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**International Journal of Primatology**  
The Official Journal of the International  
Primatological Society

ISSN 0164-0291  
Volume 38  
Number 5

Int J Primatol (2017) 38:914-941  
DOI 10.1007/s10764-017-9988-3



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# Dietary Variability in Redtail Monkeys (*Cercopithecus ascanius schmidti*) of Kibale National Park, Uganda: the Role of Time, Space, and Hybridization

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Received: 3 March 2017 / Accepted: 21 July 2017 / Published online: 2 September 2017  
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**Abstract** Studies of the diet of different groups of the same species allow us to understand intraspecific dietary variability. I collected dietary data from six neighboring groups of redtail monkeys (*Cercopithecus ascanius schmidti*) and three hybrid monkeys over 12 years at Ngogo and from one group at Kanyawara in Kibale National Park, Uganda and compared these results with previous studies of redtail diets elsewhere in Kibale and from the Kakamega Forest of Kenya. I scored feeding as a particular monkey ingesting a species-specific plant part, or catching insects from a species-specific substrate. A new feeding score was tallied for the same combination of parameters only after a 30-min interval or if the identity of one of the three parameters changed. I counted trees along transects in the home ranges of the two main study groups to calculate food selection ratios. I used chi-square tests to compare diets between groups and time periods and Spearman rank correlation coefficient tests for dietary correlates. These comparisons reveal considerable variation in plant parts and species eaten by redtails between months, years, and neighboring groups with overlapping ranges. Selection ratios show that some tree species are important sources of plant food, while others are more important as sources of invertebrates. The high incidence of insectivory by redtails demonstrates another ecological role they play in addition to seed dispersal. The intrademic variation in diets I describe for Kibale was often as great as and sometimes greater than the interademic variation. The diets of the hybrid monkeys at Ngogo differed in some ways from their parental species, particularly in their greater consumption of invertebrates. Introgression may have led to some of these differences within and between redtail demes. The pronounced variability in redtail diets demonstrates why a typological perspective of species is unwarranted and that the validity of interspecific comparisons requires a thorough understanding of intraspecific variation.

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Handling Editor: Joanna M. Setchell.

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**Keywords** Dietary variability · Hybrids · Redtail monkeys

## Introduction

Interspecific comparisons of behavior and ecology contribute to our understanding of evolutionary trends and the relative importance of genetic and environmental factors in explaining similarities and differences between species. However, any attempt at interspecific comparisons relies on a detailed understanding of intraspecific variation. For example, it is important to understand intraspecific variability in diet, when comparing diets between species, as they relate, for example, to niche partitioning, ecological specialization, interspecific competition, and the role of genetics in diet. Information on dietary variability is theoretically important and assists the development of conservation action plans because it reflects the extent of a species' ecological dependencies and flexibility.

A typological approach using average values is not likely to reflect real similarities or differences between species or even between populations or subpopulations of the same species (Chapman *et al.* 2002; Mayr 1959; Struhsaker 2008). This reality is especially relevant when studying diets of primates inhabiting rain forests, where potential foods are diverse, tree communities are typically heterogeneous over short distances, and patterns of plant phenology are often unsynchronized and aseasonal (Chapman *et al.* 2005; Struhsaker 1997). These variables are further compounded by the inherent difficulties of studying most rain forest primates due to the poor visibility afforded by the forest and because the animals are often very shy owing to hunting pressure by humans. As a consequence, there are relatively few detailed studies of rain forest monkeys that examine temporal, spatial, and intergroup variation in diet. This is particularly so for Africa's guenons (*Cercopithecus*).

Understanding the factors affecting intraspecific dietary variability must take account of temporal and spatial parameters. Among the guenons, studies demonstrate differences in diets, often profound, between species and between populations of the same species (Chapman *et al.* 2002; Cords 1987a; Gautier-Hion 1980, 1988). Several other studies have demonstrated striking intermonthly dietary variability within specific social groups (Cords 1986, 1987b; Gathua 2000; Gautier-Hion 1980, 1988; Rudran 1978). Fewer studies have compared diets between demes (subpopulations) in the same forest (Butynski 1990; Chapman and Chapman 2000; Chapman *et al.* 2002; Gathua 2000). Likewise, few have compared diets of adjacent and/or neighboring groups of the same deme (Butynski 1990; Conklin-Brittain *et al.* 1998; Gathua 2000; Rudran 1978; Wrangham *et al.* 1998). The diets of four neighboring groups of blue monkeys (*Cercopithecus mitis stuhlmanni*) differed in a 23-mo continuous study, although the analysis focused on only four gross food types and only six species-specific plant parts and did not evaluate intermonthly variation in diet (Butynski 1990). A 12-mo study evaluating gross plant food types (not invertebrates) in two neighboring groups of redtail monkeys and two groups of blue monkeys showed slight intergroup differences (Conklin-Brittain *et al.* 1998; Wrangham *et al.* 1998). Ripe fruit was the only food type the authors evaluated on a monthly basis, but they combined the data for six groups of three monkey species and did not provide information on intermonthly variation at the species level. The most thorough studies of variation within a deme are on blue monkeys in Kibale (Rudran 1978) and on redtails in Kakamega (Gathua 2000). Both studies present detailed data on intermonthly variation in species-specific plant parts eaten,



as well as invertebrates. Two neighboring groups of blue monkeys showed several dietary differences, including selection ratios, proportions of gross food types, and intermonthly diets (Rudran 1978). Redtails also showed differences between two neighboring groups, but the author concluded that the similarity in the diets of the two groups was more impressive than the differences (Gathua 2000). The study of blue monkeys is the only one that also examined intramonthly and interannual variation in diet, finding great differences in both sets of analyses for the main study group (Rudran 1978).

Here I present new data on redtail and blue  $\times$  redtail hybrid monkey diets from the Ngogo area of the Kibale National Park, Uganda that expand and compound our understanding of dietary variability in this species. I compare the Ngogo data with those from other parts of Kibale and from the Kakamega Forest of Kenya.

## Methods

### Study Sites and Subjects

My two study sites, Kanyawara (ca. 0°34'N, 30°21'E) and Ngogo (ca. 0°29'N, 30°26'E), are located in the Kibale National Park, Uganda. The ecology of these two rain forest sites is described in Struhsaker (1975, 1997). Redtails in Kibale live in groups ranging in size from 14 to 50, usually with only one adult male (Struhsaker 1988). I collected dietary data on one group of redtails at Kanyawara (TTK group) and six groups at Ngogo (S, Ss, Sn, BTP, RAT, and SW), and on two adult female and one adult male hybrid at Ngogo. The three hybrids were crosses between redtail and blue monkeys and each of them was spatially and socially integrated into one of the redtail social groups I studied (Struhsaker *et al.* 1988). Of the six Ngogo groups, two (Sn and Ss) were formed when group S divided (Struhsaker and Leland 1988). The ranges of the S, Sn, and Ss groups partially overlapped that of the BTP group to the south, whose range also partially overlapped the RAT group even further south. The SW group was located ca. 1 km to the west and southwest of the other groups (map in Struhsaker and Leland 1988). Its range did not overlap that of any of the other study groups. An adult male blue monkey was a full-time resident in the BTP group from 1980 to 1986.

I use the term deme to refer to subpopulations within Kibale, as have others (Chapman and Chapman 2000; Chapman *et al.* 2002). The two demes in my study are Kanyawara and Ngogo, separated from one another by ca. 10 km within the continuous forest of Kibale (map in Struhsaker 1997).

### Data Collection

I used the same method to collect feeding data as that of Butynski (1990), Cords (1986, 1987b), Rudran (1978), and Struhsaker (1975). I scored feeding as a particular monkey ingesting a species-specific plant part or, in the case of invertebrates, from a species-specific substrate using the same method of capture. I scored a new feeding event for the same combination of parameters only after a 30-min interval or if one of the three parameters changed. The categories of plant parts I recognized are generally self-explanatory (see key in Table I). Young leaves were usually smaller and of a different color and texture (softer, more pliable) than mature leaves. I combined uncommon foods (<0.2% of all samples for any one group) into the category "Other."

I sampled the TTK and S (1975–1976) groups with the primary goal of collecting ecological and behavioral data during all-day (>11.5 h) samples. I collected feeding data from the other groups primarily during partial-day samples (<11.5 h) and less frequently during all-day samples.

I considered redtails to be eating invertebrates based on the motor patterns they used when removing and then eating small objects off plant substrates that showed no damage after the removal of the item. I categorized the motor patterns used in capturing invertebrates as slow, e.g., slow pick, mouth direct, or fast, e.g., rapid grab, slap hand against branch, the same as those described in detail by Cords (1986) and Rudran (1978). In most cases I was unable to see the ingested item well enough to identify it. However, in those cases where I could, the objects were always insects.

I collected the data I present here as follows:

TTK group (Kanyawara): 35 all-day samples (usually 10–12 h/day) distributed as 5 continuous days in each of 7 mo (November 1973–June 1974)

Ngogo groups:

S group: 35 all-day samples distributed as 5 continuous days in each of 7 mo (July 1975–March 1976) and then 78 partial days distributed in 19 mo from 1978 to 1980

Sn group: 19 partial days in 18 mo from 1980 to 1986

Ss group: 31 partial days in 23 mo from 1980 to 1986

BTP group: 78 partial days in 51 mo from 1978 to 1986

RAT group: 22 partial days in 19 mo from 1978 to 1980

SW group: 27 partial days in 25 mo from 1979 to 1987

One advantage of sampling several groups over many months and years is that it is more likely to be representative of a deme than a study that concentrates on only one or two groups during a 1-yr. period. This is because a study of more groups over a longer period will cover a larger area and include more of the dietary diversity that is due to forest heterogeneity and interannual variability in food availability resulting from temporal asynchrony and variation in plant phenology.

