Similar generation lengths of plants and birds may allow evolutionary interactions.

Godschalk's work (1983, 1985) suggests that the savanna species *P. chrysoconus* may be as closely associated with mistletoes as *P. leucomystax* is in montane forest — but it remains to be shown that other food plants are of secondary importance. On the other hand, *P. bilineatus* has a more varied diet and is not closely dependent on mistletoes for food (see above).

Similar associations exist between certain flowerpeckers (Dicaeidae) and parasitic mistletoes in the Oriental and Australasian Regions (Salomonsen, 1964), some species acting both as pollinators and dispersers (Davidar, 1985). It is noteworthy that despite their highly specialized fruit diet, Dicaeidae and *Pogoniulus* barbets all take insects regularly. In the Neotropics, more than one family of birds is involved in the dispersal of mistletoes (Parker, 1981 ; Davidar, 1983), and the existence of close interactions there between mistletoes and particular bird species remains to be proven or investigated further (B.K. & D.W. Snow, *in litt.*).

Seed dissemination in Afromontane forests

There is no doubt that recent climatic variations during and since the last glaciation (*ca* 12 000 years B.P.) have affected the distribution and extent of evergreen forest at high altitudes — though the magnitude of the changes is still debated (Livingstone, 1975 ; White, 1981, 1983b). Even though many species of trees may have evolved long before their present-day vertebrate dispersers (cf. Herrera, 1985, pp. 134-135), recolonization of upland areas by forest after the last interpluvial must have been influenced by present-day fruit consumers. The potential dispersal role of various species is discussed below.

African Columbidae have been considered to be no more than seed predators by recent reviewers (Snow, 1981). However, Snow overlooked the exhaustive

study by Phillips (1927) of captive *Columba arquatrix* : he demonstrated that a large proportion (25 to 75 %) of ingested fruits of 40 species were unharmed ; he also showed that seeds voided germinated more quickly than those that did not go through the birds' gut. *C. arquatrix* was never seen to eat seeds in Malawi. Several handbooks report it to take both fruit and seeds (e.g. Macworth-Praed & Grant, 1952 ; Rowan, 1983 ; Maclean, 1985), but it appears that most specific records of « seed-eating » are erroneous and refer in fact to whole fruit being swallowed. For instance, when Chapin (1939) compares the « hard seeds » of *Croton macrostachyus* to castor-oil seeds, he evidently means the whole woody capsules (which are of the same size and shape as castor-oil seeds). Rowan (1983) reports *C. arquatrix* taking the « seeds » of the exotic *Acacia cyclops*, but pigeons actually swallow them with the attached red funicle (*per. obs.*) which is rich in oils (Glyphis *et al.*, 1981).

Snow (1981) also assumed *Treron* pigeons to be seed predators. The only evidence for Africa comes from two gizzards of *T. australis* which contained damaged *Ficus* seeds (Cowles & Goodwin, 1959). The possibility that these seeds might have been damaged by parasitic wasps in the first place (Janzen, 1979) was not considered. However, an Asiatic species of *Treron* is known to pass some *Ficus* seeds unharmed (F.R. Lambert, *pers. comm.*). From the faeces of *T. australis* roosting in a Transvaal garden, W.R.J. & S. Dean (*pers. comm.*) observed the emergence of the following seedlings : *Cassine transvaalensis*, *Croton gratissimus*, *Diospyros lycioides* and *Pappea capensis*.

From the above evidence, it is clear that both *C. arquatrix* and *T. australis* can be efficient seeds disseminators. Seed passage in pigeons can be fairly slow : Ridley (1930) noted that the defecation of seeds by captive birds could be spread over 6-7 hours, and Proctor (1968) had *Columbia livia* (a smaller bird than *C. arquatrix*) retain seeds for up to 24 hours. *C. arquatrix* and *T. australis* are highly mobile species : the former has home ranges of many km², non-breeders wandering daily over 10-20 km or more from their roosts (*pers. obs.*). *Treron* flocks visiting forest after breeding range daily over similarly large areas. Given this high mobility and their migratory habits, both pigeons must play an important role in both short- and long-distance seed dispersal. In Natal, *C. arquatrix* consumes large quantities of the exotic berries *Solanum mauritianum*, and the rapid spread of this plant through the province has been associated with the pigeons' movements and roosting habits (Oatley, 1984). Within East, Central and southern Africa there is a very good match between the distribution of *C. arquatrix* and that of one of its key fruit plants *Olea capensis* (F. White, *in prep.*).

