

---

# Dietary selection of L'Hoest monkeys in Kalinzu forest reserve, southwestern Uganda

C. U. Tolo\*, J. Baranga and Grace Kagoro-Rugunda

Department of Biology, Faculty of Science, Mbarara University of Science and Technology, PO Box 1410, Mbarara, Uganda

## Abstract

Reports on patterns of dietary selection of forest guenons tend to be general and often classify *Cercopithecus lhoesti* as a frugivores–folivores species just like the other guenons, and to date there has been no systematic investigation into the inventory of the species' food items in the remaining forest fragments to guide major conservation and management decisions. Here we report on the L'Hoest monkeys' main food species and how the selection of these foods varies among different age groups of the troop in Kalinzu Forest, Uganda for a period of 12 months. Behavioural observations were determined using scan samples [*Behaviour*, 49 (1974) 227]. Two hypotheses were evaluated in this study. Results indicate that individuals of different age groups have the ability to select a variety of both plant and invertebrate food items in the vicinity to supplement their diets. There was no significant difference in dietary selection between different age groups of L'Hoest monkey for a particular food type (ANOVA: Column analysis,  $F_{3,84} = 1.541337$ ,  $P = 0.209827$ ). However, significant difference was realized in dietary selection of the different food types by a particular age group (ANOVA:  $F_{22,46} = 40.86429$ ,  $P = 3.69 \times 10^{-23}$ ). Selective predation pressure against the infants and juveniles by *Stephanoaetus coronatus* was believed to be one of the likely reasons why infants and juveniles least exposed themselves in the trees feeding on fruits of *Musanga leo-errerae* and *Ficus* spp. Invertebrate feeding was found to constitute high percentage (47.2%) of the species diet and plant materials comprised (52.8%) than previously reported in other study sites. These data provide potentially useful insight on the feeding ecology of the little studied *C. lhoesti* and can provide baseline information on conservation of its food items in the remaining forests.

*Key words:* *Cercopithecus lhoesti*, dietary selection, Kalinzu forest

## Résumé

Des rapports sur le schéma de sélection alimentaire des cercopithèques forestiers semblent plutôt généraux et classent souvent le cercopithèque de l'Hoest *Cercopithecus lhoesti* parmi les frugivores et folivores, avec les autres cercopithèques. A ce jour, il n'y a eu aucune investigation systématique de l'inventaire de la nourriture de l'espèce dans les fragments de forêts restants pour orienter les décisions majeures en matière de conservation et de gestion. Nous rapportons ici les principales espèces consommées par ce cercopithèque et comment la sélection de ces aliments varie selon les différents groupes d'âge dans la troupe de la Forêt de Kalinzu, en Ouganda, pendant 12 mois. Les observations comportementales ont été déterminées au moyen d'échantillons (Altmann, 1974). Cette étude passe en revue deux hypothèses. Des résultats indiquent que les individus des différents groupes d'âge ont la possibilité de choisir parmi une variété d'aliments végétaux et animaux (invertébrés) dans le voisinage pour compléter leur régime. Il n'y avait pas de différence significative dans le choix alimentaire entre les différents groupes d'âge des cercopithèques de l'Hoest pour un type d'aliment particulier (ANOVA: analyse en colonne  $F_{d3,84} = 1.541337$ ,  $P = 0.209827$ ). Il y avait cependant une différence significative dans la sélection alimentaire des différents types de nourriture chez un groupe d'âge particulier (ANOVA:  $F_{d22,46} = 40.86429$ ,  $P = 3.69E-23$ ). La pression prédatrice exercée de façon sélective sur les jeunes et les juvéniles par *Stephanoaetus coronatus* était, semble-t-il, une des raisons pour lesquelles ceux-ci se risquaient moins dans les arbres pour manger les fruits de *Musanga leo-errerae* et de *Ficus* Spp. On a découvert que les invertébrés composaient un fort pourcentage (47,2%) du régime de l'espèce et que la matière

---

\*Correspondence: E-mail: tolocas2000@yahoo.co.uk

végétale représentait le reste, 52,8%, ce qui diffère d'études antérieures réalisées à d'autres endroits. Ces données fournissent un aperçu qui pourrait être utile sur l'écologie de ce primates peu étudié et peut constituer une information de base pour conserver la végétation dont il se nourrit dans les forêts restantes.

