African Primates 7 (2): 156-162 (2012)

Adaptation by Budongo Forest Chimpanzees (*Pan troglodytes schweinfurthii)* to Loss of a Primary Source of Dietary Sodium

V. Reynolds[1,2], A. W. Lloyd[3] and C. J. English[3]

[1]*Budongo Forest Field Station, Masindi, Uganda*
[2]*School of Anthropology, Oxford University, Oxford, United Kingdom*
[3]*Faculty of Science and Engineering, University of Brighton, Brighton, United Kingdom*

Abstract: Chimpanzees of the Sonso community living in the Budongo Forest Reserve in western Uganda have in the past obtained sodium from the pith of decaying *Raphia farinifera* (RF) palm trees, which occur in areas of Swamp Forest. In recent years there has been a decline in numbers of trees of this species, mainly owing to the demand for leaf stems for the production of *Raphia* string, used by local tobacco farmers to tie tobacco leaves during drying and curing. Faced with a declining number of dead *Raphia* trees, the chimpanzees of the Sonso community have increased their feeding on a different tree species, *Cleistopholis patens* (CP), which also occurs in Swamp Forest. We analysed samples of dead wood from CP and found it to contain higher concentrations of sodium than other plant species tested, but lower concentrations than found in RF. CP has now become the main vegetative provider of sodium for the Sonso chimpanzees. Discussions are currently taking place with British American Tobacco (BAT) and local tobacco farmers in an effort to get them to switch from *Raphia* string to cotton string.

Key words: Chimpanzees, sodium, Budongo Forest, diet, tobacco, *Raphia, Cleistopholis*

Résumé: *Les chimpanzés de la communauté de Sonso habitant la forêt de Budongo située dans l'ouest de l'Ouganda, ont par le passé été observés obtenant du sodium à partir de la moelle pourrissante de palmiers de l'espèce* Raphia farinifera *(RF), qui poussent dans les parties marécageuses de cette forêt. Au cours des dernières années, les arbres de cette espèce ont vu leur nombre décliner, en particulier en raison de la demande pour les tiges de leurs feuilles, utilisées dans la fabrication de la ficelle de raphia par les producteurs de tabac, avec laquelle ils attachent les feuilles de tabac entre elles pendant les étapes de séchage et fumaison. Confrontés à une quantité déclinante de raphias morts, les chimpanzés de Sonso ont augmenté leur consommation de bois d'arbres morts d'une autre espèce,* Cleistopholis patens *(CP), qui poussent également dans les zones marécageuses de la forêt. Nous avons analysé des échantillons de bois mort de CP et avons trouvé qu'ils contenaient des concentrations en sodium plus élevées que celles d'autres espèces, à l'exception de RF. CP a donc remplacé RF comme principal pourvoyeur végétal de sodium. Des discussions ont actuellement lieu avec la compagnie British American Tobacco (BAT) et les producteurs de tabac locaux pour tenter de remplacer la ficelle de raphia par de la ficelle de coton.*

Mots-clés: *chimpanzés, sodium, forêt de Budongo, régime alimentaire, tabac,* Raphia, Cleistopholis

INTRODUCTION

All mammals require small amounts of sodium for proper physiological functioning and this mineral is ingested in the diet, sometimes being sought out from particular sources (Michell, 1989). Reynolds *et al.* (2009) showed that chimpanzees of the Budongo Forest Reserve in western Uganda obtain sodium from the pith of decaying palm trees of the species *Raphia farinifera* (RF) (Figure1).

This decaying pith was a rich source of sodium. We also showed that sodium was present in very much smaller quantities in bark, leaves and fruits of other species tested (*ibid.*, Table 1). Leaves and fruits form the staple diet of the Budongo chimpanzees, with *Raphia* being eaten only occasionally. *Raphia* palms in Budongo are being depleted to the point of extinction by the actions of local people: palm wine makers who cut down palm trees to ferment the sap for alcohol, and tobacco farmers who remove palm leaves, and sometimes cut down whole trees, for conversion into string to tie tobacco leaves during the drying and curing process (Atuhe, 2010a). Depletion of the stock of *Raphia* palms thus poses a threat to the health and survival of chimpanzees. Feeding on decaying *Raphia* pith can be seen in the supplemental file appended to this article: Video 1 Feeding on Decaying *Raphia* (all video clips courtesy of Cat Hobaiter).