I enumerated trees along 5-m-wide transects of variable lengths using the trail grid system in the home ranges of the TTK group at Kanyawara and the S group at Ngogo to calculate selection ratios (Crawley 1983). I tallied all trees  $\geq 10$  m tall whose trunk center fell within the 5-m-wide strip. I tallied 430 trees in 1.05 ha, representing ca. 4% of the TTK group's home range and 650 trees in 1.9 ha representing ca. 2.8% of the S group's range. I used the scientific names for trees published in Hamilton (1981) and Beentje (1994), as well as those provided by the staff at the National Museums of Kenya and the Kew Royal Botanic Gardens.

## Data Analysis

I used chi-square tests to compare the gross food types in TTK and S groups, and to compare dietary food types between months in these groups. I used Spearman rank correlation coefficient tests to test the relationship between monthly proportional

consumption of different food types. I did not compare the Ngogo groups statistically because I did not think it was warranted given the opportunistic and unequal way I sampled groups other than S (1975–1976) and TTK groups. I compared hybrids and the redtail members of their group using chi-squared tests, because I sampled them simultaneously in the same area. Where expected values were low, I combined categories of food types because of the restrictions of the chi-square test. I calculated selection ratios for TTK and S groups. This ratio is calculated by dividing the percentage a tree species represents in the diet by the percentage of that species in the tree enumeration sample (Crawley 1983). Ratios  $>1$  indicate that a species was highly selected, whereas values  $<1$  indicate that a species was used less than expected based on its abundance (Crawley 1983). Values close to 1 show that a species was fed upon in proportion to its occurrence.

## Ethical Note

I conducted this research with permission from the Uganda Forestry Department and National Research Council. I have no conflict of interest.

## Results

### Plant Foods

I observed TTK group at Kanyawara feeding on a minimum of 52 plant species and possibly as many as 80 (Table I). The minimum number of plant species fed on by the six groups at Ngogo was 88 and the possible maximum was 119. The maximum number of plant species depends on how many of the unidentified species the redtails fed upon were different from one another. Unidentified plant foods were usually due to the fact that I was unable to collect specimens for identification. Some of the difference in numbers of species fed upon is due to the fact that I sampled only one group at Kanyawara compared to six groups at Ngogo. Furthermore, my sample for the TTK group at Kanyawara spanned only 16 mo (March 1973–June 1974), whereas my sample for the six Ngogo groups spanned 12 yr. (1975–1987).

### Uncommon Food Items

Uncommon food items included mushrooms (maroon and white colored types), nectar licked from the flowers of *Symphonia globulifera* and *Spathodea campanulata* (flowers left intact and attached to tree; redtail muzzles were covered with pollen, making them likely pollinators), the milky latex sap from *Ficus vallis-choudae*, pitch off *Teclea nobilis* branches, young stems of *Urera cameroonensis* and *Monodora myristica*, galls off the flowers of *Funtumia africana*, clay termite tunnels on tree branches and trunks, and water from tree holes (a total of 14 scores for all Ngogo groups combined).

Redtails were sometimes very selective in what they ate from a particular plant part. They ate only the base of the flowers of *Dictyandra arborescens* and *Tabernaemontana holstii*. This is where the nectar is located. Redtails ingested the fruits of most species they fed on in their entirety. However, they ate only the mesocarp (aril) of *Trichilia*

**Table 1** Plant food species and parts eaten by redtail monkeys in Kibale Forest, Uganda, 1973–1987

Species	Kanyawara (TTK group)	Ngogo (all groups)
<i>Acacia monticola</i>	FL	YL
<i>Acalypha bipartita</i>	ML, PYL	ML
<i>Albizia ferruginea</i>		FL, S
<i>Albizia glaberrima</i>		FL
<i>Albizia gummifera</i>		FL, FLB
<i>Aningeria altissima</i>	FLB, FL	
<i>Aphania senegalensis</i>	RF, YL	RF, GML
<i>Apodytes dimidiata</i>		YL
<i>Balanites wilsoniana</i>	LB, ML, YL	
<i>Bosqueia phoberos</i>	F, RF, UF, LB, YL	F, RF, UF, FLB, LB, YL, S
<i>Canthium</i> sp. cf. <i>brownii</i>	UF	
<i>Canthium vulgare</i>		FLB
<i>Cardiospermum grandiflorum</i>	ML	
<i>Casearia battiscombei</i>	RF	
<i>Casearia engleri</i>		RF
<i>Cassipourea ruwensorensis</i>		F
<i>Celtis africana</i>	F, RF, FLB, LB	F
<i>Celtis durandii</i>	F, RF, YL	F, RF, UF, LB, L, GML
<i>Celtis mildebraedi?</i>		F
<i>Chaetacme aristata</i>	F, RF, FL GML	RF, YL, GS <sub>t</sub>
<i>Chrysophyllum albidum</i>	na	RF, UF, FL, FLB, LB, PYL, T <sub>pi</sub>
<i>Chrysophyllum gorungosanum</i>	RF, FL, FLB	na
<i>Cissus oliveri</i>		F, RF, UF, FL, FLB, YST
<i>Cordia millenii</i>	UF	RF, UF
<i>Cyphomandria</i>	YL	ML, YL
<i>Dasylepis eggelingii</i>		F, RF
<i>Dictyandra arborescens</i>		RF, FL
<i>Diospyros abyssinica</i>	RF, FL, FLB, YL, GML	F, RF, UF, S, GYL
<i>Dombeya mukole</i>	LB, ML, YL	
<i>Dovyalis macrocalyx</i>		F, RF, FL
<i>Drypetes gerrardii</i>		RF
<i>Ehretia cymosa</i>	RF, UF, LB	
Epiphyte (monocot) > 3	ML, YL, YST	
Epiphyte (monocot) > 2		UF, FL
<i>Erythrina excelsa</i>		FL
<i>Fagaropsis angolensis</i>	UF	F, RF
<i>Ficus brachylepis</i>	F	RF, LB
<i>Ficus capensis</i>		RF
<i>Ficus cyathistipula</i>		F, LB
<i>Ficus exasperata</i>	F, RF	F, RF, UF, LB, YL, PYL
<i>Ficus mucuso</i>		F, RF, LB
<i>Ficus natalensis</i>		F
<i>Ficus polita</i>		RF
<i>Ficus pseudomangifera</i>		RF, F
<i>Ficus saussureana</i> ( <i>dawei</i> )		F, RF
<i>Ficus vallis-choudae</i>		F, RF, UF, LB, YL, Latex



**Table I** (continued)

Species	Kanyawara (TTK group)	Ngogo (all groups)
Fungus dark red		Entire
Fungus white sp.	Entire	Entire
Fungus, red, off <i>Dombeya</i>	Entire	
<i>Funtumia africana</i>	S	S, GFL
<i>Harrisonia abyssinica</i>		F, RF
<i>Harungana madagascariensis</i>	RF	
Herb sp.	YL, YST	
Herb sp.		YL
<i>Jasminum glabra</i>		YL
<i>Kigelia moosa</i>	LB, YL	
Liana sp. >20		F, UF, FL, FLB, ML, YL, YST
Liana sp. >19	F, FL, YL, YST, ML	
<i>Linociera johnsonii</i>	UF	F, RF, UF, FL, YL, S, GML
<i>Markhamia platycalyx</i>	YL, PYL	FL
<i>Milletia dura</i>	FL, FLB, LB, YL	FL, FLB
<i>Mimusops bagshawei</i>	F, RF, UF, FLB, FL	F, RF, UF, FL, FLB
<i>Morus lactea</i>		F, S
<i>Monodora myristica</i>	LB, YL	F, RF, FL, FLB, LB, YL, PYL, YST, N
<i>Neoboutonia melleri</i>		UF
<i>Olea welwitschii</i>	F, FL, FLB, ML, YL	F, RF, UF, FL, FLB, YL, ML, MLP, GML
<i>Oncoba spinosa</i>		LB, YL, YST
Orchid, epiphytic >7		FL, roots, ML, MLP, YST
<i>Pancovia turbinata</i>	UF	
<i>Parinari excelsa</i>	F, RF	
<i>Parkia filicoidea</i>		LB, YL
<i>Piper guineense</i>		RF
<i>Piper</i> sp.		RF
<i>Piptadeniastrum africanum</i>		LB, L, US
<i>Pleiocarpa pycnantha</i>		RF, YL
<i>Premna angolensis</i>	FLB, LB	F, FLB, LB, YL, YST
<i>Prunus africana</i>		F
<i>Pseudospondias microcarpa</i>	F, UF	F, RF, UF, YL, PYL
<i>Psychotria lauracea</i>		RF
<i>Pterygota mildbraedii</i>	na	FL, FLB
<i>Randia lucidula</i>		F, RF, FL
<i>Randia malleifera</i>		FL, FLB
<i>Rawsonia lucida</i>		F, RF
<i>Rhipsalis baccifera</i>	F, RF	F, RF
<i>Rothmannia urcelliformis</i>	F, RF, YL	F, RF, UF, FL, FLB, LB, YL, L, S, A
Rubiaceae sp.	YL	YL
<i>Rytiginia ruwenzoriensis</i>		FLB
Shrub 3 sp	F, LB, YL	
Shrub sp. >1		YL
Shrub sp. Rubiaceae > 2		F, RF
<i>Spathodea campanulata</i>		FL, FLB, LB, YL, N
<i>Strombosia scheffleri</i>	RF	

