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Presence of Alkaloids and Cyanogenic Glycosides in Fruits Consumed by Sympatric Bonobos and the Nkundo People at LuiKotale/Salonga National Park, Democratic Republic of Congo and Its Relationship to Food Choice

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Abstract: The importance of secondary compounds remains poorly studied in wild plants eaten by bonobos (*Pan paniscus*) and humans. As part of this study, alkaloids and cyanogenic glycosides (cyanide) were investigated in wild fruits consumed by bonobos at LuiKotale in Salonga National Park. In high concentrations, the two components can become toxic. Therefore, we investigated whether the bonobos and the Nkundo people avoid high concentrations of these components in their food. To analyze alkaloids and to detect the presence of cyanogenic glycosides, we used semi-quantitative methods. Of the 75 species of fruit analyzed, 28 species (37%) were revealed to have alkaloids at different proportions and 47 species (63%) were shown to be without alkaloids, 12 species (16%) with low concentrations (+), 14 species (19%) with moderate concentrations (++), and two species (3%) with high concentrations (+++). Of the 75 species, 60 were eaten, of which 46 were consumed only by bonobos, 13 were eaten by both bonobos and the Nkundo people, and one species (*Piper guinensis*) was eaten only by the Nkundo people. In total, bonobos ate 59 species and the Nkundo people 14 species. Of the 60 species consumed, the majority, i.e., 39 species (65%) did not show the presence of alkaloids, while 11 species (18%) showed a low concentration and 10 species (17%) moderate concentrations. As for cyanogenic glycosides (cyanide), this was detected in only three of the 75 species of fruit analyzed. Two species, *Camptostylus mannii* and *Dasylepsis seretii*, belong to the Achariaceae family, with *Oncoba welwitschii* in the Salicaceae family. The two species of Achariaceae both contain alkaloids and cyanogenic glycosides. No species eaten by the Nkundo contained cyanogenic glycosides. Hence, we infer that bonobos and the Nkundo people both avoid eating fruit species that contain high concentrations of alkaloids and cyanogenic glycosides, and this might have relevance linked to the evolution of seed dispersal.

Key words: Secondary compounds, fruits, bonobo, Nkundo, Salonga National Park

Résumé: L'importance des composés secondaires dans les plantes sauvages consommées par *Pan paniscus* (bonobo) reste encore peu étudiée. Dans le cadre de cette étude, les alcaloïdes et les hétérosides cyanogénétiques (cyanures) ont été recherchés dans les fruits consommés par la population Nkundo et les bonobos de Luikotale,

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Parc National de la Salonga ainsi que dans ceux qui ne sont pas consomés. A travers cette étude, nous avons cherché à connaître si les bonobos et les Nkundo évitent de fortes concentrations en ces éléments dans leur nourriture. Notre méthodologie a consisté à rechercher les alcaloïdes et les glycosides cyanogénétiques en utilisant la méthode semi-quantitative. Sur les 75 espèces de fruits analysées, 28 (37%) ce sont révélées avec alcaloïdes à différentes proportions et 47 (63%) espèces de fruits ce sont révélées sans alcaloïdes. Parmi les 75 espèces de fruits analysées, 60 ont été mangés dont, 59 ont été mangés par les bonobos parmi lesquelles, 13 ont été mangées par les Nkundo et par les bonobos et une espèce (*Piper guineensis*) a été mangée uniquement par les Nkundo. Parmi les 60 espèces mangées, la grande majorité, soit 39 espèces (65%) n'ont pas montré la présence d'alcaloïdes, onze espèces (18 %) ont montré une faible concentration et dix espèces (17%) ont montré une concentration moyenne. Quant aux hétérosides cyanogénétiques (cyanures), les tests fait sur les 75 espèces de fruits nous ont permis d'identifier trois (4%) espèces qui en contiennent. Parmi ces trois espèces, deux d'entre elles appartiennent à la famille des Achariaceae, il s'agit de: *Camptostylus mannii*, et *Dasylepsis seretii*. L'espèce *Oncoba welwitschii* par contre appartient à la famille des Salicaceae. La proportion de fruits sans alcaloïdes était plus élevée que ceux avec alcaloïdes. Ces proportions sont plus élevées pour les glycosides cyanogénétiques. Par conséquent, nous pouvons dire que les bonobos et la population Nkundo évitent de manger des espèces de fruits qui contiennent une forte concentration en alcaloïdes et glycosides cyanogénétiques.