Correspondence to: Vernon Reynolds, School of Anthropology, University of Oxford, Orchard House, West Street, Alfriston, East Sussex, UK; and Budongo Conservation Field Station, P.O. Box 362, Masindi, Uganda. Email: vreynolds@btopenworld.com

Figure 1. *Raphia farinifera* tree growing in Swamp Forest in the Budongo Forest Reserve. Photo: V. Reynolds.

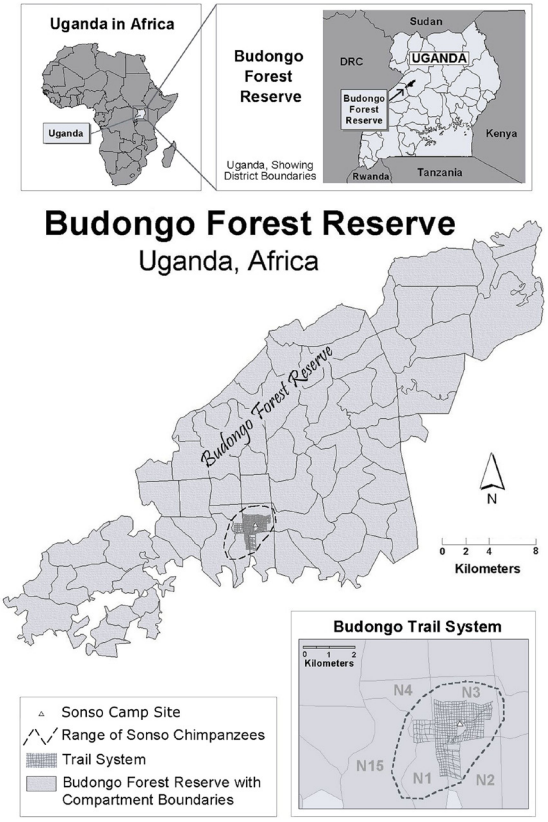

Figure 2. Map of the Budongo Forest Reserve, showing the range of the Sonso community of chimpanzees. Copyright L. Hazzah and M. Reuling.

With fewer *Raphia* trees to exploit, feeding competition at remaining trees became more marked. Observations in Budongo Forest have indicated that feeding on decaying *Raphia* pith has become more competitive as the availability of *Raphia* has declined (G. Muhumuza, C. Hobaiter; pers. comm.). This competition can be seen in supplemental file Video 2 Competition over *Raphia*. At the same time, it was noticed that feeding by chimpanzees on rotting wood of dead *Cleistopholis patens* (CP) trees lying on the forest floor in Swamp Forest had become more frequent (Atuhe, 2010b). Feeding on CP can be seen in supplemental file Video 3 Feeding on *Cleistopholis patens*. As a result, we have analysed CP for mineral content. In this paper we show that CP, like RF, provides a prominent source of sodium.

LOCATION

This study took place in the Budongo Forest Reserve in western Uganda. Budongo is a moist semi-deciduous tropical forest containing a number of forest types, including Swamp Forest (Eggeling, 1947). The River Sonso runs through the range of this community, the core area of the range measuring around 15 km^2. It is in the areas of Swamp Forest, bordering the R. Sonso, that both RF and CP occur (see map, Figure 2).

SUBJECTS AND METHODS

Subjects

The Sonso community of chimpanzees, consisting of around 60 individuals, lives towards the centre of the forest and has been habituated by members of the Budongo Conservation Field Station since 1990 (Reynolds, 2005). All members of the Sonso community, including infants, have been seen ingesting both RF and CP. Infants observe this while attending with their mothers. It seems probable that this feeding is culturally acquired, by observational learning.

