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The Ecological Role of the Bonobo

Seed dispersal service in Congo forests

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Aux jardiniers des forêts. Puissent-ils encore vivre… tout simplement

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Abstract

Bonobos (*Pan paniscus*) are threatened with extinction. They are the largest primates, and the only apes (except human), of the southern bank of the Congo Basin. Along with chimpanzees, they are our closest living relatives and are studied by anthropologists to include/understand our hominid origins; but what about their functional role in the forest? Would their disappearance have serious consequences for forest ecology? Answering this question is the aim of this new project, with several years of observations of a free-ranging habituated group of bonobos on the LuiKotale research station (DR Congo). In this tropical rainforest, the very great majority of plants need animals to reproduce and disperse their seeds. Bonobos are the largest frugivorous animals in this region, after elephants. During its life, each bonobo will ingest and disperse nine tons of seeds, from more than 91 species of lianas, grass, trees and shrubs. These seeds will travel 24 hours in the bonobo digestive tract, which will transfer them over several kilometers (mean 1.3 km; max: 4.5 km), far from their parents, where they will be deposited intact in their feces. These dispersed seeds remain viable, germinate better and more quickly than unpassed seeds. For those seeds, diplochory with dung-beetles (Scarabaeidae) imrpoves post-dispersal survival. Certain plants such as *Dialium* may even be dependent on bonobos to activate the germination of their seeds, characterized by tegumentary dormancy. The first parameters of the effectiveness of seed dispersal by bonobos are present. Behavior of the bonobo could affect the population structure of plants whose seeds they disperse. The majority of these zoochorous plants cannot recruit without dispersal and the homogeneous spatial structure of the trees suggests a direct link with their dispersal agent. Few species could replace bonobos in terms of seed dispersal services, just as bonobos could not replace elephants. There is little functional redundancy between frugivorous mammals of the Congo, which face severe human hunting pressures and local exctinction. The defaunation of the forests, leading to the empty forest syndrome, is critical in conservation biology, as will be illustrated here. The disappearance of the bonobos, which disperse seeds of 65% of the tree species in these forests, or 11.6 million individual seeds during the life of each bonobo, will have consequences for the conservation of the Congo rainforest.

Keywords Congo Basin, coevolution, conservation, ecological service, forest ecology, mutualism, seed dispersal.

Résumé

Les bonobos (*Pan paniscus*) sont menacés d'extinction. Ils sont les plus grands primates et les seuls grands singes de la rive sud du bassin du Congo. Ils sont nos plus proches parents avec les chimpanzés et sont étudiés dans l'urgence par les anthropologues pour comprendre nos origines Hominidé. Mais qu'en est-il de leur rôle fonctionnel dans la forêt ? Leur disparition aurait-elle des conséquences graves sur l'écologie forestière ? Telles sont les questions de ce projet inédit, dont les réponses sont apportées par plusieurs années d'observations d'un groupe en liberté habitué au site de recherche LuiKotale (RD Congo). Dans cette forêt tropicale humide, la très grande majorité des plantes a besoin des animaux pour se reproduire et disperser leurs graines. Les bonobos sont les plus grands frugivores après les éléphants. Au cours de sa vie, chaque bonobo ingèrera et dispersera 9 tonnes de graines, de plus de 91 espèces de lianes, herbes, arbres et arbustes. Ces graines voyageront 24 heures dans le tube digestif des bonobos, qui les transporteront sur plusieurs kilomètres (≈1.3km; max : 4.5 km), loin de leur plante mère, où ils seront déposées intactes dans leurs fèces. Ces graines dispersées restent viables, germent mieux et plus rapidement que les graines non passées par le tube digestif d'un bonobo. La diplochorie, impliquant les bousiers (Scarabaeidae), favorise leur survie post dispersion. Certaines plantes comme les *Dialium* pourraient même être dépendants du bonobo pour activer la germination de leurs graines en dormance tégumentaire. Les premiers paramètres de l'efficacité des bonobos comme disperseurs de graines sont présents. Leurs comportements pourraient affecter la structure des populations végétales. La majorité de ces plantes zoochores ne peuvent recruter sans dispersion et la structure spatiale homogène des arbres laisse penser à un lien direct avec leur agent de dispersion. Peu d'espèces remplaceraient les bonobos en terme de leur rôle fonctionnel, tout comme les bonobos ne remplacent pas les éléphants. Il y a peu de redondance fonctionnelle entre les mammifères frugivores très différents du Congo, qui doivent faire face aux pressions de chasse des hommes et disparaissent localement. La défaunation des forêts, résultant dans le syndrome des forêts vides, est un problème grave de biologie de la conservation illustré ici. La disparition des bonobos qui dispersent les graines de 65% des arbres de leur forêt, ou encore 11.6 millions de graines au cours de la vie d'un bonobo, est liée à la conservation des forêts tropicales humides du Congo.

Mots clefs Bassin du Congo, coévolution, conservation, dispersion de graines, écologie forestière, mutualisme, service écologique.

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Photos by David Beaune

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Introduction

This project was born in the middle of the Congo in 2008, in one of the few free-ranging bonobo communities studied by a permanent team of scientists. I was camp manager in the Max Planck Institut‘s field station: Luikotale (LK, Figure 1, Figure 2). Looking at the bonobos and how they behave in the wild, obvious questions arise for an ecologist. ‘These animals interact with many plants and seem to be very important, but how? For how many species? What is the effect on forest structure and on ecological network?’ Additionally, these great apes are critically threatened by extinction (IUCN 2012). They might disappear from the system. What risk would their extinction entail for the ecosystem? The project on the ecological role of the bonobo was thus born, profiting from the expertise of the Max Planck institute for evolutionary anthropology in primatology and the Biogéosciences laboratory in ecology. This project is an international collaborative project focusing on an original chapter in the life of bonobos: their ecological services in the ecosystem.

