Erschienen in: Behavioural processes. Elsevier. 2017, 142, pp. 131-137
https://doi.org/10.1016/j.beproc.2017.06.007

How bonobo communities deal with tannin rich fruits: Re-ingestion and other feeding processes

David Beaune[a,b,*], Gottfried Hohmann[a], Adeline Serckx[c,d,e], Tetsuya Sakamaki[f], Victor Narat[g,h], Barbara Fruth[i,j,k]

[a] *Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Deutscher Platz 6, Germany*
[b] *Laboratoire Biogéosciences, UMR CNRS 6282, Université de Bourgogne, 6 bd Gabriel, 21000 Dijon, France*
[c] *Primatology Research Group, Behavioural Biology Unit, University of Liege, Liege, Belgium*
[d] *Conservation Biology Unit, Royal Belgian Institute of Natural Sciences, Brussels, Belgium*
[e] *Ecole Régionale post universitaire d'Aménagement et de gestion Intégrés des Forêts et Territoires tropicaux, Kinshasa, Democratic Republic of the Congo*
[f] *Primate Research Institute, Kyoto University, Kanrin 41, Inuyama, Aichi 484 8506, Japan*
[g] *Department of Infection and Epidemiology, Epidemiology of Emerging Diseases Unit, Pasteur Institute, Paris, France*
[h] *Eco Anthropology and Ethnobiology, National Museum of Natural History, Paris, France*
[i] *Liverpool John Moores University, Faculty of Science/School of Natural Sciences and Psychology; Liverpool, UK*
[j] *Centre for Research and Conservation, Royal Zoological Society of Antwerp, Antwerp, Belgium*
[k] *Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany*

ABSTRACT

Keywords:
Coprophagy
Canarium schweinfurthii
Culture
Feeding behavior
Seed dispersal
Pan paniscus
Zoochory

This report describes bonobo (*Pan paniscus,* Hominidae) behavioral flexibility and inter-community differences with high tannin level fruit processing. In fruiting plants, tannin should discourage certain seed dispersers (direct deterrence hypothesis) such as primates. Based on data deriving from five study sites; LuiKotale, Lomako, Wamba, Malebo and Manzano, we compare consumption and dispersal of fruit species rich in tannins: *Parinari* and *Musanga* pulp was chewed across all communities probably for saliva tannin neutralisation. However, consumption of the fruits of *Canarium schweinfurthii* was observed in few communities only with differences in the food process: While bonobos of Wamba, Lomako and Manzano crunched and swallowed the pulp, bonobos of LuiKotale ingested entire fruits, extracted intact fruits from feces, and re-ingested their pulp, spitting the seed after a retention time of 24 h in the digestive tract (*i.e.* endozoochory). We discuss potential functions of this peculiar feeding technique, likely to be a cultural behavior.

1. Introduction

One common form of the multiple and sometimes complex interactions between plants and animals is the consumption of seeds. In the seed dispersal effectiveness framework, a plant can have several consumers that differ in terms of their impact on dispersal distance and germination (Schupp et al., 2010). Plants might be able to 'choose' higher-quality seed dispersal vectors and avoid those of lower quality. The directed deterrence hypothesis (Cipollini and Levey, 1997; Levey et al., 2006) proposes that fruits' secondary compounds or chemical defense mediated by plant secondary metabolites (PSMs) have evolved to escape the action of damaging consumers such as seed predators while not inhibiting those that dispersers intact seeds. The secondary compounds protecting from seed consumption include alkaloids, various glycosides, and saponins, that are potentially toxic to consumers (Johns, 1999), as well as substances such as lectins that inhibit enzymatic activity. Tannins are both toxics and digestive inhibitors. The major effects of most of them are dilution of nutritional content, reduced digestibility, and limitation of food intake (Cooper and Owen-Smith, 1985; Robbins et al., 1991). The effect of tannins has been explored in insects, fish, birds and mammalian species (Clauss, 2003; Barboza et al., 2010; Omnes et al., 2017). One mammalian taxon that is particularly interesting in this context is primates. The majority of contemporary primate species is frugivorous or consumes at least temporarily large amounts of fruit (Hohmann et al., 2010; Hawe and Peres, 2014 Hawe and Peres, 2014). Not surprisingly, primates have evolved specific adaptation to frugivory such as color vision (Osorio and Vorobyev, 1996), dentition (Scott, 2011), and digestive morphology (Milton, 2003). Accordingly, it is reasonable to ask if primates have evolved mechanisms to cope with high tannin concentrations in

---

[*] Corresponding author at: Ornithological Society of Polynesia SOP - *Manu* BP 7023 - 98719 Taravao - Tahiti - French Polynesia.
E mail address: david.beaune@gmail.com (D. Beaune).

Konstanzer Online-Publikations-System (KOPS)
URL: http://nbn-resolving.de/urn:nbn:de:bsz:352-2-1i5jsyf6ibf1d1