---

## Introduction

L'Hoest monkey (*Cercopithecus lhoesti* Sclater, 1899) is a primate species endemic to Africa, commonly restricted to the montane forests in around the albertine rift region. *C. lhoesti* has a disjunct distribution, with one population in the upper eastern Congo basin and southwestern Uganda, and the other in Western Cameroon and East Nigeria (Wolfheim, 1983). In Uganda, it is found in forests of Kibale, Bwindi impenetrable and Kalinzu (Kingdon, 1974). Its eastern limit is about 31°E (Rahm, 1970), and its western limit is near the Cross river at about 8°E (Booth, 1958). In the east it occurs as far north as 2°N just north of the Ituri river, and as far south as 2°30' south of the Ulindi river (Rahm, 1970). The eastern and western populations are separated by a gap of more than 1609 Km wide, in which no *C. lhoesti* are known to occur. Some authors consider the western race of this species (*C. lhoesti preussi*) and the eastern race (*C. lhoesti lhoesti*) to be separate species (Tappen, 1960; Napier & Napier, 1967). Nevertheless, most researchers (e.g. Rahm, 1970; Kingdon, 1971) listed them as conspecific.

*Cercopithecus lhoesti* is listed as endangered to extinction in the IUCN threat category (IUCN, 2006). The species prefers mature forests in montane and lowland areas, it also occurs in gallery and secondary forest with thick regenerating growth in felled compartments (Lee, Thornback & Bennet, 1988; Lernould, 1988; Rahm, 1970). Kalinzu forest, having undergone a lot of timber felling to supply the Kilembe mines since 1970s, provides such a suitable habitat for this species. L'Hoest monkey has been recorded to be mainly a frugivorous and folivorous species, although invertebrate feeding also constitutes a substantial quantity of its diet. A few studies have been carried out to reveal the feeding ecology of this species. For example, it has been found out that L'Hoest monkey eats mainly fruit of *Podocarpus* spp, *Pygmaea* spp, *Hagenia* spp, *Polycias fulva*, *Myrianthus arboreus* and other plants' leaves in montane forests (Haddow, 1952). Gautier-Hion (1988) stated that L'Hoest monkeys' diet is composed of between

43% and 83% fruit. However, according to Kaplin & Moermond (2000), L'Hoest monkeys consume less fruit and a greater proportion of terrestrial herbaceous vegetation than other guenons. L'Hoest monkeys have also been documented to raid crops as parties regularly come down the montane forests of Rwenzori to raid crops in the foot hills (Haddow, 1952).

The assessment of diet is critical to address many theoretical questions about primates' ecology such as continued existence, ranging patterns and social organization all of which ensure survival of species. It has also been documented that <1% of the plant diversity in the tropics sustains frugivore communities (Terborgh, 1983). In Kalinzu Forest Reserve, like many have been in Uganda, the management policy is to provide timber and little attention is paid to the conservation of biological resources. Forest wildlife is a vital component of the forest ecosystem among which primates play a significant role in the functioning of this ecosystem. Hence, the main challenge is to manage natural forests to maintain stable ecosystems for a wide range of benefits and sustainable supply of food resources for primates and other wildlife to ensure the perpetuation of these stable ecosystems.

The main aim was to compile comprehensive L'Hoest monkey's main food species and determine proportion of selection and consumption of these foods by different age groups of these monkeys. A lot of studies have been done on primates in general and other guenons. However, not much work has been done on the endangered L'Hoest monkey. Results of this study will close the gap in this knowledge and will aid decision making, planning and management of Kalinzu Forest Reserve so that even other primates in this forest like chimpanzees, baboons, black and white monkeys, red tailed monkeys and blue monkeys can be sustained.

## Materials and methods

### Study site

This study was conducted at Kalinzu Forest Reserve, situated in southwestern Uganda (30°07'E, 0°17'S) and altitudes of 1200–1500 m above sea level (Howard, 1991; Hashimoto, 1995). This forest covers an area of 137 km<sup>2</sup> and it is contiguous to the Maramagambo Forest Reserve, which is part of Queen Elizabeth National Park (Fig. 1). The area experiences two rainy seasons (from mid-March to the end of May and from mid-September to the end of

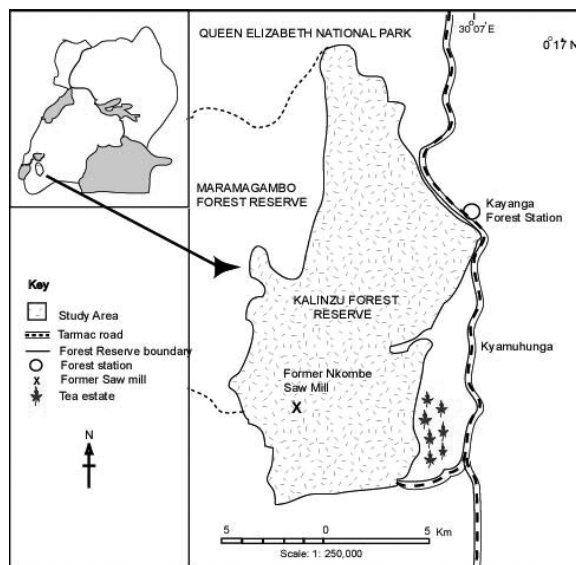


Fig 1 Location of Kalinzu forest reserve in south-western Uganda. Expanded is map of Kalinzu forest reserve