Figure 1 Map of the field site: LuiKotale in DRC.

Only recently described by science (Coolidge 1933) and studied in the wild only since the late 1970s (Kano 1980), the bonobos gained popular interest only recently. They gained interest because of their phylogenic proximity to humans and their peculiar social behavior (de Waal 1997). They were thus mainly studied by anthropologists without a particular interest in ecology and forests. Since the appearance of the young field of "bonobology", only two short notes published in *Journal of Tropical Ecology* stated the understandable role of these large frugivores in seed dispersal; with seeds found in feces and remaining viable, and secondly about the long dispersal distance infered by bonobos (Idani 1986; Tsuji, Yangozene & Sakamaki 2010).

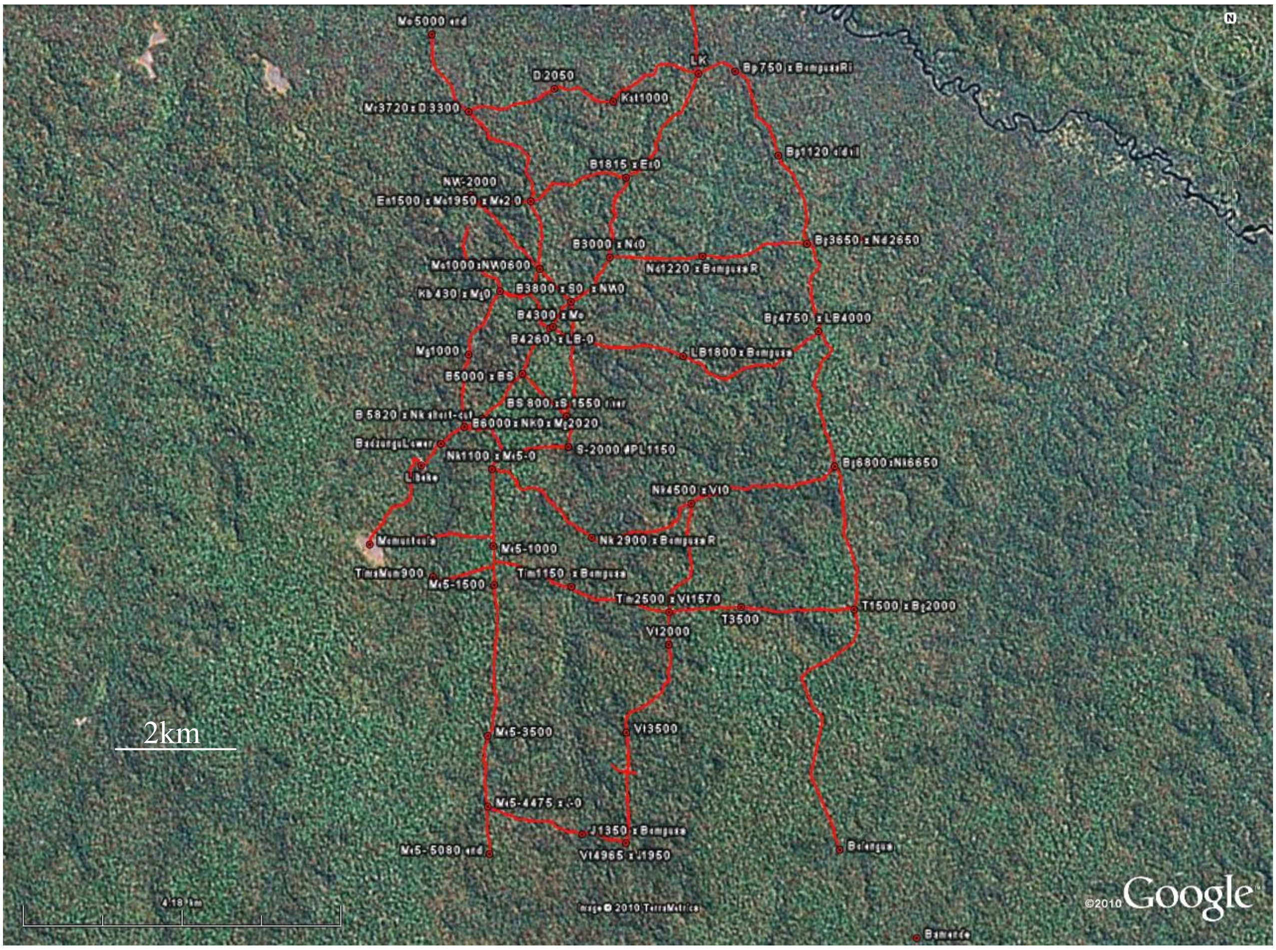

Figure 2 Trail network (76 km) of the LuiKotale field site. South-west of the Salonga NP. DRCongo.

The goal of this study is to investigate these questions and eventually analyze the ecological role of the bonobo in the ecosystem.

Bonobos are frugivores and primates are well known to be important seed dispersers (Sussman 1991; Lambert & Garber 1998; Poulsen, Clark & Smith 2001a; Vulinec, Lambert &

Mellow 2006; Gross-Camp, Masozera & Kaplin 2009). Not surprisingly, the main ecological service investigated is seed dispersal.