Tauraco corythaix, a close relative of the green turacos of Malawi, was also shown by Phillips (1928) to defecate seeds uninjured for a large number of fruit species. Hornbills in Gabon are known to pass many small seeds undamaged (Gautier-Hion *et al.*, 1985a). *Pogoniulus* barbets are efficient seed dispersers of mistletoe berries (this study ; Frost, 1980 ; Godschalk, 1983, 1985) but do so within short distances of the food source : Godschalk (1985) saw *P. chrysoconus* regurgitate seeds usually within 50 m and no further than 75 m from the fruit plant. *P. leucomystax* and *P. chrysoconus* (*pers. obs.*) may occasionally disperse seeds further when removing them from nestlings. For longer-distance dispersal mistletoe epiphytes must presumably rely on the few bird consumers that retain seeds longer through defecation (Godschalk, 1985).

Small bird species that defecate seeds do so usually in periods of 5-35 minutes (see Godschalk, 1985, for *Pycnonotus barbatus* and a barbet *Lybius torquatus*; Herrera, 1981, for *Sylvia atricapilla*). A species like the blackbird *Turdus merula* (90 g, the size of *Onychognathus walleri*) may retain seeds for up to six hours (Herrera, 1981) and the starling *Sturnus vulgaris* (75 g) for up to 15 hours (Proctor, 1968). Overall, turacos (with limited home ranges and movements: Dowsett-Lemaire, 1983a) and passerines can be expected to contribute to seed dissemination over distances of 50 m to a few km, but some longest-retained seeds could be dispersed much further by migrants (e.g. *Cinnyricinclus leucogaster*, *Sylvia borin*) and wanderers with inter-forest movements (e.g. *Onychognathus walleri* and *O. tenuirostris* crossing distances of 10 km or more, *pers. obs.*). Captive hornbills were shown by Ridley (1930) to defecate seeds from a batch of fruits over 6-7 hours. In Malawi, *Bycanistes* hornbills have wandering and migratory movements, *B. brevis* visiting forest up to 100-110 km from the nearest breeding population. Thus they may occasionally disperse small-seeded fruits over long distances.

Monkeys *Cercopithecus albogularis* do limited damage to seeds (according to fruit type). Several studies in Africa have shown that Cercopithecinae contribute efficiently to seed dissemination (Hladik & Hladik, 1967; Gautier-Hion, 1984) or dispersal (Jackson & Gartlan, 1965). Squirrels *Paraxerus lucifer* are mostly seed predators but disseminate seeds by dropping parts of multi-seeded fruit; I have no observation on seeds dispersed by scatter-hoarding in Malawi, but this dispersal method has been demonstrated for other species (e.g. *Paraxerus palliatus* in Natal: Viljoen, 1983). Some ground mammals may also aid in seed dissemination (e.g. bushpig, Phillips, 1926, and occasionally rodents and ruminants, Gautier-Hion *et al.*, 1985a).

To summarize this review and discussion, most seed dissemination in the Malawi upland forests must be attributed to birds (some over long distances) and a few mammals such as monkeys (locally only). However, there remain in the Afromontane flora (i.e. trees and shrubs with scattered distribution on mountains) two main types of diaspores that are not eaten by frugivorous birds nor transported by wind. One consists of the large fleshy fruits of trees such as *Myrianthus holstii*, *Tabernaemontana stapfiana*, the Sapotaceae *Aningeria adolfi-friedericii* and *Chrysophyllum gorungosanum*. These are well distributed in the Afromontane Region, e.g. *Aningeria* is widespread along the East African chain from Ethiopia to Zimbabwe and west of the Rift in the Zaire mountains. The fruits are usually brown (yellow in *Myrianthus*), foetid, of large size (the indehiscent capsules of *Tabernaemontana stapfiana*, equivalent to berries, are 15-20 cm in diameter), often with flattened slippery seeds. They have the characteristics of « bat fruits », and fruit species of the same genera or families are known to be eaten by bats (van der Pijl, 1957). The massive fruits of *Tabernaemontana* have structural similarities with those of *Treulia africana*, eaten by an unidentified bat (Appendix 2). Frugivorous bats have been poorly studied in Africa; what we know so far of the feeding behaviour of the large *Eidolon helvum* (Osmaston, 1965; Ayensu, 1974), a highly mobile species (even a seasonal migrant in Malawi), should encourage further investigation into that field.

