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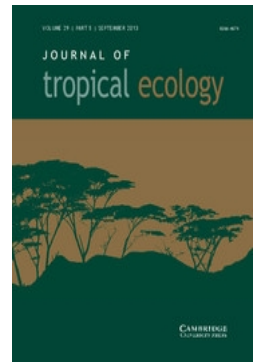
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Ecological services performed by the bonobo (*Pan paniscus*): seed dispersal effectiveness in tropical forest

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Abstract: Survival of Afrotropical primary forests depends not only on habitat protection but also on the protection of animal species such as frugivorous primates, recognized as the most important seed dispersers for many plants. Here we investigate seed-dispersal services by the bonobo (*Pan paniscus*) in an evergreen lowland tropical rain forest of the Congo Basin. In the long-term research site of LuiKotale, we investigated food habits and seed processing based on 22 mo of behavioural observation, seed trial experiment and long-term daily GPS tracking of a habituated ape community. Bonobos were mainly frugivores (66% of all feeding sessions), spending about 3.5 h d⁻¹ swallowing seeds that were transported for an average of 24 h in the gut. On average, an individual bonobo dispersed 172 kg y⁻¹ of seeds (or 220 000 seeds y⁻¹) of more than 91 plant species by endozoochory over an average distance of 1.2 km from the parent tree. Passed seeds germinated more rapidly, more successfully and had greater post-dispersal survival than unpassed seeds. Bonobo-dispersed plants accounted for 40% of tree species and 65% of individual trees in the study site (12 1-ha plots census). Since bonobos show little functional overlap with other frugivores, the loss of their seed-dispersal services is likely to affect forest structure and dynamics. Our results justify description of the threatened bonobo as a gardener of the Congo forest.

Key Words: Africa, Congo basin, forest ecology, long-distance dispersal, seed dispersal, seed rain, seed shadow, zoochory

INTRODUCTION

In tropical forests, frugivore species are embedded in a complex plant–animal network that strongly influences composition, diversity and structure of plant species communities. From 70% to more than 90% of woody species rely on animals for seed dispersal (Beaune *et al.* 2013a, Gautier-Hion *et al.* 1985, Janson 1983, Jordano 2000, Muller-Landau 2007, Wright *et al.* 2007). Frequently, many frugivore species interact with one woody plant species but the disperser species differ in their effectiveness, i.e. the ‘number of new adults produced by the dispersal activities of a disperser’ (Schupp 1993). The seed-dispersal effectiveness (SDE) is affected by the

number of seeds dispersed (quantity) and the quality of dispersal, i.e. the probability that a dispersed seed produces a new adult (Schupp *et al.* 2010). The quality of dispersal is strongly influenced by the treatment of the seed during the feeding/digestion process and by the quality of seed deposition including dispersal distance. Many characteristics of the frugivore such as its feeding behaviour and physiology, its diet, and its spatial movement, may influence SDE (Schupp *et al.* 2010). Among frugivores, large-bodied mammals are considered as major seed dispersers because of their diet diversity (tens to hundreds of species), the large quantities of dispersed seeds, and because of their capacities to feed on large fruits or large seeds (Vidal *et al.* 2013). In particular, plants producing large seeds depend on large-bodied vertebrates for their dispersal and regeneration (Poulsen *et al.* 2001, Vanthomme *et al.* 2010, Vidal *et al.* 2013, Wright *et al.* 2007). Large mammals are also involved in long-distance dispersal (LDD) that influences survival and

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genetic patterns of plant species, with an ultimate effect on forest structure (Bohrer *et al.* 2005). However, animals are extracted from African tropical forests at about six times the sustainable rate (Fa *et al.* 2005). This 'bushmeat crisis' generates myriads of cascading effects on the mutualistic tree-disperser network that will critically affect the Central African forest ecosystems (Brodie *et al.* 2009, Fa *et al.* 2005, Milner-Gulland & Bennett 2003, Muller-Landau 2007). The plight of vertebrate communities generates an obvious modification of the spatio-temporal dynamics of seedling diversity in the forest regeneration and this worldwide process is termed 'defaunation syndrome' (Howe & Miriti 2004, Redford 1992, Wright *et al.* 2007). The great ape species of the African forests (chimpanzee, bonobo and gorilla) are considered as key dispersers of woody species but little is known concerning the relationship between the diversity of their fruit diet and SDE (Chapman & Onderdonk 1998, Effiom *et al.* 2013, Gross-Kamp & Kaplin 2011, Voysey *et al.* 1999, Wrangham *et al.* 1994). However, this information is important in order to assess whether or not the dispersal service provided by these species could be compensated for, at least partially, by other frugivore species (Effiom *et al.* 2013).

In the present study, we investigate fruit consumption of one bonobo community in order to assess SDE. First, we estimate the dispersal curve/kernel (the function that describes the probability of dispersal to different distances from the source, Nathan & Muller-Landau 2000). Second, we assess the ecological importance of bonobos in the ecosystem by investigating the plant community's diversity, abundance and ability to recruit without seed dispersal. Third, we compare seed rain resulting from dispersal by bonobos with that produced by other seed dispersers by reviewing the literature. We hypothesize that several plant species are adapted to endozoochory through the bonobo gut and that these passed seeds germinate better than do unpassed seeds.

MATERIALS AND METHODS

Study site and species

Least is known for the bonobo (*Pan paniscus* Schwarz 1929), the last of the three African great ape species (family Hominidae) discovered. It is endemic in the Democratic Republic of Congo (DRC) and lives south of the Congo River. More than 50% of the diet of the bonobo is fruit, characterizing the bonobo as an important fruit consumer, but little is known about its role in seed dispersal (Beaune 2012, Idani 1986, Tsuji *et al.* 2010). The role of this species as seed disperser is of particular interest due to its critical conservation status (Hart *et al.*

2008). Population estimates of this threatened species currently fluctuate between 15 000 and 20 000 animals (Fruth *et al.* 2013).