To do this, a wild bonobo group exists and can help to improve our knowledge on plant-animal interactions. Near the Salonga National Park, the Bompusa community is a free-ranging group of 25-30 bonobos habituated by scientists beginning a decade ago (Hohmann & Fruth 2003c); Figure 3). Plant biodiversity has been studied over the long term and the great majority of trees, shrubs, lianas and herbs are identified to species level (Fruth 2011).

Figure 3 An habituated bonobo community with identifiable individuals: Bonobos of the Bompusa community are indifferent to human observers, allowing collection of behavioral data (left : Zed felling asleep in front of me ; right : Ida eating *Haumania* stem)

This thesis is organised in sections which can be read independently. Each section is based on a paper submitted or in the process of being submitted, to a peer-reviewed journal in ecology, conservation biology or primatology. The introductive part is an introduction the studied model, *Pan paniscus*, in which I review the most recent research on bonobos. The second sub-section introduces the different seed dispersal strategies of plants in the LuiKotale forest and the importance of frugivores in this system. This sub-section also identifies the seed disperser and seed predator guilds and the human pressure on each of them.

Part I is the core of the project, presenting data on the ecological role of the bonobo. The first sub-section is a general analysis of how bonobos affect seed survival, germination rate and speed, and examines the number of plant species whose reproduction is affected by bonobos. The functional redundancy with other primates is also tested, in addition to an estimation of the seed rain infered by a bonobo population and an examination of how plants deal with the absence of seed dispersal. The second sub-section focuses more specifically on a dominant tree genus in examining the mutualism between bonobo and *Dialium* (Fabaceae: Caesalpinioideae). This part documents the bonobo's positive effect in this animal-plant interaction (Figure 4). Another investigation (third sub-section) focuses on fruits that produce chemical components such as tannins that deter consumers (direct deterrence hypothesis) and how these chemicals affect interaction with bonobos.

The last sub-section ends with an examination of the effect of bonobos on seed germination. In this section the seed dormancy of a dominant tree species, important ecologically, economically and in conservation, was broken by imitation of an ecological process. Artificial activation of seed germination in *Dialium corbisieri* is tested.

Part II examines more fundamental aspects of the ecology of bonobos. Dispersal distances are compared among plant species dispersed by bonobos, in order to see whether fruit traits can affect the dispersal behaviour of this dispersal vector.