The other type of diaspore belongs to shrubs of the understorey (particularly in the families Acanthaceae, Urticaceae, some Euphorbiaceae such as *Acalypha*) and herbs such as Gramineae. These diaspores are small and dry and not adapted for anemochory nor zoochory. However, *Cryptospiza reichenovii* and other

Estrildidae eat the seeds of several species in these groups (Appendix 2). In Tanzanian mountains the dove *Aplopelia larvata* is reported to be attracted in large numbers to mass seeding of *Acanthopale* and *Isoglossa* Acanthaceae shrubs (L. Tanner & S.N. Stuart, *pers. comm.*). It is well known that granivorous birds of several families pass a small proportion of seeds unharmed (Roessler, 1936 ; van der Pijl, 1969). The distribution of these understorey shrubs in forests on scattered mountains can be best explained by accidental dispersal by seed-eaters. Granivorous passerines in Malawi are subject to local movements (e.g. Dowsett, 1985) ; the localized species *Linurgus olivaceus* is known to wander to small forests 15-20 km away (*pers. obs.*). *Aplopelia* doves have been reported to wander to isolated forests up to 80 km from the nearest breeding site (as in the Malawi Hills in the extreme south of the country : Long, 1967 ; N. Johnston-Stewart, *pers. comm.*, and *pers. obs.*).

SUMMARY

The present study analyses the frugivorous diet of birds and some mammals (mainly the monkey *Cercopithecus albogularis*) in the upland evergreen forests of Malawi, south-central Africa. Among birds, only a few non-passerines are obligate frugivores. There is a wide dietary overlap between most bird species (including some that are not closely related), and the overlap between birds as a whole and *Cercopithecus albogularis* is over 90 %. The pigeon *Columba arquatrix* is, however, fairly selective and prefers woody, fibrous capsules and oily drupes. There is an example of close plant-disperser mutualism between the small barbet *Pogoniulus leucomystax* and parasitic mistletoes (Loranthaceae/Viscaceae).

The great bulk of the fruit sample (134 species) consists of berries (56) and drupes (58). The most frequent colours of fruit eaten by birds and monkeys are purple/black and red, but green is by no means avoided. Gape width in birds somewhat imposes an upper size limit on fruits swallowed whole : small-fruited plant species draw significantly more species of birds than large-fruited ones, as large-gaped birds commonly feed on small fruits.

Observations on fruiting phenology in relation to frugivores do not overall suggest an evolutionary influence of consumers on the timing of fruiting.

It is shown that the pigeons *Columba arquatrix* and *Treron australis* have been wrongly considered as seed predators and are potentially important in short- and long-distance seed dispersal. Most seed dissemination in Afromontane plant species (i.e. with scattered distribution on isolated mountains) must be attributed to frugivorous birds. However, the role of bats for some fruit species not eaten by birds remains to be investigated ; the dry diaspores of certain understorey shrubs are probably dispersed accidentally by seed-eating birds.

RÉSUMÉ

Cette étude analyse le régime frugivore des oiseaux et de quelques mammifères (surtout le singe *Cercopithecus albogularis*) dans les forêts d'altitude du Malawi, Afrique tropicale-aus-trale. Parmi les oiseaux, seuls certains non-passereaux sont frugivores à part entière. Les régimes frugivores de la plupart des oiseaux se chevauchent largement, même entre espèces peu apparentées. Entre

l'ensemble des oiseaux et le singe *Cercopithecus albogularis*, ce chevauchement alimentaire dépasse 90 %. Toutefois, le pigeon *Columba arquatrix* est assez sélectif et montre une préférence pour les capsules dures et fibreuses et les drupes grasses. Il y a un exemple très marqué de mutualisme plante-disperseur entre le petit barbu *Pogoniulus leucomystax* et les baies de Loranthaceae/Viscaceae.