**Table I** (continued)

Species	Kanyawara (TTK group)	Ngogo (all groups)
<i>Symphonia globulifera</i>	RF, FL, FLB, N	
<i>Tabernaemontana holsti</i>		F, RF, UF, FL, FLB, LB, PYL, PML, S
<i>Tarenna pavettoides</i>		F, RF, UF, ML
<i>Teclea nobilis</i>	F, RF, YL	F, RF, UF, P
<i>Toddalia asiatica</i>		RF
<i>Treculia africana</i>		UF, FL
<i>Trema guineensis</i>	F, RF, UF	
<i>Trichilia splendida</i>		RF
Tree sp. > 5		UF, ML, YL, PYL
Tree spp. >7	FL, LB, YL, YST	
<i>Urera cameroonensis</i>		YL, YST
<i>Uvaria angolensis</i>	FLB	
<i>Uvariopsis congensis</i>	F, RF, UF	F, RF, UF
<i>Vangueria apiculata</i>	UF	F, UF, ML
<i>Ventilago africana</i>	UF	
<i>Vitex amboniensis</i>		UF
<i>Voaganga thouarsii</i>		F, UF, FL, FLB
<i>Warburgia ugandensis</i>		F, UF
<i>Zanha golungensis</i>		YL

F fruit undetermined ripeness, RF ripe fruit, UF unripe fruit, FL flowers, FLB floral buds, LB leaf buds, ML mature leaf, YL young leaf, YLP young petiole, MLP mature petiole, YST young stem tip, S seed, US unripe seed, A anther, GML mature leaf gall, GYL young leaf gall, GFL floral gall, GSt stem gall, Tpi twig pith, N nectar, P pitch, na not present

*splendida* and *Casearia engleri* and the thin layer beneath the epicarp of *Linociera johnsonii*, discarding the seeds beneath or very near the parent tree. Although they often ingested seeds when eating fruit, it appeared that they usually, if not always, either spat them out or, in the case of figs, passed them in the feces. I observed the redtails eat seeds only on 10 occasions out of thousands of observations and from only six species (Table I). The consumption of unripe fruit may have also involved the consumption of insects, but I was unable to confirm this. In any event, the consumption of unripe fruit likely resulted in seed mortality.

### Comparison of TTK (Kanyawara, 1973–1974) and S (Ngogo, 1975–1976) Groups

The TTK and S groups differed in the gross food types they ate during comparable sampling periods (5 all-day samples in each of 7 mo, Table II;  $\chi^2 = 89.4$ ,  $df = 7$ ,  $P < 0.0001$ ). TTK group ate more flowers and floral buds combined, mature leaves, and mature-leaf galls than S group, while S group ate invertebrates more often than did TTK group. Fruit and invertebrates dominated the feeding scores for both groups, with unripe fruit representing  $\geq 5.9\%$  to 8%.

Both groups differed significantly in their dietary food types between months (TTK group:  $\chi^2 = 628.7$ ,  $df = 36$ ,  $P < 0.0001$ , Table III; S group:  $\chi^2 = 273.3$ ,  $df = 24$ ,  $P < 0.0001$ , Table IV). For TTK group 72% of the “Other” category items were mature-leaf galls.

**Table II** Comparison of gross food types in redbtail monkeys in five all-day samples in each of 7 mo for Kanyawara (1973–1974) and Ngogo (1975–1976) sites, Uganda

Food type	TTK group		S group	
	No. of times eaten	% of records	No. of times eaten	% of records
Fruit undetermined Ripeness	181	16.3	165	19.6
Ripe fruit	210	18.9	162	19.2
Unripe fruit	65	5.9	67	8.0
Flowers	47	4.2	35	4.2
Floral buds	135	12.2	31	3.7
Leaf buds	79	7.1	74	8.8
Mature leaf	44	4.0	6	0.7
Young leaf	60	5.4	41	4.9
Young leaf petioles	8	0.7	10	1.2
Gall on mature leaf	39	3.5	3	0.4
Invertebrates	226	20.4	241	28.6
Other	15	1.4	7	0.8
Sample size	1109		842	

These items were very important in April and May 1974. Both groups showed pronounced intermonthly variation in all categories, except mature leaves for S group.

In the S group there was a significant inverse correlation between the monthly proportional consumption of all fruit and the combined categories of flowers and floral and leaf buds ( $r_s = -0.82$ ,  $P = 0.024$ ,  $N = 7$ ) during the 7-mo sample. In other words, buds and flowers increased in the diet as fruit decreased. I found no significant correlations between any of the other food types of the S group (all fruit vs. all leaves:  $r_s = 0.10$ ,  $P > 0.83$ ; all leaves vs. invertebrates:  $r_s = 0.10$ ,  $P > 0.83$ ; all fruit vs. invertebrates:  $r_s = 0.32$ ,  $P = 0.48$ ; all leaves vs. all buds and flowers:  $r_s = 0.14$ ,  $P = 0.76$ ; all buds and flowers vs. invertebrates:  $r_s = 0.14$ ,  $P = 0.76$ ). Like S group, TTK group also showed a significant inverse correlation

**Table III** Monthly variation in food type (% of monthly sample) for TTK group of redbtails, Kanyawara, Uganda, 1973–1974

Date	All fruit	Flowers and floral buds	Leaf bud	Mature leaf	Young leaf/ Young leaf petiole	Invertebrates	Other	<i>N</i>
Nov 73	66.7	0	0	0.9	0.9	30.7	0.9	114
Dec 73	68.7	0.9	0	0.9	0.9	27.8	0.9	115
Jan 74	81.3	0	0	1.5	0	17.2	0	134
Feb 74	56	25	6	1.5	5	6.5	0	200
Apr 74	15.2	23.9	9.1	9.6	11.2	15.2	15.7	197
May 74	13.2	29.1	24.7	4.4	8.2	11	9.3	182
June 74	15.6	18.6	2.4	6	11.4	43.7	2.4	167
Total <i>N</i>								1109

**Table IV** Monthly variation in food type (% of monthly sample) for S group of redtails, Ngogo, Uganda, 1975–1976

Date	All fruit	Flowers and floral buds	Leaf bud	Mature leaf	Young leaf/Young leaf petiole	Invertebrates	N
July 75	21.3	23.6	2.2	2.8	3.9	44.9	89
Sept 75	43.1	1.8	30.3	0	4.6	20.2	109
Oct 75	49	2.1	21	1.4	13.3	12.6	143
Nov 75	56	0	2.6	0.4	7.3	31.9	116
Dec 75	65.1	0.9	3.8	0	3.8	24.5	106
Jan 76	44.5	7	0	0	3.9	44.5	128
Mar 76	44.4	19.9	1.3	0.7	4	27.2	151
Total N							842

between the dietary proportion of fruit and the combined categories of buds and flowers ( $r_s = -0.84$ ,  $P = 0.0003$ ,  $N = 13$ ) (Struhsaker 1978a). Unlike S group, however, TTK group showed two more inverse correlations between gross food types: fruit vs. all leaves ( $r_s = -0.78$ ,  $P = 0.002$ ,  $N = 13$ ) and leaves vs. buds and flowers ( $r_s = -0.69$ ,  $P = 0.009$ ,  $N = 13$ ) (Struhsaker 1978a). TTK group showed no significant correlation between the following food types: all fruit vs. invertebrates:  $r_s = 0.10$ ,  $P = 0.74$ ,  $N = 13$ ; all leaves vs. invertebrates:  $r_s = -0.29$ ,  $P = 0.34$ ,  $N = 13$ ; all buds vs. invertebrates:  $r_s = -0.44$ ,  $P = 0.14$ ,  $N = 13$  (Struhsaker 1978a).

Intermonthly variability was also apparent for both groups in the two most common species-specific plant foods eaten each month (Tables V and VI). The top two items accounted for 37–90% of the monthly diet, being more variable for TTK than for S group. The proportion these top two items represented in the monthly dietary sample did not correlate with the corresponding monthly sample size; i.e., smaller sample sizes did not result in higher proportions of the top two items (TTK group:  $r_s = -0.66$ ,  $P = 0.11$ ,  $N = 7$ ; S group:  $r_s = -0.25$ ,  $P = 0.59$ ,  $N = 7$ ). However, there were significant negative correlations between the percentage the top two items represented each month and the total number of species-specific plant parts eaten (TTK group:  $r_s = -0.86$ ,  $P = 0.018$ ,  $N = 7$ ; S group:  $r_s = -0.93$ ,  $P = 0.002$ ,  $N = 7$ ), and the total number of plant species eaten in the corresponding month (TTK:  $r_s = -0.88$ ,  $P = 0.009$ ,  $N = 7$ ; S:  $r_s = -0.96$ ,  $P = 0.0006$ ,  $N = 7$ ; Tables V and VI). In other words, when two species-specific items constituted higher proportions of the plant diet, the plant species richness of the diet was lower. None of these monthly top two species-specific foods were common to the two groups and the only species shared in this category was *Mimusops bagshawei*. In some months unripe fruit constituted  $\geq 14.5$ –14.9% of the diet.