Fieldwork took place between September 2009 and June 2011 at the research site LuiKotale (LK) (2°47'S–20°21'E), located at the south-western fringe of Salonga National Park, Democratic Republic of Congo (DRC) (Hohmann & Fruth 2003). The study site consists of > 100 km² of primary evergreen lowland tropical rain forest (for details see Beaune *et al.* 2013a, 2013b, 2013c; Fruth 2011). Studies of the members of the *Bompusa bonobo* community are ongoing since 2002. The community consists of 33–35 mature individuals inhabiting a home-range of about 40 km². They are fully habituated to human observation since 2007. Bonobos are individually known by physical traits such as limb deficiencies, form, structure and colouration of genitals and face. The study group is free ranging; all methods of data-collection are non-invasive. Researchers did not constrain, contact or interact with their study subjects. Animal welfare had greater priority than 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, and adhere to the legal requirements of the host country, the Democratic Republic of Congo.

Bonobo feeding behaviour

From September 2009 to June 2011, behavioural data were recorded for bonobos over 22 mo, corresponding to 1879 h of observations over 315 d. Bonobos live in a fission–fusion society in which, depending on season and time of day, the community splits up into smaller foraging subgroups called parties. As parties are largely cohesive (most animals conducting the same activities at the same time), we considered group activity to be that of the majority (> 50% of the bonobos) of the visible animals during a continuous record of feeding activities (i.e. continuous focal sub-group; Altmann 1974, Beaune *et al.* 2013c). The continuous record stopped when the group went out of view or contact was lost. In order to record the part of feeding sessions (starting with the first hand-to-mouth movement, stopping with another behaviour) in daily activities and among feeding sessions we analysed interactions with consumed plants (i.e. granivory, herbivory, frugivory with positive or neutral seed-dispersal effect). We recorded the duration of the feeding session, the item consumed and seed processing such as spitting, handling and swallowing. Food items were classified into five categories: (1) fruits (including either the whole fruit ingested with its seeds or the pulp without its seeds), (2) leaves/stem/bark/gum, (3) seeds,

(4) animals and (5) other items (honey, mushrooms, soil).

Dispersal distance

Actual bonobo dispersal distances were calculated from direct observations. Whenever possible, bonobos were followed daily from nest to nest (c. 05h30–17h30). Daily travel routes of parties were tracked with a GPS (Garmin® 60CSX) using one point position every 5 min for georeferencing. Whenever an individual bonobo swallowed the fruit of a species not eaten in the previous 36 h, its seed was considered as a marker seed and the individual was monitored continuously (but not at night) until the seeds of the newly ingested species were found in its faeces. The straight-line dispersal distance was calculated with GPS positions from the parent tree to the georeferenced seed deposition. When several bonobos of the group had ingested new marker seeds, only one random individual was included in the dispersal model to avoid bias in the dispersal distance, while all were included in the calculation of transit time. We estimated the dispersal curve/kernel using a mechanistic model based on empirical movement georeferenced with a mean transit time of 24 h for free-ranging bonobos (Beaune *et al.* 2013c, Nathan & Muller-Landau 2000). This curve is frequently used as a quantitative descriptor of seed dispersal in plants because it combines information on movements (distances, positions) and gut passage time.

Plants ingested

Plants ingested by bonobos were identified by vernacular name and determined post hoc with data from the herbarium collection of the long-term project The Cuvette Centrale as Reservoir of Medicinal Plants, consisting of 7300 vouchers by May 2010 (Fruth 2011). If unknown, samples were recorded as NID (non-identified), and collected for later species identification. All feeding plants (trees, lianas and shrubs) were marked. Plant species were considered as dispersed by endozoochory when seeds were observed to be swallowed and defecated intact. Such cases were classified as frugivory with seed-dispersal mutualism and constituted our list of bonobo-dispersed species. Seeds that were not ingested but spat out in place without primary horizontal dispersal we classified as frugivory without endozoochory. Bonobo-dispersed plant species of the LK community were compared with those of communities from Wamba (Kano & Mulavwa 1984) and Lomako (Badrian & Malenky 1984), the two long-term field sites for bonobo research, to assess cross-site similarities.

Representation of bonobo-dispersed trees

To assess the impact of bonobo seed dispersal on the forest tree community, we calculated both relative diversity and abundance of bonobo-dispersed species (effectively dispersed as determined in the other paragraphs) within 12 plots set up in heterogeneous primary forest on terra firme soil. Plots were positioned randomly within the home range of the bonobo community. From February to June 2011 all trees > 10 cm dbh were censused in these 12 plots of 1 ha (100 × 100 m) each. Relative diversity was calculated as the number of species within the plot observed at least once to be effectively dispersed by bonobos, divided by the total number of species found in the plot. Relative abundance was calculated as the total number of individual trees of all species dispersed by bonobos, divided by the total number of trees in the plot.

Seed dispersal/viability/germination/survivorship

Bonobo faeces were collected at the study site between April 2002 and June 2011 (N = 1152). Faeces and seeds therein were weighed (fresh mass); the number of seeds per faeces was counted for each species. To test germination viability of seeds that passed the bonobo digestive tracts, we extracted seeds from faeces collected between January 2010 and June 2011. Seeds were packed in leaves of *Haumania* spp. and deposited in a nursery within the same day. The nursery was an elevated platform (height 170 cm) *in situ* under natural canopy cover. It was 200 cm long × 100 cm wide, filled with natural soil (6 cm deep), and secured with predator-proof table legs. Each seed was marked and observed daily. We recorded emergence of the radicle (germination) (Beaune *et al.* 2013d) and viability ratio (proportion of seeds that germinated).

To assess the influence of either seed manipulation or ingestion on germination, we compared the germination percentage of seeds collected on the same parental tree submitted to three different treatments mimicking three dispersal modes: (1) by barochory (seed embedded in its pericarp (fruit)); (2) by seed-spitting zoochory (seed with pericarp removed); and (3) by swallowing endozoochory (seeds collected after gut transit on bonobo). When bonobo were observed to ingest a new species, some fruits were directly collected from the parent tree and submitted to barochory and seed-spitting zoochory treatments. Ingested seeds (swallowing zoochory) were collected the next day in the faeces from identified bonobos. Seeds were marked, alternately positioned in line in the nursery platform (mixing local effects) the evening of collection (D_0), and monitored daily until they rot or germinate.