La plupart des fruits consommés (n = 134 espèces) sont des baies (56) et des drupes (58). Les couleurs les plus fréquentes des fruits mangés par les oiseaux et les singes sont pourpre/noir et rouge, cependant les fruits de couleur verte ne sont pas ignorés. Chez les oiseaux, le diamètre maximum des fruits avalés entiers correspond (avec quelques exceptions) à la largeur de la base du bec : ainsi les plantes à petits fruits attirent davantage d'espèces de consommateurs que celles à grands fruits, les oiseaux à bec large se nourrissant communément de petits fruits.

Les observations sur la phénologie de la fructification par rapport aux consommateurs ne permettent pas de mettre en évidence une influence évolutive de ceux-ci sur la périodicité de la fructification.

Les pigeons *Columba arquatrix* et *Treron australis* ont été considérés à tort comme des prédateurs de graines. Ils sont potentiellement importants dans la dispersion des graines à courte et longue distance. L'essentiel de la dissémination des graines de plantes afromontagnardes (i.e. dont la distribution se restreint à une mosaïque de forêts de montagne) doit être imputé aux oiseaux frugivores. Cependant, pour certains types de gros fruits non consommés par les oiseaux, le rôle des chauves-souris devrait être étudié ; les diaspores sèches de certains arbustes du sous-bois sont probablement dispersés (accidentellement) par des oiseaux granivores.

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APPENDIX 1

Systematic checklist of plant species.

Gymnospermae	
Cupressaceae	<i>Juniperus procera</i> Hochst. ex Endl.
Podocarpaceae	<i>Podocarpus latifolius</i> (Thunb.) R. Br. ex Mirb.
Angiospermae	
Monocotyledones	
Agavaceae	<i>Dracaena afromontana</i> Mildbr. <i>D. laxissima</i> Engl. <i>D. usambarensis</i> Engl.
Gramineae	<i>Olyra latifolia</i> L. <i>Panicum adenophorum</i> K. Schum. <i>Setaria longiseta</i> P. Beauv. <i>Streblochaete longiarista</i> (A. Rich.) Pilg. <i>Asparagus setaceus</i> (Kunth.) Jessop <i>Ensete ventricosum</i> (Welw.) E.E. Cheesman
Liliaceae	
Musaceae	
Dicotyledones	
Acanthaceae	<i>Hypoestes verticillaris</i> (L. f.) Roem. & Schult.
Anacardiaceae	<i>Rhus longipes</i> Engl.
Apocynaceae	<i>Carvalhoa campanulata</i> K. Schum. <i>Landolphia buchananii</i> (Hall. f.) Stapf <i>Rauwolfia caffra</i> Sond. <i>Tabernaemontana stapfiana</i> Britten
Aquifoliaceae	<i>Ilex mitis</i> (L.) Radlk.
Araliaceae	<i>Cussonia spicata</i> Thunb. <i>Polyscias fulva</i> (Hiern) Harms <i>Schefflera abyssinica</i> (A. Rich.) Harms <i>S. umbellifera</i> (Sond.) Baill.
Boraginaceae	<i>Ehretia cymosa</i> Thonn.
Cactaceae	<i>Rhipsalis baccifera</i> (J. Mill.) Stearn
Celastraceae	<i>Cassine aethiopica</i> Thunb. <i>C. transvaalensis</i> (Burt Davy) Codd <i>Maytenus acuminata</i> (L. f.) Loes. <i>M. heterophylla</i> (Eckl. & Zeyh.) N. Robson
Chrysobalanaceae	<i>Parinari curatellifolia</i> Planch. ex Benth. <i>P. excelsa</i> Sabine
Connaraceae	<i>Jaundeia pinnata</i> (P. Beauv.) Schellenb.
Cornaceae	<i>Afrocrania volkensii</i> (Harms) Hutch.
Cucurbitaceae	<i>Coccinia mildbraedii</i> Harms
Ebenaceae	<i>Diospyros abyssinica</i> (Hiern) F. White subsp. <i>chapmaniorum</i> F. White <i>D. lycioides</i> Desf. <i>D. mespiliformis</i> Hochst. ex A. DC. <i>D. whyteana</i> (Hiern) F. White <i>D. zombensis</i> (B.L. Burtt) F. White <i>Euclea divinorum</i> Hiern
Euphorbiaceae	<i>Acalypha psilostachya</i> Hochst. ex A. Rich. <i>Bridelia brideliifolia</i> (Pax) Fedde <i>B. micrantha</i> (Hochst.) Baill. <i>Clusia abyssinica</i> Jaub. & Spach <i>Croton gratissimus</i> Burch. <i>C. macrostachyus</i> Del. <i>C. sylvaticus</i> Krauss <i>Drypetes gerrardii</i> Hutch. <i>Erythrococca hirta</i> Pax <i>Macaranga capensis</i> (Baill.) Sim <i>M. kilimandscharica</i> Pax <i>Neoboutonia macrocalyx</i> Pax <i>Sapium ellipticum</i> (Krauss) Pax