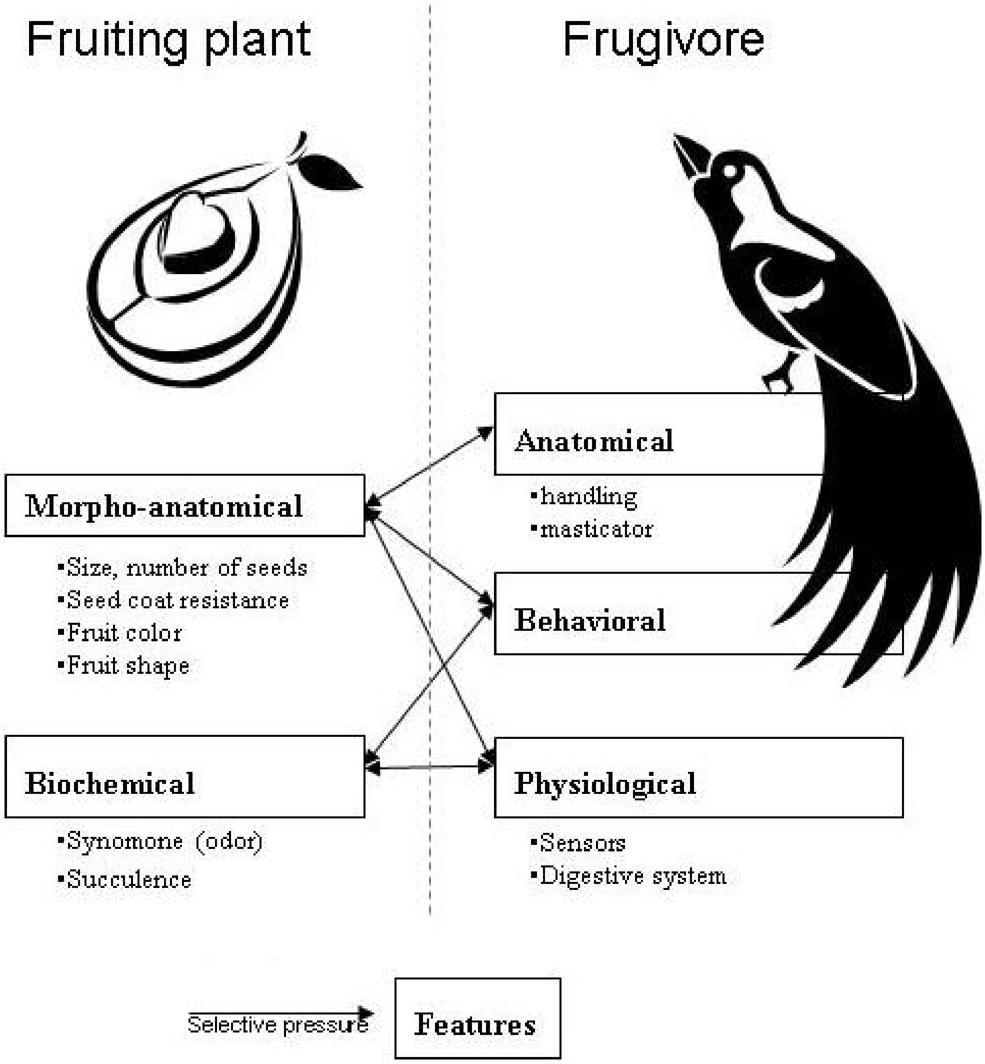

Figure 4 Interactive effects between frugivores and fruiting plants

Part III includes other actors of the ecological network that affect post-dispersal seed fate. One subsection starts with the biggest seed predators of the system, bush pigs (Beaune *et al.* 2012a), and the second introduces rodents and dung beetles (Beaune *et al.* 2012b). Other important actors in the Congo forest are elephants (Campos-Arceiz & Blake 2011). However, forest elephants are seriously threatened with extinction in Africa (Blake *et al.* 2007). It is thus critical to assess if another animal vector, such as bonobo, can replace the ecological service of seed dispersal that was previously assured by elephants. Functional overlap between the two biggest frugivorous mammals of the forest is then investigated

This project does not fill the gap in data on processes occurring between seed deposition and the arrival to maturity of an adult plant. However, it provides a base for future work on seed dispersal processes in Congo forests, and new evidence for the urgent need to protect our cousin, the bonobo, and the other animals of the forest.

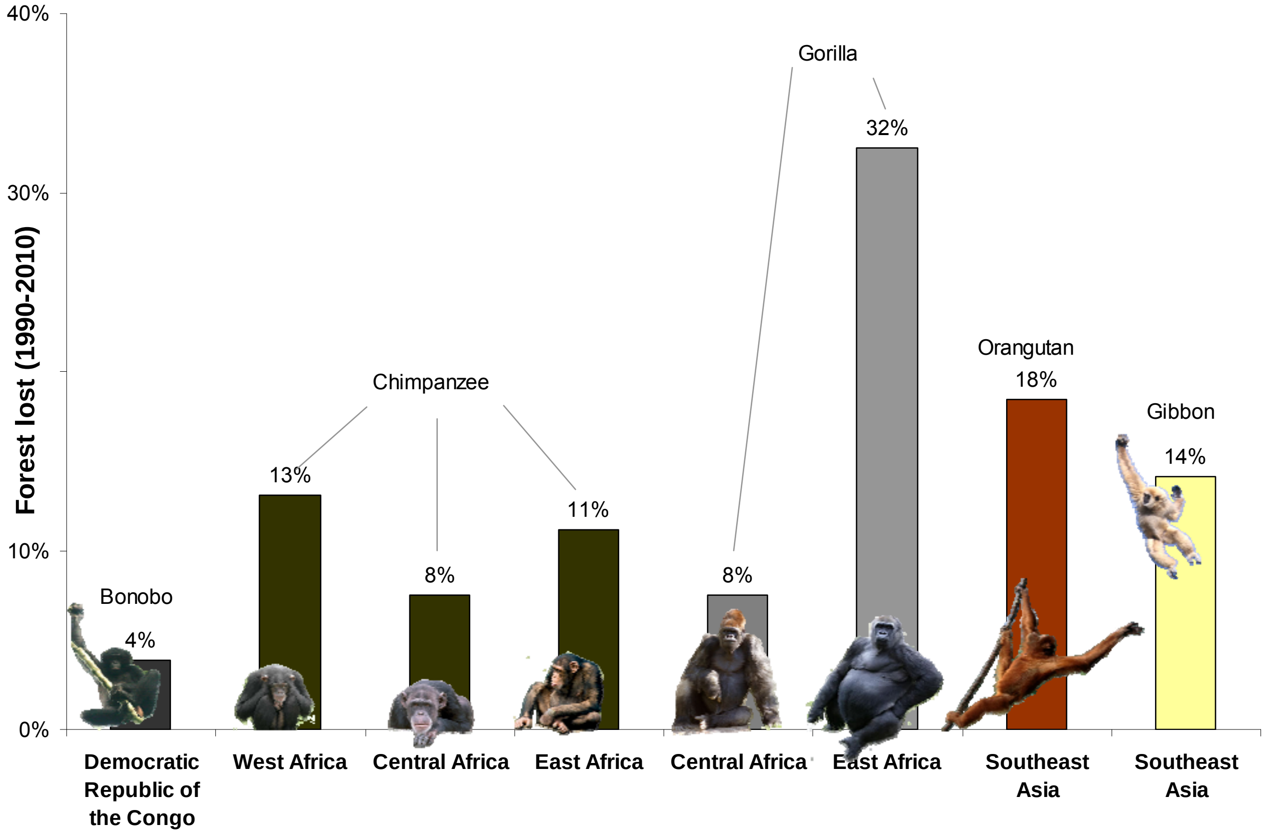

Figure 5 Percentage forest area losses between 1990 and 2010 for regions within the ranges of ape species. Percentage values express the total area deforested between 1990 and 2010 relative to forest cover in 1990. Calculation based on FRA FAO 2010

In forest conservation, deforestation is the most obvious and visible fact. Based on FAO data (FAO 2010), we can see the deforestation rate of countries hosting apes. Figure 5 shows major forest area loss for all ape species over the last two decades. However, tropical forests face another threat: defaunation. Many countries conserve rare primary forests and relatively large forested areas (Table 1), but without protection, hunting pressures empty the forest of its large and medium-sized animals and thus affect ecological functions such as seed dispersal (Redford 1992). The forests remain structurally intact, with large healthy trees and large areas of ‘intact’ forest that we can assess in tables. Nevertheless the functional effects of emptying the forest of its animals (Terborgh *et al.* 2008) are not revealed by tables and deforestation reports. Forest conservation should be considered not only in terms of surface area protected against deforestation but in temrs of survival of the entire system that assures ecological services, and this is the point of the main chapter of this thesis.