### Dietary Variation among Ngogo Groups and Hybrids

The Ngogo groups varied in gross food types (Table VII). One of the most striking differences is the very high proportion of invertebrates and lower proportion of fruit in the diets of S (1978–1980) and RAT groups and the redtail-blue hybrids, namely females MBT and PT and male AMH, compared to the other groups. The two groups

**Table V** Monthly variation in species-specific plant foods (top two per month) for TTK group of redtails, Kanyawara, Uganda, 1973–1974

Species	% by month						
	Nov 73	Dec 73	Jan 74	Feb 74	Apr 74	May 74	June 74
<i>Teclea nobilis</i> ripe fruit	22.8						
<i>Mimusops bagshawei</i> ripe fruit	21.5	42.2	62.2				
<i>Bosqueia phoberos</i> fruit, undetermined ripeness		15.7	27.9				
<i>Aningeria altissima</i> flower bud/flower				25.1			
<i>Harungana madagascensis</i> ripe fruit				18.2			
<i>Millettia dura</i> flower bud/flower					20.4		
<i>Chaetacme arista</i> mature leaf gall					15.6		
<i>Premna angolensis</i> leaf bud						24.7	
<i>Mimusops bagshawei</i> flower						17.3	
<i>Uvariopsis congensis</i> unripe fruit							14.9
<i>Diospyros abyssinica</i> flower bud/flower							22.3
Total %	44.3	57.9	90.1	43.3	36.0	42.0	37.2
Total <i>N</i> for plant foods	79	83	111	187	167	162	94
Total no. species-specific parts	18	20	6	24	38	41	32
Total no. plant food species	15	15	5	20	27	35	26

**Table VI** Monthly variation in species-specific plant foods (top two per month) for S group of Redtails, Ngogo, Uganda, 1975–1976

Species	% by month						
	July 75	Sept 75	Oct 75	Nov 75	Dec 75	Jan 76	Mar 76
<i>Chrysophyllum albidum</i> flower bud/flower	42.9						
<i>Linociera johnsonii</i> unripe fruit	10.2						
<i>Celtis durandii</i> fruit undetermined ripeness		28.7	32.8				
<i>Ficus vallis-choudae</i> leaf bud		27.5	20.8				
<i>Monodora myristica</i> ripe fruit				40.5	41.3	53.5	
<i>Ficus exasperata</i> fruit undetermined ripeness				13.9			
<i>Tarenna pavettoides</i> ripe fruit					15.0		
<i>Mimusops bagshawei</i> ripe fruit						8.5	
<i>Millettia dura</i> flower bud/flower							23.6
<i>Rothmannia urcelliformes</i> unripe fruit							14.5
Total %	53.1	56.2	53.6	54.4	56.3	62.0	38.1
Total <i>N</i> for plant foods	49	87	125	80	80	71	110
Total no. species-specific parts	20	18	23	18	18	14	30
Total no. plant food species	16	12	17	14	11	11	24



**Table VII** Inter- and intragroup variation in redtail diets at Ngogo and Kanyawara (TTK), Uganda, 1973–1987: Group or individual name, years of sample, and % of food type

Food type	Group S 1975–1976	Group S 1978–1980	Group Sn 1980–1986	Group Ss 1980–1986	Group BTP 1978–1986	Adult female MBT hybrid of BTP group 1978–1986
All fruit	46.8	26.7	59.6	42.0	49.2	26.9
Flower/floral bud	7.8	7.6	7.1	13.7	15.9	7.6
Leaf bud	8.8	3.5	3.8	2.7	2.3	3.4
Mature leaf	0.7	1.0	0.4	0.2	0.3	2.5
Young leaf and young petiole	6.1	7.6	3.0	5.9	2.6	4.2
Anthers	0.0	2.3	1.1	1.2	0.1	0
Other	1.2	2.8	2.1	2.0	2.2	3.4
Invertebrates	28.6	48.6	22.9	32.4	27.5	52.1
Total N	842	869	266	410	738	119
Adult male RD mitis of BTP group 1980–1986		Group RAT 1978–1980	Adult male hybrid AMH of RAT group 1978–1979	Group SW 1979–1987	Adult female PT hybrid of SW group 1979–1987	Group TTK 1973–1974
All fruit	51.1	38.7	28.2	58.8	24.3	41.1
Flower/floral bud	11.1	3.8	2.6	6.6	2.7	16.4
Leaf bud	0	2.8	0	1.9	0	7.1
Mature leaf	4.4	0	0	0	0	4
Young leaf and young petiole	8.9	2.8	0	3.8	6.8	6.1
Anthers	0	0	0	0	0	0
Other	6.7	1.4	2.6	2.4	0	4.9
Invertebrates	17.8	50.5	66.7	26.5	66.2	20.4
Total N	45	212	39	211	74	1109

(Sn and Ss) resulting from the fission of the S group differed in their consumption of fruit and flowers/floral buds, although their home ranges overlapped and they were sampled in the same months (Struhsaker and Leland 1988).

The hybrids differed in their food types from the redbtail members of their social groups. Statistical analysis is warranted here because the hybrids and the redbtail members of their group were sampled simultaneously in the same area. The hybrid adult female MBT, who physically resembled a blue monkey more than a redbtail, differed from the redbtails of her group (BTP) in that she ate fruit and flowers/floral buds less frequently, but invertebrates more often ( $\chi^2 = 37.9$ ,  $df = 3$ ,  $P < 0.0001$ ; Table VII). The hybrid adult male AMH, most closely resembling a blue monkey, differed from the redbtails of his RAT group by eating fruit less frequently and invertebrates more often than they did ( $\chi^2 = 5.79$ ,  $df = 2$ ,  $P = 0.055$ ; Table VII). The hybrid adult female PT, most closely resembling a redbtail, ate fruit less frequently and invertebrates more often than did the redbtails in her SW group ( $\chi^2 = 10.9$ ,  $df = 1$ ,  $P = 0.001$ ; Table VII). A general pattern is apparent. The hybrids, regardless of sex or phenotypic prevalence, ate fruit less often and invertebrates more often than did redbtails with but two exceptions, the 1978–1980 sample for the S group in which fruit represented only 26.7% of feeding scores and the redbtails of the RAT group, which had a high frequency of invertebrate feeding but still 16% less than the hybrid male (AMH) of that group (Table VII).

Differences between groups are also apparent when examining the five most common species-specific plant foods (Table VIII). Some of these differences are surely due to differences in sampling times and duration, as well as to differences in the vegetation between home ranges. Despite these issues, certain foods consistently rank high in all or the majority of Ngogo groups and hybrids, e.g., fruit of *Celtis durandii*, *Uvariopsis congensis*, and *Pseudospondias microcarpa*. None of the five most common plant foods of the Kanyawara TTK group are shared with the five most common plant foods of the Ngogo groups.

### Invertebrate Diet: General

In most cases, I could not identify the invertebrates eaten. Larvae and cocoons were the most common forms of insects I identified as eaten by the redbtails. Redtails typically rubbed hairy caterpillars on tree branches or picked them apart, squeezing the internal organs out and eating them and discarding the exoskeleton. Other identifiable prey included: the cocoon of the moth *Avitta lineosa* (Noctuidae), adult beetles, adult bush crickets (Tettigonidae), adult praying mantis, eggs of praying mantis, and plant hopper nymphs (Flatidae). Redtails licked Flatidae nymphs off the mature leaves of *Pterygota mildbraedii*. These nymphs had numerous white, waxy, and sticky filaments and when the monkeys finished feeding on them, they typically had white sticky remains on their cheek whiskers and around their mouths, which they removed by rubbing their mouths and cheeks back and forth on tree branches. On the rare occasion when redbtails fed on the arboreal clay tunnels of termites that were situated on tree trunks and branches, I could not determine if they ate only the clay or if they also ate termites. They ate galls off of mature leaves, especially TTK group, and these galls may have contained insect eggs and/or larvae. However, leaf galls can also be formed as the result of the plant's reaction to infections by bacteria, viruses, fungi, nematodes, mites, and algae (Mani 1964). I treated galls as plant food because of this uncertainty and because the bulk of the gall was plant tissue.