December) and two dry seasons (from the beginning of January to mid-March, and from the beginning of June to mid-September). The study site which is located in the northeastern side of the forest reserve comprised a small section of the Reserve, with an area of 25 km<sup>2</sup> and the centre of which the Nkombe sawmill headquarters was located. Annual rainfall of the study area from June 1997 to May 1998 was 1584 mm (Hashimoto, Furuichi & Tashiro, 2001), while the annual rainfall during this study from October 2003 to September 2004 was 1116.2 mm.

#### Determining dietary selection

We observed focal animals of *C. lhoesti* group from dawn to dusk (06.30–18.30 hours) to determine dietary selection

using scan samples (Altmann, 1974) at 5 min interval, and each scan lasted for 40–60 s. This was done five times a week for twelve consecutive months, from October, 2003 to September, 2004, during which time we recorded the sex and age class of the members of the focal group (Lambert, 2004) of the animal and all feeding events in which the entire process of food acquisition, processing and ingestion could be fully observed without interruption. To standardize feeding frequency, a feeding event was defined as all ingestion that took place during a period of a single scan (Lambert, 2004). During this period, we recorded the food species/part being consumed by each member of the group aided by use of a binocular.

The types of food consumed by focal animals were recorded and categorized into two: the plant species and the part eaten (leaves, fruits, flowers, flower buds, pith/stem among others) and animal materials (normally invertebrate of the phylum arthropoda). Each scan was treated as one data point in the analysis of feeding frequency. Only important food plant species were included in the analysis of dietary selection. Food plant species were defined as being important if at least 0.1% of all the feeding observations were on that species (Table 1). Identification of most food plant species was done according to (Lind & Tallantire, 1971; Katende, Segawa & Birnie, 1999).

#### Data analysis

Observations were made on a habituated focal troop of L'Hoest monkeys which consisted of 29–32 individual members, including one adult male, three young males, ten adult females (estimated to be more than 5 years old), fifteen juveniles (1–4 years old), and 1–3 infants (<1 year of age). Both male and female juveniles in the same troop were treated as one 'individual' with their data being

Table 1 Diurnal activity patterns of L'Hoest monkey age groups in Kalinzu forest reserve

Age group	Activity category							Total time
	Feeding time	Foraging time	Moving time	Grooming time	Vocalization time	Resting time	Others time	
Adult male	1452 (25.38)	346 (6.05)	1605 (28.06)	418 (7.31)	611 (10.68)	1194 (20.87)	95 (1.66)	5721 (100)
Adult Female	1788 (26.5)	518 (7.67)	1967 (29.1)	574 (8.5)	656 (9.72)	1141 (16.9)	106 (1.57)	6750 (100)
Juvenile	1255 (27.0)	326 (7.02)	1366 (29.4)	348 (7.49)	513 (11.05)	782 (16.84)	53 (1.14)	4643 (100)
Infant	1288 (25.51)	328 (6.33)	1517 (30.04)	343 (6.79)	639 (12.65)	834 (16.52)	101 (2)	6050 (100)

Values in parentheses are indicated as % total.

pooled and averaged. The same method did apply to infants.

A single factor analysis of variance was carried out to ascertain the differences in dietary selection between different age groups of L'Hoest monkey for a particular food type (column analysis). A similar test was carried out to ascertain the differences in dietary selection by a particular age group for the different food types (row analysis), with the criterion of significance set at 0.05 (Siegel & Castellan, 1988). Both *F* and *P*-values were recorded for all tests (Tables 2 and 3) respectively. Level of significance was

0.05 and tests were two-tailed. Statistical tests were performed using computer program SPSS 11.0 for PC.

## Results

All age groups of L'Hoest monkeys spent at least slightly above one-fourth of their total activity time feeding; in the order adult male (25.38%), adult female (26.5%), juvenile (27.0%) and infant (25.51%) respectively (Table 1). However, within the total average time devoted to feeding, by all age groups in a year, infants spent 53% (*n* = 682)