Field methods

Samples of CP weighing <50g were collected by trained field assistants. The period of sample collection was from April 2009 to August 2010. Samples of CP consisted of decaying wood, with samples of living trees, herbs, bark and fruits collected for comparison. Samples were collected with latex gloves or tweezers, taking care not to allow contact between samples and human skin. These were placed in glass collection tubes which were then closed and marked. When back at camp, samples were dried and when dry, were placed in polythene bags and returned to the UK for analysis, as described in Reynolds *et al.* (2009).

Laboratory methods

Analysis was undertaken by drying samples of each material to constant weight prior to oven pyrolysis at 550°C. Samples of the pyrolysed material (*ca*. 0.1 g) were subsequently digested in 3 ml of aqua regia at 100°C for 2 hours. Following appropriate dilution of the digested samples, a Perkin Elmer Optima 2100 DV Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES) was used to determine the elemental content of each sample, using 5 and 10 mg L−1 elemental standards. The elemental content per kg of dried material was calculated from the raw data.

Statistical analysis

For purposes of comparison, samples were divided into 3 groups: RF, CP and all other samples. RF samples consisted of the original 11 samples described in Reynolds *et al.* (2009); CP samples (N=20) were those newly collected, as described above. Samples of other species were the original 16 samples (Reynolds *et al.,* 2009), plus an additional 8 newly collected samples (N=24). All samples were independent, having been collected from different trees. Data were not normally distributed in any of the three groups and therefore, nonparametric tests were used to establish whether concentrations of minerals differed between the groups.

RESULTS

Tables 1-3 show the results of the chemical analysis expressed as mg per kg of twice dried material for each sample yielding results. This is the same method in all respects as was used in Reynolds *et al.* (2009). Table 1 uses the results from that study; Tables 2 and 3 are new.

Table 1 - Results for *Raphia farinifera*; mg kg^{-1}

Sample no.	Species	Plant part	Decaying?	Magnesium	Sodium	Potassium	Calcium	Manganese	Iron	Phosphorus	Sulfur
1	RF	pith	yes	293	7096	5118	815	60	90	58	16485
2	RF	pith	yes	621	3365	4892	1282	266	140	190	24472
3	RF	pith	yes	556	14616	6594	1332	139	23	293	19375
4	RF	pith	yes	440	1431	4518	421	366	67	88	6499
5	RF	pith	yes	5771	1666	12559	2756	1024	71	906	61301
6	RF	pith	yes	1118	5152	3165	679	254	37	204	47232
7	RF	pith	yes	6586	7194	11708	4568	1785	515	1057	127516
8	RF	pith	yes	1449	1095	3915	1223	308	229	338	24984
9	RF	pith	yes	4560	8666		1829	232	20	261	21974
10	RF	pith	yes	2847	3216	7384	1327	145	159	437	31490
11	RF	pith	yes	2490	1920		962	97	60	205	13843

Species: RF=*Raphia farinifera*

Table 2 - Results for *Cleistopholis patens;* mg kg^{-1}

Sample no.	Species	Plant part	Decaying?	Magnesium	Sodium	Potassium	Calcium	Manganese	Iron	Phosphorus	Sulfur
14	CP	wood	yes	443	800	2261	1005	14	301	364	7886
CP 9	CP	wood	yes	1397	1917	4419	7095	26	111	150	286
CP10	CP	wood	yes	1299	2408	5027	8874	18	71	115	492
CP11	CP	wood	yes	2064	151	3724	26620	7	61	582	421
CP2	CP	wood	yes	1152	937	4467	1864	12	618	1539	390
CP6	CP	wood	yes	421	92	603	2219	7	265	228	225
CP8	CP	wood	yes	695	165	1986	4571	2	22	445	256
CP1	CP	wood	yes	1627	2111	4953	4076	25	170	130	568
CP4	CP	wood	yes	2514	865	3448	2080	2	81	648	410
CP3	CP	wood	yes	1242	797	3632	1699	4	59	782	622
CP7	CP	wood	yes	945	276	1708	2322	2	42	296	548
SA1	CP	wood	yes	2186	565	9937	2598	56	52	583	720
SA2	CP	wood	yes	549	1236	2411	1359	20	15	726	508
SA3	CP	wood	yes	960	706	5403	1921	27	20	804	578
SA4	CP	wood	yes	3333	1622	29038	4303	31	44	2176	936
SA5	CP	wood	yes	7090	4753	71212	6123	645	344	2847	1546
22	CP	wood	yes	5110	14331	33706	9398	38	240	11597	4468
JK6	CP	wood	yes	6983		14018	20243	62	367	3313	1945
JK7	CP	wood	yes	724	749	3564	2748	4	51	401	617
JK8	CP	wood	yes	1985	1061		2531	5	24	769	461