**Table VIII** Comparison of the five most common species-specific plant foods in redtail diets at Ngogo and Kanyawara (TTK Group), Uganda, 1973–1987

S group (1975–1976)	% of N	S group (1978–1980)	% of N
<i>Monodora myristica</i> ripe fruit	17.5	<i>Celtis durandii</i> fruit, ripe fruit, unripe fruit	9.2
<i>Celtis durandii</i> fruit, ripe fruit, unripe fruit	12.1	<i>Uvariopsis congensis</i> fruit, ripe fruit	8.0
<i>Ficus vallis-choudae</i> leaf buds	9.2	<i>Rothmannia urcelliformes</i> young leaves	7.8
<i>Rothmannia urcelliformes</i> fruit, ripe fruit, unripe fruit	6.5	<i>Rothmannia urcelliformes</i> anthers	4.5
<i>Ficus exasperata</i> fruit	4.5	<i>Ficus saussureana</i> fruit, ripe fruit	4.2
Total % of N (601)	49.8	Total % of N (447)	33.7
Sn group (1980–1986)		Ss group (1980–1986)	
<i>Teclea nobilis</i> ripe fruit, unripe fruit	12.2	<i>Celtis durandii</i> fruit, ripe fruit,	13.0
<i>Uvariopsis congensis</i> ripe fruit, unripe fruit	11.2	<i>Pseudospondias microcarpa</i> fruit, ripe fruit	7.6
<i>Pseudospondias microcarpa</i> ripe fruit, fruit, unripe fruit	7.8	<i>Uvariopsis congensis</i> ripe fruit, unripe fruit	6.1
<i>Celtis durandii</i> ripe fruit, fruit, unripe fruit	6.8	<i>Chrysophyllum albidum</i> ripe fruit	6.1
<i>Ficus vallis-choudae</i> leaf bud	4.4	<i>Randia malleifera</i> flower bud	5.4
Total % of N (205)	42.4	Total % of N (277)	38.2
BTP group (1978–1986)		MBT hybrid of BTP (1978–1986)	
<i>Celtis durandii</i> fruit, ripe fruit	11.0	<i>Pseudospondias microcarpa</i> fruit, ripe fruit, UF	14.3
<i>Rothmannia urcelliformes</i> flower bud	8.4	<i>Celtis durandii</i> fruit, ripe fruit	10.7
<i>Uvariopsis congensis</i> ripe fruit	8.0	<i>Ficus exasperata</i> fruit, ripe fruit	7.1
<i>Pseudospondias microcarpa</i> fruit, ripe fruit, unripe fruit	8.0	<i>Diospyros abyssinica</i> fruit	3.6
<i>Monodora myristica</i> flowers	6.0	<i>Ficus saussureana</i> fruit	3.6
Total % of N (535)	41.4	<i>Uvariopsis congensis</i> ripe fruit	3.6
		Total % of N (56)	42.9
Adult Male mitis RD of BTP (1980–86)		RAT group (1978–1980)	
<i>Celtis durandii</i> fruit, ripe fruit	16.2	<i>Celtis durandii</i> fruit, ripe fruit	21.0
<i>Uvariopsis congensis</i> ripe fruit	16.2	<i>Ficus saussureana</i> fruit, ripe fruit	10.5
<i>Ficus saussureana</i> fruit, ripe fruit	8.1	<i>Uvariopsis congensis</i> ripe fruit	10.5
<i>Ficus vallis-choudae</i> ripe fruit	5.4	<i>Monodora myristica</i> fruit	6.7
<i>Funtumia africana</i> seed	5.4	<i>Diospyros abyssinica</i> fruit, ripe fruit, unripe fruit	5.7
<i>Monodora myristica</i> flowers	5.4	<i>Ficus mucuso</i> ripe fruit	5.7
<i>Pseudospondias microcarpa</i> fruit, ripe fruit	5.4	Total % of N (105)	60.1
<i>Vangueria apiculata</i> mature leaves	5.4		
Total % of N (37)	67.5	SW group (1979–1987)	
AMH hybrid of RAT (1978–79)		<i>Uvariopsis congensis</i> ripe fruit	18.1
<i>Celtis durandii</i> fruit, ripe fruit	30.8	<i>Monodora myristica</i> fruit	12.3
<i>Ficus mucuso</i> ripe fruit	23.1	<i>Pseudospondias microcarpa</i> fruit, ripe fruit	11.6
<i>Diospyros abyssinica</i> fruit	15.4	<i>Morus lactea</i> fruit	10.3
<i>Diospyros abyssinica</i> seeds	7.7	<i>Celtis durandii</i> fruit, unripe fruit	8.4
<i>Linociera johnsonii</i> fruit	7.7	Total % of N (155)	60.7
<i>Monodora myristica</i> flowers	7.7		
<i>Uvariopsis congensis</i> ripe fruit	7.7	TTK ggroup (1973–1974)	
Total % of N (13)	100.0	<i>Mimusops bagshawei</i> fruit, ripe fruit	14.2
PT hybrid of SW (1979–1987)			
<i>Uvariopsis congensis</i> ripe fruit	16.0		

**Table VIII** (continued)

S group (1975–1976)	% of N	S group (1978–1980)	% of N
<i>Celtis durandii</i> fruit	12.0	<i>Bosqueia phoberos</i> fruit, ripe fruit, unripe fruit	6.2
<i>Zanha golungensis</i> young leaves	12.0	<i>Celtis africana</i> fruit, ripe fruit	6.0
<i>Pseudospondias microcarpa</i> fruit, ripe fruit	8.0	<i>Premna angolensis</i> leaf buds	6.0
<i>Rothmannia urcelliformes</i> young leaves	8.0	<i>Aningeria altissima</i> flower buds	5.2
<i>Ficus natalensis</i> fruit	8.0	Total % of N (883)	37.5
<i>Monodora myristica</i> fruit	8.0		
Total % of N (25)	72.0		

fruit fruit of undetermined ripeness

### Invertebrate Diet: Substrates Exploited

Redtails took the great majority of their invertebrate prey from mature leaves (Table IX). This was true for all groups and the three hybrids (MBT, AMH, PT) and is probably related to the fact that mature leaves were the most common substrate available. Tree branches, trunks, and twigs were the second most common substrates exploited for invertebrates. This category includes bare and moss- and lichen-covered surfaces. The hybrids caught a greater proportion of their invertebrate prey from branches than did the redtails of their respective social groups.

Intermonthly variation in gross substrates occurred during the all-day, systematic samples of TTK and S groups (Tables X and XI). Variation was greatest for the TTK group in all substrates, but was most apparent in prey taken from mature leaves (30–74%) and tree branches, trunks, and twigs (13–56.7%). This was also true for S group with the addition of empty pods of *Pterygota mildbraedii*, which ranged from zero in most months to 37.5% of the substrates in July 1975. The large pods of *Pterygota*

**Table IX** Redtail invertebrate diet: Gross substrates exploited as % of total invertebrate scores, Kanyawara and Ngogo, Uganda, 1973–1987

Group/ Individual (years)	Mature leaves	Branches, trunks, twigs	Dead leaves	Young leaves	Empty pod of <i>Pterygota mildbraedii</i>	Other	N
Group TTK (73–74)	61.6	26.9	5.9	3.2	0	2.3	219
Group S (75–76)	61.3	18.5	8.4	4.2	6.7	0.8	238
Group S (78–80)	75.9	13	6.6	1.7	2.2	0.5	407
Group Sn (80–86)	76.7	8.3	6.7	6.7	0	1.7	60
Group Ss (80–86)	72.4	7.9	5.5	12.6	0	1.6	127
Group BTP (78–86)	74.9	12.6	3.5	7	1	0.5	199
Hybrid female MBT (78–86)	56.5	22.6	8.1	11.3	0	1.6	62
Group RAT (78–80)	90	5.6	2.2	1.1	0	1.1	90
Hybrid male AMH (78–79)	76.9	19.2	3.9	0	0	0	26
Group SW (79–87)	76.4	5.5	12.7	1.8	3.6	0	55
Hybrid female PT (79–87)	59.2	24.5	10.2	4.1	2	0	49

**Table X** Intermonthly variation in substrate exploited for invertebrates by TTK group of redtails, Kanyawara, Uganda, 1973–1974

Date	N	% of monthly scores					
		Mature leaf	Branch	Dead leaf	Young leaf	Flower	Substrate undetermined
Nov 73	35	67.1	25.7	2.9	4.3		
Dec 73	32	56.3	25	12.5	3.1		3.1
Jan 74	23	69.6	13	13		4.3	
Feb 74	13	46.2	53.8				
Apr 74	30	30	56.7	6.7	3.3		3.3
May 74	20	50	35	5	5		5
June 74	73	74	13.7	2.7	6.8		5.5
Total N	226						

remain open and dry on the tree long after their winged seeds disperse. I was unable to see what kind of insect the redtails were picking out of these pods with their fingers. This tree species was not present in the home range of TTK group.

TTK and S groups differed from one another in the percentage of captures they made from moss- and lichen-covered tree branches, trunks, and twigs vs. bare surfaces; 34% moss/lichen vs. 66% bare for TTK and 15.6% moss/lichen and 84.4% bare for S.

There were differences between groups, including hybrids, in the species-specific substrates exploited for invertebrates. Some of these differences are seen when comparing the eight most important substrates during the systematic all-day samples of S group (1975–1976) with another time period (1978–1980) and with other groups and the hybrids. In this comparison I included three more substrates that were important to at least one other group (Table XII). These 11 substrates accounted for ≥50% of the substrates exploited, with the exception of the hybrid female MBT (49.3%) and TTK

**Table XI** Intermonthly variation in substrate exploited for invertebrates by S group of redtails, Ngogo, Uganda, 1975–1976

Date	N	% of monthly scores						
		Mature leaf	Empty <i>Pterygota</i> pod	Branch	Dead leaf	Young leaf	Spider web	Substrate undetermined
July 75	40	40	37.5	15	5	2.5		
Sept 75	22	50	4.5	18.2	9.1	13.6		
Oct 75	18	44.4		38.9	11.1	5.6		
Nov 75	37	73		21.6	5.4			
Dec 75	26	65.4		23.1	3.8	3.8	3.8	
Jan 76	57	70.2		19.3	3.5	7		
Mar 76	41	65.9		7.3	22			4.9
Total N	241							



(41.6%) group from the Kanyawara study site ca. 10 km northwest of Ngogo. I also present the 8 (11 because of tied percentages) most important substrates for the TTK group in Table XII, representing 65% of the total substrates they exploited.