To assess actual viability and recruitment of seeds embedded in bonobo faeces *in situ*, 45 faeces defecated

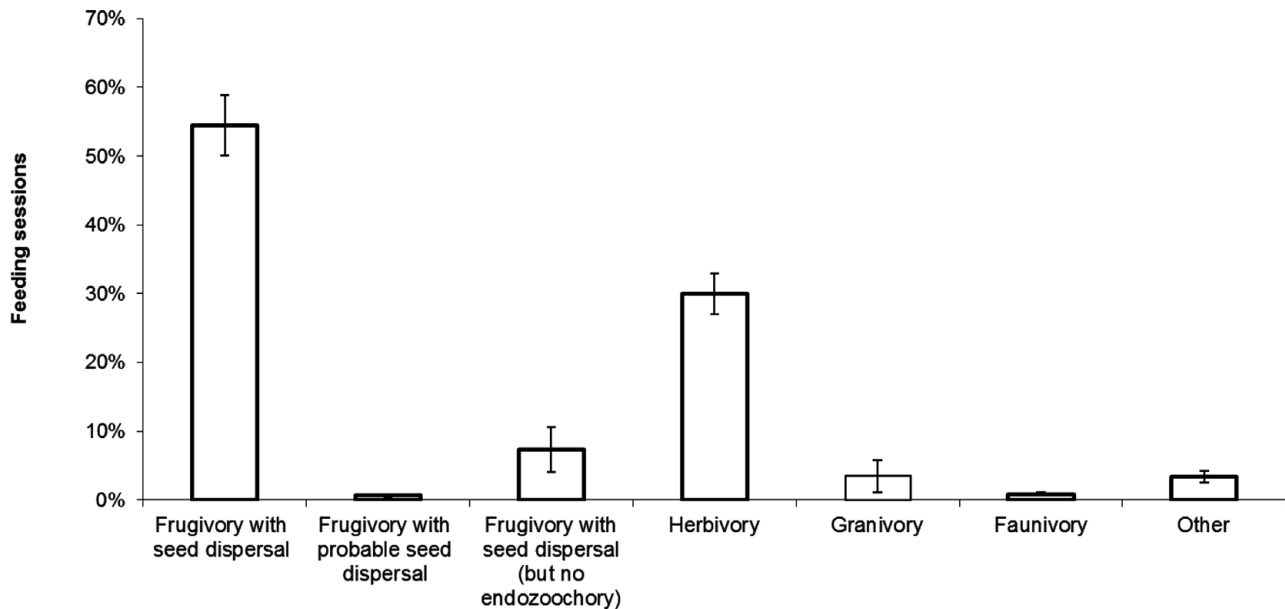


Figure 1. Percentage of each bonobo interaction (herbivory, faunivory, frugivory including seed dispersal service, etc.) during the feeding sessions (22 mo; 1879 h of continuous group scans); Error bars indicate SE. Other = honey, mushrooms, soil and unknown. Location is LuiKotale, DRC.

between January 2010 and May 2011 (and not collected for the above experiments) were monitored from 1 to 18 mo. Seed species composition was determined by visual inspection of the dung. Seedling recruits were counted once a week.

Seed rain

The daily seed rain dispersed by bonobos was calculated according to Poulsen *et al.* (2001):

Seed rain = number of seed deposited per faecal clump × defecation rate × bonobo density

Population density was taken from Mohnke & Fruth (2008) where it was calculated to be 0.73 bonobos km⁻². Defecation rate was calculated on the basis of defecation records deriving from continuous follows of individual bonobos, resulting in an average number of dung piles per individual per day. The number of seeds deposited was calculated as the average of seeds found from dung piles collected (N = 157). Influences of sex and age (adult, sub-adult) were tested with analyses of variance (ANOVA), with factors considered as fixed effects.

Functional overlap – the primate community

In addition to the bonobo, 41 other species of frugivorous vertebrates were recorded in LuiKotale, including birds, fruit bats, civets, monkeys and others (Beaune *et al.* 2013a). We assessed seed handling and overlap in food-plant species among seven species of the diurnal

primate community of LK from February to June 2011. Observations were simultaneously performed by two teams (one observing bonobos, the other monkeys). In contrast to bonobos, monkeys were not habituated (Bourson 2011). Feeding and seed handling were assessed by the above-mentioned protocol. The functional overlap was calculated using the Jaccard similarity coefficient (Real & Vargas 1996).

RESULTS

Bonobo food identified and quantified

A total of 133 plant species were recorded in the bonobo diet during the 22-mo study period (Appendices 1 and 2). Of these, 107 species (80%) had fruit ingested by bonobos. Feeding behaviour represented 992 h of continuous records (from 1879 h of observation). The bonobo group spent (mean ± SE) 52.8% ± 1.1% of its daily activity engaged in feeding sessions. During the 315 d with an average observation time of 6 h d⁻¹ (without difference between morning and afternoon data), we observed 4129 feeding sessions. We recorded fruits of 91 species being ingested with their seeds being swallowed. These species belonged to 45 genera of 25 plant families. Seeds of 56 of these species were found intact in faeces, confirming endozoochory.

Of these feeding sessions, 54.5% ± 4.4% included the ingestion of fruit with subsequent seed dispersal (i.e. frugivory with seed ingestion and deposition observed, Figure 1), 0.6% ± 0.2% included the ingestion of fruit but

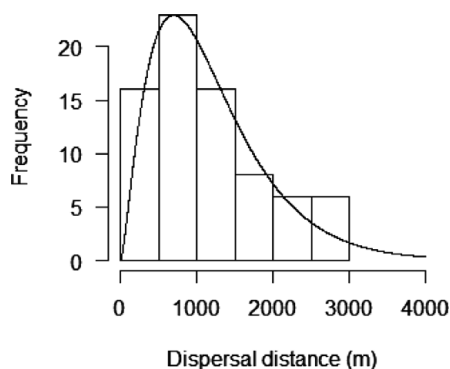


Figure 2. Dispersal-distance kernel induced by bonobos in LuiKotale, DRC (N = 75 dispersal events of 12 different plant species recorded).

deposition of seeds was not confirmed (insufficient data) and $7.3\% \pm 3.0\%$ consisted of the ingestion of fruit but with large seeds that were not swallowed (e.g. *Mammea africana* with average seed size = 62 ± 1 mm, *Anonidium mannii* = 42 ± 2 mm, *Irvingia gabonensis* 55 ± 2 mm) (for each of these species measured, $N \geq 10$). Transport of these large seeds over distances of about 100 m by hand or mouth (max = 426 m) were opportunistically observed. Ingestion of food other than fruit such as leaves, terrestrial herbaceous vegetation, flowers, stems and bark consisted of $30.0\% \pm 3.3\%$ of the feeding sessions. The remainder could be attributed to granivory ($3.4\% \pm 2.4\%$), carnivory (squirrels, monkeys: *Procolobus tholloni*, bird chicks, duikers: *Cephalophus* spp.) ($0.9\% \pm 0.2\%$) and other foods (honey, termite soil, digging session for truffles and probably insect larvae, etc.) ($3.3\% \pm 0.9\%$).

