

## RESEARCH ARTICLE

The Bonobo–*Dialium* Positive Interactions: Seed Dispersal MutualismDAVID BEAUNE<sup>1,2\*</sup>, FRANÇOIS BRETAGNOLLE<sup>2</sup>, LOÏC BOLLACHE<sup>2</sup>, GOTTFRIED HOHMANN<sup>1</sup>, MARTIN SURBECK<sup>1</sup>, CHLOÉ BOURSON<sup>1,2</sup>, AND BARBARA FRUTH<sup>1</sup><sup>1</sup>Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Leipzig, Germany<sup>2</sup>Laboratoire Biogéosciences, UMR CNRS 6282, Université de Bourgogne, Dijon, France

A positive interaction is any interaction between individuals of the same or different species (mutualism) that provides a benefit to both partners such as increased fitness. Here we focus on seed dispersal mutualism between an animal (bonobo, *Pan paniscus*) and a plant (velvet tamarind trees, *Dialium* spp.). In the LuiKotale rainforest southwest of Salonga National Park, Democratic Republic of Congo, seven species of the genus *Dialium* account for 29.3% of all trees. *Dialium* is thus the dominant genus in this forest. *Dialium* fruits make up a large proportion of the diet of a habituated bonobo community in this forest. During the 6 months of the fruiting season, more than half of the bonobos' feeding time is devoted to *Dialium* fruits. Furthermore, *Dialium* fruits contribute a considerable proportion of sugar and protein to bonobos' dietary intake, being among the richest fruits for these nutrients. Bonobos in turn ingest fruits with seeds that are disseminated in their feces (endozoochory) at considerable distances (average: 1.25 km after 24 hr of average transit time). Endozoochory through the gut causes loss of the cuticle protection and tegumentary dormancy, as well as an increase in size by water uptake. Thus, after gut passage, seeds are better able to germinate. We consider other primate species as a potential seed disperser and conclude that *Dialium* germination is dependent on passage through bonobo guts. This plant–animal interaction highlights positive effects between two major organisms of the Congo basin rainforest, and establishes the role of the bonobo as an efficient disperser of *Dialium* seeds. *Am. J. Primatol.* 75:394–403, 2013. © 2013 Wiley Periodicals, Inc.

**Key words:** Congo basin; forest ecology; germination activation; plant–animal interaction; seed dispersal; zoochory

## INTRODUCTION

Seed dispersal mutualism between fruiting trees and frugivores is an important interaction in rainforest ecology [Forget et al., 2011; Howe & Miriti, 2004; Howe & Smallwood, 1982; Lambert & Garber, 1998; Levin et al., 2003; Nathan & Muller-Landau, 2000]. Fruiting plants bear fruit that attracts frugivorous animals. Animals in turn disperse the seeds by zoochory. Animals seem to be so efficient that the majority of tropical plants use zoochorous strategies for seed dispersal [Howe & Miriti, 2000; Beaune et al., 2013].

Within tropical rainforests, birds, mammals, and to a lesser extent reptiles and even fishes are known to be frugivores and seed dispersers [Asquith et al., 1997]. In particular, primates have been cited to be efficient seed dispersers in tropical rainforest ecosystems, as they often occur in high densities, show high rates of frugivory and are often of considerable body size [Chapman, 1995; Lambert & Garber, 1998]. Studies from Cameroon [Clark et al., 2001] and Ivory Coast [Koné et al., 2010] show that seed dispersal services provided by primates are of

ten taxon-specific. These processes have been shaped by sophisticated evolutionary histories and the disappearance or declining abundance of one partner may raise serious challenges for conservation [Chapman, 1995; Chapman & Onderdonk, 1998]. For a wide range of plant species in African rainforests, great apes such as chimpanzees and gorillas play key roles in seed dispersal [Voysey et al., 1999a,b; Wrangham et al., 1994]. In a comprehensive study investigating the diurnal primate community in the Dja reserve, Poulsen et al. [2001] were able to show

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that despite lower densities compared to monkeys, apes accounted for one-half of all seeds dispersed by primates, highlighting their major role as dispersal agents.

Of the 32 species of the tree genus *Dialium* (Caesalpinoideae) known worldwide, 16 occur in tropical Africa [Senesque, 1995]. *Dialium* trees are tall, sometimes more than 40 m, and reach the highest level of the canopy. They produce black-brown velvety pods, each enclosing a single seed embedded in luscious sugary fruit that is produced throughout most of the year. These trees provide food for populations of many apes in Africa, including gorillas, chimpanzees, and bonobos [Kuroda et al., 1996; White & Abernethy, 1997], not only with fruit, but also with flushes of young leaves. In the southern part of the Congo basin, south of the Congo River, in the Democratic Republic of Congo (DRC), the bonobo (*Pan paniscus*) is the only great ape. Like gorillas and chimpanzees on the northern bank of the Congo River, this primate is thought to play an important role in seed dispersal [Idani, 1986]. So far, however, their role in seed dispersal and germination processes has been poorly addressed [Idani, 1986; Tsuji et al., 2010].