Although the mature leaves of *Celtis durandii* are generally of great importance to most groups, there were three notable exceptions. Sn and Ss groups and adult female hybrid PT exploited this substrate less than did the other groups and hybrids. These exceptions cannot be obviously explained on the basis of habitat differences because Sn and Ss groups were the result of a fission of the S group and used the same home range that had been used by S group from 1975 to 1980. Sn used mature leaves of *Diospyros abyssinica* and *Uvariopsis congensis* more than the Ss and S groups, whereas the Ss group used the mature leaves of *Strombosia scheffleri* and *Tabernaemontana holstii* more than did S and Sn groups. Likewise, hybrid PT was sampled at the same time and place as her SW group of redtails and yet there were important differences between them in the substrates exploited, e.g., mature leaves of *Monodura myristica*, *Chrysophyllum albidum*, and *Uvariopsis congensis*.

### Invertebrate Diet: Mode of Capture

All groups, regardless of location or sample size, used slow methods of capturing invertebrates much more than they used rapid methods (Table XIII). Adult female MBT and adult male AMH, the two hybrids whose appearance closely resembled a blue monkey, used slow methods of capture more than any redtail group (93.6% and 92.3%), with the exception of the RAT group (90.4%). In this way, they behaved more like blue monkeys than redtails. Blue monkeys used the slow methods 93.4% of the time (Rudran 1978; Struhsaker 1978a). By contrast, the hybrid adult female PT, who most closely resembled a redtail, used methods of capture indistinguishable from those of a redtail.

### Dietary Selection Ratios

The systematic, all-day samples of both the TTK and S groups demonstrated selectivity in the tree species upon which they fed (Tables XIV and XV). Selection ratios for a given species often differed depending on whether the redtails fed on it for plant material or as a source of invertebrates, e.g., *Bosqueia phoberos*, *Celtis africana*, *Newtonia buchanani*, *Premna angolensis*, and *Strombosia scheffleri* for TTK group and *Ficus exasperata*, *Millettia dura*, *Monodura myristica*, *Pterygota mildbraedii*, *Rothmannia urcelliformis*, and *Strombosia scheffleri* for S group. Furthermore, although a species may have had a low selection ratio, it could still be an important component of the diet; e.g., the invertebrate selection ratio for *Diospyros abyssinica* was low (0.8), but it represented 21.7% of the substrates exploited for invertebrates by TTK group. *Uvariopsis congensis* represents a similar example for S group.

## Discussion

### Interdemic vs. Intrademic Variation

The significant differences in both the annual and monthly gross food types between TTK group of Kanyawara and S group of Ngogo are not obviously due to gross differences

**Table XII** Important species-specific substrates exploited for invertebrates by redtails: Group, sample years, and % of total invertebrate scores at Kanyawara (1973–1974) and Ngogo (1975–1987)

Substrate	Group S 1975–1976	Group S 1978–1980	Group Sn 1980–1986	Group Ss 1980–1986	Group BTP 1978–1986
Total <i>N</i>	240	392	56	121	192
<i>Celtis durandii</i> mature leaf	11.7	18.1	7.1	3.3	18.8
<i>Celtis durandii</i> branch	6.7	2.8	3.6	3.3	2.1
<i>Chrysophyllum albidum</i> mature leaf	3.8	5.4	5.4	5.8	5.2
<i>Diospyros abyssinica</i> mature leaf	12.5	7.4	21.4	7.4	7.3
<i>Monodura myristica</i> mature leaf	0	0.3	0	0.8	1
<i>Piptadeniastrum africanum</i> mature leaf	0	2.6	0	0	1.6
<i>Pseudospondias microcarpa</i> mature leaf	0.8	0.8	0	0.8	0.5
<i>Pterygota mildbraedii</i> empty pod	6.7	2.3	0	0	1
<i>Strombosia scheffleri</i> mature leaf	5	1.5	0	10.7	2.6
<i>Tabernaemontana holstii</i> mature leaf	3.3	13.5	2.5	14.9	10.9
<i>Uvariopsis congensis</i> mature leaf	5.8	6.1	12.5	9.1	5.2
% of total <i>N</i>	56.3	60.8	52.5	56.1	56.2
	Hybrid MBT 1978–1986	Group RAT 1978–1979	Hybrid AMH 1978–1979	Group SW 1979–1987	Hybrid PT 1979–1987
Total <i>N</i>	59	88	26	54	48
<i>Celtis durandii</i> mature leaf	11.9	26.1	19.2	13	6.3
<i>Celtis durandii</i> branch	6.8	1.1	0	1.9	6.3
<i>Chrysophyllum albidum</i> mature leaf	6.8	6.8	15.4	11.1	2.1
<i>Diospyros abyssinica</i> mature leaf	5.1	15.9	11.5	5.6	8.3
<i>Monodura myristica</i> mature leaf	3.4	1.1	0	0	10.4
<i>Piptadeniastrum africanum</i> mature leaf	1.7	14.8	7.7	1.9	0
<i>Pseudospondias microcarpa</i> mature leaf	3.4	1.1	0	0	8.3
<i>Pterygota mildbraedii</i> empty pod	0	0	0	3.7	2.1
<i>Strombosia scheffleri</i> mature leaf	3.4	0	0	5.6	4.2
<i>Tabernaemontana holstii</i> mature leaf	6.8	3.4	0	1.9	2.1
<i>Uvariopsis congensis</i> mature leaf	0	0	7.7	20.4	4.2
% of total <i>N</i>	49.3	70.3	61.5	65.1	54.3
	Group TTK 1973–1974				
Total <i>N</i>	212				
<i>Celtis durandii</i> mature leaf	9.9				
<i>Celtis durandii</i> branch	2.8				
<i>Chrysophyllum albidum</i> mature leaf	na				
<i>Diospyros abyssinica</i> mature leaf	18.4				
<i>Monodura myristica</i> mature leaf	0				
<i>Piptadeniastrum africanum</i> mature leaf	na				
<i>Pseudospondias microcarpa</i> mature leaf	0				
<i>Pterygota mildbraedii</i> empty pod	na				
<i>Strombosia scheffleri</i> mature leaf	8.5				
<i>Tabernaemontana holstii</i> mature leaf	0				
<i>Uvariopsis congensis</i> mature leaf	0				
% of total <i>N</i>	41				

**Table XII** (continued)

	Group TTK 1973–1974
Total <i>N</i>	212
<i>Celtis durandii</i> mature leaf	9.9
<i>Celtis durandii</i> branch	2.8
<i>Chaetacme aristata</i> mature leaf	1.9
<i>Diospyros abyssinica</i> mature leaf	18.4
<i>Mimusops bagshawei</i> mature leaf	3.3
<i>Parinari excelsa</i> branch	9
<i>Parinari excelsa</i> mature leaf	4.2
<i>Olea welwitschii</i> mature leaf	1.9
<i>Strombosia scheffleri</i> mature leaf	8.5
<i>Strombosia scheffleri</i> branch	1.9
<i>Teclea nobilis</i> mature leaf	3.3
% of total <i>N</i>	65.1

between the two sites in tree species richness, diversity, or species-area curves (Struhsaker 1997). Differences in the densities of some tree species between the home ranges of these two study groups likely account for differences in their species-specific diets. However, in terms of gross diet, a difference of greater importance between the two sites was that of fruit production. Indices of monthly fruit abundance indicate that there was significantly more fruit available at Ngogo than at Kanyawara, perhaps twice as much (Butynski 1990). This may explain why S group ate fruit significantly more often than TTK group. Production of less fruit at Kanyawara may have resulted in TTK group concentrating more on floral buds, mature leaves, and leaf galls. Alternatively, the increased consumption of floral buds by

**Table XIII** Redtail invertebrate diet: Mode of capture as % of Total Captures. Kanyawara (1973–1974) and Ngogo (1975–1987)

Group (year)	Slow	Fast	<i>N</i>
TTK (73–74)	81.9	18.1	226
S (75–76)	85.8	14.2	233
S (78–80)	88.2	11.8	416
Sn (80–86)	76.3	23.7	59
Ss (80–86)	82.8	17.2	128
BTP (78–86)	88.3	11.7	197
MBT (78–86)	93.6	6.4	62
RAT (78–80)	90.4	9.6	94
AMH (78–79)	92.3	7.7	26
SW (79–87)	83.6	16.4	55
PT (79–87)	79.6	20.4	49

Hybrids: females MBT and PT, male AMH

**Table XIV** A comparison of plant food and invertebrate substrate dietary selection ratios for TTK group of redtails, Kanyawara, 7-mo sample (1973–1974)

Species	% trees in sample	% plant diet	Plant selection ratio	% substrate from which invertebrates were captured	Invertebrate selection ratio
<i>Bosqueia phoberos</i>	1.5	7	4.7	0.4	0.3
<i>Celtis africana</i>	1.2	7.4	6.2	1.4	1.2
<i>Celtis durandii</i>	11.9	2.7	0.2	13.2	1.1
<i>Chaetacme aristata</i>	3.7	4.6	1.2	3.3	0.9
<i>Diospyros abyssinica</i>	26.6	3.3	0.1	21.7	0.8
<i>Ficus exasperata</i>	0.3	4.5	15	0.9	3
<i>Millettia dura</i>	2	6.2	3.1	0.4	0.2
<i>Mimusops bagshawei</i>	1	18.1	18.1	3.8	3.8
<i>Newtonia buchanani</i>	0.3	0		3.3	11
<i>Olea welwitschii</i>	0.7	3.6	5.1	1.9	2.7
<i>Pancovia turbinata</i>	1.5	3.2	2.1	2.4	1.6
<i>Parinari excelsa</i>	0	0.3		15.6	
<i>Premna angolensis</i>	1	6	6	0	
<i>Strombosia scheffleri</i>	1.5	0.6	0.4	12.3	8.2
<i>Teclea nobilis</i>	7	2.5	0.4	4.7	0.7
<i>Uvariopsis congensis</i>	8.4	2.7	0.3	0	
% of total	68.6	72.7		85.3	
<i>N</i>	403	883		212	

TTK group may, in turn, have negatively affected fruit production. It is not apparent to me why S group ate invertebrates more often than did TTK group.