**Table 2** Comparison of foods eaten by different age groups of L'Hoest monkeys in Kalinzu forest reserve

Food eaten	Part(s) eaten	Frequency				Total	% Total of each food type
		AM	AF	Ju	If		
Arthropods	Whole body	692	835	555	682	2764	47.20
<i>Musanga leo-errerae</i>	Fruits	249	201	47	23	520	8.88
<i>Selicostacions</i> spp	Leaves/fruits/ flowers/buds	122	143	95	109	469	8.01
<i>Landolphia dawei</i>	Leaves only	90	74	67	73	304	5.19
<i>Carapa grandiflora</i>	Young leaves /buds	68	74	46	69	257	4.39
<i>Pallisota manii</i>	Stems/fruits/leaves	60	61	38	21	180	3.07
Mushrooms	Whole body	42	73	13	6	134	2.29
<i>Pteridium aquilinum</i>	Sporangium	33	39	28	40	140	2.39
Other plant species	Stems/leaves/buds/ flowers /fruits	32	33	23	36	124	2.65
<i>Ficus</i> spp	Leaves/buds/flower / fruits	20	24	10	2	56	0.96
<i>Impatiens</i> spp	buds/flowers /fruits	20	23	18	24	85	1.45
<i>Caesalpinia decapitata</i>	Leaves/flowers/ fruits	17	21	6	30	74	1.26
<i>Celtis</i> spp	Leaves/buds	16	72	38	29	155	2.65
<i>Strombosia scheffleri</i>	Young leaves/buds	16	35	16	7	74	1.26
<i>Craterispermum laurinum</i>	Young leaves	15	56	40	54	165	2.82
<i>Asplenium</i> spp	Leaves/fruits	12	23	9	7	51	0.87
<i>Funtumia africana</i>	Fruits/buds/flowers	11	20	8	5	44	0.75
<i>Trema orientalis</i>	Leaves only	7	14	4	9	34	0.58
'Ekinyesengye'	Young leaves only	7	12	4	2	25	0.43
<i>Neoboutonia cacrocarlyx</i>	Leaves only	6	19	20	20	65	1.11
<i>Syzygium</i> spp	Leaves only	4	25	19	21	69	1.18
<i>Sapium ellipticum</i>	Leaves / buds	3	18	13	8	42	0.72
<i>Macaranga schweinfurthii</i>	Leaves / buds	2	12	8	3	25	0.43
Total		1544	1907	1125	1280	5856	100
% total for each age group		26.37	32.57	19.21	21.86	100	

Source of variation	SS	d.f.	MS	<i>F</i>	<i>P</i> -value	<i>F</i> <sub>crit</sub>
Between groups	7612.545	3	2537.515	1.541337	0.209827	2.713229
Within groups	138289.8	84	1646.307			
Total	145902.4	87				

**Table 3** ANOVA: a single factor analysis of variance carried out to ascertain the differences in dietary selection between age group of L'Hoest monkey for particular food type (column analysis)