Species: CP=*Cleistopholis patens*

Table 3 - Results for all other species; mg kg^{-1}

Sample no.	Species	Plant part	Decaying?	Magnesium	Sodium	Potassium	Calcium	Manganese	Iron	Phosphorus	Sulphur
JK10	TR	wood	no	778	0	383	11275	198	1651	440	766
JK11	HG	wood	no	143	3	345	15004	12	376	180	204
JK12	FA	wood	no	388	23	764	8368	215	3443	105	201
JK13	AB	wood	no	378	904	5622	2775	19	689	347	205
JK14	TT	wood	no	620	1	412	2542	116	385	150	352
JK17	BP	wood	no	1151	116		10798	6	40	330	125
JK18	FM	wood	no	3415	59	1266	154913	73	563	1337	1605
JK19	FS	wood	no	271	8	534	19852	112	2344	212	254
JK24	DD	wood	no	2075	326	1439	13391	75	5322	264	350
12	FU	bark	no	2655	66	3048	1521	20	12	59	5519
13	FU	bark	no	340	75	2770	1452	28	14	73	6962
15	AB	bark	no	383	2455		1723	28	29	409	9368
16	AB	bark	no	393	100	835	6912	11	37	533	7576
17	ME	bark	no	1203	198	1141	16183	106	57	213	15521
18	ZG	leaf	no	2740	289		2518	16	117	2273	95695
19	FE	leaf	no	4114	408	24993	12449	81	118	1187	51291
20	CM	leaf	no	3738	436		5790	253	86	1106	32835
21	FV	leaf	no	1112	156	7479	3130	23	16	729	11478
22	MI	fruit	no	1132	321		2007	44	21	815	16878
23	BP	fruit	no	3634	546		10878	23	63	4381	32879
24	LC	fruit	no	767	164	10073	2823	20	34	1359	15070
25	FM	fruit	no	1751	135		4895	20	49	1145	26913
26	FE	fruit	no	2889	192		7563	41	72	1962	41893
27	BO	fruit	no	1305	55		791	43	30	818	48638

Species: TR=*Trichilia rubescens*, HG=*Holoptelia grandis*, FA=*Fagara angolensis*, AB=*Alstonia boonei*, TT=*Tetrapleura tetraptera*, BP=*Broussonettia papyrifera*, FM=*Ficus mucuso*, FS= *Ficus saussureana*, DD=*Desplatsia dewevrei*, FU=*Funtumia elastica*, ME=*Maesopsis eminii*, ZG=*Zanha golungensis*, FE=*Ficus exasperata*, CM=*Celtis mildbraedii*, FV=*Ficus varifolia*, MI=*Mangifera indica*, LC=*Lantana camara*, BO=*Beoquaertiodendron oblanceolatum*

The direction of differences is shown in Table 4. As can be seen from this Table, concentration of sodium (Na) is highest in RF, intermediate in CP, and low in other species. These differences are presented graphically in Figure 3, illustrating the mean, SD, range and outliers for Na concentrations in the three sample groups. These comparisons indicate that CP is now serving as a source of sodium for the Budongo chimpanzees, though not at the same concentration as RF formerly did. Additional differences noted include the richness of CP in potassium (K), another salt. Manganese (Mn) and sulphur (S) are found in higher concentrations in RF than in CP and other species. Ca (calcium) is, as expected, found mainly in living samples (all other species).