Across all field sites where food plant inventories have been published and some investigations conducted, *Dialium* has been mentioned as a major food resource for *P. paniscus*. In terms of time, the apes spend feeding on them and the availability of foods they produce throughout the year, *Dialium* trees make up a major part of the diet of the bonobos inhabiting LuiKotale [Hohmann et al., 2006]. At Wamba, fruit pulp of *Dialium* spp. is eaten as a staple food during several periods of the year [Kano & Mulavwa, 1984]. In the Lomako long-term field site, *Dialium* is one of the most important bonobo foods [Badrian & Malenky, 1984]. Although *Dialium* is widely considered to be an important resource for bonobos, and thus plays an important role in the daily foraging activities of the groups, the relative importance of species of this genus compared to species of other genera with which these animals interact is largely unknown. Moreover, the role of the bonobo in the regeneration process of *Dialium* spp. is largely unknown. The aim of the present article is to investigate the interactions between *Dialium* and bonobos, testing the hypothesis that they are engaged in a positive interaction (seed dispersal mutualism), by studying both (i) the efficiency of seed dispersal by bonobos, including *Dialium* seed rain and the effects of interactions with bonobos on seed viability and germination, and (ii) the benefits that bonobos receive by including *Dialium* in their diet, indexed by comparing the nutritional value of *Dialium* fruit to those of other plants at the site.

In addition, to investigate the importance of interactions of bonobos with *Dialium* compared to other primates, we (iii) explore how other primates of

the community at LuiKotale interact with *Dialium*. Our objective is to quantify the possible functional redundancy between primate species, addressing the question of whether other primates could replace the ecological services provided by bonobos and *Dialium* seed dispersal. We hypothesize that bonobos and *Dialium* trees are mutually interdependent.

We consider bonobo-mediated seed dispersal as being efficient, if the number of seeds spread through endozoochory by bonobos exceeds that spread by other consumers (here, monkeys). We predict that *Dialium* provides critical food resources for bonobos, as its fruits are among the most important items in the animals' annual diet in terms of both, quantity and quality.

## METHODS

### Study Site

The LuiKotale research site (LK) is located within the equatorial rainforest (2°47'S, 20°21'E), at the south-western fringe of Salonga National Park (DRC), within the same continuous forest block. The study site comprises >60 km<sup>2</sup> of primary evergreen lowland tropical forest with a trail network of 76 km. The climate is equatorial with abundant rainfall (>2,000 mm/year). Mean temperatures at LuiKotale range between 21°C and 28°C with a minimum of 17°C and a maximum of 38°C (2007–2010). Investigations were conducted with a habituated group of 35 bonobos. Field work with these primates has been carried out since 2002 [Hohmann & Fruth, 2003].

### Impacts of Bonobos for *Dialium*

#### *Dialium* seed rain

A total of 1,152 bonobo feces were collected between April 2002 and June 2011 to contribute to the project's long-term database. These samples were analyzed for the presence of *Dialium* seeds. In addition, the number of *Dialium* seeds per feces was counted for 160 feces collected between 2009 and 2011.

#### Seed transformation and viability

To assess seed transformation allowing control for both intake and output, seeds were ingested by the first author and measured again after passage through the digestive tract. A total of 112 seeds from a bonobo feeding tree were collected. Seed diameter (length and breadth) in millimeter was measured using a slide caliper (0–10 cm ± 1 µm). Retention time was 24 hr, which is similar to that calculated in the wild bonobo population of LK (24 hr 00 min ± SE. 9 min, see below).

We collected *Dialium* fruit samples during bonobo feeding sessions. The trees where feeding was observed were our target trees. To avoid other

confounding factors such as the genotype of the fruiting plant, fruit samples were used from these target trees as controls. We took only intact fruit that had fallen to the ground incidentally as the bonobos moved through a feeding tree. Fruit that was clearly discarded by a feeding animal was not collected. If bonobos had not been observed feeding in any other *Dialium* tree 36 hr prior to and 24 hr after the feeding bout under investigation, we collected their feces the next day to obtain seeds from the target tree. The seeds were extracted manually from the feces. Unchanged seeds, that is, seeds that were identical in size and shape to fresh seeds, were separated from transformed seeds, that is, seeds that were visibly swollen (imbibed). All seeds were placed on an elevated platform (1 × 2 m, 1.70 m high with predator-proof legs) in natura in LuiKotale forest (under canopy) and monitored daily.