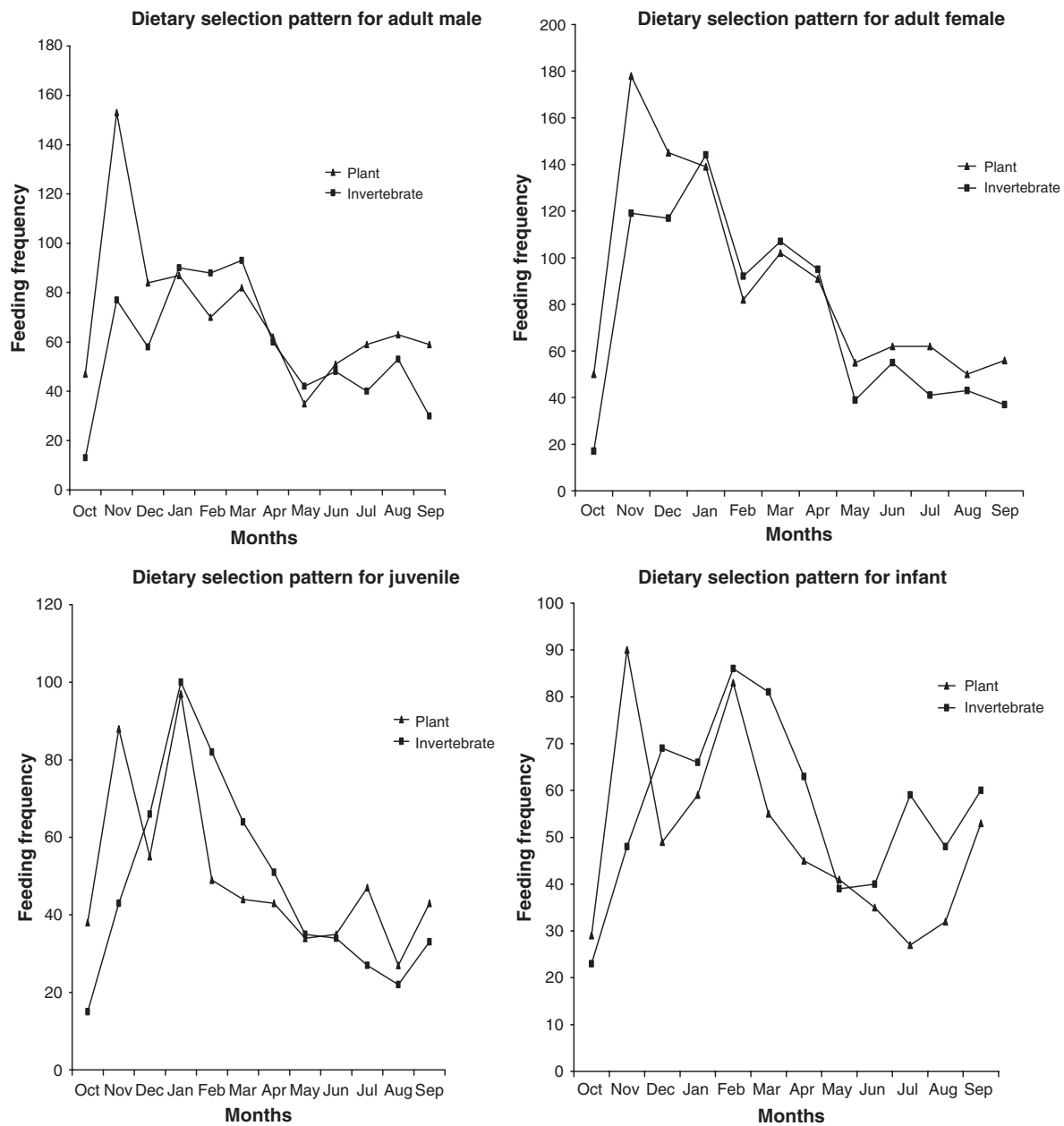


Fig 2 Dietary selection patterns for different age groups of L'Hoest monkeys in Kalinzu forest reserve

feeding on invertebrates (mainly arthropods), juvenile 49% ( $n = 555$ ), adult male 45% ( $n = 692$ ) and adult female only 44%, ( $n = 835$ ) respectively during the study period. Nevertheless, despite monthly variations in dietary selection, overall, majority of the individuals in different age groups devote slightly more than half of their total feeding

time enjoying plant materials rather than animal materials. The reverse is true only for the infant, in this case it spent on average 47% ( $n = 5980$ ) feeding on plant materials. Figure 2 illustrates monthly variations in the patterns of dietary selection for different age groups of L'Hoest monkey in Kalinzu Forest Reserve. It was also

Source of variation	SS	d.f.	MS	F	P-value	F <sub>crit</sub>
Between groups	1290099	22	58640.84	40.86429	$3.69 \times 10^{-23}$	1.77963
Within groups	66010.67	46	1435.014			
Total	1356109	68				

**Table 4** ANOVA: a single factor analysis of variance was carried out to ascertain the differences in dietary selection by a particular age group for the different food types (row analysis)

surprising to note that considerable variations exist in the way different food types are selected by a particular age group. This was particularly true when selecting different plant species as food for the L'Hoest monkey.

All age groups of L'Hoest monkeys exploited similar forest strata for feeding on invertebrates and plant materials. They used the lower strata or ground for feeding on invertebrates, terrestrial herbs and mushrooms among others. Higher forest strata were normally exploited while feeding on fruits and other plant materials. In general, plant materials consumed were ripe fruits normally small in size, young leaves, buds, flowers and succulent stems of herbaceous plants (Table 2). However, the group most frequently used upper forest strata of above 20 m above the ground feeding on fruits in the canopy of *Musanga leo-errerae* and *Ficus* spp. In some cases, adult male and adult females were frequently observed feeding on fruits of *M. leo-errerae* and *Ficus* spp well above 20 m from the ground level. This observation however, was uncommon in infants and juvenile.

Feeding on invertebrates was not limited to particular species or particular parts of plant. L'Hoest monkeys searched for arthropods on trunks, branches, fallen dry leaves on the forest floor. They also searched for invertebrates in small shallow streams and stagnant water bodies within the forest. Most of the invertebrates consumed were; small insects, eggs of insects, earthworms, ants, spiders, larvae of moth or butterfly and grasshoppers. L'Hoest monkeys frequently caught prey from the surface of live or dead leaves both on the tree and on the ground, and from old nests of chimpanzees. However, identification of invertebrates consumed by these monkeys to species level was very difficult and therefore not done because the monkeys ate the invertebrates quickly, the prey was very small and the whole body was eaten. Fruits of *M. leo-errerae* and *Ficus* spp appeared to be the most important for the monkeys and were especially frequently selected for by the adult male and adult females within the troop. On the contrary, *Selicostacions* spp seemed to be the most important food plant species for the infants and juveniles in the group (Table 2).