Interdemic differences also occurred between four other sites in Kibale, the most extreme differences being in the feeding scores for young leaves, fruit, flowers, and insects (Chapman and Chapman 2000). The authors suggested these gross dietary differences might be due to phenological differences or the availability of other preferred foods. Although it is true that habitat characteristics, especially tree species composition, will affect diets, some of these interdemic differences in feeding scores might be the consequence of monthly and/or annual variation in food availability or habitat heterogeneity within demes rather than between demes. For example, at both the Kanyawara and Ngogo study sites in Kibale there was pronounced phenological variation in trees at all levels, i.e., between individuals, species, months, and years (Struhsaker 1997). Likewise, vegetation within a tropical forest can vary greatly over relatively short distances, such as the catena effect described for the Kanyawara area (Struhsaker 1975, p. 117–118). This means that neighboring groups of monkeys in the same deme can be in habitats with different tree-species compositions and food availability that will affect their diets. Dietary comparisons both within and between demes will also be affected by when and how the sampling was conducted, who collected the data, how well the monkeys were habituated (Wrangham *et al.* 1998), and how finely food items were categorized. For example, some studies of redtails employed multiple observers with different levels of training and experience (Bryer *et al.* 2013, 2015; Lambert 2002; Rode *et al.* 2003; Wrangham *et al.* 1998), while other

**Table XV** A Comparison of plant food and invertebrate substrate dietary selection ratios in S group of redtails, Ngogo, 7-mo sample (1975–1976)

Species	% trees in sample	% plant diet	Plant selection ratio	% substrate from which invertebrates were captured	Invertebrate selection ratio
<i>Celtis durandii</i>	12.6	12.5	1	19.3	1.5
<i>Chrysophyllum albidum</i>	8.3	4	0.5	5.8	0.7
<i>Diospyros abyssinca</i>	15.7	1.7	0.1	15.2	1
<i>Ficus exasperata</i>	0.3	7.7	25.7	0	
<i>Ficus vallis-choudae</i>	0	10		0.4	
<i>Millettia dura</i>	1.4	4.7	3.4	0.4	0.3
<i>Monodora myristica</i>	1.5	19.3	12.9	0.8	0.6
<i>Pseudospondias microcarpa</i>	0.5	3	6	2.9	5.8
<i>Pterygota mildbraedii</i>	3.5	0	0	9.9	2.8
<i>Randia urcelliformes</i>	1.2	10	8.3	1.6	1.3
<i>Tabernaemontana holstii</i>	5.1	0.3	0.06	4.5	0.9
<i>Strombosia scheffleri</i>	1.9	0	0	6.6	3.5
<i>Uvariopsis congensis</i>	9.1	0.5	0.05	6.6	0.7
% of total	60.2	73.7		73.1	
N	650	601		241	

studies had only one observer (Butynski 1990; Cords 1986, 1987b; Struhsaker 1978a, 1980; Rudran 1978; this study). I used the same sampling method in my studies of redtails at Kanyawara and Ngogo as did Cords (1986, 1987b) and Gathua (2000) in their studies of redtails at Kakamega, Kenya. In contrast, other studies of redtails at Kanyawara used a variety of methods: instantaneous, 10-min focal animal samples (Wrangham *et al.* 1998), 5-point scan samples every 30 min (Bryer *et al.* 2013; Chapman and Chapman 2000), and all-day focal animal samples of adult females only (Bryer *et al.* 2015). All of these studies defined feeding as the actual ingestion of an item, except that of Wrangham *et al.* (1998), who defined feeding as picking, handling, or chewing a food item. Some of the studies combined plant items together as one category. Despite differences in nutritional value (Conklin-Brittain *et al.* 1998), Bryer *et al.* 2013 treated fruit, flowers, and seeds as one category and Wrangham *et al.* (1998) classed mature and young leaves, leaf petioles, and leaf buds as one category.

These differences in methods may account for some of the intradividual variation between redtail studies at Kanyawara, but not all. For example, using the same 5-point scan sample every 30 min method, two studies of redtails in the same general area and perhaps of the same group at Kanyawara yielded radically different results. Insects constituted 31.2% of the scores in one study (Chapman and Chapman 2000), but 71.4% in the other (Bryer *et al.* 2013). Reproductive parts (a combination of fruit, flowers, and seeds) were 39.4% of the scores in the former study, but only 16% in the latter. Wrangham *et al.* (1998) did not score insect, floral, or leaf bud foods in their study of two redtail groups at Kanyawara, but their results for other plant foods were very different from what I observed in my study of the TTK group at Kanyawara, ca. 1 km from their site. Unripe fruit constituted 31–35% of their plant food scores, but only 7.4% or 12% for my group when I assumed that unripe fruit was 23.6% of the fruit



scores whose ripeness was undetermined, i.e., the same percentage as fruit scores with known ripeness. Leaves (mature and young) made up 37.5–38.5% of their scores, but only 11.8% of mine. Seeds were 3.7–6.2% of their scores, but only 0.002% of mine and zero for a group studied by the Chapmans at Kanyawara (Chapman *et al.* 2002). These intrademic differences in food types are comparable to or exceed some of the interdemic differences reported by Chapman and Chapman (2000) and here in my comparison of TTK and S groups. The intrademic differences at Kanyawara are consistent in a general way with those that I report here for the Ngogo redtails, where the variables of interobserver reliability and methodological differences can be eliminated because I collected all of the data using the same method.

Some of the intrademic differences I recorded at Ngogo might be due to differences in tree communities between the different home ranges, although the ranges of four of the study groups were contiguous and partially overlapping with at least one other group and only SW group was separated from them by ca. 1 km. Habitat differences cannot, however, explain dietary contrasts between the two sample periods for the S group because they used the same range. Similarly, habitat is not likely to explain differences in fruit, flower, floral bud, and invertebrate scores between Sn and Ss groups because their ranges overlapped extensively and I sampled them in the same time period.

Intrademic differences are also apparent at Kanyawara when comparing the species of plant foods fed on by TTK group with a redtail group  $\leq 1$  km away studied by Chapman and Chapman (2000). *Mimusops bagshawei* was the most common species fed on by the TTK group (18% of diet), but was only 1.2% of the dietary scores of the Chapman and Chapman (2000) group, despite similar densities, 3.8 and 3.3 trees per ha., respectively. In contrast, while *Celtis durandii* (14.8%) was the most common species fed on by the Chapmans' group, this species represented only 2.7% of the TTK group's diet. Densities of this species were high in both of our Kanyawara study sites, 47.1 and 45.7 per ha. Similarly, *Teclea nobilis* was only 2.5% of TTK group's plant diet, but 7.1% of the Chapmans' group. None of these intrademic differences at Kanyawara are related to the density of these tree species, which were similar within the ranges of the two groups (Chapman and Chapman 2000; Struhsaker 1975). It is beyond the scope of our data to say whether or not these intrademic dietary differences are the consequence of the availability of alternative and preferred foods.

## Hybrid Diets

Although the sample sizes for the three hybrid monkeys at Ngogo were relatively small, the results demonstrate that they ate more invertebrates than redtails did and more than their other parental species, blue monkeys (Butynski 1990; Rudran 1978; Struhsaker 1978a). The proportion of fruit in the hybrid diets was less than that of redtails, but similar to that of blues. Otherwise, much of the hybrids' plant diet was the same as that of redtails. However, some of their species-specific plants foods were shared primarily or only with blue monkeys and some were not eaten by either redtails or blues (Struhsaker *et al.* 1988). These results, combined with the fact that the hybrids were spatially and socially integrated with their redtail groups and not peripheral to them, suggested to us that there was a strong genetic component to dietary selectivity (Struhsaker *et al.* 1988) and the data presented here on invertebrate and fruit consumption lend additional support for this idea. Not only did the hybrids eat more invertebrates, but they also did so using motor patterns consistent with

those of the parental type they most resembled. The two hybrids that most closely resembled blues caught invertebrates using motor patterns more like blues than redtails. Hybrid female PT, who most closely resembled a redtail, used motor patterns like that of a redtail. Furthermore, the hybrids captured more of their prey from branches than did the redtails in the respective social groups, a distinction similar to that between blue and redtail monkeys at Kanyawara where the blues took 21% more of their prey from branches than did redtails (Struhsaker 1978a, b). Although hybrids were not common at Ngogo, it is possible that introgression was widespread throughout this subpopulation, much more so than indicated by phenotypes. This possibility raises the question as to whether or not introgression could be contributing to some of the intrademic dietary variation among the Ngogo redtails.