Mots clés : Composés secondaires, fruits, bonobo, Nkundo, Parc National de la Salonga

INTRODUCTION

The forests of the Central Congo Basin contain a diverse mix of plants and animals, including many plants producing a wide variety of fruits, of which most are edible by animals (FAO 2006). Much scientific research looking at animal food choice has concentrated on the nutrient content (e.g., Hohmann *et al*. 2006; Kamungu *et al*. 2015). This approach assumes that foraging is focused on optimizing the supply of macronutrients, such as fats, carbohydrates, and proteins (Pasquet *et al.* 2011).

However, other studies have shown that food choice is influenced by the avoidance of substances that alter the organoleptic quality (Hohmann *et al.* 2006; Doran-Sheehy *et al.* 2009). Some field and experimental studies have indicated that the choice of foods as well as food intake efficiency are affected by a number of parameters, including nutritional quality, distribution, and abundance of resources (Carlo *et al.* 2003; Saracco *et al.* 2004). Some studies even suggest that the presence of secondary compounds may be the major driver of food selection by animals (Alm *et al.* 2000; Clauss *et al.* 2003). For example, fruits may occasionally contain undesirable substances for nutrition, such as secondary compounds, and depending on their concentration, these substances may become toxic for their consumers. These include very active plant poisons with a specific action, some of which can be used medicinally (Hopkins 2003; Irina *et al*. 2012).

Bonobos (*Pan paniscus*) live only in the equatorial forests south of the Congo River (IUCN & ICCN 2012). These forests provide a high diversity of ligneous plants bearing fruit, 85 % of which produce fleshy fruits to attract animals for primary seed dispersal (Beaune *et al.* 2013). In addition, the habitat is not markedly seasonal, providing fruit throughout the year. This is similar to Rubondo National Park, an island in the southwestern corner of Lake Victoria, Budongo Forest, and Bwindi Impenetrable National Park in Uganda, where important chimpanzee fruit foods are available across all months, with no distinct periods of habitat-wide fruit scarcity (Newton-Fisher 1999; Newton-Fisher *et al.* 2000; Stanford & Nkurunungi 2003; Moscovice *et al.* 2007). Thus, as bonobos are primarily frugivores (Badrian *et al.* 1981; Kano 1983; Wrangham 1986), it is likely that they avoid foods containing high concentrations of antifeedants, and rather select for macronutrients, including sugars. This avoidance of toxic secondary metabolites may be triggered by an unpleasant taste, which for most primates has been shown to correspond to a primary rejection reaction by the gusto-facial reflex, considered as an adaptation for avoiding more or less toxic plant products (Hladik 2002).

The prevalence of secondary metabolites, including alkaloids and cyanogenic glycosides, in wild plant foods consumed by bonobos and the local Nkundo population is almost completely unknown. As with other secondary metabolites, there are a number of arguments in favor of a defensive (antifeedant) role for alkaloids (Hartmann 1991; Lebreton 1982; Douglas & Martin 1998). However, alkaloids also have diverse medicinal properties (Bernhoft 2008).

Cyanogenic glycosides are present in some species of plants and offer an immediate chemical defense against herbivores and pathogens causing damage to the plant tissue (Moller 2010). Nevertheless, the sensitivity of animals towards cyanogenic glycosides varies considerably, depending on the species (Jones 1988).

Here, we investigate alkaloids and cyanogenic glycosides in both fruits consumed and not consumed by bonobos and the Nkundo population, the local human inhabitants of the neighboring area. Through this investigation, we seek to understand whether bonobos avoid high concentrations of alkaloids or the presence of cyanogenic glycosides in their food. In addition, we investigate bonobo and human food choice with respect to the concentration of these components.

MATERIALS AND METHODS

This investigation was conducted between June 2007 and March 2008 at the study site of LuiKotale, located at the southwestern fringe of Salonga National Park (2° 45.610 S, 20° 22.723 E; Hohmann & Fruth 2008; Figure 1). The study site was started in 2002 and hosts projects focusing on plant diversity and bonobo behavioral ecology, conducted by shifting teams of researchers, students, and volunteers. The