ANOVA: column analysis summary (Table 3), the  $F_{3,84} = 1.541337 < F_{critical} = 2.713229$  at 95% level of significance and it's associated  $P$ -value  $0.209827 > 0.05$ . There is no significant difference in dietary selection between different age groups of L'Hoest monkey for a particular food type. On the contrary, ANOVA: row analysis summary (Table 4), gives an  $F_{22,46} = 40.86429 > F_{critical} = 1.777963$  and a very small associated  $P$ -value  $3.69 \times 10^{-23} < 0.05$ , depicting a significant difference in dietary selection of the different food types by a particular age group.

## Discussion

Interpreting the significance of dietary variation on the basis of field documentation is difficult and will often depend on the questions being asked (Chapman *et al.*, 2002). In general, the members of the focal troop of the L'Hoest monkey observed in this study typically ate fruits, young leaves, buds, flowers and succulent herbaceous stems in addition to invertebrates. This agrees to a greater extent with the findings of (Gathua, 2000) who worked on the intraspecific variation in foraging patterns of *Cercopithecus ascanius* a species closely related to *C. lhoesti*, in the Kakamega forest, Kenya. However, no systematic data exist on the patterns of dietary selection of L'Hoest monkeys in other forest habitats to compare findings with this study. Nevertheless, Kaplin & Moermond (2000) presented the first systematic field study on the feeding ecology of L'Hoest monkey in Nyungwe Forest, Rwanda. Their finding revealed that *C. lhoesti* spent 35% of observation time feeding on terrestrial herbaceous vegetation. Thirty-five fruits and seed species comprised 42% of their diet, and invertebrates composed only 9% of the diet. In this case, the feeding data from Nyungwe forest, Rwanda, contradicts sharply the findings from Kalinzu forest, Uganda which put invertebrate and plant material feeding by L'Hoest monkey at 47.2% and 52.8% of the diet respectively during this study.

On the other hand, Tashiro (2005), working in the same study area Kalinzu forest, came close to agreeing with the

finding of this study. He found the L'Hoest monkey and the blue monkey spent as much as 66% and 50% of their time on insectivory respectively. Nevertheless, these proportions of time spent on invertebrate feeding are higher than those reported elsewhere for forest guenons. However, in the absence of a long-term study data on feeding ecology of L'Hoest monkey both in Kalinzu and other forest sites in the albertine rift region where the species is predominantly known to occur, it remains highly speculative to tell why high invertebrate feeding by the species in Kalinzu forest. Primates have the ability to change their feeding habits according to habitat transition (Bourliere, 1985). L'Hoest monkeys have high flexibility to various types of available food resources found in their habitats (Table 2). Despite seasonal variations plant feeding exceeds invertebrate feeding for most of the months except for infants (Fig. 2).

The nutrient factor, that invertebrate feeding may compensate protein shortage, could possibly be one of the explanations for high invertebrate feeding by different age groups of L'Hoest monkeys. Invertebrate feeding is considered to be a protein rich source (Kay, 1984; Egler, 1992). Insect might be eaten to supply essential amino acids, such as histidine, leucine and lysine, not present in sufficient amounts in plants (Hladik, 1977). If the plant foods do not include enough proteins, invertebrate feeding may help compensate for a lack of essential nutrients (Y. Tashiro, unpublished data). This suggestion however, fall short in providing convincing explanation on the high incidence of invertebrate feeding observed in Kalinzu Forest Reserve during this study as no data is available to compare protein contents of the other food items selected by these monkeys except for the *M. leo-errerae* fruits which is 10.2% (Y. Tashiro, unpublished data). The abundance of invertebrates in the study area could yet be another factor in influencing high invertebrate feeding; but comparison of abundance of invertebrates in Kalinzu forest and those in other forests was beyond the scope of this study and therefore could not be verified. However, preliminary research on ant species diversity found three species of army ant genus *Dorylus* to be abundant in Kalinzu forest reserve (M. Kiyono, unpublished data).