To assess seed viability, we scored germination as defined by radicle emergence [Heß, 1999; Knogge et al., 2003]. We monitored the germination rate of seeds that had passed the human digestive tract as mentioned above and seeds collected from target trees artificially activated by scraping the hard testa responsible for physical seed dormancy, in an attempt to imitate processes occurring in the bonobos' gut [Beaune, 2012; Beaune et al., personal observation].

#### *Transit time (TT) and dispersal distance*

The probability distribution of *Dialium* seeds is based on empirical bonobo movements, georeferenced from January 15, 2008 to September 21, 2011. With bonobo movements after feeding sessions in *Dialium* trees georeferenced and mean TT of seeds known, a mechanistic model of seed dispersal distance can be calculated [Côrtes & Uriarte, 2012; Tsuji et al., 2010; Westcott et al., 2005]. Whenever possible, bonobos were followed daily from nest to nest (approximately 05:30–17:30). Daily travel routes of parties were tracked with a global positioning system (Garmin® 60CSX) using 1 point position/5 min for georeferencing [Beaune, 2012]. Bonobo TT was calculated from direct observations. Whenever an individual bonobo swallowed a new fruit species not eaten in the previous 36 hr, its seed was considered as a marker seed indicating the onset of passage time, and the individual was monitored continuously (except at night) until the seeds of the newly ingested species were found in its feces. The time between ingestion of the marker seeds and appearance of the first seeds in the dung was taken as gut TT. Influences of the sex and seed size on TT were tested with Student's *t*-test and analyses of variance (ANOVA) with all the effects considered as fixed and homoscedasticity tested (Breusch–Pagan test). Seed size was arbitrarily categorized as follows: small: <2 mm; medium-sized: 2–10 mm; large: >10 mm).

## Data Analysis

To test the germination success of different *Dialium* seeds, the R program [R Development Core Team 2011] was used. Each relevant statistical test is specified in the results section.

## Impact for the Apes

### *Dialium as part of the bonobo diet*

Bonobos have a fission–fusion society. Depending on season and time of day, the community splits up into smaller foraging subgroups called parties. From December 2007 until July 2009, we preferentially followed parties containing males and performed hourly scans on the activity of individuals ( $n = 5,605$ ). If they were observed feeding, the food item and species were determined. Based on these scans, we calculated the proportion of observations of *Dialium* feeding relative to feeding on other items. From August 2009 until June 2011, 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 subgroup sampling [Altmann, 1974]). Start and end times of feeding for each plant species and part consumed were recorded starting from August 2009 for focal subgroups. We thereby assessed the proportion of feeding sessions on *Dialium* relative to those of feeding on other plant species. We distinguished fruit from leaves and sap consumption. *Dialium* tree and seed species have subtle differences, making them difficult to distinguish. The genus level *Dialium* was used for all seven of the species, considering that seed biology was similar among species.

## Nutritional Value of *Dialium* Compared to That of Other Fruits

### *Collection of plant samples*

Data collection covered 25 months between February 2002 and July 2010. The study included 95 species whose fruits were observed to be eaten by bonobos. Samples were preferably collected from individual plants that were visited by bonobos and, whenever possible, came from feeding patches while the animals fed. When this was impossible, we collected a sample either from the same feeding patch after the animals had left, or from a patch that was similar in size and phenophase. As for the *Dialium* control fruits, samples were made up of intact fruit that had fallen to the ground. The samples were brought back to camp within a few hours. Samples were processed the same day and stored in liquid nitrogen until lyophilization. For further details see Hohmann et al. [2010].

### Phytochemical analyses

Macronutrient analyses of all samples were performed at the Nutritional Lab of the Leibniz Institute for Zoo and Wildlife Research (Berlin). Analyses of antifeedants such as phenols and tannins were carried out at Hamburg University following the protocol described in Hohmann et al. [2006]. For methodological details see Hohmann et al. [2010].

### Functional Overlap—Preliminary Report on the Primate Community

To assess the importance of monkeys as dispersers of *Dialium* seeds, we investigated seed handling and food plant overlap among seven species of the diurnal primate community of LK from February to June 2011 as a preliminary report. The following species were involved: *Allenopithecus nigroviridis*, *Colobus angolensis*, *Ptilocolobus tholloni*, *Lophocebus aterrimus*, *Cercopithecus neglectus*, *Cercopithecus ascanius*, and *Cercopithecus wolfi*. For reasons of sample size and because *C. angolensis*, *A. Nigroviridis*, and *C. neglectus* are restricted to riparian forest where *Dialium* does not occur, we included only data for the following four species: *P. tholloni*, *L. aterrimus*, *C. ascanius*, and *C. wolfi*. Observations were simultaneously performed by two teams, one focusing on bonobos and one focusing on the monkey species. In contrast to bonobos, monkeys were not habituated [Bourson, 2011]. Feeding and seed handling of *Dialium* fruit were assessed by direct observation. Fecal samples were collected whenever possible. Seeds were collected from feces as described above. A total of 440 monkey feces were collected between February and June 2011. In addition, we collected seeds that had been spat out by monkeys.