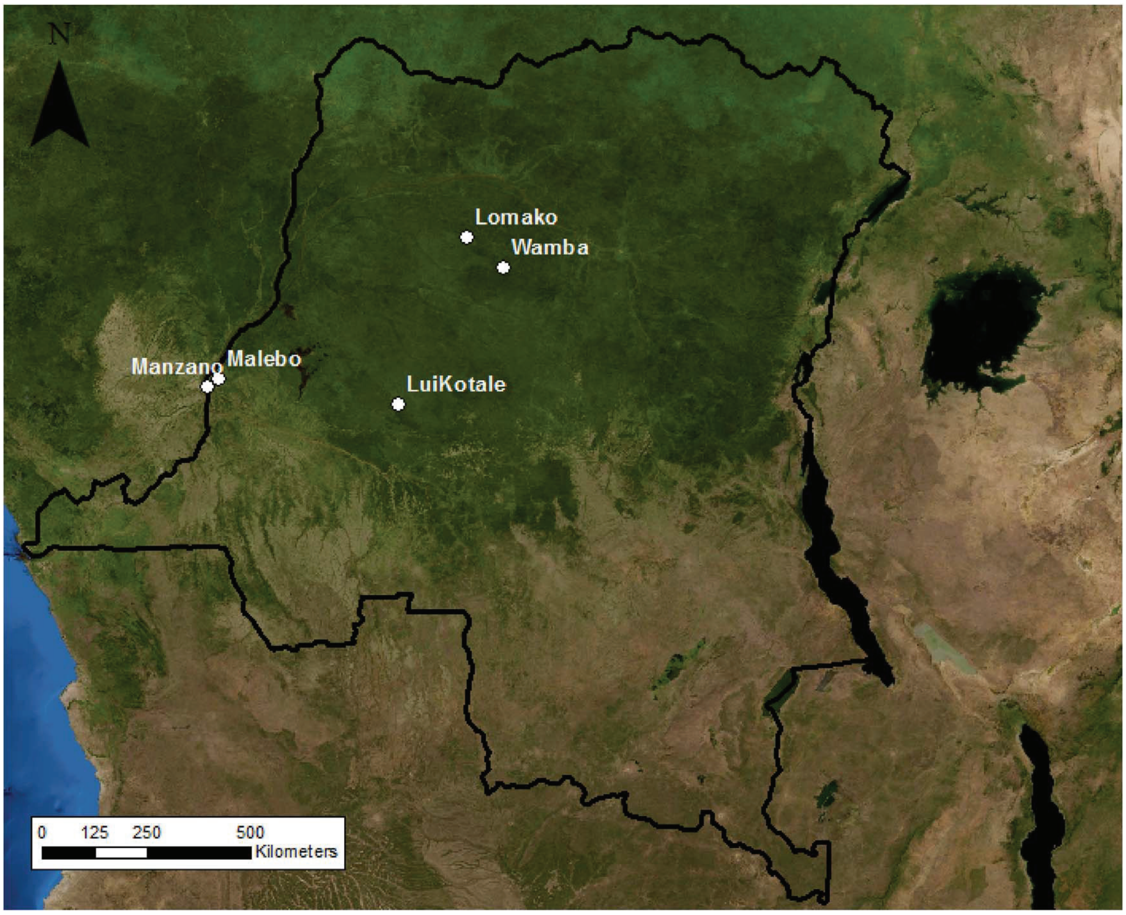

Fig. 1. Map of the field sites with five bonobo communities: LuiKotale (S2°47′- E20°21′), Lomako (N0°51′, E21°5′), Wamba (N0°11′, E22°37′), Malebo (S2°33′, E16°29′) and Manzano (S2°38, E16°23′), Democratic Republic of the Congo.

their diet. There is some evidence that wild primates are sensitive to the astringency caused by tannins (Dominy et al., 2001). In a recent experimental study with three hominoid species, species-differences were found in terms of facial expression of subjects consuming a cereal with relatively high concentrations of tannin. Other studies reported that consumers avoid food with polyphenolic compounds, in both condensed and hydrolysable forms (Wrangham and Waterman, 1981; Oates et al., 1977; Glander, 1982; McKey et al., 1981). While this information makes evident that primates are sensitive to tannins and their deleterious effects, major components such as ecological variation of tannin distribution and specific adaptability to cope with fruit that provide important food but contain high concentrations of tannin are virtually lacking. This study explores patterns of consumption of tannin rich fruit by bonobos (*Pan paniscus*) across different sites and populations differing in terms of forest composition, habitat heterogeneity, and seasonal changes in food availability. Moreover, having observational data from multiple sites, we ask to what extent bonobos differ in the techniques of food processing to cope with high tannin concentrations. Finally, we explore if bonobos disperse seeds of tannin rich fruit as predicted by the directed deterrence hypothesis (Levey et al., 2006), by describing the fruit handling and its effect on the dispersal of intact seeds.

Bonobos are restricted to the tropical lowland forests south of the Congo River. The species has an omnivorous diet and, besides forest elephants, is one of the largest seed dispersers in this habitat providing critical seed dispersal service to the majority of the tree species (Idani, 1986; Tsuji et al., 2010; Beaune et al., 2013a; Beaune et al., 2013b; Beaune et al., 2015; Beaune, 2015). Previous studies at one site revealed concentrations of tannins being relatively low, and that variation of macronutrients was independent of tannin content (Hohmann et al., 2006). From this, one would assume that bonobos ingest low levels of tannin when compared with other species and that fruit with high concentrations of tannin are avoided. Yet, evidence from the same and other sites indicate that bonobos do consume tannin rich fruit, suggesting that they are able to cope with the deleterious effects of dietary tannins. This raises the following questions: (a) how are bonobos adapted to process fruit with high concentrations of tannin, and (b) is there geographic variation in the way bonobos process fruit with high tannin concentrations? The latter question is particularly relevant as other studies on African and Asian apes have shown considerable variation in dietary patterns, social behavior, and material culture.