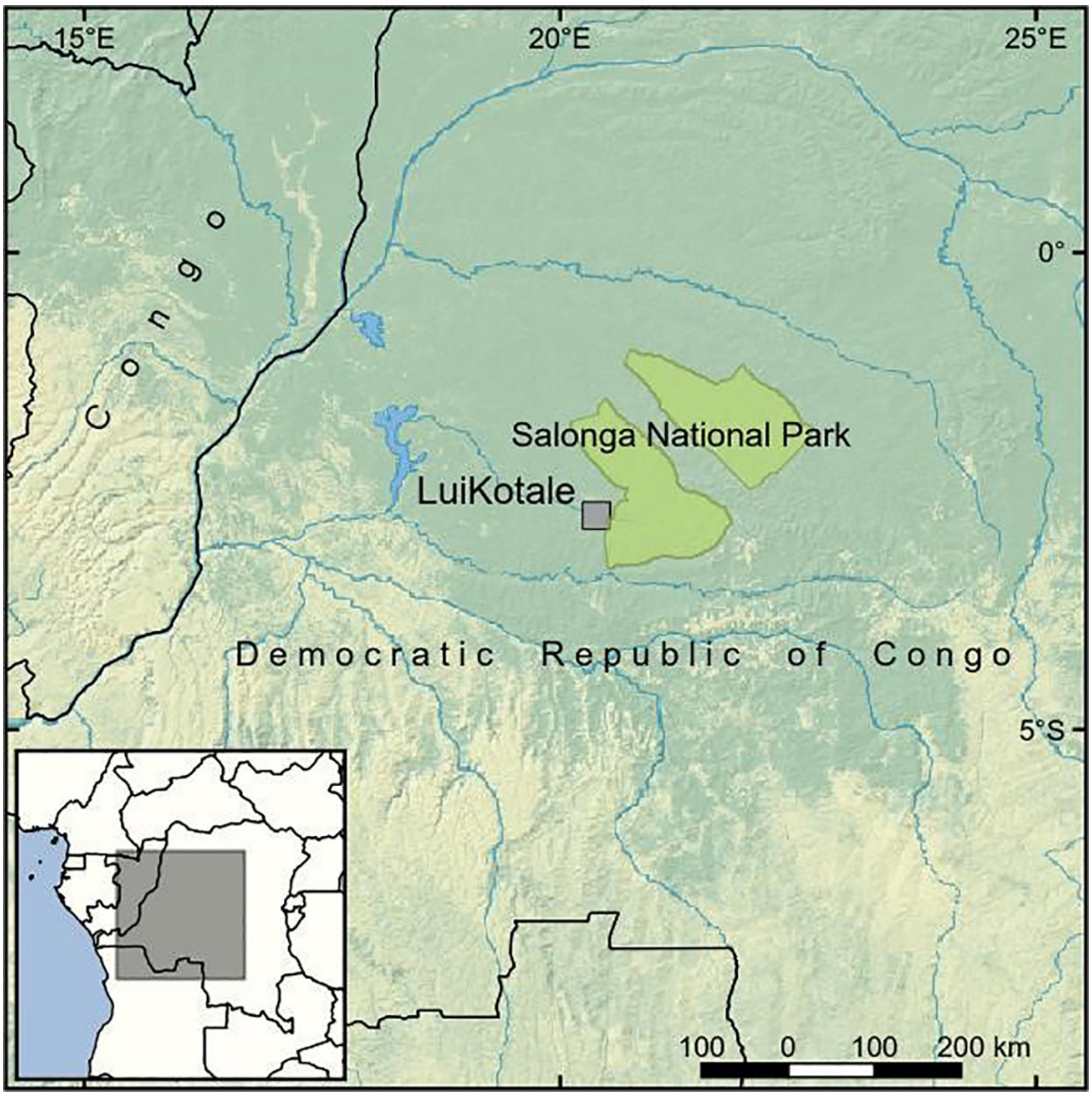

Figure 1. Location of the study site at LuiKotale, in Salonga National Park, Democratic Republic of Congo. Map courtesy (http://scalar.usc.edu/works/graphics-for conservation/media/LuiKotale_781.jpg).

climate is equatorial with abundant rainfall (>2000 mm/year), a short dry season in February and a long dry season between May and August. The monthly average temperature ranges between 18 and 29° C, with a minimum of 15.7° C and a maximum of 37.3° C (Fruth *et al*. 2014).

We focused our investigation on those species that produce fruits seasonally. Identification was confirmed with the help of a reference herbarium, established during the framework of the long-term project, "The Cuvette Central as a reservoir of medicinal plants" (Fruth 2011). After cross-checking, plant samples were deposited at the herbarium of the INERA, located at the University of Kinshasa.

Fruits were collected along standardized phenological transects, as well as opportunistically outside transects when following bonobos, and brought back to camp for analysis (Figure 2). Only ripe fruit was taken into consideration as the state that is eaten by both bonobos and the Nkundo people. Alkaloids were identified following a semi-quantitative method described by Ganzhorn (1989) using three reagents: Dragendorff´s, Wagner´s, and Mayer's. The fruit pulp was crushed using a porcelain or steel mortar. Sulfuric acid (0.1 M) was added, and the solution was passed through filter paper (Rotilabo R, 80 mm in diameter). A drop of the filtrate was deposited in each of four petri dishes. One served as a control. Next, a drop of each reagent was pipetted onto the filtrate. The reaction was either immediate or took up to a few minutes to occur. In the cases where alkaloids were present, the reaction produced a precipitate. The concentration of alkaloids in the filtrate was ranked on a scale of 0 – 3. When almost all the reagent reacted with the filtrate, it was assigned a 3 or +++, when half of the filtrate reacted it was assigned a 2 or ++ and when 1/3 of the filtrate reacted, it was assigned a 1 or +. When there was no precipitate formation in the filtrate it was assigned a 0.