### Ethics Statement

The studied apes are free-ranging bonobos and monkeys observed without invasive methods, constraint, contact, and any interaction with the researchers. Animal welfare was of higher priority than scientific interest. 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 adhere to the legal requirements of the host country, the DRC, and to the American Society of Primatologists principles for the ethical treatment of primates.

## RESULTS

### Impacts of Bonobos for *Dialium*

#### *Dialium* seed rain

Among the 1,152 feces analyzed from April 2002 to June 2011,  $36.1 \pm \text{SE } 0.0\%$  contained *Dialium* seeds. Of 416 feces that contained seeds, the num-

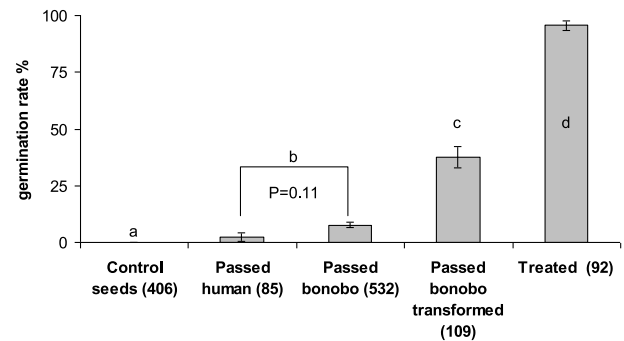


Fig. 1. Germination rates of seeds of different preconditions. Columns along the X-axis show seeds subjected to different preconditions: Control seeds, seed passed through digestive tracts of human and bonobos, naturally transformed, and artificially activated seeds. Number in brackets indicates sample size (N). Error bars indicate SE. Horizontal brackets indicate significance of differences (multiple pairwise comparisons, binomial test, power analysis = 100%).

ber of *Dialium* seeds varied greatly between 1 and 781. The median was 50.0 *Dialium* seeds/feces with an average of  $82.9 \pm \text{SE } 14.3$ , right skewed ( $=3.52$ ). By extrapolation, an individual bonobo should disperse 82,623,471 *Dialium* seeds/year. Considering 40 years as an average lifespan [Rowe, 1996], and an average number of dung produced per day (7.55; this study), a bonobo may disseminate about 3.3 million *Dialium* seeds in its lifespan.

### Seed Transformation and Viability

In the human-gut passage experiment, a total of 112 measured *Dialium* seeds were swallowed, 85 of these were excreted and found 24 hr later. Of these 85 seeds, only five had transformed into bigger seeds (from 1,148 to 1,502  $\mu\text{m}$  of length, Wilcoxon's rank-sum test:  $W = 1$ ,  $P < 0.05$ ; and from 542 to 739  $\mu\text{m}$  of breadth:  $W = 0$ ,  $P < 0.05$ ), whereas the remainder of 80 seeds remained unchanged (length:  $W = 4,107.5$ ,  $P = 0.72$ ; breadth:  $W = 4,244.5$ ,  $P = 0.9912$ ). In the transformed seeds, the protective cuticle was partially removed, and the cotyledon reserve was visible. In the rest of passed seeds no change was visible, which is similar to what we observed in bonobo dung (Wilcoxon's rank-sum test for length ( $\mu\text{m}$ ):  $W = 91$ ,  $P = 0.09$ ).

None of the control seeds ( $n = 406$ ) germinated during the 8 months of monitoring (Fig. 1). Only seeds transformed by passage through the human or bonobo digestive tract and artificially treated seeds germinated. One-third ( $37.6\% \pm \text{SE } 4.7$ ) of these transformed seeds showed radicle emergence becoming visible between 24 and 96 hr after plantation. All of the other transformed seeds that did not germinate were infected with pathogens. Of 532 seeds collected from bonobo feces, 109 were transformed and 423 were untransformed. The germination rate was  $7.7\% \pm 1.3$  for seeds that passed through the bonobo