Intra group feeding frequency comparisons put adult female L'Hoest monkey ahead of the other group members (Table 2). The likely reason for this may be due to greater nutritional requirements of the female arising from additional physiological demand because of lactation; as well as scramble and competition for food resources from the other females as the troop comprised a single leading male,

multi-females, juveniles and infants. In Boabeng-Fiema monkey Sanctuary Ghana, intra group comparisons between the sexes of *Colobus vellerosus* show that females in the large group spent more time feeding than males (Teichroeb *et al.*, 2002), which precisely agrees with the above finding. The adult males and adult females; with relatively huge body mass within the troop seemed to frequently feed on the fruits of *M. leo-errerae* and *Ficus* spp contrary to the juveniles and infants which in turn go for *Selicostacions* spp more than the latter to supplement their nutritional demands. These differences in dietary selection within group members were common for different food items. It is possible that the difference in dietary selection between different age groups could be due to difference in their nutritional requirements among other factors. However, one notable field observation fact during this study was selective predation pressure against the relatively small bodied individuals in the group. Infants and juveniles generally fear to expose themselves high above in the trees while feeding especially on fruits of *M. leo-errerae* because of frequent attacks from crowned hawk eagles (*Stephanoaetus coronatus*) which normally target the infants and juveniles L'Hoest monkeys, lending support to the idea that adult male and adult females were the most frequently seen feeding high on *M. leo-errerae* fruits.

Forest guenons, the medium sized primates, are basically considered to be frugivores or frugivore-folivores (Kay, 1984). Although the main food resource is different for each species in each habitat (Gautier-Hion, 1988), invertebrate feeding is widespread across species and localities of guenons. More over, most studies revealed that guenons did not spend much time feeding on invertebrate compared with food plants. This however, is in sharp contrast with the finding of this study which suggests otherwise. Ideally, feeding data are used to specify the proportions of the diet comprising different food items and thus to classify species according to their main dietary constituent; for example frugivores, folivores or insectivore (Chapman *et al.*, 2002). It seems *C. l'hoesti* is flexible in dietary selection and has the ability to change its diet according to the availability and accessibility to food in its disposal in a given habitat in a given time of the year. Chapman *et al.* (2002) also cautions that, a study of the diet of a single group in a specific habitat at one time may not be representative of the species as a whole. Kagoro (2006), found that abundance of *M. leo-errerae* fruits influences both the ranging patterns and increases greatly the time spent on invertebrate feeding by Chimpanzees (*Pan troglodytes*) of Kalinzu

forest reserve, in that presences of *M. leo-errerae* fruits provides the animals with quick sources of food to feed on within a short time leaving plenty of time for invertebrate feeding for the Chimpanzees. It is most likely therefore, that the same reason applies to explain the high proportions of invertebrates in the diet of L'Hoest monkeys in Kalinzu forest reserve as the two studies were conducted in the same study area, although on different animal species.

## Acknowledgements

Our field work at Kalinzu forest reserve was greatly facilitated by the ground work done by Dr Chie Hashimoto and Ugandan staff of the Kalinzu Forest Project, including the initial construction of the line-transects in the area and habituation of the L'Hoest monkeys. We thank the Administration of Mbarara University of Science and Technology for granting us time to do this research. This research was solely and absolutely financed by Deutscher Akademischer Austausch Dienst (DAAD) scholarship awarded to C.U. Tolo (No. A/02/18375), to them we make grateful acknowledgement.