Figure 6 Charcoal-making and agriculture are the main causes of deforestation linked to human encroachment. (here for manioc cultivation, DR Congo).

Species	**Countries**	**Extent of forest in 2010 (1000ha)**		**Forest % of land area**	**Primary forest annual change rate (2005-2010)**		**Forest annual change rate (2005-2010)**		**Forest area lost (1990-2010)**	**Population status**
		Primary	All forest		1000ha/yr	%	1000ha/yr	%	1000ha	
Pan paniscus										
Central Africa	Democratic Republic of the Congo	-	154135	68	-	-	-311	-0.2	-6228	
Pan troglodytes										
West Africa	Benin	0	4561	41	0	-	-50	-1.06	-1200	extinct
	Burkina Faso	0	5649	21	0	-	-60	-1.03	-1198	extinct?
	Ivory Coast	625	10403	33	0	0	-	-	181	
	Gambia	1	480	48	-	-4.36	2	0.38	38	extinct
	Ghana	395	4940	22	0	0	-115	-2.19	-2508	
	Guinea	63	6544	27	0	0	-36	-0.54	-720	
	Guinea-Bissau	0	2022	72	0	-	-10	-0.49	-194	
	Liberia	175	4329	45	0	0	-30	-0.68	-600	
	Mali	0	12490	10	0	-	-79	-0.62	-1582	
	Senegal	1553	8473	44	-9	-0.57	-40	-0.47	-875	
	Sierra Leone	113	2726	38	-4	-3.21	-20	-0.7	-392	
	Togo	0	287	5	0	-	-20	-5.75	-398	extinct
Central Africa	Angola	0	58480	47	0	-	-125	-0.21	-2496	
	Cameroon	-	19916	42	-	-	-220	-1.07	-4400	
	Central African Republic	2370	22605	36	-76	-2.94	-30	-0.13	-598	
	Congo	7436	22411	66	-6	-0.08	-12	-0.05	-315	
	Democratic Republic of the Congo	-	154135	68	-	-	-311	-0.2	-6228	
	Equatorial Guinea	0	1626	58	0	-	-12	-0.71	-234	
	Gabon	14334	22000	85	-330	-	0	0	0	

						2.16				
	Nigeria	-	9041	10	-65	-	-410	-4	-8193	
East Africa	Burundi	40	172	7	0	0	-2	-1.01	-117	
	Rwanda	7	435	18	0	0	10	2.47	117	
	Sudan	13990	69949	29	-11	-0.08	-54	-0.08	-6432	
	Uganda	0	2988	15	0	-	-88	-2.72	-1763	
	United Republic of Tanzania	0	33428	38	0	-	-403	-1.16	-8067	
	Zambia	0	49468	67	0	-	-167	-0.33	-3332	extinct
			529558						-51506	
Gorilla										
Central Africa	Angola	0	58480	47	0	-	-125	-0.21	-2496	
	Cameroon	-	19916	42	-	-	-220	-1.07	-4400	
	Cameroon	-	19916	42	-	-	-220	-1.07	-4400	
	Central African Republic	2370	22605	36	-76	-2.94	-30	-0.13	-598	
	Congo	7436	22411	66	-6	-0.08	-12	-0.05	-315	
	Democratic Republic of the Congo	-	154135	68	-	-	-311	-0.2	-6228	Western= extinct?
	Equatorial Guinea	0	1626	58	0	-	-12	-0.71	-234	
	Gabon	14334	22000	85	-330	-2.16	0	0	0	
	Nigeria	-	9041	10	-65	-	-410	-4	-8193	
East Africa	Rwanda	7	435	18	0	0	10	2.47	117	
	Uganda	0	2988	15	0	-	-88	-2.72	-1763	
			333553						-28510	
Pongo										
Southeast Asia	Indonesia	47236	94432	52	-103	-0.22	-685	-0.71	-24113	
	Malaysia	3820	20456	62	0	0	-87	-0.42	-1920	
			114888						-26033	
Hylobatidae										
Southeast Asia	Bangladesh	436	1442	11	0	0	-3	-0.18	-52	
	Brunei Darussalam	263	380	72	-2	-0.89	-2	-0.47	-33	
	Cambodia	322	10094	57	0	0	-127	-1.22	-2850	
	East India	-	-	-	-	-	-	-	-	
	Indonesia	47236	94432	52	-103	-	-685	-	-24113	

					0.22		0.71	
Lao People's Democratic Republic	1490	15751	68	0	0	-78	-0.49	-1563
Malaysia	3820	20456	62	0	0	-87	-0.42	-1920
Myanmar	3192	31773	48	0	0	-310	-0.95	-7445
Thailand	6726	18972	37	0	0	15	0.08	-577
Viet Nam	80	13797	44	-1	-1.21	144	1.08	4434
Yunnan (south China)	-	-	-	-	-	-	-	-

Table 1 Deforestation rate for all countries harbouring populations of ape species (1990-2010). "-": unavailable data.