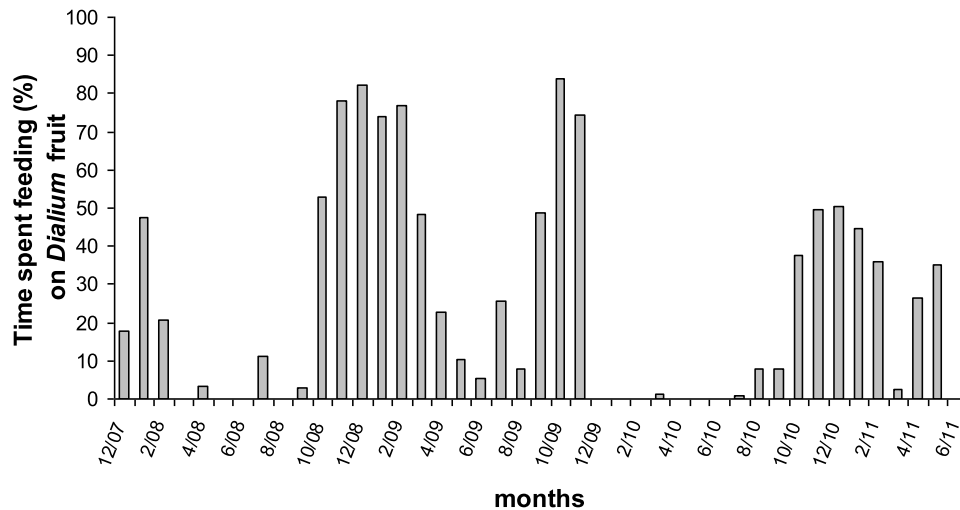


Fig. 2. Time spent feeding on *Dialium* fruit.

Bars indicate feeding sessions on *Dialium* fruit as proportion of overall time spent feeding for 43 months between December 2007 and June 2011.

digestive tract. This rate was not significantly different from the germination rate of seeds that passed through the human digestive tract ( $\chi^2$  test = 2.4019,  $df = 1$ ,  $P = 0.1212$ ).

## TT and Dispersal Distance

### Transit time

We recorded 124 marker seeds from ingestion to first deposition. Marker seeds were identified from 13 different genera. These marker seeds were swallowed and defecated by 19 different bonobos, seven males and 12 females. The resulting TT was 24 hr 00 min on average  $\pm$  SE 9 min (range: 20 hr 03 min–28 hr 17 min). Neither sex nor seed size affected TT ( $t = 0.0253$ ,  $df = 15.285$ ,  $p = 0.9801$ ;  $n = 61$  large, 28 medium-sized, 35 small;  $F_{2,119} = 0.382$ ,  $p = 0.683$ ).

### *Dialium* dispersal distance

In the fission–fusion bonobo society, subgroups (parties) are often composed of males and females of various ages. Thus, movement behavior ought to be similar for both sexes. Based on 344 bonobo travel distances from 344 *Dialium* feeding session in trees, the average dispersal distance for *Dialium* seeds was  $1,248 \pm 45$  m, median = 1,115; range = 1–4,151 m.

## Impact for the Apes

### Proportion of *Dialium* in the bonobo diet

**Fruit:** Bonobos consume *Dialium* fruit during several months of the year (32/43 months studied, from December 2007 to June 2011; Fig. 2). This includes times when we observed bonobos eating unripe fruits before the start of the fruiting season. However, this consumption is negligible compared

with the high consumption of ripe fruit during the season. During the 43 months of feeding ecology assessment, *Dialium* fruit feeding sessions made up  $25.5\% \pm \text{SE } 1.0$  of the overall time spent feeding. By excluding months when *Dialium* was not in fruit, the average proportion of feeding sessions on *Dialium* fruit rose to  $34.2\% \pm 1.5$ . During certain months of the year, *Dialium* fruit also made up the majority of feeding time such as in December 2008 and October 2009, when it accounted for 82.4% and 83.4% of the feeding time, respectively. On certain days, *Dialium* fruits were the only fruits eaten by the group. From September 2009 to June 2011, 951 hr of group feeding sessions were recorded across 22 months (totaling 315 days). Among all fruit species eaten during this period, *Dialium* were the most consumed fruits (19.0%) beyond *Cissus dinklagei* (7.9%); *Grewia* spp. (4.7%); *Polyalthia* (= *Greenwayodendron*) *suaveolens* (3.8%); and others. Bonobos were observed eating more than 100 plant species (see Beaune [2012]).

**Leaves:** Bonobos also ate young leaves of this tree. Therefore, bonobos also feed on *Dialium* trees outside the fruiting season (Fig. 3). Considering *Dialium* leaf-consumption, the species appears to be present in the bonobo diet all year round.

**Sap:** Bonobos were anecdotally observed feeding on *Dialium* sap ( $n = 1$ ). After removing a dozen or so centimeters of bark, bonobos ate the leaking sap.

## Nutritional Value of *Dialium* Compared to That of Other Fruits

Table I shows nutritional values of *Dialium* seeds in comparison to the averaged values of 94 other fruits. It becomes clear that *Dialium* has a special place within the bonobo diet with respect



Fig. 3. Bonobos eating *Dialium* leaves outside of the fruiting season of *Dialium*. LuiKotale, DRC. Democratic Republic of Congo. D. Beaune/MPI.

to macronutrients such as protein (145.7 mg/g) and sugar (101.4 mg/g). Although not reaching significance, *Dialium* also shows the tendency to contain less antifeedants than the average fruit. When compared with other important fruit consumed by bonobos (*C. dinklagei* and *G. suaveolens*), *Dialium* fruits still provide more protein while the other two fruits are richer in sugar.