1.1. Possible counter strategies to high tannin values

Salivary proline-rich proteins (PRPs) have the capacity to bind tannins forming stable complexes that prevent dilution of dietary protein and facilitate excretion of detrimental tannins. To facilitate this technique, food matter has to be exposed to saliva prior to ingestion. In fact, bonobos and other hominid primates sometimes chew on fruits without swallowing food pulp and by doing so plant material is extensively exposed to saliva. Yet, the technique of wadging could also be used to separate those parts of the fruit containing high concentrations of tannin from those that are easily digested. Another form of oral food processing that may serve a similar purpose is separating seeds from mesocarp and discarding the former while ingesting the latter (Lambert, 1998). As tannins tend to occur in higher concentrations in seeds rather than mesocarp, a simple way to reduce tannin intake is removal of seeds. If all consumers share the capacity of secreting salivary proline to an extent that even high concentrations of tannin are neutralized one would expect them to do so because the two other techniques, wadging and seed removal increase handling time and slow down food intake. On the other hand, foraging techniques may be acquired by social learning and members of one population may use wadging while others may remove seeds to lower the amount of dietary tannin. This study is the first to compare preliminary data on local habits of food processing of tannin rich foods by bonobos at five sites differing in terms of forest structure, plant community composition, and climate.

2. Methods

2.1. Study sites

The field sites, LuiKotale, Lomako, Wamba, Malebo and Manzano are situated in the Cuvette Centrale (DRC), south of the Congo River. LuiKotale (S2°47′, E20°21′), Lomako (N0°51′, E21°5′), and Wamba (N0°11′, E22°37′) are situated within the same lowland equatorial rainforest block, and are about 400 km apart (Fig. 1). Annual rainfall is > 2000 mm per year and temperature averages 24 °C. For more details on climate see (Hohmann and Fruth, 2003; Furuichi et al., 2008). At all sites, bonobos were habituated to human observers and were monitored on a daily basis by research teams. Food species overlap is high across these three sites (Kano and Mulavwa, 1984; Badrian and Malenky, 1984; Beaune et al., 2013a). Bonobo populations are considered to share the same genotype and similar ecosystem (Eriksson et al., 2004). The fourth site, Malebo WWF Station (S2°33′, E16°29′) is located in a forest-savanna mosaic in northwestern DRC. Annual rainfall oscillates around 1500–1600 mm and is interrupted by two dry seasons in February and July-August. The mean daily temperature fluctuates around 25 °C. Bonobos involved in this study live in two distinct forest patches of 32 km^2 and 54 km^2 in the vicinity of the villages of Nkala and Mpelu respectively. Since 2007 subjects are under habituation (see Serckx et al., 2015 for more details). Manzano forest (S2°38′, E16°23′) is included in the Mbou-Mon-Tour community based conservation area (Narat et al., 2015a) and is independent of the 15 km distant Malebo site where one bonobo community is under habituation since 2010 (Narat et al., 2015b) (Fig. 1).

2.2. Ethics statement

The studied apes are habituated, free-ranging bonobos observed without invasive methods, constraint, contact and any interaction from the researchers. Animal welfare is the top priority beyond scientific interests. The methods used to collect data in the field are in compliance with the requirements and guidelines of the Institut Congolais pour la Conservation de la Nature (ICCN) and to the legal requirements of the host country, the Democratic Republic of the Congo.

2.3. Tannins content analysis

In previous studies, ninety-five species of fruit available from LuiKotale forest were collected for nutritional analyses and antifeedants. Phenols and tannins were measured in the lab of the Institute for Zoo and Wildlife Biology Berlin. Information on the lab protocol and original results are published by Hohmann et al. (2006).

2.4. Feeding process

From September 2009 to June 2011 behavioral data were collected from bonobos at LK for 22 months corresponding to 1879 h of observation or 315 days. Grouping patterns of bonobos are dynamic with groups fissioning and fusing multiple times per day. Feeding parties tend to be fairly cohesive in terms of food extraction and the majority or all party members consume the same type of food at a given time. Thus, this study considers feeding as a communal activity provided that the majority (> 50% of all party members) of individuals is visible to the human observer and converges on the same activity, i.e. continuous focal sub-group (Altmann, 1974). The continuous record terminated when visual contact was lost or when subjects engaged in another activity (Beaune et al., 2013a; Beaune et al., 2013b). For one fruit species with the highest tannin content (*C. schweinfurthii*), we described the fruit processing distinguishing between the following modes: (i) pulp consumption with manual seed removal, (ii) fruit consumption without seed removal, (iii) seed consumption, and (iv) mastication of fruit pulp with or without ingestion. The latter mode of food processing infers salivary neutralisation of tannins. Data from LuiKotale are compared with records from Wamba (provided by TS) and Lomako (provided by BF). Descriptions of diet composition and feeding behavior of bonobos at Malebo are based on two data sets: One is analysis of feces collected between May 2011 and June 2013 (by AS). Samples (N = 2252) were collected every morning underneath fresh nest sites, taking one sample below each fresh nest for 270 days (see Serckx et al., 2015 for more details). The other is based on direct observations of feeding behavior between February and June 2015 (270 h, 42 days), using scan-sampling. For each feeding event, the food species, the plant part eaten, and the type of food processing were scored (AS). At Manzano, diet information is based on long-term data using *ad libitum* sampling (1000 h,) from May 2012 to July 2016 and fecal analysis (N = 668, 257 days).

To test the directed deterrence hypothesis, we scored the mode of seed dispersal that is, being horizontally with relation to the parent plant by either seed-spitting or by endozoochory (promotion of dispersal of intact seeds). If bonobos ate the fruit without horizontal seed dispersal (neutral effect) or chewed the seed (negative effect), we inferred that tannin content was not sufficient to prevent consumers from destroying seeds making bonobos an inefficient partner for the plant (Table 1).

3. Results

3.1. Fruits with high tannin

Based on the nutrient analyses of 95 fruit species collected at

Table 1

Compares the mode of fruit processing (FP) of fruit with high tannin concentrations and the mode of seed dispersal (SD) across five bonobo sites. SD can be neutral (0), positive (−), or limited (−). Salivary neutralisation implies long mastication process.