Similarly, semi-quantitative analyses were used for the detection of cyanogenic glycosides according to the method of Feigl and Anger (1966). This simple field detection method detects the presence of cyanide from small amounts of plant material. Fruits were crushed in a mortar, mixed with distilled water, and poured into a tube. Feigl-Anger paper was placed in the tube without contacting the solution, and the top was sealed. Within approximately five minutes, if cyanide was present, a reaction turned the paper from white to blue.

RESULTS

1. Alkaloids

Almost 2/3 of the 75 species (63%) did not show the presence of alkaloids, while 28 species (37%) revealed alkaloids of different proportions: 12 species (16%) showed a low concentration (+), 14 species (19%) showed an average concentration (++), and 2 species (3%) had a high concentration (+++). Of the 75 species of fruit analyzed, 60 were eaten, of which 46 were eaten only by bonobos, 13

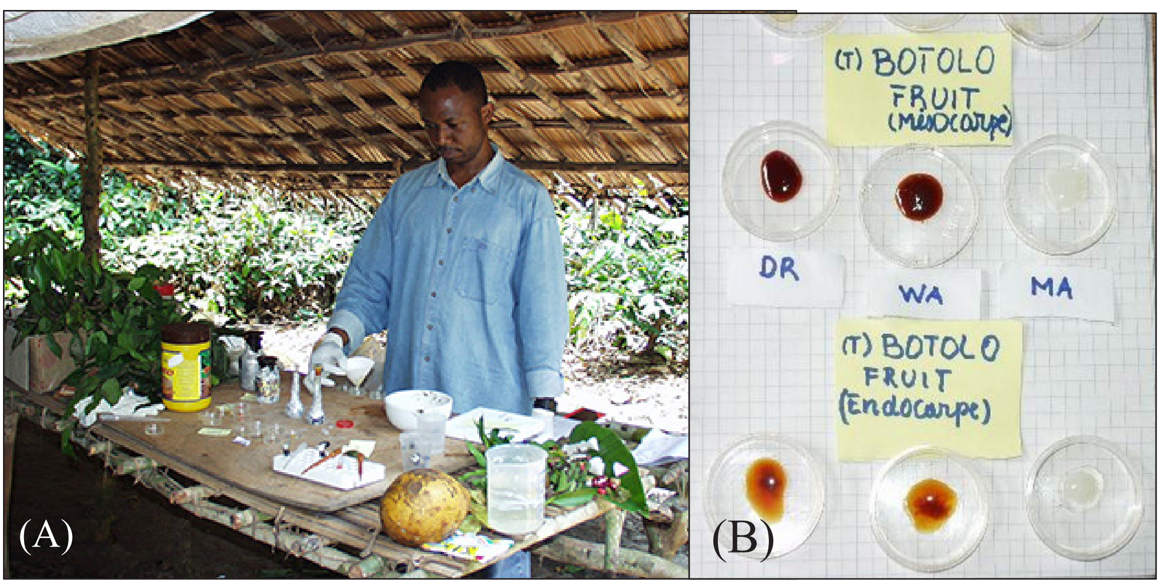

Figure 2. (A) Analyses of the alkaloids and cyanogenic glycosides in the laboratory at Luikotale, (B) Results of the analysis of alkaloids in the fruit of *Picralima nitida.*

were eaten by both bonobos and the Nkundo people, while one species (*Piper guinensis*) was eaten only by the Nkundo. In total, bonobos ate 59 species and the Nkundo consumed 14 species. Of the 60 species eaten, 11 species (18%) showed a low concentration (+) of alkaloids, while 10 species (17%) showed a moderate concentration (++). No species of fruit consumed by bonobos and the Nkundo people showed an alkaloid abundance rank of +++ (Table 1).

Table 2 indicates the number of species consumed by humans and bonobos. Looking at the alkaloid content, nine (64%) of the 14 species consumed by the Nkundo people had no alkaloids, while four species (29%) contained low (+) concentrations, with just one species (7%), *Canarium schweinfurthii*, having a moderate concentration (++) of alkaloids. None of the fruits consumed by the Nkundo had a high concentration (+++) of alkaloids.