### Functional Overlap—Preliminary Report on the Primate Community

The diurnal primate community of the study area is composed of three families as follows: Homiidae: *P. paniscus*; Colobidae: *C. angolensis*, *P. tholloni*; Cercopithecidae: *L. aterrimus*, *C. wolfei*, *C. ascanius*, *C. neglectus*, and *A. nigroviridis*. Based on 5 months of daily survey, *L. aterrimus*, *C. wolfei*, *C. ascanius* were observed eating *Dialium* fruits, while *C. neglectus* and *A. nigroviridis* did not. Although we could not confirm that the two latter species interact with *Dialium*, these monkeys were mainly restricted to riparian forest where the genus *Dialium* is not present. The monkeys mainly spit out the *Dialium* seeds as they did with seeds from other species. Overall, 440 feces from four monkey species were collected. Of these, only 12.5% ( $N = 55$ ) contained intact seeds. Of these, only two feces contained *Dialium* seeds: one feces of *L. aterrimus* (1/124) with three *Dialium* seeds and one feces of *C. ascanius* (1/118) with one *Dialium* seed. The number of all plant seeds per feces was low, *L. aterrimus*:  $0.19 \pm \text{SE. } 0.06$  ( $N = 124$ ), *C. wolfei*:  $0.39 \pm 0.99$  ( $N = 78$ ), *C. ascanius*:  $2.80 \pm 0.15$  ( $N = 118$ ). *Dialium* seed handling by monkeys is different than that of bonobos. Seeds were mainly dispersed by seed spitting. Whether spit out or passed, *Dialium* seeds resulting from monkey foraging activity never germinated.

### DISCUSSION

In this study, we investigated ecological interactions between an animal (bonobo, *P. paniscus*) and a plant (velvet tamarind trees, *Dialium* spp.). Concerning the impact for the tree, we investigated

TABLE I. Nutritional Values of Fruits Consumed by Bonobos at LuiKotale

		<i>Dialium</i> spp.	Other fruits average $\pm$ SE	Direction of difference	Wilcoxon's signed- rank test	<i>Cissus</i> <i>dinklagei</i>	<i>Polyalthia</i> <i>suaveolens</i>
Macronutrient	Protein (mg/g)	145.7	92.8 $\pm$ 43.1	>	$P < 0.001$	106.1	96.8
	Crude protein/acid detergent fiber (ADF) ratio	1.7	0.8 $\pm$ 0.7	>	$P < 0.001$	0.4	0.4
	Protein	14.6%	9.3% $\pm$ 4.3	>	$P < 0.001$	10.6%	9.7%
	Sugar (mg/g)	101.4	84.8 $\pm$ 70.5	>	$P < 0.001$	119.2	128.5
	Starch (mg/g)	3.0	37.8 $\pm$ 86.8	<	$P < 0.001$	14	9.9
	Crude fat	1.8%	6.4% $\pm$ 8.8	<	$P < 0.001$	10.6%	NA
Energy	Energy (kJ/g dry matter)	16.3	18.2 $\pm$ 2.8	<	$P < 0.001$	20.4	18.3
Fiber	Neutral detergent lignin	32.0%	29.1% $\pm$ 15.9	=	$P = 0.05$	38.7%	29.7%
	ADF	8.6%	18.5% $\pm$ 11.5	<	$P < 0.001$	27.3%	22.2%
	Acid detergent lignin	0.5%	6.2% $\pm$ 5.3	<	$P < 0.001$	7.4%	7.6%
	Cellulose	8.1%	12.3% $\pm$ 7.1	<	$P < 0.001$	19.9%	14.6%
	Hemicellulose	23.3%	10.6% $\pm$ 7.0	>	$P < 0.001$	11.4%	7.5%
Antifeedant	Total phenol	0.4	0.7 $\pm$ 1.2	=	$P = 0.09$	0.7	0.5
	Total tannin	0.3	0.6 $\pm$ 1.2	=	$P = 0.32$	0.6	0.3
	Condensed tannin	4.5	4.9 $\pm$ 9.3	=	$P = 0.06$	8.3	1.2

Note: Column *Dialium* and other fruits show mean nutritional values or concentration of macronutrients expressed as percent of dry matter. Direction of difference indicates > (higher), < (lower), or = (no difference) revealed by application of Wilcoxon's signed-rank test. Nutritional values of other highly consumed fruits (*C. dinklagei* and *Polyalthia* [= *Greenwayodendron*] *suaveolens*) are presented for comparison.