Species		LuiKotale	Lomako	Wamba	Malebo	Manzano
Canarium schweinfurthii	FP	ingestion of entire fruit and re-ingestion after passage	only pulp ingestion	only pulp ingestion		only pulp ingestion
	SD	+	Limited	Limited		Limited
Musanga cecropioides	FP	salivary neutralisation	salivary neutralisation	salivary neutralisation	salivary neutralisation	salivary neutralisation
	SD	+	+	+	+	+
Strombosia pustulata	FP	not consumed	not consumed	not consumed	species absent	salivary neutralisation
	SD		+			limited
Parinari excelsa	FP	salivary neutralisation	salivary neutralis.	salivary neutralis.	Not observed	salivary neutralisation
	SD	neutral/limited	neutral/limited	neutral/limited		neutral/limited

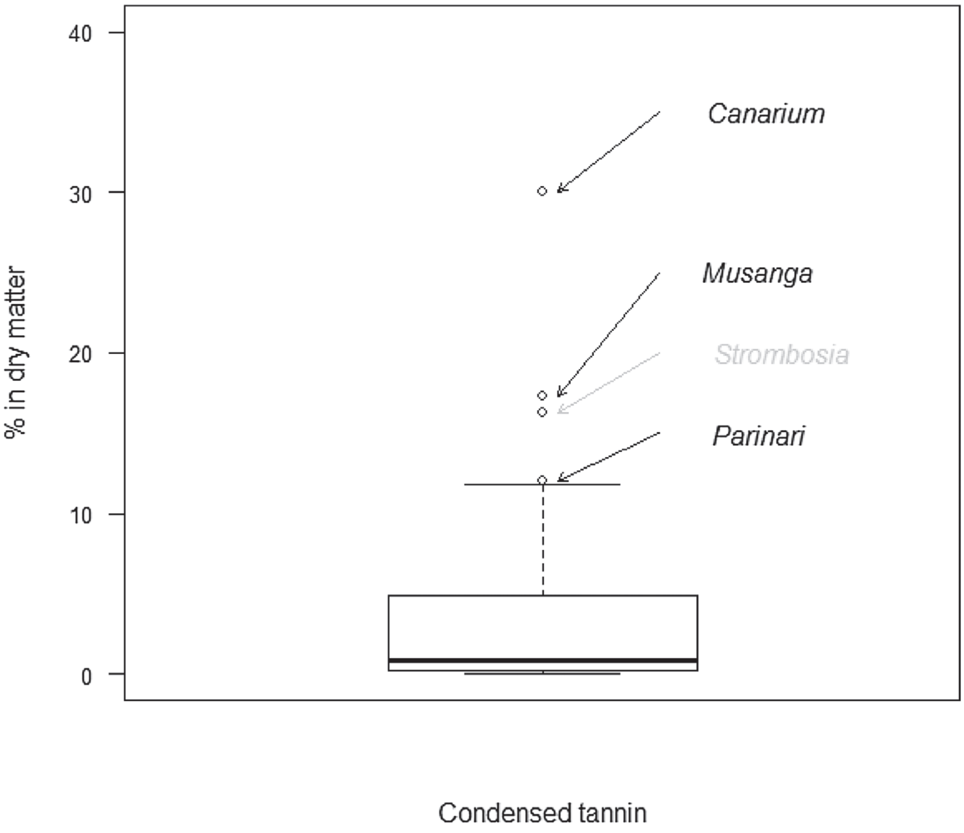

Fig. 2. Condensed tannin (% in dry matter) in fruit. Outliers are *Canarium schweinfurthii*, *Musanga cecropioides, Strombosia pustulata* and *Parinari excelsa*. The fruits of *S. pustulata* are only consumed by bonobos at Manzano. Botanical nomenclature follows the African Plants Database (version 3.4.0) from http://www.ville-ge.ch/musinfo/bd/cjb/africa/.

LuiKotale, the average percentage of condensed tannin in dry matter of fruits (100 mg) was 3.8 ± SE.0.2% ($CI_{95\%}$ = [1.9-5.7%]). In four species, levels of condensed tannin in the pulp (mesocarp) were significantly higher than in the other fruits (Wilcoxon signed rank-tests; Fig. 2). *Canarium schweinfurthii* Engl. (Sapindales: Burseraceae) (30%; V = 0, $P < 0.001$), *Strombosia pustulata* Oliver (Santalales: Strombosiaceae) (15%; V = 54, $P < 0.001$), *Parinari excelsa* Sabine (Malpighiales: Chrysobalanaceae) (12% of condensed tannin in the fruit flesh (mesocarp); V = 54, $P < 0.001$) and *Musanga cecropioides* R. Br. (Rosales: Urticaceae) (10%; V = 15, $P < 0.001$). These values are significantly different from the averages of total phenol found in fruits: 0.75 ± 1.17%; CI95% = [0.38-1.12%]; and average total tannin: 0.55 ± 1.16%; CI95% = [0.21-0.92%].

3.2. Food processing

When feeding on high tannin fruits, food processing was observed for *Canarium schweinfurthii*, *Musanga cecropioides* and *Parinari excelsa* at LuiKotale, Lomako, Wamba and Manzano. At Malebo, the three species were present in the forests but only *Musanga cecropioides* was seen to be consumed and at this site, accounted for the largest record of seeds obtained from fecal samples (present in 55% of fecal samples). At Manzano the seeds of the species were present in 69% of the feces (N = 668 feces within 257 days), which was the most represented species found in feces. Consumption of fruit pulp of *Strombosia pustulata* was neither observed for LuiKotale nor Wamba (Kano and Mulavwa, 1984), although seed consumption is reported from Lomako (Kano and Mulavwa, 1984; Badrian and Malenky, 1984) and pulp consumption with potential saliva neutralisation in Manzano. The species was not observed at Malebo and *Strombosia* sp. present at the site were only found once in the feces.