As for the fruits not consumed by the local people and bonobos, these comprise a total of 15 species. Of these, seven species (47%) contained alkaloids, with three fruit species found to have a high concentration (+++), three species with an average concentration (++), and one species with a low concentration (+). The eight remaining species (53%) did not contain alkaloids (Table 3).

2. Cyanogenic glycosides

Table 4 indicates the results of the 75 species of fruits analyzed for cyanogenic glycosides content. Only 3 (4%) of the 75 species tested contained cyanogenic glycosides: *Camptostylus mannii, Dasylepsis seretii* and *Oncoba welwitschii.* The first two species belong to the Achariaceae family and *Oncoba welwitschii* is in the Salicaceae family.

DISCUSSION

Out of the 75 species of fruit collected, we have identified 59 species of fruit consumed by bonobos, of which 13 are consumed concurrently by both bonobos and the Nkundo, and one species consumed only by the Nkundo people (*Piper guinensis*). These results show that bonobos consume a larger number of species compared to the local Nkundo population. This can be explained partly by the fact that fruits comprise only a minor part of the human diet, and that a number of cultivated fruits are also available such as oranges, papayas, mangoes, pineapples, etc. In contrast, wild fruits form the main component of the bonobo diet (Rafert & Vineberg 1997). Like chimpanzees, bonobos are primarily frugivorous, with fruit accounting for 49-63% of their diet (Badrian *et al.* 1981; Kano 1983; Boesch *et al.* 2002). The fruits observed to be consumed here are also consumed by bonobos elsewhere: most of these species are cited by Idani *et al.* (1994) as part of the bonobo diet at Wamba/Lopori, while the fruit of *Dialium zenkeri* is noted in other studies (Yamamoto *et al.* 2009; Beaune *et al.* 2013).

The alkaloid tests carried out on 75 different species of fruit showed that 47 species (63%) did not show the presence of alkaloids, while 28 species (37%) contained alkaloids of different proportions: 12 species (16%) showed low concentration (+), 14 species (19%) a moderate concentration (++) and 2 species (3%) a high concentration (+++). Of the 60 species of fruit consumed by bonobos and the local population of Nkundo people, 39 fruit species (65%) did not contain alkaloids; 11 species (18%) showed a low concentration (+) and 10 species (17%) a moderate concentration (++), but no species contained alkaloids in high concentration. To confirm the presence or absence of alkaloids, our procedure involved using three reagents, including Dragendorff, Wagner and Mayer. Chapman *et al.* (2003) used only Dragendorff's reagent to test for the presence of alkaloids, which sometimes produces false positive results (Waterman 1993).

In Gabon, tests carried out on samples of 382 plant species collected at random in the Ipassa-Mingouli rainforest and on 38 plant species eaten by chimpanzees gave only 15% positive results for the presence of alkaloids, using Mayer and Dragendorff reagents (Hladik & Hladik 1977). These results indicate that chimpanzees, like bonobos, showed little selection against plants containing alkaloids (Clutton-Brock 1977).

According to Whitten (1980), the Kloss gibbon (*Hylobates klossi*), found on islands off the west coast of Sumatra, has been observed to eat the fruits of Arenga obtusifolia which contain oxalate, though the gibbon may avoid toxicity by careful selection of ripe fruit. Moreover, Waser (1977) recorded that mangabeys (*Lophocebus albigena*) avoid the alkaloid-rich fruits of Rauvolfia and Strychnos. Similarly, chimpanzees avoid alkaloid-rich fruits of Picralima (Hladik & Hladik 1977). Meanwhile, Remis *et al.* (2001) concluded that lowland gorillas in the Central African Republic appear to avoid nitrogen-based alkaloids, even when preferred foods are scarce.

The chimpanzee's food selection strategy may be to prefer non-poisonous alkaloid-free foods, ingest astringent foods when they are also sweet, and consume some foods containing alkaloids when they have some nutritional or possibly medicinal

Table 1. The 75 species of fruits, indicating the presence of both alkaloids and cyanides, as well as consumption by bonobos and humans.