	<i>Uapaca kirkiana</i> Müll. Arg.
	<i>U. nitida</i> Müll. Arg.
	<i>U. sansibarica</i> Pax
Flacourtiaceae	<i>Aphloia theiformis</i> (Vahl) Benn.
	<i>Casearia battiscombei</i> R.E. Fr.
	<i>Kiggelaria africana</i> L.
	<i>Scolopia stolzii</i> Gilg
Guttiferae	<i>Garcinia kingäensis</i> Engl.
	<i>Harungana madagascariensis</i> Poir.
Lauraceae	<i>Cryptocarya liebertiana</i> Engl.
	<i>Ocotea usambarensis</i> Engl.
Loganiaceae	<i>Anthocleista grandiflora</i> Gilg
Loranthaceae	<i>Dendrophthoe pendens</i> (Engl. & Krause) Danser
	<i>Englerina inaequilatera</i> (Engl.) Balle
	<i>Erianthemum dregei</i> (Eckl. & Zeyh.) v. Tieghem
	<i>Phragmanthera usuiensis</i> (Oliv.) M.G. Gilbert
	<i>Tapinanthus bipartitus</i> Polh. & Wiens (= <i>T. sansibarensis</i> auct. non (Engl.) Danser in Dowsett-Lemaire, 1985a)
	<i>T. subulatus</i> (Engl.) Danser
Meliaceae	<i>Ekebergia capensis</i> Sparrm.
	<i>Lepidotrichilia volkensii</i> (Gürke) Leroy
	<i>Trichilia dregeana</i> Sond.
Meliantaceae	<i>Bersama abyssinica</i> Fresen.
Menispermaceae	<i>Stephania abyssinica</i> (Dill. & A. Rich.) Walp.
Mimosaceae	<i>Acacia cyclops</i> A. Cunn.
Monimiaceae	<i>Xymalos monospora</i> (Harv.) Warb.
Moraceae	<i>Ficus capensis</i> Thunb.
	<i>F. exasperata</i> Vahl
	<i>F. ingens</i> (Miq.) Miq.
	<i>F. kirkii</i> Hutch.
	<i>F. lutea</i> Vahl
	<i>F. polita</i> Vahl
	<i>F. sansibarica</i> Warb.
	<i>F. sycomorus</i> L.
	<i>F. thonningii</i> Bl.
	<i>F. vallis-choudae</i> Del.
	<i>Myrianthus holstii</i> Engl.
	<i>Treulia africana</i> Decne.
Myricaceae	<i>Myrica salicifolia</i> A. Rich.
Myrsinaceae	<i>Maesa lanceolata</i> Forssk. subsp. <i>lanceolata</i>
	<i>Rapanea melanophloeos</i> (L.) Mez
Myrtaceae	<i>Eugenia capensis</i> (Eckl. & Zeyh.) Harv. & Sond.
	<i>Syzygium cordatum</i> Hochst. ex Krauss
	<i>S. guineense</i> (Willd.) DC. subsp. <i>afromontanum</i> F. White
Ochnaceae	<i>Ochna holstii</i> Engl.
	<i>O. stolzii</i> Gilg ex Engl.
Oleaceae	<i>Chionanthus battiscombei</i> (Hutch.) Stearn
	<i>Jasminum abyssinicum</i> Hochst. ex DC.
	<i>Olea africana</i> Mill.
	<i>O. capensis</i> L.
Oliniaceae	<i>Olinia rochetiana</i> Juss.
Passifloraceae	<i>Adenia stolzii</i> Harms
Pittosporaceae	<i>Pittosporum viridiflorum</i> Sims
Rhamnaceae	<i>Rhamnus prinoides</i> L'Hérit.
Rosaceae	<i>Hagenia abyssinica</i> (Bruce) J.F. Gmel.
	<i>Prunus africana</i> (Hook. f.) Kalkm.
	<i>Rubus ellipticus</i> J.E. Sm.
Rubiaceae	<i>Aulacocalyx diervilloides</i> (K. Schum.) Petit
	<i>Canthium gueinzii</i> Sond.
	<i>Chassalia parvifolia</i> K. Schum.
	<i>Coffea ligustroides</i> S. Moore
	<i>Galiniera coffeoides</i> Del.
	<i>Psychotria ealaensis</i> De Wild.