3.3. Potential salivary neutralisation

Parinari excelsa: At LuiKotale, 54 feeding sessions were observed at 27 different *P. excelsa* trees during two field seasons (June-July 2007 and June-July 2010). Fruit were within the crown or on the ground within the fruit fall zone. Fruit size was 3.6 × 4.4 cm and weight was 32.7 g (N = 10) on average. Bonobos scraped both exo- and mesocarp from the seed chewing it without swallowing by forming wadges that placed in the lower lip and squeezed allow extraction of juice and nutrients (Fig. 3). Seeds may have been too large for ingestion rendering them to endozoochory. As bonobos remained in the fruit fall zone, horizontal seed dispersal was limited, but seeds sometimes were carried for up to 50 m suggesting that bonobos are neutral or limited seed dispersers for *Parinari*.

Bonobos at Wamba, Lomako and Manzano show the same mode of food processing with forming wadges of the pulp that were discarded as were the intact seeds. No records are available from Malebo.

Musanga cecropioides: At LuiKotale, we recoded 27 feeding sessions on Musanga in 14 different trees. Bonobos ate young leaf stems, flowers and fruit. On average, the flat fruit weighs 21,36 g, has a length of 6.5 cm and a width of 3.4 cm. It contains thousands of small seeds (< 2 mm ø, N = 10). Bonobos chewed fruits for several minutes before swallowing or formed wadges that were discarded lateron. In this case, bonobos served as endozoochoric seed dispersers for *Musanga* trees.

The same type of food processing was observed at all other sites but the data are not sufficient for comparing rates of dropping versus swallowing *Musanga* wadges.

Strombosia pustulata: From February 2015 to July 2016, two occurrences of *S. pustulata* fruit consumption were observed at Manzano (August 2015 and February 2016). Bonobos were observed wadging fruits, suggesting a saliva neutralisation process, but no detailed data were collected on the process of that consumption.

3.4. Reingestion

Canarium schweinfurthii: is consumed at all sites except for Malebo where the species may be absent. At all sites, bonobos ingest the entire fruit but drop seeds prior to ingestion while the re-ingestion of seeds

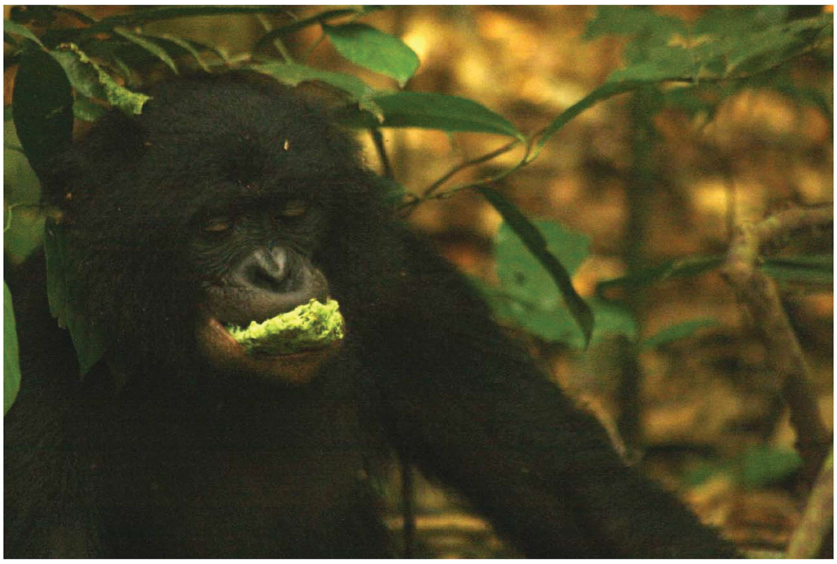

Fig. 3. Emil chewing on a wadge of *Parinari excelsa*. LuiKotale, DR Congo. D Beaune/MPI LKBP.

was only observed at LuiKotale: Here, records refer to 14 feeding sessions at 10 different *Canarium* trees. Bonobos, both adult and juvenile, extracted larger amounts of fruit from the canopy and swallowed entire fruits without biting or chewing (Avg. size: 3.4 cm long, 2.0 cm ø, avg. weight: 8.2 g, N = 10). On the next day, bonobos inspected their feces and removed entire *Canarium* fruits. Prior to re-ingestion of the pulp, bonobos removed and dropped the seeds (2.6 cm long, 1.2 cm ø, 2.2 g, N = 10). Independent juvenile bonobos did the same, similarly to all members of the observed parties. While two different infants observed their mothers when they held and checked their own feces, they did the same only during these events and without waiting 24 h prior to *Canarium* fruit ingestion. After this second ingestion of the fruit (mesocarp only), the remaining and still intact seeds of *C. schweinfurthii* were dispersed (with a maximum dispersal distance recorded of 1947 m from the parent tree). Accordingly, bonobos at LuiKotale were endozoochoric partners of *C. schweinfurthii*.

Bonobos at Lomako and Wamba removed the pulp around the seeds and, depending on the stage of ripeness, chewed and ingested the pulp or, if unripe, discarded it without any oral processing. After the ingestion of pulp, they either dropped the seeds or swallowed them. Therefore, they were occasionally endozoochoric and had limited horizontal dispersal. However, process described for LK was observed several times.

Food processing at Manzano resembled that observed at Wamba and Lomako except that bonobos tended to eat unripe fruit of *C. schweinfurthii*. In 668 dung samples, no seeds and/or fruits of this species were detected.

At Malebo, no observation of food processing was observed.