Dispersal distance

To assess the dispersal distance of seeds, we used georeferenced records of 75 events from 12 different plant species, when observation was continuous from first ingestion to first defecation. The average distance of dispersal from the parent tree was 1183 ± 88 m ($CI_{95\%} = 1007\text{--}1358$ m); range = 0–2995 m, Figure 2). The resulting dispersal distance kernel is a probability density function, characterized by a unimodal leptokurtic distribution, with a fat-tailed dispersal kernel (right skewness = 0.63; kurtosis = 2.61). Bonobos disperse seeds over long distances, with 93.3% of the dispersal events longer than 100 m.

Seed viability/survivorship

Of the 56 species whose seeds were observed to be swallowed and defecated intact, seeds of 35 species were submitted to a viability census in the nursery (it was not possible to bring samples of the other 21 species due to

field conditions). Of these, 97% were viable, that is, we were able to observe emergence of the radicle (n.b. for the ungerminated species only five seeds of *Momordica foetida* were monitored) (Appendix 1).

In order to assess the influence of seed manipulation on germination, we first compared manipulated but unpassed seeds and unmanipulated seeds. Overall germination percentage was higher for manipulated than for unmanipulated seeds, although differences were significant for only four out of seven species with sufficient sample size ($P < 0.001$; power analyses = 100%) (Figure 3a).

Second we compared germination percentage of passed seeds and unpassed but manipulated seeds. Overall germination percentage was higher for passed (swallowing endozoochory) than for unpassed seeds (seed-spitting zoochory). Differences were significant for only four out of eight species with sufficient sample size ($P < 0.05$; power analyses $\geq 99\%$) (Figure 3b).

To assess the viability of seeds *in situ*, a total of 45 bonobo faeces (defecated from January 2010 to May 2011 and not collected for the above experiments) was localized, marked and monitored. Each dung pile was monitored for 1–18 mo. Of all these dung piles, $67\% \pm 8\%$ produced seedlings ($CI_{95\%} = 53\text{--}81\%$). Overall, we identified seedlings of eight genera. We think it highly likely that faeces continued to yield seedlings after monitoring ceased (the shorter monitoring of a dung lasting 1 mo). In an unpublished experiment we found the following T_{50} values (time when 50% of the seedlings germinated) for seeds passed in bonobo: *Zeyherella longepedicellata*, 50 d; *Diospyros* sp., 7 d; *Guarea laurentii*, 20 d; *Garcinia* sp., 63 d; *Manilkara yangambiensis*, 44 d.

Diversity and abundance of trees dispersed by bonobos

Focusing on trees only, we found 5233 adults in the 12 1-ha plots. A total of $40.1\% \pm 0.8\%$ of these tree species in these plots are dispersed by bonobos via endozoochory through the gut (Figure 4). These account for a total of $64.7\% \pm 1.3\%$ of all tree individuals recorded in these plots. Abundance of endozoochorous species is not equally distributed. A few species only account for the majority of individuals, such as *Greenwayodendron suaveolens* and *Dialium* spp., which together account for 32% of individual trees.

Seed rain

To assess defecation interval, we observed 16 mature individuals, five males and 11 females. A total of 74 defecations were recorded (1 May 2010–31 May 2011), resulting in an average of 7.55 dung piles between dawn

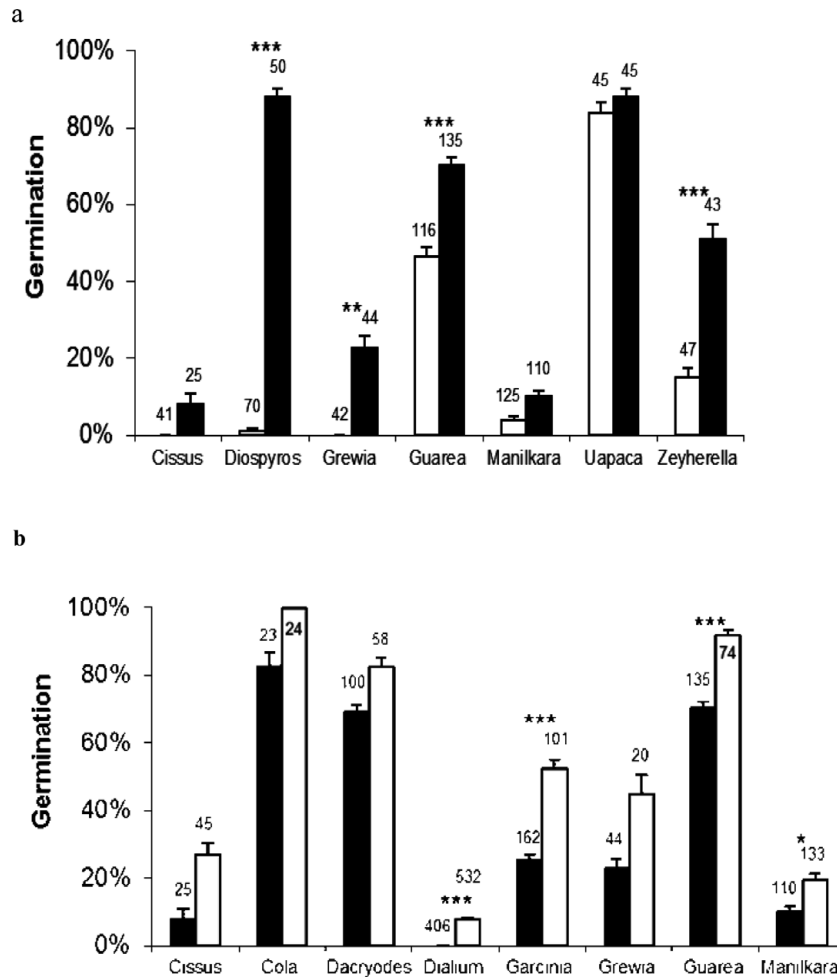


Figure 3. Germination percentage of seven species (a) (*Cissus dinklagei*, *Diospyros* sp., *Grewia* sp., *Guarea laurentii*, *Manilkara yangambiensis*, *Uapaca* sp., *Zeyherella longepedunculata*) with (white) and without fruit (black bars) and germination percentage of eight species (b) (*Cissus dinklagei*, *Cola gigantea*, *Dacryodes yangambiensis*, *Dialium corbisieri*, *Garcinia ovalifolia*, *Grewia* sp., *Guarea laurentii*, *Manilkara yangambiensis*) comparing passed through bonobos (white) and unpassed seeds without fruit (black bars). Location is LuiKotale, DRC. ***: $P < 0.001$, *: $P < 0.05$ after *t*-test. Error bars indicate SE. Numbers on the bars are N.