Table 5 gives the results of statistical tests comparing the three groups (RF, CP and all other species) with each other. As this Table shows, 5 of the 8 comparisons yield significant results: Na, Ca, Mn, and P ($p<.000$) and K ($p<.05$).

Table 4 - Means and (ranges) (mg $^{kg-1}$) for groups 1-3

	Magnesium	Sodium	Potassium	Calcium	Manganese	Iron	Phosphorous	Sulphur
RF	2430 (293-6586)	5038 (1095-14616)	6650 (3165-12559)	1563 (421-4568)	425 (60-1785)	128 (20-515)	367 (58-1057)	35925 (6499-127516)
CP	2067 (421-7090)	1822 (92-14330)	10462 (603-71212	5474 (1005-26620)	48 (1-645)	142 (15-618)	1376 (115-11597)	1153 (225-7886)
All other species	1457 (143-4114)	293 (0-2455)	4073 (345-24993)	13314 (791-154913)	66 (6-253)	649 (12-5322)	851 (59-4381)	17607 (125-95695)
All samples	1877 (143-7089)	1798 (0-14616)	7505 (345-71212)	8066 (421-154913)	130 (1-1785)	357 (12-5322)	953 (58-11597)	15034 (125-127516)
Total N	56	55	44	56	56	56	56	56

Species: RF=*Raphia farinifera,* CP=*Cleistopholis patens*

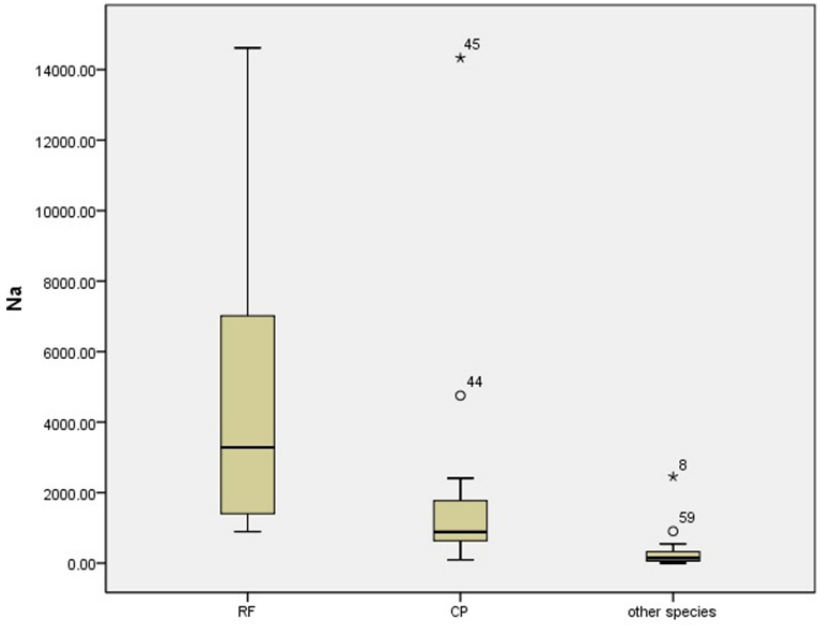

Figure 3. Boxplot showing the Na results for *Raphia, Cleistopholis* and all other species.

Table 5 - Kruskal-Wallis test results for groups 1-3

	Magnesium	Sodium	Potassium	Calcium	Manganese	Iron	Phosphorous	Sulfur
Total N	56	55	44	56	56	56	56	56
Test statistic (H)	2.322	31.000	8.494	16.551	20.857	.134	4.647	19.379
Degrees of freedom	2	2	2	2	2	2	2	2
P (2-sided test)	.313 n.s.	.000 ***	.014 *	.000 ***	.000 ***	.935 n.s.	.098 n.s.	.000 ***

DISCUSSION

Ingestion by mountain gorillas (*Gorilla gorilla beringei*) of decaying wood to provide sodium was reported by Rothman *et al.* (2006). Magliocca and Gautier-Hion (2002) reported that lowland gorillas in Congo obtained sodium from herbaceous swamp clearings. Subsequently, Reynolds *et al.* (2009) reported on the ingestion of decaying *Raphia farinifera* (RF) pith by chimpanzees (*Pan troglodytes schweinfurthii*) as a source of sodium in Swamp Forest in Budongo.