4. Discussion

Hominoid primates such as bonobos are adapted to consume fruit with tannins. Indeed, several communities of bonobos regularly consumed fruiting species having levels of condensed tannins significantly higher than other fruit of the forest. While the chemical defense of the pulp of the different fruit species may be sufficient to prevent other consumers that destroy seeds or act as neutral seed dispersers, bonobos seemed to cope with fruit such as *Canarium schweinfurthii*¸ *Parinari excelsa*, and *Musanga cecropioides* containing tannins in relatively high concentrations. Given the mode of food processing, extensive salivary exposure may neutralize the deleterious effects of tannins. Differences across plant species exist in terms of seed dispersal effectiveness. While certain bonobo populations appear to avoid *S. pustulata* (not recorded for Lomako and Malebo) or remove seeds of *P. excelsa* prior to ingestion, they are considered to be efficient endozoochoric partners for *M. cecropioides* and, at least locally, for *C. schweinfurthii* (LuiKotale). By spiting the seeds of species such as *P. excelsa* the seed dispersal induced by bonobos in the fruit fall zone can be deleterious for seeds of *P. excelsa*, due to the negative density dependent effect and the predation by bush pigs (Beaune et al., 2012b; Beaune et al., 2012c). In contrast, seeds embedded in feces and dispersed by endozoochory (*Musanga cecropioides*) escape seed predators and may benefit from the actions of dung beetles (Beaune et al., 2012a).

This report highlights subtle population differences in terms of dietary composition, food processing of one species (*C. schweinfurthii*), and by inference, the consumers' tolerance towards tannin content across the five sites that contributed data to this study (LuiKotale, Wamba, Lomako, Malebo and Manzano). As a consequence, bonobos at the different sites vary with regard to their seed dispersal services provided to specific food trees, albeit at a modest scale. Dispersal of *C. schweinfurthii* depends on large frugivorous birds such as hornbills (White and Abernethy, 1997) but is also dispersed by bonobos at LuiKotale. Since dispersal distances and seed dispersal effectiveness are different between birds and apes (Whitney et al., 1998; Holbrook et al., 2002; Poulsen et al., 2002; Beaune et al, 2013c), this bonobo effect should impact gene flow, population biology and structure of *C. schweinfurthii* comparatively to Wamba, Lomako, Manzano and Malebo.

4.1. *The Canarium handling technique and coprophagy*

At the study sites, coprophagy was linked to food plants such as *Dialium* sp. (e.g. at LuiKotale, Lomako, Wamba and Manzano) or *Placodiscus pynaertii* (at LuiKotale). At LuiKotale, coprophagy with reingestion of mesocarp was observed for *Canarium*. While coprophagy and seed reingestion has been reported from wild gorillas and chimpanzees (Krief et al., 2004; Bertolani and Pruetz, 2011; Payne et al., 2008; Krief et al., 2006; Harcourt and Stewart, 1978; Kuroda et al., 1996), this report is the first one on a more complex interaction between plants and consumers were seeds and pulp are separated after they have passed the digestive tract. Given the high concentration of tannins in the fruit of *Canarium*, the ingestion of the entire fruit could be seen as a strategy combining minimal food processing with decreased passage time when tannin activity is high. Once tannins are neutralised, separation of seeds and reingestion of pulp may optimize nutrient absorption by the consumer. As a side-effect, germination of plant seeds may be enhanced, indicating a mutualistic relation between bonobos and *Canarium*. Corresponding observations have been reported from chimpanzees and it was suggested that the first gut passage serves to reduce the mechanical resistance to digestion of *Canarium* fruit (Krief et al., 2006; Bertolani and Pruetz, 2011) which does not exclude the possibility of neutralising tannin activity. Measures of physical resistance and tannin content before and after gut passage would be required to explore the effect of gut passage in more detail. Another interesting question is the emergence of such behaviour. While *Canarium* consumption was reported from all populations reported here, only one practiced reingestion and seed removal. At this stage, we cannot exclude that reingestion behavior is practiced by bonobos of other populations but the fact that it is absent in all other populations contributing to our data set indicates that it is not a common behavior. More detailed inter-site comparisons on forest composition, diet, and modes of food processing will illuminate the extent of behavioral diversity, their functional significance, and modes of transmission.

At LuiKotale, bonobos probably found a remarkable handling technique to process and extract food problematic for its tannin or simply too hard. This indicates that bonobos are able to anticipate, eating a fruit for which digestion will be delayed, which potentially requires prospects and by that cognition. This undigested food encumbers the bolus and is a clear trade-off (*i.e.* bad meal today for a better tomorrow). With prospective ability, they should ‘remember’ the next day to check the feces containing ‘appetizing’ food from the day before. This holding process of *Canarium* fruits is the first case described in *Pan paniscus* in one out of five study sites and requires promising investigations in future.

5. Conclusions

In this study, we show that bonobos 1) can consume fruit with particularly high tannin content (*C. schweinfurthii)*. 2) show different strategies to cope with tannins such as chewing the pulp to neutralise the tannin with saliva (*P. excelsa*, *M. cecropioides*) or applying peculiar handling techniques such as reingestion (*C. schweinfurthii*). 3) are differential efficient seed dispersers for some of these fruiting species depending of the bonobo community. Reingestion behavior is an interesting candidate to investigate cultural differences in food processing and cognitive abilities in wild bonobos.

.

Acknowledgements

We thank the Institut Congolais pour la Conservation de la Nature (ICCN) for granting permission to conduct research in all the sites, and Lompole villagers for granting permission to access the forest of their ancestors at LuiKotale. Research at LuiKotale was conducted under the auspices and with the financial support of the Max-Planck-Society, the German Ministry of Education and Research, le conseil regional de Bourgogne, the Société Française d'Écologie and Société Francophone De Primatologie). We thank all the international and local staff, field assistant of all the field sites and Mbou-Mon-Tour, and two anonymous reviewers for their valuable comments and suggestions.