and dusk of a day. Thus, the interval of defecation for each individual was on average 95 ± 3 min. We detected no effect of sex ($t = 0.244$, $df = 12.5$, $P = 0.811$) or of age (adult, sub-adult) ($t = -0.332$, $df = 4.38$, $P = 0.755$) on the interval between two defecations. Taking into account bonobo population density, the average seed rain induced by bonobos in the LuiKotale area is estimated to be $441 \text{ seeds d}^{-1} \text{ km}^{-2}$. Extrapolating based on their average lifespan in the wild (50–55 y), an individual bonobo disperses 9.1 Mg of seeds or 11.6 million seeds (not including seeds < 2 mm length such as those of *Ficus* spp. and *Musanga cecropioides*).

Functional overlap – the primate community

The diurnal primate community of the study area is composed of members of three families: Hominidae:

P. paniscus; Colobidae: *Colobus angolensis* P. Sclater, 1860, *Piliocolobus tholloni* (Milne-Edwards, 1886); Cercopithecidae: *Lophocebus aterrimus* (Oudemans, 1890), *Cercopithecus wolffi* (A. Meyer, 1891), *Cercopithecus ascanius* (Audebert, 1799), *Cercopithecus neglectus* Schlegel, 1876 and *Allenopithecus nigroviridis* (Pocock, 1907). In 16 faeces of *C. angolensis* that were investigated, and 124 faeces of *P. tholloni*, we did not discover a single seed. Allen's swamp monkey (*A. nigroviridis*) and de Brazza's monkey (*C. neglectus*) are restricted to riparian forests. While the bonobo can visit these habitats and feed on riparian plants, we cannot assume functional overlap due to insufficient data. We investigated 124 dung piles of *L. aterrimus*. Of these, 11.3% contained intact seeds, 62.9% fragmented seeds. The average number of intact seeds per faeces was 0.19 ± 0.06 ($N = 124$). The only species indicating food overlap and dispersal of intact seeds was *Dialium* sp. for *C. wolffi*, we investigated 78 dung piles.

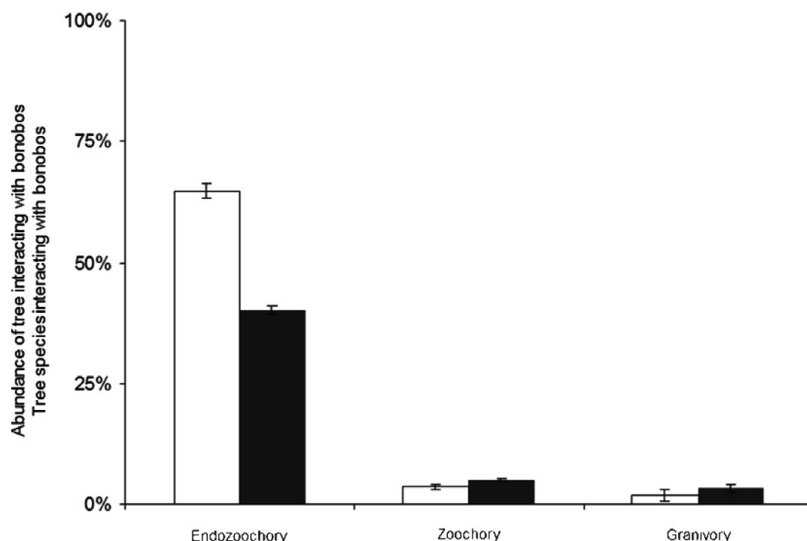


Figure 4. Tree species richness (black) and abundance of trees (white) affected by bonobo seed dispersal service (endozoochory and zoochory; 'zoochory' implies seed dispersal without internal transport) and predation (granivory). The y-axis depicts the average proportion of tree species (diversity) or tree individuals (abundance ($N = 12$ 1-ha plots)). Error bars indicate SE. Location is LuiKotale, DRC.

Of these, 17.9% contained intact seeds of six different species. On average, each dung pile contained 0.39 ± 0.99 seeds per faeces. For *C. ascanius*, we investigated 118 faeces, discovering seeds in 35.2% of them, originating from 16 species. On average, each dung pile contained 2.8 ± 0.15 seeds. Based on direct observations, both species disperse additional species by seed spitting. Thus, the total number of dispersed species during the observation period was $N = 18$ for *C. wolfi* and $N = 23$ for *C. ascanius*. Based on this 5-mo survey, the values of Jaccard's index show that functional overlap between the monkeys and the bonobo seems to be low. The bonobo shared 17.1% of species dispersed with *C. ascanius* and 16.1% with *C. wolfi*. Only 4.8% of the plants dispersed by *L. aterrimus* were also dispersed by the bonobo.

DISCUSSION

Here we investigated seed dispersal by the bonobo (*Pan paniscus*), a large, mainly frugivorous, great ape species inhabiting the evergreen lowland forests of the Central Congo Basin, restricted to the area south of the Congo river. For our study site LK we compiled a list of 133 plant species whose fruits were observed to be ingested by bonobos, of which 91 were ingested including seeds. Among these plant species shown to be bonobo-dispersed, trees represented 40% of all tree species found in the area and account for 65% of all adult trees. Examining data from the two other long-term field sites, Wamba and Lomako (Appendices 1 and 2), shows that our findings are in line with plant species observed to be consumed in

these sites. Kano & Mulavwa (1984) reported 113 species for the Wamba site, representing an overlap of 44% at the generic level with our site. Badrian & Malenky (1984) reported 81 species for Lomako, of which 40% overlap at the generic level with our site. The fact that the overlap at the species level is small (8% and 9% respectively) merits further investigation, suggesting a much higher diversity across the Congo Basin than usually anticipated.