*Dialium* seed rain, seed transformation, and seed viability. With ingestion observed during almost 75% of all months investigated, *Dialium* is consumed over long periods of the year. Over one-third of all feces collected between 2002 and 2011 contained *Dialium* seeds. We showed that the majority of *Dialium* seeds are adapted to survive digestion in apes and to a lesser extent in monkeys (*L. aterritimus* and *C. ascanius*). One of the major risks for a tree using the endozoochorous strategy is the passage through a digestive system, where seeds are exposed to a high level of acidity. Adaptation to these endozoochorous partners implies a trade-off for the cuticle, which must be thin enough to be removed by acid attack and strong enough to survive digestion. This is the case for *Dialium* seeds. Here, *Dialium* seeds seem to be adapted to resist acid erosion of the primate's gut. However, seed protection decreases with time in the digestive tract. This affects some of the seeds that become porous. When hermetic protection of the coat is perforated, seeds swell and probably become digestible. Prolonged retention in the gut may increase the likelihood of perforation. This can explain the coprophagy described in young chimpanzees [Krief et al., 2004] and bonobos at Wamba [Sakamaki, 2009]. In addition, this may explain the coprophagy observed in bonobos in times of reduced food abundance and extended *Dialium* availability (own observations), although these observations remain exceptional. The number of seeds passing through the bonobo's digestive tract is considerable and exceeds by far that of *L. aterritimus*, the monkey with the highest proportion of *Dialium* seeds found in feces.

Of the seeds that passed through the digestive tract, a small proportion (8%) had become porous and managed to start germination within 24–96 hr from the moment of being positioned on the ground. This effect is known as germination activation by animals, and this was the first example observed in bonobos. In mammals, elephants are best known for germination activation. *Detarium* or *Balanites* seeds are able to germinate only after passing through the elephant's digestive tract, and the consequences of the considerable decline in elephant populations for these trees has already become apparent [Babweteera et al., 2007; Chapman et al., 1992; Cochrane, 2003].

In seed dispersal mutualisms, dispersal by animal partners shows high dependence on population survival. In cases when the animal partner becomes extinct (e.g., elephants by poaching) and when no alternative partner exists, the dependent plant population cannot recruit effectively and the number of seedlings falls [Babweteera et al., 2007]; this is more difficult to demonstrate for the dispersal of medium-sized and small seeds such as *Dialium*, which involves many consumers and is thus multi-vectorial. In Afrotropical forests, birds and primates

consume and disseminate plants located in different canopy strata and there is thus low overlap in dispersed seed species [Clark et al., 2001; Fleming, 1979; Poulsen et al., 2002]. In LK neither birds nor bats have so far been observed feeding on *Dialium*. However, we showed that other frugivorous primates consume and disperse *Dialium* seeds, although to a much lesser extent than bonobos. Even though monkey densities in LK are larger than bonobo densities, *Dialium* endozoochorous seed rain through the gut from monkeys might be lower than seed rain from bonobos. This phenomenon has been observed in other sites [Poulsen et al., 2001]. We cannot prove that *Dialium* trees are dependent on the bonobo, but monkeys, as a dispersal vector for *Dialium*, are surely different from bonobos in terms of handling techniques, seed treatment, and dispersal distance and thus seed dispersal effectiveness.

Monkeys disperse seeds by seed spitting and endozoochory. Seed spitting by monkeys also allows plant reproduction, although the quantity and quality of seeds are different from those dispersed by bonobos [Gross-Camp & Kaplin, 2011; Gross-Camp et al., 2009; Lambert & Garber, 1998]. Thus, *Dialium* may be able to survive even without bonobos, although the process of reproduction would be slowed down, and this would probably have an impact on *Dialium* populations, and their genetic and spatial structures [Schupp et al., 2010]. The role of monkeys in *Dialium* seed dispersal deserves further exploration. The current data are a preliminary report and more observations and data collection during other seasons are required before final conclusions are made.

Thanks to the dormancy coat, *Dialium* seeds can resist pathogens until germination after being dispersed by any primate. However, they are highly vulnerable to seed predators when on the ground. In other experiments, we showed that, when on the ground, *Dialium* seeds are often removed by seed predators such as the giant pouched rat (*Cricetomys emini*) [Beaune et al., 2012a]. In addition, herds of bush pigs (*Potamochoerus porcus*), which are important seed predators, are regularly observed foraging beneath *Dialium* trees [Beaune et al., 2012b] and they readily ingest and chew available seeds. The same is true for forest duikers (*Cephalophus nigrifrons*, *Cephalophus callipygus*) that are often found in the company of troops of monkeys eating fruit and/or seeds that have fallen to the ground. In these cases, the seeds are a valuable source of nutrients to their predators. However, such seeds will no longer be able to germinate.