	<i>P. mahonii</i> C.H. Wright
	<i>P. zombamontana</i> (O. Kuntze) Petit
	<i>Rutidea fuscescens</i> Hiern
	<i>R. orientalis</i> Bridson
	<i>Rytigynia adenodonta</i> (K. Schum.) Robyns
	<i>Tricalysia acocantheroides</i> K. Schum.
	<i>T. verdcourtiana</i> Robbrecht (= <i>T. myrtifolia</i> auct. non S. Moore in Dowsett-Lemaire, 1985a)
Rutaceae	<i>Clausena anisata</i> (Willd.) Benth.
	<i>Vepris stolzii</i> I. Verdoorn
Santalaceae	<i>Osyris lanceolata</i> Hochst. & Steudel
Sapindaceae	<i>Allophylus abyssinicus</i> (Hochst.) Radlk.
	<i>A. chaunostachys</i> Gilg
	<i>Blighia unjugata</i> Bak.
	<i>Pappea capensis</i> Eckl. & Zeyh.
Sapotaceae	<i>Aningeria adolfi-friedericii</i> (Engl.) Robyns & Gilb.
	<i>Bequaertiodendron natalense</i> (Sond.) Heine & J.H. Hemsl.
	<i>Chrysophyllum gorungosamum</i> Engl.
Scrophulariaceae	<i>Halleria lucida</i> L.
Solanaceae	<i>Solanum mauritianum</i> Scop.
	<i>S. torvum</i> Swartz
Sterculiaceae	<i>Cola greenwayi</i> Brenan
	<i>Dombeya torrida</i> (J.F. Gmel.) P. Bamps
Ulmaceae	<i>Celtis africana</i> Burm. f.
	<i>C. gomphophylla</i> Bak.
	<i>Trema orientalis</i> (L.) Bl.
Urticaceae	<i>Ureia hypselodendron</i> (Hochst. ex A. Rich.) Wedd.
Verbenaceae	<i>Clerodendrum johnstonii</i> Oliv.
	<i>C. quadrangulatum</i> Thomas
Viscaceae	<i>Viscum capense</i> L. f.
	<i>V. nervosum</i> Hochst. ex A. Rich.
	<i>V. shirensense</i> Sprague
Vitaceae	<i>Cyphostemma kilimandscharicum</i> (Gilg) Descoings
	<i>C. masukuense</i> (Bak.) Descoings
	<i>C. vandenbrandeanum</i> (Dewit) Descoings
	<i>Rhoicissus tridentata</i> (L. f.) Wild & R.B. Drumm.

APPENDIX 2

Fruit- and seed-eating records in birds and mammals with fewer than 10 species recorded for each.

Birds

Columba delegorguei : fruits of *Ficus thonningii*.

Streptopelia semitorquata : fruits of *Macaranga capensis*.

Turtur tympanistris : seeds of *Croton macrostachyus*, *Neoboutonia macrocalyx*, *Polyscias fulva*.

Poicephalus robustus : seeds of *Aningeria adolfi-friedericii*, *Cola greenwayi*, *Parinari excelsa*.

Tauraco porphyreolophus : fruits of *Dracaena usambarensis*, *Ficus thonningii*, *Sapium ellipticum*, *Uapaca kirkiana*, *U.sansibarica*.

Colius striatus : fruits of *Cussonia spicata*, *Maesa lanceolata*, *Maytemus heterophylla*, *Rhus longipes*.

Tockus alboterminatus : fruits of *Allophylus abyssinicus*, *Ficus sansibarica*.

Stactolaema leucotis : fruits of *Ficus capensis*, *F. exasperata*, *F. kirkii*, *F. lutea*, *F. sansibarica*, *F. thonningii*, *Trema orientalis*.