As reported by Reynolds *et al.* (2009), RF has become scarce because of the actions of local people. They use this tree for making palm wine. The main threat, however, comes from local tobacco farmers who strip the outer layer of the leaves to make string for hanging their tobacco leaves during curing and drying. Because young leaves are preferred for string, the trees are often damaged or killed before flowering (RF flowers and fruits once only in its life time), thus preventing it from reproducing and leading to its extirpation. Today, there are few RF remaining in the area occupied by the Sonso community of chimpanzees, and possibly in the Budongo Forest as a whole. Other primate species are also affected; e.g., black and white colobus monkeys (*Colobus guereza*). Oates (1978) found high levels of sodium and other minerals in swamp plants eaten by black and white colobus monkeys. This species is also present in Budongo Forest and it also ingests decaying *Raphia* pith from the same trees used by chimpanzees. That source of minerals has now largely disappeared.

The results reported in this paper indicate that with the decline of RF, chimpanzees have come to rely more on an alternative source of sodium, decaying wood of a swamp forest tree species, *Cleistopholis patens* (CP). As shown in our analyses, however, CP is not as rich as RF in sodium. Rothman *et al.* (2006) found a mean dry sodium weight of 810 mg kg^{-1}, with a range of 100-1920 mg kg^{-1}, in their analyses of decaying wood sources of Na for mountain gorillas. In the present study, the mean dry sodium weight for RF was 4892 mg kg^{-1} with a range of 892-14616 mg kg^{-1} - a higher concentration than found for the mountain gorillas. The mean dry sodium weight for CP was 1822 mg kg^{-1} with a range of 92-14330 mg kg^{-1}; this is lower than RF, but still higher than for mountain gorillas. In view of this, it is likely that CP can provide the required sodium needs of the Sonso chimpanzees, but how long the supply of decaying CP trees will last is not known. It also should be noted that RF is also richer than CP in manganese and sulphur.

Following the discovery of the rapid decline of RF, steps have been taken to try to find alternatives to the exploitation of this species by tobacco farmers. In 2008, Concy Olanya initiated discussions with tobacco farmers in local villages, explaining the need to conserve RF in the interests of the chimpanzees. This work was continued in 2009 by James Knights (Knights, 2009), and is being continued at the present time by Gilbert Atuhe (2010a, 2010b). Figure 4 shows one of the meetings being held with local tobacco growers.

Senior members of the Budongo Conservation Field Station (BCFS) also have been involved in these discussions, which have moved from farmers and their representatives to senior staff in the large companies operating in the area, British American Tobacco (BAT), Continental, and the Uganda Tobacco Growers Association. A number of alternatives to raffia string have been discussed, including plastic twine, sisal, jute, and cotton string. Of these, cotton string has proved to be an acceptable alternative; however, unlike *Raphia*, it is not freely available and must be purchased. We also have been in discussion with the National Forest Authority to make the harvesting of RF illegal. These discussions are continuing with both farmers and senior staff of the big companies.

A number of specific meetings have been held with BAT to discuss the raffia/cotton problem in the Budongo area. So far, uptake of cotton here has been very low. Elsewhere, however, cotton is supplied by BAT and used extensively by tobacco farmers. This is the case in Hoima District to the south of Budongo, in the Diima, Kigumba and Bweyale areas. The cotton is financed with loans from BAT which are later deducted from the proceeds of tobacco sales. The cotton loans are part of a wider loan scheme operated by BAT, and it is hoped that with a publicity scheme emphasising the need to conserve *Raphia* palms in Budongo forest, uptake in the Budongo area will increase. In the meantime, BCFS is investigating the reasons for low uptake in our area.