Families	Species	Nkundo name	BFT	HS	FrDr	FrMa	FrWa	Result	HCN
Achariaceae	*Camptostylus mannii*	Bonkasa ya esobe	1	0	2	2	2	++	+
Achariaceae	*Dasylepis cfr.seretii*	Imbedzi ya pembe	1	0	0	0	0	0	+
Anacardiaceae	*Antrocaryon nannanii*	Bokongwende	1	1	0	0	0	0	0
	Sorindea sp.	Ipambua II	1	0	0	0	0	0	0
	Trichoscypha arborescens	Bohungwu	1	0	0	0	0	0	0
Annonaceae	*Anonidium mannii*	Bodzingo	1	1	1	1	1	+	0
	Enantia olivacea	Ikodzi konga	1	0	1	1	1	+	0
	Friesoldielsia enghiana	Impimbo ya pembe	1	0	0	0	0	0	0
	Polyalthia suaveolens	Bodzinda	1	0	2	2	2	++	0
	Uvariopsis letestui	Bodzungu IIa	1	0	0	0	0	0	0
	Uvariopsis solheidii	Bodzungu IIb	1	0	0	0	0	0	0
Apocynaceae	*Dictyophleba ochracea*	Baole	1	1	2	2	2	++	0
	Landolphia owariensis	Botsuatope	1	1	0	0	0	0	0
	Picralima nitida	Botolo	0	0	3	3	3	+++	0
	Pleiocarpa pycnantha	Elongo kodzi ya moindo	0	0	3	3	3	+++	0
	Tabernanthe iboga	Losekola	1	0	0	0	0	0	0
Burseraceae	*Canarium schweinfurthii*	Boele	1	1	2	0	2	++	0
	Dacryodes yangambiensis	Saw saw	1	0	0	0	0	0	0

BFT: Bonobo Feeding Tree, FrDr: Fruit analyzed with Dragendorff's reagent, FrMa: Fruit analyzed with Mayer's reagent, FrWa: Fruit analyzed with Wagner´s reagent, CN: Cyanide, Hs: *Homo sapiens*, Pp: *Pan paniscus.*

Table 1. The 75 species of fruits, indicating the presence of both alkaloids and cyanides, as well as consumption by bonobos and humans. (Cont.)

Families	Species	Nkundo name	BFT	HS	FrDr	FrMa	FrWa	Result	HCN
Chrysobalanaceae	*Parinari congensis*	Bondzale	1	0	1	0	1	+	0
	Parinari excelsa	Bodzilompongo	1	0	0	0	0	0	0
Clusiaceae/ Clusiodeae	*Garcinia chromocarpa*	Botendo	1	0	0	0	0	0	0
Ebenaceae	*Garcinia punctata*	Bosepe	1	0	0	0	0	0	0
	Garcinia smeathmannii	Itatalongo	1	0	0	0	0	0	0
	Mammea africana	Bokoli	1	0	0	0	0	0	0
	Diospyros melanocarpa	Mandza	1	0	0	0	0	0	0
Euphorbiaceae	*Drypetes gossweileri*	Bopambe	0	0	3	3	3	+++	0
	Drypetes leonensis	Kalanga ya pembe	1	0	0	0	0	0	0
	Phyllantus pynaertii	Bontepfu	1	1	0	0	0	0	0
	Plagiostyles africana	Bondenge ya zamba	1	0	0	0	0	0	0
Fabaceae/ Caesalpinioideae	*Dialium angolense*	Maku pembe	1	0	0	0	0	0	0
	Dialium corbisieri	Maku rouge	1	0	0	0	0	0	0
	Dialium zenkeri	Maku rouge II	1	0	0	0	0	0	0
	Macrolobium fragrans	Atsangila	0	0	0	0	0	0	0
	Tessmannia africana	Buaka	1	0	0	0	0	0	0
Fabaceae/ Faboideae	*Pterocarpus soyauxii*	Bofulu	0	0	0	0	0	0	0
Irvingiaceae	*Irvingia gabonensis*	Boseki ya pembe	1	0	1	1	0	+	0
	Klainedoxa gabonensis	Boseki ya moindo	1	0	0	0	0	0	0

BFT: Bonobo Feeding Tree, FrDr: Fruit analyzed with Dragendorff's reagent, FrMa: Fruit analyzed with Mayer's reagent, FrWa: Fruit analyzed with Wagner´s reagent, CN: Cyanide, Hs: *Homo sapiens*, Pp: *Pan paniscus.*

Table 1. The 75 species of fruits, indicating the presence of both alkaloids and cyanides, as well as consumption by bonobos and humans. (Cont.)