References

Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour 49 (3), 227 267.

Badrian, N., Malenky, R., 1984. ‘Feeding ecology of Pan paniscus in the Lomako forest, Zaire'. In: Susman, R.L. (Ed.), The Pygmy Chimpanzee: Evolutionary Biology and Behavior. Plenum Press, New York, pp. 275 299.

Barboza, P.S., Bennett, A., Lignot, H.J., Mackie, R.I., McWhorter, T.J., Secor, S.M., Skovgaard, N., Sundset, M.A., Wang, T., 2010. Digestive challnages for vertebrate animals: microbial diversity, cardiorespiratory coupling, and dietary specialization. Phys. Biochem. Zool. 83, 764 774.

Beaune, D., Bollache, L., Bretagnolle, F., Fruth, B., 2012a. Dung beetles are critical in preventing post-dispersal seed removal by rodents in Congo rain forest. J. Trop. Ecol. 28, 507 510.

Beaune, D., Bollache, L., Fruth, B., Bretagnolle, F., 2012b. Bush pig (Potamochoerus porcus) seed predation of bush mango (Irvingia gabonensis) and other plant species in Democratic Republic of Congo. Afr. J. Ecol. 50 (4), 509 512.

Beaune, D., Bollache, L., Fruth, B., Hohmann, G., Bretagnolle, F., 2012c. Density-dependent effect affecting elephant-seed dispersed tree recruitment (*Irvingia gabonensis*) in Congo forest. Pachyderm 52, 97 100.

Beaune, D., Bretagnolle, F., Bollache, L., Bourson, C., Hohmann, G., Fruth, B., 2013a. Ecological services performed by the bonobo (Pan paniscus): seed dispersal effectiveness in tropical forest. J. Trop. Ecol. 29 (05), 367 380.

Beaune, D., Bretagnolle, F., Bollache, L., Hohmann, G., Surbeck, M., Bourson, C., Fruth, B., 2013b. The Bonobo Dialium positive interactions: seed dispersal mutualism. Am. J. Primatol. 75 (4), 394 403.

Beaune, D., Bretagnolle, F., Bollache, L., Hohmann, G., Surbeck, M., Fruth, B., 2013c. Seed dispersal strategies and the threat of defaunation in a Congo forest. Biodivers. Conserv. 22 (1), 225 238.

Beaune, D., Bretagnolle, F., Bollache, L., Hohmann, G., Fruth, B., 2015. Can fruiting plants control animal behaviour and seed dispersal distance? Behaviour 152 (3 4), 359 374.

Beaune, D., 2015. What would happen to the trees and lianas if apes disappeared? Oryx 49 (03), 442 446.

Bertolani, P., Pruetz, J.D., 2011. Seed reingestion in savannah chimpanzees (Pan troglodytes verus) at Fongoli, Senegal. Intl. J. Primatol. 32 (5), 1123 1132.

Cipollini, M.L., Levey, D.J., 1997. Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. Am. Nat. 150 (3), 346 372.

Clauss, M., 2003. Tannins in the nutrition of wild animals: a review. In: In: Fidgett, A., Clauss, M., Ganslosser, U., Hatt, J.M., Nijboer, J. (Eds.), Zoo Animal Nutrition Vol. II. Filander Verlag, Furth, Germany, pp. 51 87.

Cooper, S.M., Owen-Smith, N., 1985. Condensed tannins deter feeding by browsing ruminants in a South African savanna. Oecologia 67 (1), 142 146.

Dominy, N.J., Lucas, P.W., Osorio, D., Yamashita, N., 2001. The sensory ecology of primate food perception. Evol. Anthropol. 10 (5), 171 186.

Eriksson, J., Hohmann, G., Boesch, C., Vigilant, L., 2004. Rivers influence the population genetic structure of bonobos (Pan paniscus). Mol. Ecol. 13 (11), 3425 3435.

Furuichi, T., Mulavwa, M., Yangozene, K., Yamba-Yamba, M., Motema-Salo, B., Idani, G.i., Ihobe, H., Hashimoto, C., Tashiro, Y., Mwanza, N., 2008. Relationships among fruit abundance, ranging rate, and party size and composition of bonobos at Wamba. The bonobos. In: Furuichi, T., Thompson, J. (Eds.), Developments in Primatology: Progress and Prospects. Springer, New York, pp. 135 149.

Glander, K.E., 1982. The impact of plant secondary compounds on primate feeding behavior. Am. J. Phys. Anthropol. 25 (S3), 1 18.

Harcourt, A.H., Stewart, K.J., 1978. Coprophagy by wild mountain gorilla. Afr. J. Ecol. 16 (3), 223 225.

Hawe, J.E., Peres, C.A., 2014. Ecological correlates of trophic status and frugivory in neotropical primates. Oikos 123, 365 377.

Hohmann, G., Fruth, B., 2003. Lui Kotal − A new site for field research on bonobos in the Salonga National Park. Pan Afr. News 10, 25 27.

Hohmann, G., Fowler, A., Sommer, V., Ortmann, S., 2006. Frugivory and gregariousness of Salonga bonobos and Gashaka chimpanzees: the influence of abundance and nutritional quality of fruit. In: Hohmann, G., Robbins, M., Boesch, C. (Eds.), Feeding Ecology in Apes and Other Primates. Cambridge University Press, Cambridge, pp. 123 159.