Bonobo: a brief presentation

Pan paniscus myths and realities

David Beaune

Published in Revue de primatologie

Abstract

Bonobos are our closest living relatives along with chimpanzees. They attract much attention from anthropologists who want to better understand our primate origins and more recently from the public because of their remarkable behavior and matriarchal social system. New published insights from recent years allow us to better know *Pan paniscus*. This review describes the most recent findings: bonobos, chimpanzees, and humans ought to be part of the same genus (*Homo* or *Pan*) according to our genetics. bonobos have impressive cognitive ability to communicate with lexigram and sign-language, solve problems and use tools. Females have high social status in the group due to female association and coalition. The society is not really characterized by female dominant but rather by co-dominance of associated females. They are not purely egalitarian but non-violent and tolerant. Neither lethal aggression nor infanticide were observed and are not expected. Sex has a pivotal role in this pacifist society, which lacks sexual restrictions with the one exception of incest. Bonobos are probably a key species in forest ecology through their seed dispersal mutualism with plants whose fruits they eat. We continue to discover fascinating biological facts about our cousins who are in danger of extinction. A few of these are described here.

Key words: Great apes, Hominid, homosexuality, matriarchal, Pan, sexual behavior.

Résumé

Les bonobos sont nos plus proches parents vivants avec les chimpanzés. Ils attirent beaucoup d'attention de la part des anthropologues qui cherchent à comprendre nos origines simiesques. Plus récemment, ils attirent l’attention du grand public en raison de leur comportement remarquable et de leur système social matriarcal singulier. Les médias et certaines aspirations philosophiques ont rapidement érigé les bonobos comme nos plus proches parents, vivant en société pacifique de végétariens féministes, et gouvernée par le sexe. Mais la barrière entre l’homme et l’animal était sauve pour beaucoup tant que ce lubrique primate ne manifestait aucune capacité à exécuter ce qui fait le propre de l’homme. Or les nouvelles découvertes publiées ces dernières années nous permettent d’en savoir plus sur *Pan paniscus*. Cette revue décrit les résultats les plus récents : Selon les généticiens, bonobos, chimpanzés et humains appartiennent au même genre (*Homo* ou *Pan*) avec plus de 98% de gènes communs et un ancêtre partagé il y à 5 à 6 millions d’années. Il est récemment prouvé que les bonobos possèdent les capacités cognitives pour communiquer mais sans pharynx (langage des signes, lexigramme). Les bonobos peuvent résoudre des problèmes complexes et utiliser des outils. En captivité certains bonobos taillent des pierres, allument du feu avec un briquet ou utilisent une pelle pour creuser. Les femelles ont le statut social le plus élevé du groupe grâce à l'association et à la coalition entre femelles. La société n'est pas vraiment femelles-dominantes, mais plutôt co-dominante. La société n’est pas purement égalitaire, mais non violente et tolérante. Ni les agressions mortelles ni l'infanticide n'ont été observés à ce jour en milieu naturel ou en captivité. Le sexe a un rôle primordial dans cette société pacifique. Il n’y a pas de restriction sexuelle excepté l'inceste. Les bonobos sont une espèce clef dans leur écosystème, grâce au service écologique fournit de dispersion de graines. De plus en plus de découvertes fascinantes naissent au sujet de nos cousins qui sont en danger d'extinction et pourraient disparaître d’ici quelques décennies.

Mots clefs : Comportement sexuels, grands singes, Hominidé, homosexualité, matriarchale, *Pan*

Introduction

Bonobos are one of the large mammal species most recently discovered by science. First informally described in 1929, they were named *Pan paniscus* in 1933 (Coolidge 1933). Since Robert Yerkes in the thirties, bonobos were studied in captivity and more recently in the wild beginning in 1973 with Takayoshi Kano at Wamba field site, DR Congo (Kano 1980). With Congolese wars and political instability, studies in the field were slowed down but research teams persevered and new exciting discoveries about this great ape allow us to better know our cousins' biology and also allow insights into our own origin. This paper reviews the latest news from the bonobos. Some old views of bonobos are obsolete; some previous questions have been answered while others remain unsolved. This review based on recent literature is also punctuated by my own observations with an habituated free-ranging bonobo community at the LuiKotale field site (Hohmann & Fruth 2003c). My main research focused on the bonobo ecology. I recorded 1879 hours of behavioral data within this community of 25-35 identifiable bonobos, through 22 months of field work (2008-2011). Other discoveries, I hope, will astonish you with new insights about one of the planet's most fascinating animals and one of our closest living relatives.

Our closest living relative?

Within our own family of the Hominidae, great apes of the genus *Pan*, including bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), are our closest living relatives. Chimpanzees live in four major populations, including those located in western Africa (*P. t. verus*), equatorial Africa (*P. t. troglodytes* and *P. t. schweinfurthii*), and the Gulf of Guinea region (*P. t. ellioti*); with distinct and full species proposed and still debated today (Gonder *et al.* 2011). Described as pygmy chimpanzees in literature before the 1980s, bonobos have more gracile limbs than chimpanzees but are similar in many other morphological traits and in body size (♀≈33-36kg, ♂≈43-46kg; (Coolidge & Shea 1982; Parish 1996)) to the other *Pan* species. However, their frequently bipedal posture (D'Août *et al.* 2004), their morphology, and neotenic characteristics (Shea 1983) which they share with us (*Homo sapiens sapiens*), caused many anthropologists to propose the bonobo as the best model for our closest living relative.

However, contrary to popular belief, bonobos are not more closely related to us than are chimpanzees. We share a common ancestor with both *Pan* which dates to 5-6 million years ago, and approximately 98% of our DNA (Wildman *et al.* 2003; Patterson *et al.* 2006; Prufer *et al.* 2012) with both species. Bonobos and chimpanzees diverged from 0.93 (Won & Hey 2005) to 2 million years ago (Raaum *et al.* 2005) and are separated by the Congo River, which acts as a biogeographic barrier by splitting the Congo basin. Therefore, both are genetically equidistant to us.