Stactolaema olivacea : fruits of *Ekebergia capensis*, *Ficus capensis*, *F. kirkii*, *F. polita*, *F. sansibarica*, *F. thonningii*, *Macaranga capensis*, *M. kilimandscharica*, *Rauwolfia caffra*.

Stactolaema whytii : fruits of *Ficus capensis*, *Rauwolfia caffra*.

Pogoniulus bilineatus : fruits of *Clausena anisata*, *Ficus thonningii*, *Macaranga capensis*, *Rhipsalis baccifera*, *Tapinanthus subulatus*, *Trema orientalis*, *Viscum shirensense*.

Oriolus auratus : fruits of *Ficus ingens*, *F. lutea*, *Trema orientalis*.
Oriolus larvatus : fruits of *Ficus ingens*, *F. thonningii*.
Oriolus chlorocephalus : fruits of *Ficus thonningii*.
Alcippe abyssinica : fruits of *Jasminum abyssinicum*, *Ochna holstii*.
Andropadus virens : fruits of *Bridelia brideliifolia*, *B. micrantha*, *Canthium gueinzii*, *Harungana madagascariensis*, *Macaranga capensis*, *M. kilimandscharica*, *Rhus longipes*, *Trema orientalis*.
Andropadus masukuensis : fruits of *Bridelia micrantha*, *Canthium gueinzii*, *Ficus thonningii*, *Rhoicissus tridentata*, *Xymalos monospora*.
Phyllastrephus flavostriatus : fruits of *Harungana madagascariensis*, *Polyscias fulva*.
Cossypha natalensis : fruits of *Macaranga capensis*.
Turdus olivaceus : fruits of *Afrocrania volkensis*, *Myrica salicifolia*, *Polyscias fulva*, *Syzygium guineense afromontanum*.
Turdus gurneyi : fruits of *Aulacocalyx diervilloides*, *Xymalos monospora*.
Sylvia atricapilla : fruits of *Aphloia theiformis*, *Macaranga capensis*, *Maesa lanceolata*, *Myrica salicifolia*, *Polyscias fulva*, *Urea hypselodendron*.
Malacotus olivaceus : fruits of *Kiggelaria africana*.
Onychognathus morio : fruits of *Polyscias fulva*.
Onychognathus tenuirostris : fruits of *Allophylus abyssinicus*, *Polyscias fulva*.
Petronia superciliaris : seeds of *Ficus vallis-choudae*.
Cryptospiza reichenovii : seeds of *Acalypha psilostachya*, *Hagenia abyssinica*, *Hypoestes verticillaris*, *Panicum* spp. including *P. adenophorum*, *Setaria longiseta*, *Streblochaete longiarista*, *Urea hypselodendron*.
Hypargos niveoguttatus : seeds of *Olyra latifolia* and other grasses.
Mandingoa nitidula : seeds of *Amaranthaceae* and *Gramineae* spp.
Estrilda melanotis : seeds of *Urea hypselodendron*.
Serinus mozambicus : seeds of *Ficus lutea*.
Serinus canicollis : seeds of *Hagenia abyssinica*.
Serinus citrinelloides : seeds of *Cussonia spicata*, *Ficus capensis*, *F. vallis-choudae*, *Hagenia abyssinica*.
Mammals
Unidentified bat (*Megachiroptera*) : fruits of *Coccinia mildbraedii*, *Treulia africana*. *Eidolon helvum* : fruits of *Ficus* spp., *Parinari excelsa* (J.D. Chapman, pers. comm.).
Galagoides zanzibaricus : fruits of *Drypetes gerrardii*.
Cercopithecus pygerythrus : fruits of *Diospyros zombensis*, *Myrianthus holstii*.
Potamochoerus porcus : fruits of *Ficus kirkii*, *Ocotea usambarensis*, *Olea capensis*, *Podocarpus latifolius*, *Syzygium guineense afromontanum*.
Cephalophus monticola : fruits of *Adenia stolzii*, *Chrysophyllum gorungosanum*, *Garcinia kingäensis*.
Cephalophus natalensis : fruits of *Croton macrostachyus*, *Drypetes gerrardii*.
Helioscurus mutabilis : seeds of *Chrysophyllum gorungosanum* and *Parinari excelsa*, fruits of *Neouboutonia macrocalyx*, *Ocotea usambarensis* and *Syzygium guineense afromontanum*.
Unidentified rodent : fallen fruits of *Tabernaemontana stapfiana*.