We are aware that there may be several dispersers per plant species and that primary dispersal can be followed by secondary or tertiary dispersal and followed by post-dispersal predation. Nevertheless, we single out the bonobo to illuminate seed dispersal services performed by a single vector in the extremely complex system of the tropical rain forest under consideration.

Almost all bonobo faeces (98%) contained seeds, which represented over half of the dung's weight (67%), with an average of two species in each dung pile.

With regard to the quality and viability of passed seeds, our results show that ingested seeds remained viable after gut transit (97%). These seeds germinated faster and in higher frequency than unpassed seeds, suggesting removal of coat dormancy and endozoochorous processes shaped by co-evolutionary interactions with the bonobo (Beaune *et al.* 2013c, 2013d; Howe & Smallwood 1982, Robertson *et al.* 2006). Similar results have been documented for all other great ape species, highlighting their determinant role in regeneration of the forests they inhabit (Gross-Camp & Kaplin 2011, Nielsen *et al.* 2011, Poulsen *et al.* 2001). Although we did not

quantify all the aspects of seed-dispersal effectiveness, in particular the probability that a viable dispersed seed survives, germinates and produces an adult tree, our study shows that the bonobo fits many crucial criteria characterizing efficient dispersers of tree species. Like other large primates, the bonobo exploits a large home range and consequently may disperse seeds to relatively long distances from parent plants. Our study shows that the seeds ingested are dispersed to an average distance of 1.2 km from the parental tree. Nevertheless, time of last appearance is longer than 24 h (63 h for chimpanzees; Lambert 1998) and other seeds could travel even further. Overall, 93.3% of dispersal events were longer than 100 m. Long-distance dispersal (Nathan *et al.* 2003) is of critical importance in plant population dynamics (Cain *et al.* 2000) and in LuiKotale, the majority of the adult zoochorous plants dispersed by bonobos (95% of the investigated species: 18 tree and 1 liana species) could not self-recruit without dispersal beyond the parent tree's crown (Beaune 2012). This can be due either to the incapacity of seeds to germinate without handling and/or to higher mortality under the parental crown due to density-dependent effects (Beaune *et al.* 2012a, 2012b, 2012c, 2013b; Connell 1971, Janzen 1970, Schupp 1992).

Furthermore, and not reported here, endozoochory by bonobos is in fact often the first stage of diplochorous seed dispersal, with dung beetles as secondary dispersers. Tunnellers such as *Catharsius* sp. bury seeds to a maximum of 3.5 cm (Beaune *et al.* 2012a) thereby enhancing the probability that a seed will escape predators, when compared with seeds that remain on the surface (by > 50%, Beaune *et al.* 2012a). Thus, small changes in predation pressures could affect plant demography (Fenner 2000).

Still a large gap exists between seed production and the growth of a reproductive adult tree (secondary/tertiary/quaternary dispersal, post-dispersal mortality, competition, abiotic and biotic factors, etc.; Forget *et al.* 2005, 2011), but we assess here the first steps of the seed-dispersal loop involving the bonobo. According to Schupp's definition, the bonobo seems to be an efficient seed disperser for the majority of fruiting plants in our site. What we found here is probably applicable to other ecosystems in which large primates are important frugivores.

If we compare seed rain produced by the bonobo with that produced by other Afrotropical primates (Poulsen *et al.* 2001), the bonobo outperforms them in seed dispersal. Accounting for density, seed rain effected by the chimpanzee turns out to be less than that effected by the bonobo. With only 96.5 seeds $d^{-1} km^{-2}$ chimpanzees at a Cameroonian site dispersed a quarter of what the bonobo dispersed in our study site (441 seeds $d^{-1} km^{-2}$). Seed rain reported for the gorilla calculated with the

high density of this ape (1.7 indiv. km^{-2}) are similar to our results (465 seeds $d^{-1} km^{-2}$). There the entire arboreal monkey community, including four species of Cercopithecidae, disperses 568 seeds $d^{-1} km^{-2}$ (Poulsen *et al.* 2001). While our hypothesis is verified, a unique and irreplaceable dispersal service provided by bonobo cannot be proved here. However, the 5 mo of observation of other primates show little functional redundancy for seed dispersal with bonobo suggesting poor functional redundancy in dispersal service. A general correlation is found between body size of frugivores and the size of fruits/seeds that are ingested (Howe & Smallwood 1982), and very few frugivorous animals reach the size of bonobos. Thus, it becomes evident that the bonobo is certainly a key seed disperser for many tree species and can be considered – next to the elephant – as a gardener of the Congo forests.

CONCLUSION

Pan paniscus is the biggest ape within its geographical range and the second-largest frugivore after the elephant. While fleshy fruit species could be dispersed by many frugivorous animals (Beaune *et al.* 2013a, Gross-Camp & Kaplin 2011) such as hornbills, ungulates, monkeys and bats, the potential dispersal vectors for fruit with large seeds are scarce, suggesting that the fate of large frugivore species such as the bonobo may disproportionately affect the regeneration process of these plants (Vanthomme *et al.* 2010). Apes with their medium/large body-size category are specialized in a certain seed size range (Forget *et al.* 2007). Moreover, the overlap in dispersal services within the LK primate community seems to be low, as we found very few plant species dispersed by bonobo endozoochory also dispersed by monkeys. In addition, monkeys (mainly *Cercopithecus*) disperse principally by seed spitting, a different mechanism in terms of recruitment (Dominy & Duncan 2005), with different effects on seed fate (Gross-Camp & Kaplin 2011). Finally, home range sizes and daily travel distances are different in monkeys and bonobos, with consequences for long-distance dispersal. In Afrotropical forests, birds and primates feed and disseminate plants located in different canopy strata and exhibit low plant species overlap in the seeds they disperse (Clark *et al.* 2001, Fleming 1979, Poulsen *et al.* 2002). In the absence of functional overlap between the bonobo and other dispersers, the extirpation of this primate from the system is likely to lead to an irreplaceable loss of current ecosystem services. Strategies for the conservation of Congo forests should therefore include strong measures for conserving their key seed dispersers, among which the bonobo represents certainly one of the most important ones.