Pan troglodytes and *P. paniscus* are so close to us that an increasing number of scientists propose a fusion of the genus of our cousins *Pan*, with our own genus *Homo*; with the proposed classification: *Homo sapiens* (humankind), *Homo troglodytes* (chimpanzee), and *Homo paniscus* (bonobo) (Wildman *et al.* 2003). This little taxonomic revolution could be difficult for the general public to accept, but an extraterrestrial taxonomist would not hesitate. One day we might accept ourselves as the third chimpanzee (Diamond 1991). Another more philosophical rapprochement is the Great Ape Project (GAP) launched in the 1990s (Cavalieri & Singer 1993). It is an appeal of 36 scientists from different disciplines aiming at the legal equalization of the non-human great apes with humans. The central point of the initiative is the "Declaration on Great Apes", claiming the inclusion of great apes in the "community of equals" and thus securing three basic rights for all great apes: 1. The Right to Life; 2. Protection of Individual Freedom**;** 3. The Prohibition of Torture. Furthermore, the project pleads for the idea of conferring the "moral status of person" on great apes. But beyond religion and ethics, rejection of this idea is mainly due to pressure for maintaining the use of living apes as “biological material” for experimentation in industry (Carlsson *et al.* 2004). We can note that the United States and Gabon are the only remaining countries allowing such research.

A tool maker?

Chimpanzees are well recognized as tool makers in the wild, with cultural variation in usage among populations across Africa (Whiten *et al.* 1999). For bonobos, tool-related behaviors are observed in wild populations but are rare and less sophisticated than those observed in chimpanzees (Kano 1982; Ingmanson 1996; Hohmann & Fruth 2003a). This bonobo difference could be explained by the fact that they inhabit a less challenging environment than chimpanzees with no need for weapons, or may simply the general lack of studies of this species compared to chimpanzees. However, in captivity, tool making and usage by bonobos have both been well described (Jordan 1982; Toth *et al.* 1993; Gold 2002; Mulcahy & Call 2006; Gruber, Clay & Zuberbühler 2010). Kanzi and Pan-Banisha, a famous male and female who have gained widespread attention for their skills in language and have lived in the stimulating environment of the Great Ape Trust of Iowa since 2005 (Savage-Rumbaugh & Lewin 1994). They can light a fire with a lighter, cook a meal, roast marshmallows and perform other impressive tasks. They have the basic stone-tool making skills required to produce usable flakes and fragments by hard-hammer percussion (Toth *et al.* 1993) and their techniques are improving (Schick *et al.* 1999). Their reported tool production and utilization for food retrieval (digging or breaking wooden logs) exhibits *Homo*-like technological competencies (Roffman *et al.* 2012).

The most recent results appear to describe bonobos as having a similar repertoire in captivity, and tool-using capabilities equal to those of chimpanzees (Herrmann, Wobber & Call 2008; Gruber, Clay & Zuberbühler 2010). Bonobos as chimpanzees use less dramatic tools for social purposes, games or comfort (cleaning with specific leaves, use of leaves as an umbrella against rain), while chimpanzees use also impressive reported tool techniques in the context of difficult food-acquisition tasks. Another remarkable point is that just like chimpanzees, female bonobos are more willing to use tools than males (Gruber, Clay & Zuberbühler 2010). Because wild and captive bonobos share the same cognitive abilities required for tool use, such behavior is expected to occur in wild bonobos as well.

Communication

Bonobos, like gorillas and chimpanzees, show a human-like asymmetry in language-related brain areas, which has been correlated with language dominance (Cantalupo & Hopkins 2001). But articulation of speech is physically impossible and language is restricted to vocalizations and gestures (Pika, Liebal & Tomasello 2005; Pollick & de Waal 2007). We share several communicative roots like the gestural NO by head shaking (Schneider, Call & Liebal 2010) and almost all of these are understood by humans. Gestural communications include sexual invitation with body posture and hand raising, begging, embracing, mouth/tongue kissing, kicking, slapping, etc. with facial nuance and context dependence (Pika, Liebal & Tomasello 2005).

Apes cannot ‘speak’. They can however communicate a wide range of information and are even able to talk with us with the help of technology. Kanzi understands spoken English and communicates with a lexigram keyboard. He also modulates his vocalization with evident structural differences produced within a specific semantic context (Taglialatela, Savage-Rumbaugh & Baker 2003). A similar structural difference was observed in other captive bonobos which use a specific acoustic structure in long and complex call sequences related to a precise type of food. This suggests that bonobo food-calling sequences convey meaningful information to other group members (Clay & Zuberbuhler 2009).

In the wild, bonobos exchange long distance calls (high hoot) between groups (Hohmann & Fruth 1994). What kind of information do they exchange? The study of communication in wild bonobos is promising and may lead to fascinating discoveries.

A female dominant society?

Bonobos live in a male-philopatric structure. This means that males are born and die in the same group while females of 6–13 years emigrate to neighboring groups (Furuichi *et al.* 2012). Males will stay all their lives with their mothers. Females are accepted into new groups weaving future alliance bonds. Female chimpanzees do not have frequent social interactions with other females, whereas female bonobos maintain close social associations with one another (Furuichi 2011).