## References

- ALTMANN, J. (1974) Observational study of behaviour: sampling methods. *Behaviour* **49**, 227–267.
- BOOTH, A.H. (1958) The zoogeography of West African primates: a review. *Bull. Inst. Fondam. Afr. Noire* **20**, 587–622.
- BOURLIERE, F. (1985) Primate communities: their structure and role in tropical ecosystems. *Int. J. Primatol.* **6**, 1–26.
- CHAPMAN, A.C., CHAPMAN, J.L., CORDS, M., GATHUA, M.J., GAUTIER-HION, A., LAMBERT, E.J., RODE, K., TUTIN, E.G. & WHITE, T.J. (2002) Variations in the Diets of *Cercopithecus* Species: Differences within Forests, among Forests, and across Species. In: *The Guenons: Diversity and Adaptation in African Monkeys* (Eds M. E. GLENN and M. CORDS). Kluwer Academic/Plenum Publishers, New York.
- EGLER, S.G. (1992) Feeding ecology of *Saguinus bicolor bicolor* (Callitrichidae: Primates) in a relict forest in Manaus, Brazilian Amazonia. *Folia Primatol. (Basel)* **59**, 61–76.
- GATHUA, M. (2000) Intraspecific variation in foraging patterns of redbtail monkeys (*Cercopithecus ascanius*) in the Kakamega Forest, Kenya. PhD thesis, Columbia University, New York.
- GAUTIER-HION, A. (1988) The diet and dietary habits of forest guenons. In: *A Primate Radiation: Evolutionary Biology of the Guenons* (Eds A. GAUTIER-HION, F. BOURLIERE, J. P. GAUTIER and J. KINGDON). Cambridge University Press, Cambridge.
- HADDOW, A.J. (1952) Field and laboratory studies on an African monkey, *Cercopithecus ascanius* Schmidt Matschie. *Proc. Zool. Society of London* **122**, 297–394.
- HASHIMOTO, C. (1995) Population census of the chimpanzees in the Kalinzu Forest, Uganda: comparison between methods with nest counts. *Primates* **36**, 477–488.
- HASHIMOTO, C., FURUICHI, T. & TASHIRO, Y. (2001) What factors affect the size of Chimpanzee parties in the Kalinzu Forest, Uganda? Examination of fruit abundance and number of estrous females. *Int. J. Primatol.* **22**, 947–950.
- HLADIK, C.M. (1977) Chimpanzees of Gabon and Chimpanzees of Gombe: some comparative data on the diet. In: *Primate Ecology* (Ed. T. H. CLUTTON-BROCK). Academic Press, New York.
- HOWARD, P.C. (1991) *Nature Conservation in Uganda's Tropical Forest Reserves*. IUCN, Gland, Switzerland and Cambridge, U.K.
- IUCN (2006) *IUCN Red Data Book. Primate Conservation*. The World Conservation Union, Gland, Switzerland.
- KAGORO, R.G. (2006). Patterns of frugivory in chimpanzees (*Pan troglodytes* Blumenbach, 1755) in Kalinzu forest reserve, South western Uganda. PhD thesis (unpublished), Mbarara University, Uganda.
- KAPLIN, B.A. & MOERMOND, T.C. (2000) Foraging ecology of the mountain monkey (*Cercopithecus l'hoesti*): implication for its evolutionary history and use of disturbed forest. *Am. J. Primatol.* **50**, 227–246.
- KATENDE, A.B., SEGAWA, P. & BIRNIE, A. (1999) *Wild Food Plants and Mushrooms of Uganda*. Regional land management unit. Swedish International Development Cooperation Agency (SIDA), Nairobi, Kenya.
- KAY, R.F. (1984) On the use of anatomical features to infer foraging behaviour in extinct primates. In: *Adaptations for Foraging in Nonhuman Primates* (Eds P. S. RODMAN and J. G. H. CANT). Columbia University Press, New York.
- KINGDON, J. (1971) East African Mammals. *An Atlas of evolution in Africa*. Vol. 1. Academic Press, London.
- KINGDON, J. (1974) East African mammals. *An Atlas of evolution in Africa*. Vol. 1. The University of Chicago Press, Chicago.
- LAMBERT, E.J. (2004) Competition, predation, and the evolutionary significance of the cercopithecine cheek pouch: the case of *Cercopithecus* and *Lophocebus*. *Am. J. Phys. Anthropol.* **126**, 183–192.
- LEE, P.C., THORNBACK, J. & BENNET, E.L. (1988) *Threatened Primates of Africa*. IUCN, Gland, Switzerland and Cambridge, UK.
- LEARNOULD, J.M. (1998) Classification and geographic distribution of guenons: A review. In: *A Primate Radiation: Evolutionary Biology of the African Guenons* (Eds A. GAUTIER-HION, F. BOURLIERE and J. GAUTIER). Cambridge University Press, Cambridge.
- LIND, E.M. & TALLANTIRE, A.C. (1971) *Some Common Flowering Plants of Uganda*. Rev. ed. Oxford University Press, Nairobi, Kenya.
- NAPIER, J.R. & NAPIER, P.H. (1967) *A Handbook of Living Primates*. Academic Press, London.
- RAHM, U. (1970) Ecology, zoogeography, and systematics of some African forest monkeys. In: *Old World Monkeys* (Eds J. R. NAPIER and P. H. NAPIER). Academic Press, New York.
- SIEGEL, S. & CASTELLAN, A.C. (1988) *Noparametric Statistics for the Behavioral Sciences*. McGraw-Hill, New York.



- TAPPEN, N.C. (1960) Problems of distribution and adaptation of the African monkeys. *Curr. Anthropol.* **1**, 91–120.
- TASHIRO, Y. (2005) Frequent insectivory by two guenons (*Cercopithecus lhoesti* and *Cercopithecus mitis*) in the Kalinzu Forest, Uganda. *J. Primates, Japan* **47**, 170–173.
- TEICHROEB, A.J., SAJ, L.T., PATERSON, D.J. & SICOTTE, P. (2002) Effect of group size on activity budgets of *Colobus vellerosus*. *Int. J. Primatol.* **24**, 743–758.
- TERBORGH, J. (1983) A method of sitting parks and reserves with special reference to Colombia and Ecuador. *Biol. Conserv.* **19**, 45–58.
- WOLFHEIM, J.H. (1983) *Primates of the world. Distribution, Abundance, and Conservation*. University of Washington Press, Seattle, U.S.A.

(Manuscript accepted 11 July 2007)

doi: 10.1111/j.1365-2028.2007.00826.x