Families	Species	Nkundo name	BFT	HS	FrDr	FrMa	FrWa	Result	HCN
	Irvingia grandifolia	Loote	1	0	2	0	2	++	0
Linaceae	*Hugonia gilletti*	Bomposo ya pembe	0	0	2	1	2	++	0
Malvaceae/ Bombacoideae	*Ceiba pentandra*	Londaa	1	0	0	0	0	0	0
Malvaceae/ Sterculioideae	*Cola griseiflora*	Bonkasa ya mai	1	0	1	1	1	+	0
Malvaceae/ Tilioideae	*Grewia coriacea*	Bopfumo	1	1	1	1	1	+	0
Marantaceae	*Hypselodelphis poggeana*	Bomomongo	0	0	0	0	0	0	0
	Sarcophrynium schweinfurthianum	Nkokoloko	0	0	2	1	2	++	0
Meliaceae	*Trichilia heudalotii*	Eonge	1	0	0	0	0	0	0
Menispermaceae	*Stephania laetificata*	NID(B 3000)	1	0	3	2	2	++	0
	Penianthus longifolius	Lopetu ya bonkoko	0	0	1	0	0	0	0
Fabaceae/ Mimosoideae	*Parkia bicolor*	Bokungu II	1	0	2	1	2	++	0
	Pentaclethra macrophylla	Boala	0	0	0	0	0	0	0
Moraceae	*Treculia africana*	Boimbo	1	1	0	0	0	0	0
	Ficus sp.	Lokumo	1	0	0	0	0	0	0
Myristicaceae	*Staudtia kamerunensis*	Bokolombe	0	0	0	0	0	0	0
Not identified	*Not identified*	Enkendu ya bundo	1	0	1	1	1	+	0
Olacaceae	*Strombosiopsis zenkeri*	Bongondo	0	0	0	1	1	+	0
Piperaceae	*Piper guineensis schum.*	Boleleko	0	1	1	1	1	+	0

BFT: Bonobo Feeding Tree, FrDr: Fruit analyzed with Dragendorff's reagent, FrMa: Fruit analyzed with Mayer's reagent, FrWa: Fruit analyzed with Wagner´s reagent, CN: Cyanide, Hs: *Homo sapiens*, Pp: *Pan paniscus*.

Table 1. The 75 species of fruits, indicating the presence of both alkaloids and cyanides, as well as consumption by bonobos and humans. (Cont.)

Families	Species	Nkundo name	BFT	HS	FrDr	FrMa	FrWa	Result	HCN
Polygalaceae	*Carpolobia glabrescens*	Boseke	1	1	0	0	0	0	0
Rubiaceae	*Colletoecema dewevrei*	Isilalongi	1	0	0	0	0	0	0
	Massularia acuminata	Welo	0	0	2	2	2	++	0
	Vangueriella orthancantha	Lilala ya dzamba	1	0	0	0	0	0	0
Salicaceae	*Oncoba welwitschii*	Saake	1	0	2	2	2	++	+
Sapindaceae	*Blighia welwitschii*	Booso	1	0	2	2	2	++	0
	Pancovia laurentii	Botende	1	1	1	0	1	+	0
	Pancovia sp	Mpanda	1	0	0	0	0	0	0
	Placodiscus paniculatus	Etende Nkema	1	0	2	1	2	++	0
Sapotaceae	*Gambeya lacourtiana*	Bopambu	1	1	1	1	1	+	0
	Manilkara obovata	Boonya	1	0	0	0	0	0	0
	Synsepalum longecuneatum	Bopfunga	1	1	0	0	0	0	0
	Synsepalum subcordatum	Bopfunga totodu II	1	0	0	0	0	0	0
	Synsepalum sp.	Pepepe	1	0	0	0	0	0	0
	Tridesmostemon omphalocar-poides	Bosanga	0	0	0	0	0	0	0
	Zeyherella longepedicellata	Ilonge Pambu	1	0	1	0	1	+	0
Thymeleaceae	*Dicranolepis disticha*	Bontole badzumba	0	0	0	0	0	0	0
Vitaceae	*Cissus dinklagei*	Botaatata	1	0	0	0	0	0	0
	Cissus sp	NID (comme Bota-atata)	1	0	0	0	0	0	0
Zingiberaceae	*Afromomum alboviolaceaum*	Mbole ya mai	1	1	0	0	0	0	0

BFT: Bonobo Feeding Tree, FrDr: Fruit analyzed with Dragendorff's reagent, FrMa: Fruit analyzed with Mayer's reagent, FrWa: Fruit analyzed with Wagner´s reagent, CN: Cyanide, Hs: *Homo sapiens*, Pp: *Pan paniscus.*

Table 2. The number of species with alkaloids, cyanogenic glycosides, and consumed by the Nkundo and bonobos.