In contrast, seeds swallowed by bonobos avoid this dangerous period on the ground. First, passage through the gut and seed dormancy both reduce the risk of predation. Second, diplocory also occurs, bonobo feces attract dung beetles (*Scarabidae*, tunnelers as *Catharsius* spp.) that bury the seeds

and thus hide them from nocturnal predators [Feer, 1999; Hanski & Cambefort, 1991]. At LK, we showed that thanks to tunnelers, *Dialium* seeds dispersed by bonobo endozoochory through the gut disappeared from the surface of the ground in less than an hour and were better able to avoid seed predators and pathogens. A high proportion (97%) of *Dialium* seeds dispersed by diplochory first by bonobos and then by dung beetles remained in place, while 74% of the surface seeds were removed by nocturnal rodents [Beaune et al., 2012a].

Furthermore, based on the follow-up of 344 *Dialium* seed dispersal events, we judged *Dialium* seed dispersal to be very long ( $1.25 \text{ km} \pm \text{SE } 0.045$ ). Considering this very long dispersal together with home range size and postdispersal survival, bonobos are more likely to affect the spatial structure of the trees than are sympatric primates [Schupp et al., 2010; Seidler & Plotkin, 2006; Westcott et al., 2005]. Although there is a gap between seedlings and adult trees that remains to be explored, bonobos seem to play an important role in *Dialium* seed dispersal, reproduction, and population biology, and thus have an impact on the evolution of *Dialium* spp. populations.

However, bonobos, like all great apes, are rare and threatened in their area of distribution [Dupain et al., 2000; Hart et al., 2008; Tranquilli et al., 2012; Walsh et al., 2003]. A decrease in the numbers, or worse, the disappearance of this species might have consequences for the ecosystem. Although other mammals such as monkeys are probable dispersers of these attractive trees, their ability to activate *Dialium* germination still remains to be demonstrated.

For *Dialium* species, this adaptation related to bonobo-facilitated germination, namely the strong protection against digestion, could become a dangerous dependence [Chapman, 1995; Chapman & Onderdonk, 1998; Howe, 1984]. In our experiment, none of the 406 seeds that had not gone through the bonobo digestive tract germinated during 8 months of monitoring. Such seeds probably germinate, though at a much lower rate and after a long and dangerous dormancy period.

Considering this and other studies, the genus *Dialium* (African velvet tamarind) seems to be a key resource for apes. *Dialium* trees have developed a highly nutritive fruit available during a long fruiting period, and thus provide food for apes and other members of the frugivore community. Although the two other great apes, chimpanzees (*Pan troglodytes*) and gorillas (*Gorilla gorilla*) overlap with the *Dialium*'s home range in their areas of distribution [White & Abernethy, 1997], only chimpanzees have a positive *Dialium*–ape interaction. Gorillas have been observed chewing the seeds and thus act as seed predators [Kuroda et al., 1996] or have been observed eating unripe fruit [Rogers et al., 1990].

In LuiKotale, *Dialium* trees represent  $29.3\% \pm \text{SE } 2.3$  of the tree community in the terra firme het-

erogeneous primary forest and are thus dominant [Beaune, 2012]. *Dialium* plays a considerable role in bonobo feeding ecology. *Dialium* is known to be an important plant in the bonobo food repertoire for the other long-term sites Lomako and Wamba [Badrian & Malenky, 1984; Kano & Mulavwa, 1984], but no study has attempted to assess the relative importance of *Dialium* in terms of quality and quantity. Here, we showed not only that *Dialium* serves bonobos as staple food for more than half of the year, but also that once in fruit, bonobos spend more time feeding for *Dialium* than for any other food item in their diet. However, we cannot exclude other exceptional fruiting species during other season not followed during our 43 months of monitoring. The extraordinary abundance of these trees across bonobo study sites and the important nutrients contained in the fruit may explain why the bonobos have this predilection. Furthermore, the fruits are richer in protein and sugar than are other fruits available in the forest. In addition to eating *Dialium* fruit, bonobos also eat the young leaves, even outside the *Dialium* fruiting season (Fig. 3). *Dialium* trees could thus be considered one of the bonobos' staple foods and are certainly of crucial importance. This importance should be highlighted in bonobo conservation plans, with regard to the assessments of suitable places for bonobo conservation or reintroduction [André et al., 2008].

Future investigations should focus on *Dialium* recruitment, population biology, spatial and genetic structure, and survival in forests where their ape partners are now extinct. In addition, to assess potential coevolution between apes and *Dialium* trees, a comparison of their respective ranges is needed. If some of the *Dialium* spp. ranges overlap with the range of bonobos and chimpanzees, the coevolution hypothesis would be reinforced.

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