In the interim, seedlings of RF can still be found in the forest, although they are heavily predated on, largely by pigs. It is to be hoped that the remaining seedlings can provide a source for the future repopulation of Budongo Forest by RF.

Figure 3. Discussion meeting with tobacco farmers. Photo: J. Knights.

ACKNOWLEDGEMENTS

Grateful thanks are due to the staff of Budongo Conservation Field Station, in particular Fred Babweteera and Geoffrey Muhanguzi. Our thanks go to Geresomu Muhumuza, Concy Olanya, Gilbert Atuhe, James Knights, Stephen Oliki, and senior staff of BAT for different parts played in the project. We are grateful to Catherine Hobaiter for permission to use video clips. For financial support we are grateful to the Mohamed bin Zayed Species Conservation Fund and to the Royal Zoological Society of Scotland. For permission to undertake the study we wish to thank the National Forest Authority, the Uganda National Council for Science and Technology, and the President's Office.

LITERATURE CITED

Atuhe, G. 2010a. Utilisation of *Raphia farinifera* by the Biiso community in Budongo Sub-county. Unpublished report available from Budongo Conservation Field Station, P.O. Box 362, Masindi, Uganda.

Atuhe, G. 2010b. The ecological status of *Cleistopholis patens* in Budongo Forest Reserve, Uganda. Unpublished report available from Budongo Conservation Field Station, P.O. Box 362, Masindi, Uganda.

Eggeling, W.J. 1947. Observations on the ecology of the Budongo Rainforest, Uganda. *Journal of Ecology* 34: 20-87.

Knights, J. 2009. *Raphia* Conservation Report. Unpublished report vailable from Budongo Conservation Field Station, P.O. Box 362, Masindi, Uganda.

Magliocca, F. & A. Gautier-Hion (2002). Mineral content as a basis for food selection by Western Lowland Gorillas in a forest clearing. *American Journal of Primatology* 57: 67-77.

Michell, A.R. 1989. Physiological aspects of the requirement for sodium in mammals. *Nutrition Research Reviews* 2: 149-160.

Reynolds, V., A.W. Lloyd, F. Babweteera, & C.J. English. 2009. Decaying *Raphia farinifera* palm trees provide a source of sodium for wild chimpanzees in the Budongo Forest, Uganda. *PLoS ONE* 4(7), e6194.

Reynolds, V. 2005. *The Chimpanzees of the Budongo Forest*. Oxford University Press.

Rothman, J.M., P.J. van Soest & A.N. Pell. 2006. Decaying wood is a Na source for mountain gorillas. *Biology Letters* 2: 321-324.

Oates, J.F. 1978. Water-plant and soil consumption by Guereza monkeys (*Colobus guereza*): a relationship with minerals and toxins in the diet? *Biotropica* 10: 241-253.

AUTHORS' CONTACT INFORMATION

Corresponding author: Vernon Reynolds, School of Anthropology, University of Oxford, Orchard House, West Street, Alfriston, East Sussex, UK; and Budongo Conservation Field Station, P.O. Box 362, Masindi, Uganda. Email: vreynolds@btopenworld.com

Andrew W. Lloyd, Faculty of Science and Engineering, University of Brighton, Cockcroft Building, Moulsecoomb, Brighton BN2 4GJ, UK. Email: a.w.lloyd@brighton.ac.uk.

Christopher J. English, Faculty of Science and Engineering, University of Brighton, Cockcroft Building, Moulsecoomb, Brighton BN2 4GJ, UK. Email: c.j.english@brighton.ac.uk.

***Musa* - Adult male, Sonso community, September 2011.**
Photo courtesy of Vernon Reynolds.

Video 1: Feeding on Decaying *Raphia*

(Please double-click on clip to start video)

Video Clip Courtesy of Cat Hobaiter

Video 2: Competition over *Raphia*

(Please double-click on clip to start video)

Video Clip Courtesy of Cat Hobaiter

Video 3: Feeding on *Cleistopholis patens*

(Please double-click on clip to start video)

Video Clip Courtesy of Cat Hobaiter