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Résumé

L'écologie des forêts d'Afrique tropicale dépend non seulement de la protection des habitats, mais également de la protection des espèces qui la composent telle que les primates frugivores, identifiés parmi les disperseurs de graines les plus importants pour de nombreuses plantes. L'étude de la dispersion de graines par des bonobos (*Pan paniscus*) dans une forêt tropicale humide du bassin du Congo est ici présentée. Les bonobos sont principalement frugivores (66% de toutes les sessions

d'alimentation). Ils passent environ 3.5 h/jour à avaler des graines qui sont transportées 24 hrs en moyenne. Pendant l'étude comportementale (22 mois), les graines de plus de 91 espèces de plantes ont été identifiées comme étant dispersées par endozoochorie dans l'estomac à une distance moyenne de 1,2 km de l'arbre-parent. Les graines passées germent plus rapidement, à des taux plus élevés et avec une plus grande survie post-dispersion que les graines non passées par le tube digestif

d'un bonobo. L'influence du bonobo dans le réseau écologique devrait affecter 40 % des espèces d'arbres et 65 % des arbres individuels. Puisque les chevauchements fonctionnels avec d'autres frugivores sont faibles, le bonobo en tant que vecteur de dispersion de graines est susceptible d'affecter la structure et la dynamique des forêts. Nos conclusions classifient le bonobo (espèce menacée d'extinction) comme probable jardinier de la forêt du Congo.

Appendix 1. Plants consumed by bonobo (X = confirmed consumption) with seed dispersal in LuiKotale, DRC. ^W indicates that the species exists in and is consumed by bonobos at Wamba (Kano & Mulavwa 1984); ^L = same for Lomako (Badrian & Malenky 1984, Fruth, unpubl. data); I = seeds were found intact in faeces, V = seeds were tested and found viable in nursery trials but ratio is not presented because census was interrupted. NID = not identified. Botanical nomenclature follows the African Plants Database (version 3.4.0) from <http://www.ville-ge.ch/musinfo/bd/cjb/africa/> and unpublished nomenclature of recently described species (Fruth *et al.* 2013).

Species	Life form	Leaf	Flower	Fruit	Seed	Stem	Sap	Bark	Seed handling	Intact passed seed	Germinated/ Total
Achariaceae											
<i>Caloncoba welwitschii</i> ^{W L}	tree			X					swallow	I	
Anacardiaceae											
<i>Antrocaryon nannanii</i>	tree			X					spit	I	
<i>Sorindeia zenkeri</i>	tree			X					swallow	I	
<i>Trichoscypha acuminata</i>	tree			X					swallow		
<i>Trichoscypha arborescens</i>	tree			X					swallow	I	
Annonaceae											
<i>Anonidium mannii</i> ^{W L}	tree			X					handle	I	15/15
<i>Enantia olivacea</i>	tree			X					swallow		
<i>Enantia pilosa</i>	tree			X					swallow		
<i>Isolona bruneelii</i>	tree			X					swallow	I	
<i>Monanthes myristicifolia</i>	liana			X					swallow		
<i>Greenwayodendron suaveolens</i> ^{W L}	tree			X					swallow	I	1/4
<i>Thonnera congolana</i>	tree			X					swallow	I	5/19
<i>Uvaria acabrida</i>	liana			X					swallow		
<i>Uvaria</i> sp.	tree			X					swallow	I	6/18
<i>Uvaria engleriana</i>	liana			X					swallow		
<i>Uvariastrum pynaertii</i>	tree			X					swallow		
Apocynaceae											
<i>Landolphia congolensis</i> ^{W L}	liana			X					swallow	I	
<i>Landolphia forestiana</i>	liana			X					swallow	I	V
<i>Landolphia owariensis</i> ^W	liana			X					swallow		
Bursaceae											
<i>Canarium schweinfurthii</i> ^{W L}	tree			X					swallow	I	
<i>Dacryodes buettneri</i>	tree			X					?		
<i>Dacryodes</i> sp.	tree			X					swallow		
<i>Dacryodes yangambiensis</i>	tree			X					swallow	I	69/142
NID	tree			X					swallow		
NID	tree			X					swallow		
<i>Santiria trimera</i> ^W	tree			X					swallow		
Caesalpiniaceae											
<i>Dialium corbisieri</i> ^{W L}	tree	X		X					swallow	I	41/542
<i>Dialium</i> sp.	tree	X		X					swallow	I	
<i>Dialium</i> sp.	tree	X		X					swallow	I	
<i>Dialium</i> sp.	tree	?		X					swallow	I	
<i>Dialium</i> sp.	tree	?		X					swallow	I	

Appendix 1. Continued

Species	Life form	Leaf	Flower	Fruit	Seed	Stem	Sap	Bark	Seed handling	Intact passed seed	Germinated/ Total
Cecropiaceae											
<i>Musanga cecropioides</i>	tree	X	X	X					swallow	I	V
Chrysobalanaceae											
<i>Parinari excelsa</i> ^{WL}	tree			X					spit	I	
Clusiaceae											
<i>Garcinia chromocarpa</i>	tree			X					swallow		
<i>Garcinia ovalifolia</i> ^L	tree			X					swallow	I	52/101
<i>Garcinia punctata</i> ^L	tree			X					Swallow		
<i>Mammea africana</i> ^{WL}	tree			X					handle	I	
Cucurbitaceae											
<i>Momordica foetida</i>	liana		X						swallow	I	0/5
Ebenaceae											
<i>Diospyros hoyleana</i> ^L	tree			X					?		
<i>Diospyros</i> sp.	tree			X					swallow	I	V
<i>Diospyros</i> sp.	tree			X					swallow	I	
Euphorbiaceae											
<i>Drypetes</i> sp.	tree			X					?		
<i>Drypetes</i> sp.	tree			X					spit	I	
<i>Maesobotrya</i>	tree			X					spit	I	
<i>bertramiana</i>											
<i>Phyllanthus</i>	tree			X					?		
<i>muellerianus</i>											
<i>Plagiostyles africana</i>	tree			X					?		
Icacinaceae											
<i>Icacina</i> sp.	shrub			X					swallow		
Irvingiaceae											
<i>Irvingia gabonensis</i> ^{WL}	tree			X					handle	I	5/100
<i>Irvingia grandifolia</i>	tree			X					handle	I	
<i>Irvingia</i> sp.	tree			X					handle	I	
<i>Klainedoxa gabonensis</i> ^L	tree			X					handle	I	
Malvaceae											
<i>Cola bruneelii</i> ^W	shrub			X					swallow	I	
<i>Cola clamidandtha</i>	tree				X				swallow		
<i>Cola gigantea</i>	tree			X					swallow	I	24/24
<i>Cola</i> sp.	shrub			X					swallow		
<i>Cola</i> sp.	shrub			X					swallow	I	
<i>Cola</i> sp.	tree				X				swallow		
<i>Grewia pinnatifida</i> ^W	tree			X					swallow	I	13/77
<i>Grewia</i> sp.	tree			X					swallow	I	29/79
<i>Grewia</i> sp.	tree			X					swallow	I	15/40
<i>Grewia</i> sp.	tree			X					swallow	I	9/20
Marantaceae											
<i>Marantochloa leucantha</i>	herb			X					swallow		
Melastomataceae											
<i>Dissotis brazeana</i>	shrub	X	X	X					?		
Meliaceae											
<i>Guarea laurentii</i>	tree			X					swallow	I	68/74
Mimosaceae											
<i>Parkia filicoidea</i>	tree			X					?		
Moraceae											
<i>Ficus cyathistipula</i>	liana			X					swallow	I	V
<i>Ficus exasperata</i> ^L	liana			X					swallow	I	V
<i>Ficus</i> sp.	liana			X			X		swallow	I	V
<i>Ficus</i> sp.	liana			X					swallow	I	V
<i>Ficus</i> sp.	liana			X					swallow	I	V
<i>Ficus</i> sp.	liana			X					swallow	I	V
<i>Morus nigrum</i>	tree			X					swallow	I	
Myristicaceae											
<i>Pycnanthus angolensis</i>	tree			X					swallow		
<i>Staudtia kamerunensis</i>	tree			X					swallow	I	3/67