### Intermonthly Variation

The intermonthly variation in food types and species-specific food items that I found among the Kibale redtails is similar to the results for the redtails of Kakamega, Kenya (Cords 1986, 1987b; Gathua 2000). Both of these latter studies, like my Kibale study, found that on a monthly basis, relatively few species-specific plant parts accounted for a large portion of the total plant diet. One of the most striking differences between the Kibale and Kakamega redtails is the low frequency with which flowers and/or floral buds were eaten in Kakamega compared to Kibale (1.1–2.7% vs. 7.9–16.4% of annual diet) (Cords 1987b; Gathua 2000). In no month did the Kakamega redtails eat flowers and floral buds as frequently as the Kibale redtails did in some months (24%). All three studies found a significant negative correlation in the monthly frequency with which fruit was eaten vs. leaves and/or buds.

### Invertebrates

Invertebrates, usually insects, represent important dietary components for redtails in all studies that recorded this food category (Bryer *et al.* 2013, 2015; Chapman and Chapman 2000; Chapman *et al.* 2002; Cords 1986, 1987b; Gathua 2000; Struhsaker 1978a). This is not surprising given the macro- and micronutritional benefits of insects (Bryer *et al.* 2015; Rode *et al.* 2003). Insect-feeding bouts are usually much shorter than feeding bouts of plant items because insects are small (Bryer *et al.* 2015). Furthermore, most insect prey occurs as a single item, compared to clumped foods such as fruit and leaves. It is much easier for an observer to detect feeding on fruit and leaves than on insects and easier to miss the consumption of an insect than consumption of most plant parts. Consequently, most sampling methods will underestimate the frequency with which insects are consumed. This also means that the very high proportion of invertebrates in the dietary scores of the three hybrid monkeys might be even higher because sample sizes for them were relatively small and small samples reduce the probability of detecting the consumption of invertebrates. Furthermore, the extent of insectivory in redtails and many other species is underestimated because no account is made of the insects infesting the fruit they eat, e.g., pollinating wasps and parasitic wasps and beetles of figs (Rudran 1978; Struhsaker 1980).

Results from the few studies that evaluated substrates from which redtails captured invertebrates are similar to what I report here (Kibale: Struhsaker 1978a, b; Kakamega, Kenya: Cords 1986; Gathua 2000). Relatively few plant species and species-specific

substrates account for a disproportionately large percentage of the substrates from which invertebrates were captured. Mature leaves were the most common substrate from which prey were taken, followed by branches, including tree trunks and twigs. This is probably because mature leaves are the most common substrate available, followed by branches, trunks, and twigs. However, I found that for at least one group (TTK), the branch substrate was used more in some months than were mature leaves. *Celtis durandii* and *Diospyros abyssinica* were important substrates in Kakamega (Gathua 2000), as they were in Kibale. At both Kakamega and Kibale, the redtails used similar methods for capturing invertebrates, 86.2% slow methods and 13.8% fast (Cords 1986) vs. 84.7% slow and 15.3% fast my study (mean of eight groups). These consistencies prevail despite differences between studies in sample size and habitat.

The importance of insectivory to redtails, which likely includes the consumption of folivorous, granivorous, and sap-sucking insects, demonstrates another important role that these monkeys play in forest ecology, in addition to being pollinators, seed dispersers, and predators of flowers and seeds.

### Selection Ratios

Plant-food selection ratios from my study cannot be compared directly with those from Kibale (Chapman and Chapman 2000) or Kakamega, Kenya (Cords 1987b; Gathua 2000) because these studies computed selection ratios differently. Nevertheless, qualitative comparisons reveal similarities and differences within Kibale and between Kibale and Kakamega. For example, *Celtis durandii*, a common species throughout most of Kibale, was not highly selected by the redtails as a source of plant food even though it was frequently fed on at Ngogo, Kanyawara, and other sites in Kibale. A similar result was reported for this species in Kakamega (Cords 1987b). One of the more striking differences in selection ratios between studies at Kanyawara was that for *Mimusops bagshawei*, which was very high for my TTK group, but low for the Chapman and Chapman (2000) group. A low selection ratio only means that a species was fed on less than expected based on its abundance. Species with low selection ratios can still be very important in the diet.

In some cases the results from my studies in Kibale were more like those from Kakamega than other studies in Kibale. *Ficus exasperata* is an example, where it occurred at low densities in my two study sites compared to those of Chapman and Chapman (2000). It accounted for 4.5–7.5% of the plant diet and had very high selection ratios in my studies, whereas it did not account for more than 2.2% of feeding scores with low selection ratios in the four study sites of Chapman and Chapman (2000). In Kakamega this species accounted for 7.7% of the diet and had a high selection ratio (Cords 1987b). Some of these differences might be attributable to the availability of alternative foods, habitat heterogeneity, and when the studies were done in relation to when a given species was producing food.

None of the other studies of redtails computed selection ratios for the plant species from which they obtained invertebrates. My results from both Kibale sites demonstrate the importance of these ratios because they show that some tree species are selected much more as a source of invertebrate than plant food. As with the selection ratios for plant foods, the invertebrate substrate ratios show that some tree species, although representing a significant proportion of the sources for invertebrates, have low selection ratios because of their abundance; i.e., they were used less than expected based on their abundance.

Some tree species were important sources of invertebrate foods at both Ngogo and Kanyawara, as well as at Kakamega (Gathua 2000), including *Celtis durandii* and *Diospyros abyssinica*. Studies of blue monkey (Rudran 1978; Struhsaker 1978a) and red colobus (Struhsaker 1975, 1978b) groups at Kanyawara that had overlapping ranges with TTK group and were sampled at the same time found that some tree species were important sources of invertebrate foods for all three of these monkey species, e.g., *Parinari excelsa* and *Strombosia scheffleri*. The extent of damage to mature leaves due to insects can sometimes be related to the preceding results. For example, the index of leaf damage was consistently high for *Strombosia scheffleri* and *Celtis durandii*, but not for *Parinari excelsa* and *Diospyros abyssinica* (Struhsaker 1978b). This suggests that these tree species were sources of invertebrate prey that differed in their food habits, e.g., folivorous vs. sap-sucking insects.

### Recommendations for Future Studies of Dietary Variability

The dietary variability described here is not restricted to redtails and other guenons. Similar variation within and between demes, between populations, and over time (monthly and annually) has been described for several taxa of colobine monkeys (Dunham 2017; Fashing 2001; Struhsaker 2010). These studies suggest that we must refine our sampling methods if we are to improve our understanding of intraspecific variability in diet, and thereby increase the reliability of interspecific comparisons. Aside from sampling as many different habitats and populations as possible for a given taxon, we must pay more attention to how we sample subpopulations. This is particularly relevant in heterogeneous habitats, such as tropical rain forests. Dietary variability within a subpopulation is likely to be a reflection of the array of sub-habitats used by the groups being studied. Ideally, we should sample according to the proportional representation and use of these sub-habitats, in a manner analogous to stratified random sampling.

Intermonthly and interannual variation in food availability and phenological asynchrony are particularly complex in tropical rain forests, further confounding attempts to understand dietary variability. Plotting measures of precision against sample time is one possible approach to determining how many days per month and how many years to sample to deal adequately with these variables. Another approach is to generate cumulative curves, plotting food species or species-specific foods against sample time.

### Conclusions

My study of dietary variability among the redtail monkeys of Kibale provides further evidence of the inadequacy of typological concepts, which assume that intraspecific variance is small relative to that between species. Furthermore, intrademic differences in redtail diets, whether in terms of gross food items, plant species, or species-specific foods, were often as great as or even greater than interdemec differences. Some of these differences might be attributed to differences between studies in methodology, but this is not the case with studies by the same observer using the same method. Habitat heterogeneity over relatively short distances, e.g., catena effect, as well as phenological asynchrony and pronounced temporal variation at all scales in food production are likely even greater sources of dietary variance. The intrademic dietary variability in the Kibale redtails suggests

that the concept of demes is not particularly useful when evaluating diets because of these spatial and temporal variables affecting food availability at a micro scale. Despite these issues, certain species-specific foods were important for most redtail groups in Kibale.

Invertebrates were important dietary items for redtails and are probably even more important than indicated by the data because they are consumed much more rapidly than plant foods and occur as single, dispersed items, which reduce the probability of their capture being seen by the observer. This reliance on invertebrates demonstrates another ecological role the redtails play, in addition to seed dispersal, pollination, and floral and seed predation. Selection ratios demonstrated that some tree species were utilized more often for invertebrates than they were for plant foods and vice versa. The Ngogo hybrid monkeys consumed significantly more invertebrates than did either of the parental species. They also showed a tendency to capture invertebrates more from branches than did the redtails of their social groups and to use capture methods more like the parental phenotype they most closely resembled. These observations provide further evidence for a strong genetic component to dietary selectivity. Consequently, introgression at the Ngogo study site might be yet another factor affecting intrademic dietary variability there.

## Data Availability

The data analyzed in this study are available from the corresponding author on reasonable request.

**Acknowledgments** I thank Dr. Alan Hamilton, the late Tony Katende, and the staff at the National Museums of Kenya and Botanic Gardens Kew for plant identifications and Lysa Leland for field assistance. My research was funded by the New York Zoological Society, African Wildlife Foundation, and the National Geographic Society grant number 2929-84. The Department of Zoology, Makerere University was my affiliation in Uganda and I was permitted to study in Kibale by the President's Office of Uganda, Uganda National Research Council, and the Uganda Forest Department. I thank all of these organizations and institutions. I thank two anonymous reviewers and Drs. Jessica Rothman and Joanna Setchell for constructive comments on my manuscript and Dr. Christine Wall for statistical advice.

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