Hohmann, G., Potts, K., N'Guessan, A., Fowler, A., Mundry, R., Ganzhorn, J.U., Ortmann, S., 2010. Plant foods consumed by Pan: exploring the variation of nutritional ecology across Africa. Am. J. Phys. Anthropol. 141 (3), 476 485.

Holbrook, K.M., Smith, T.B., Hardesty, B.D., 2002. Implications of long-distance movements of frugivorous rain forest hornbills. Ecography 25 (6), 745 749.

Idani, G., 1986. Seed dispersal by pygmy chimpanzees (Pan paniscus): a preliminary report. Primates 27 (4), 441 447.

Johns, T., 1999. The chemical ecology of human ingestive behaviors. Annu. Rev. Anthropol. 27 50.

Kano, T., Mulavwa, M., 1984. Feeding ecology of the pygmy chimpanzees (*Pan paniscus*) of Wamba. In: Susman, R.L. (Ed.), The Pygmy Chimpanzee: Evolutionary Biology and Behavior. Plenum Press, New York, pp. 435.

Krief, S., Jamart, A., Hladik, C.M., 2004. On the possible adaptive value of coprophagy in free-ranging chimpanzees. Primates 45 (2), 141 145.

Krief, S., Wrangham, R.W., Lestel, D., 2006. Diversity of items of low nutritional value ingested by chimpanzees from Kanyawara, Kibale National Park, Uganda : an example of the etho-ethnology of chimpanzees. Social Sci. Inf. 45 (2), 227 263.

Kuroda, S., Nishihara, T., Suzuki, S., Oko, R.A., 1996. Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. Great Ape Societies 71 81.

Lambert, J.E., 1998. Primate digestion: interactions among anatomy, physiology, and feeding ecology. Evol. Anthropol.: Issues, News, Rev. 7 (1), 8 20.

Levey, D., Tewksbury, J., Cipollini, M., Carlo, T., 2006. A field test of the directed deterrence hypothesis in two species of wild chili. Oecologia 150 (1), 61 68.

McKey, D.B., Gartlan, J.S., Waterman, P.G., Choo, G.M., 1981. Food selection by black colobus monkeys (Colobus satanas) in relation to plant chemistry. Biol. J. Linn. Soc. 16 (2), 115 146.

Milton, K., 2003. The critical role played by animla source foods in Humna (*Homo*) evolution. J. Nutr. 133, 3886S 3892S.

Narat, V., Pennec, F., Ledo-Bisson, L., Bokika Ngawolo, J.C., Dumez, R., Krief, S., 2015a. Bonobo conservation as a means for local development: an innovative local initiative of community-based conservation in Democratic Republic of Congo. J. Primatol. 4 (2).

Narat, V., Pennec, F., Simmen, B., Ngawolo, J.C.B., Krief, S., 2015b. Bonobo habituation in a forest savanna mosaic habitat: influence of ape species, habitat type, and sociocultural context. Primates 56 (4), 339 349.

Oates, J.F., Swain, T., Zantovska, J., 1977. Secondary compounds and food selection by colobus monkeys. Biochem. Syst. Ecol. 5 (4), 317 321.

Omnes, M.H., Le Goasduff, J., Le Delliou, H., Le Bayon, N., Quazuguel, P., Robin, J.H., 2017. Effects of dietary tannin on growth, feed utilization and digestibility, and carcass composition in juvenile European seabass (Dicentrarchus labrax L.). Aquat. Rep. 6, 21 27.

Osorio, D., Vorobyev, M., 1996. Colour vision as an adaptation to frugivory in primates. Proc. R. Soc. Lond. 263, 593 599.

Payne, C., Webster, T., Hunt, K., 2008. Coprophagy by the semi-habituated chimpanzees of Semliki, Uganda. Pan Afr. News 15, 29 32.

Poulsen, J.R., Clark, C.J., Connor, E.F., Smith, T.B., 2002. Differential resource use by primates and hornbills: implications for seed dispersal. Ecology 83 (1), 228 240.

Robbins, C.T., Hagerman, A.E., Austin, P.J., McArthur, C., Hanley, T.A., 1991. Variation in mammalian physiological responses to a condensed tannin and its ecological implications. J. Mammal. 72 (3), 480 486.

Schupp, E.W., Jordano, P., Gomez, J.M., 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytol. 188 (2), 333 353.

Scott, J.E., 2011. Folivory, frugivory, and postcanine size in the Cercopithecoidea revisited. Am. J. Phys. Anthro. 146, 20 27.

Serckx, A., Kühl, H.S., Beudels-Jamar, R.C., Poncin, P., Bastin, J.F., Huynen, M.C., 2015. Feeding ecology of bonobos living in forest-savannah mosaics: diet seasonal variation and importance of fallback foods. Am. J. Primatol. 77 (9) (pp. American journal of primatology).

Tsuji, Y., Yangozene, K., Sakamaki, T., 2010. Estimation of seed dispersal distance by the bonobo, Pan paniscus, in a tropical forest in Democratic Republic of Congo. J. Trop. Ecol. 26, 115 118.

White, L., Abernethy, K., 1997. A Guide to the Vegetation of the Lope Reserve Gabon. Wildlife Conservation Society, New York.

Whitney, K.D., Fogiel, M.K., Lamperti, A.M., Holbrook, K.M., Stauffer, D.J., Hardesty, B.D., Parker, V.T., Smith, T.B., 1998. Seed dispersal by ceratogymna hornbills in the dja reserve, Cameroon. J. Trop. Ecol. 14, 351 371.

Wrangham, R., Waterman, P., 1981. Feeding behaviour of vervet monkeys on Acacia tortilis and Acacia xanthophloea: with special reference to reproductive strategies and tannin production. J. Anim. Ecol. 715 731.