Appendix 1. Continued

Species	Life form	Leaf	Flower	Fruit	Seed	Stem	Sap	Bark	Seed handling	Intact passed seed	Germinated/ Total
NID											
NID	tree			X					swallow	I	
NID	tree			X					swallow		
NID	tree			X					swallow	I	
NID				X					swallow	I	6/83
NID	tree			X					swallow	I	1/100
NID	tree			X					swallow	I	
NID				X					swallow	I	
NID				X					swallow	I	2/100
NID				X					swallow	I	V
NID	tree			X					swallow		
Olacaceae											
<i>Olax</i> sp.	tree			X					swallow	I	
<i>Strombosiopsis tetrandra</i> ^L	tree			X					swallow		
<i>Strombosiopsis tetrandra</i> ^L	tree			X					spit	I	
Rubiaceae											
<i>Mitragyna stipulosa</i>	tree			X					swallow	I	V
NID	tree		X						swallow		
Sapindaceae											
<i>Blighia welwitschii</i>	tree			X					swallow		
<i>Chytranthus macrobotrys</i>	tree			X					swallow		
<i>Eriocoelum microspermum</i>	tree			X					swallow		
<i>Haplocoelum congolanum</i>	shrub			X					swallow		
<i>Pancovia laurentii</i> ^{WL}	tree			X					swallow	I	54/74
<i>Placodiscus paniculatus</i>	tree	X		X					swallow	I	V
Sapotaceae											
<i>Autranella congolensis</i>	tree			X					spit	I	
<i>Gambeya lacourtiana</i>	tree			X					swallow	I	2/50
<i>Manilkara malcoleus</i>	tree			X					swallow		
<i>Manilkara obovata</i>	tree			X					swallow		
<i>Manilkara</i> sp.	tree			X					swallow		
<i>Manilkara yangambiensis</i>	tree			X					swallow	I	30/133
<i>Pachystela bequaertii</i>	tree			X					?		
<i>Synsepalum</i> sp.	tree			X					swallow		
<i>Zeyherella longepedicellata</i>	tree			X					swallow	I	V
Verbenaceae											
<i>Vitex</i> sp.	tree			X					swallow		
Vitaceae											
<i>Cissus dinklagei</i> ^W	liana			X					swallow	I	12/45
Zingiberaceae											
<i>Aframomum daniellii</i>	herb			X					swallow		
<i>Aframomum</i> sp.	herb			X		X			swallow	I	V
<i>Aframomum</i> sp.	herb			X					swallow	I	
<i>Renalmia africana</i> ^{WL}	herb			X					swallow	I	

Appendix 2. Plants consumed by bonobo (X = confirmed consumption) without seed dispersal in LuiKotale, DRC. ^W indicates that the species exists in and is consumed by bonobos at Wamba (Kano & Mulavwa 1984); ^L = same for Lomako (Badrian & Malenky 1984, Fruth, unpubl. data). NID = not identified. Botanical nomenclature follows the African Plants Database (version 3.4.0) from <http://www.ville-ge.ch/musinfo/bd/cjb/africa/> and unpublished nomenclature of recently described species (Fruth *et al.* 2013).

Species	Life form	Leaf	Flower	Fruit	Seed	Stem	Sap	Bark
Caesalpinaceae								
<i>Cynometra alexandri</i> ^W	tree				X			
<i>Cynometra sessiliflora</i>	tree	X						
<i>Cynometra</i> sp.	tree	X						
<i>Dialium gossweileri</i>	tree	X		?				
<i>Erythrophleum suaveolus</i>	tree	X						
<i>Gilbertiodendron dewevrei</i> ^{W L}	tree	X			?			
<i>Gilbertiodendron ogouense</i>	tree				X			
<i>Hymenostegia mundungu</i>	tree				X			
<i>Julbernardia seretii</i>	tree	X						
<i>Monopetalanthus microphyllus</i> ^L	tree				X			
<i>Scorodophloeus zenkeri</i> ^{W L}	tree	X	X		X			
Euphorbiaceae								
<i>Manniophyton fulvum</i> ^W	liana	X					X	
Marantaceae								
<i>Haumania leonardiana</i>	liana					X		
<i>Haumania liebrechtsiana</i> ^{W L}	liana					X		
<i>Megaphrynium macrostachyum</i> ^L	herb	X						
Melastomataceae								
<i>Ochthocharis ancellandroides</i>	shrub	X	X					
<i>Ochthocharis dicellandroides</i>	shrub	X	X	?				
<i>Tristemma mauritianum</i>	shrub	X	X	?				
Mimosaceae								
<i>Pentaclethra macrophylla</i> ^W	tree		X					
<i>Piptadeniastrum africanum</i>	tree				X			
Moraceae								
<i>Treculia africana</i> ^{W L}	tree			X	X			
NID								
NID	epiphyte	X						
Nymphaeaceae								
<i>Nymphaea lotus</i>	herb					X		