n=75 species	Yes	No
With alkaloids	27	48
With cyanogenic glycosides	3	72
Consumed by *H. sapiens*	14	61
Consumed by *P. paniscus*	59	16

value, as observed in Mahale National Park, western Tanzania (Nishida 2012). This may similarly explain the absence of a high concentration of alkaloids in the fruits consumed by bonobos and humans in this study. Among the species eaten by the Nkundo people, only *Canarium schweinfurthii* showed a moderate concentration of alkaloids in the raw state as consumed by the bonobo. However, before being eaten by humans, the fruit is softened in hot water (Bondjengo 2011). Therefore, it is likely that the fruit of *Canarium schweinfurthii* is not only cooked to be softened, but also to eliminate some alkaloids that give a bad taste to the fruit in its raw state. This treatment is also known to occur in Cameroon (Njoukan 1998; Tchouamo *et al.* 2000). According to Irina *et al.* (2012), humans have used alkaloid-containing plants and animals since ancient times as poisons, stimulants, aphrodisiacs, and medicines. Indeed, alkaloid-containing plants have been – and still are – part of our regular diet (Irina *et al.* 2012). However, it is not only alkaloids that give a bad taste to fruits, but also other compounds (such as tannin) that may prevent bonobos from eating these fruit species (Hladik *et al.* 2011). Nevertheless, great apes may be more tolerant to bitter tastes than humans. For example, Hladik and Simmen (1996) showed that Pan troglodytes can drink bitter solutions containing almost 150 micromoles of quinine, a concentration four times higher than the median threshold measured for humans. Furthermore, Nishida *et al.* (2000) found that chimpanzees are able to tolerate food species that to humans taste unpleasant, bitter, or astringent, as well as others that are neutral or sweet. But, in general, a diverse environment such as the LuiKotale Forest reveals few fruits rich in alkaloids (Hladik *et al.* 2011). Abiodun *et al.* (2014) reported that high alkaloid content causes toxicity when ingested by human beings, which is linked primarily with their ability to interfere with various neurotransmitters (Krief 2003). Alkaloid over-consumption could be the origin of many cases of poisoning in veterinary medicine, as is the case in domestic herbivores after ingestion of excessive amounts of lupine, rich in alkaloids known as quinolizidiniques (Mazid *et al.* 2011). These items when consumed in small amounts have been referred to as 'medicinal foods' by Huffman (1997), and by Masi *et al.* (2012) as unusual items of consumption; both propose some kind of medicinal value. The great ape diet is indeed rich in plants containing secondary compounds of non-nutritional, sometimes toxic, and medical value (Huffman 2003).

Regarding cyanogenic glycosides, we used the same test of Feigl-Anger as Chapman *et al.* (2003). Only three species were found to contain these substances out of the 75 species surveyed. Our results are in line with Bouquet and Fournet (1975), who also found the same species with cyanogenic glycosides: *Oncoba welwitschii, Camptostylus mannii* and *Dasylepis cfr. seretii*. The two species of the Achariaceae family contain both alkaloids and cyanogenic glycosides. Indeed, Bouquet (1972) confirmed that all Congolese species of the Salicaceae family contain cyanogenic glycosides. However, according to Conn (1979), cyanogenesis appears to be limited only to certain families such as the Leguminosae, Rosaceae, Euphorbiaceae and

Table 3. The number of species consumed by humans and bonobos that contain alkaloids or not.

Species	Hs	Pp
Species with	7 (50%)	20 (34%)
Species without	7 (50%)	39 (66%)
Sample size	14	59

Table 4. Number of species consumed by humans and bonobos, with respect to cyanogenic glycosides content.

Species	Hs	Pp
Species with	0 (0%)	3 (5%)
Species without	14 (100%)	56 (94%)
Species size	0	3

Passifloraceae. Nevertheless, our study reconfirms the work of Bouquet (1972) that some species in the Achariaceae and Salicaceae families contain cyanogenic glycosides.

Rothman *et al.* (2006) analyzed the chemical content of a total of 127 food plant parts, representing 84 plant species, eaten by two groups of mountain gorillas, from Bwindi Forest National Park, Uganda, but found only two foods that contained cyanogenic glycosides.

Thus, the small proportion (5%) found among the fruits consumed by bonobos at LuiKotale is in line with what has been reported elsewhere, e.g., the results found by Bouquet and Fournet (1975) in the study of the Congolese flora and the investigation by Rothman *et al.* (2006). Similarly, independent findings show that red colobus monkeys in Kibale National Park, Uganda also avoid plants with high levels of secondary compounds (Chapman & Chapman 2002).

In summary, the results provided here show that none of the ingested fruit species showed high concentrations of either alkaloids or cyanogenic glycosides. Using semi-quantitative analyses of bonobo and local human fruit foods, we have provided an overview into the presence/absence of two major secondary metabolite groups in the diet. However, future studies should quantify and qualify these compounds to assess their importance for the health of bonobos and humans. This investigation has contributed to our understanding the food choices in bonobos and the Nkundo people, as they relate to the presence or absence of alkaloids and cyanogenic glucosides. Furthermore, we have contributed valuable data about the presence of secondary compounds in the fruits of certain species from the African rainforest.

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