The result is a singular primate society: a matriarchal bonobo society in clear contrast with the patriarchal societies of chimpanzees, other primates and most human societies (Parish 1996; Sommer *et al.* 2011). This unique trait attracted feminists, public attention and debate about male-female dominance. In early studies (mainly male) scientists described this behavior as "strategic male deference" or males being chivalrous to females as a strategy to obtain sex. This made it easier to admit female dominance in bonobo groups (Parish, De Waal & Haig 2000). Females most often initiate sexual interactions and ranging behavior (Furuichi 2011), have priority of access to preferred food (Hohmann & Fruth 1993; White & Wood 2007) and will sometimes chase or be aggressive towards males (i.e. the definition of 'dominance'; NB: not within chimpanzees). Females are so influential in the groups that mothers improve the mating success of their sons when present (Surbeck, Mundry & Hohmann 2011). In male-male aggression, mothers and females can intervene and decide the outcome of the situation, and eventually influence their son's rank in the hierarchy (Furuichi 2011). Despite modest physical dimorphism (female body size is 82.5% that of males) females gain power by cooperation and coalition formation (Parish 1996; White & Wood 2007). However, female dominance over males is not a rule. Males are consistently dominant in dyadic interactions (White & Wood 2007). To conclude, it is clear that adult females occupy high dominance status in bonobo societies and that females are rather co-dominant to males (Surbeck *et al.* 2012). Differences in dominance among individuals are slight but measurable (see below) but we should keep in mind that bonobos show nothing that is comparable to the strong dominance with submission enforced by violence that is characteristic of chimpanzee societies. Are we close to an egalitarian society? Not really, but non-violence gives us this impression.

A peaceful vegetarian society?

Because they use sexual behavior in several contexts where other species use aggression, bonobos may be viewed as peaceful. However several injuries have been observed in captivity and in the wild, resulting from beatings, or biting on fingers, faces, or genitals (Parish, De Waal & Haig 2000), pers. obs). Recently, the public was shocked by a case of cannibalism among wild bonobos where a baby was consumed by a group, including the mother (Fowler & Hohmann 2010). We should note that the cause of death remains unknown and violence was not observed. Before the carcass was eaten (it was, after all, meat), the mother, with great affection, carried her offspring's body around with her for a whole day. Indeed, bonobos are not the pure vegetarians that we first thought them to be (Figure 7). Bonobos kill and eat duikers, birds, rodents and monkeys (Hohmann & Fruth 1993; Hohmann & Fruth 2008; Surbeck & Hohmann 2008; Surbeck *et al.* 2009). However, although bonobos appreciate and are excited by meat, they are not organized hunters and carnivory thus remains opportunistic and accounts for only a marginal part of their diet (Oelze *et al.* 2011), i.e., 0.9% ± SE 0.2 of feeding sessions; N = 1879 hrs of observation (Beaune 2012).

Although linear dominance can be determined by agonistic interactions, bonobos are non-violent and mainly engage in chasing acts, submissive behaviours and deference (Hohmann & Fruth 2003b; Surbeck, Mundry & Hohmann 2011). Bonobos are highly tolerant and cooperative (Hare *et al.* 2007). While most primate groups have territorial conflicts, bonobos behave peacefully with neighbouring community, with a large inter-group home range overlap (at Wamba 66% of the group's home range overlaps with those of neighbour groups (Kano & Mulavwa 1984)). When two groups meet, they often engage in inter-group sexual relations (often female-female), grooming, feeding and foraging together, and sometimes sleeping at the same nesting place (Hohmann & Fruth 2002; Furuichi 2011). So far, infanticide and lethal aggression have never been observed in *Pan paniscus*. We can definitively say that the bonobo has a peaceful nature.

Figure 7 Female Olga and her daughter Opale eating a red colobus (*Procolobus tholloni*), opportunistically killed by the group.

The most lascivious hominid?

For the public, the bonobo is our lubricous cousin, performing Kama Sutra positions all day long (de Waal 1997). Actually, the frequency with which bonobos engage in sex is less than an average of 0.3 copulation/hour (Furuichi & Hashimoto 2002), with intercourse lasting less than a minute (usually a few seconds). Compared to us, bonobos' frequency of intercourse is definitely higher, with humans averaging 1 to 3 marital coitus per week, the freqeuncy declining with age (Kinsey Institute 2012). The length of coitus fo rhumans is generally longer than a minute with an average of 5 min for humans (Kinsey Institute 2012). Bonobos do not have more sex than chimpanzees, nevertheless females of this species do have more sex and start earlier in life than male bonobos (Takahata, Ihobe & Idani 1999; Hashimoto & Furuichi 2006). Most importantly females have sex during non-fertile periods or in non-swelling episodes (Furuichi & Hashimoto 2004). And when fully tumescent, sexual swelling signals occur even during non-conceptive periods. This is called "pseudo-estrus" (Furuichi 2011). Thus females with true and confusing estrus signals are proportionally more numerous than females displaying no estrus signals so they are less monopolizable by an alpha male (preventing sexual harassment and infanticide) (Furuichi 2011). See Figure 8 for swellings). Male bonobos do not sexually coerce females (Hohmann & Fruth 2003b) and therefore, their sexual solicitation has to be accepted by the female for intercourse to occur. This strategy, contrasting with chimpanzees, is evolutionarily stable and quite similar to behaviour in most human societies (except that our species lost the receptive signals potentially as a result of similar selective pressures).

Sex is routinely used for non-reproductive goals (tension-reduction, reconciliation, bartering for social favors, and sex for food exchanges). Behavioral observations support the hypothesis that sex reduces tension and is the basis of this largely peaceful society (Hohmann & Fruth 2000; Palagi, Paoli & Tarli 2004; Hare *et al.* 2007) and now scientists are trying to test this hypothesis through hormonal experimentation (Hohmann, Mundry & Deschner 2009; Wobber *et al.* 2010).

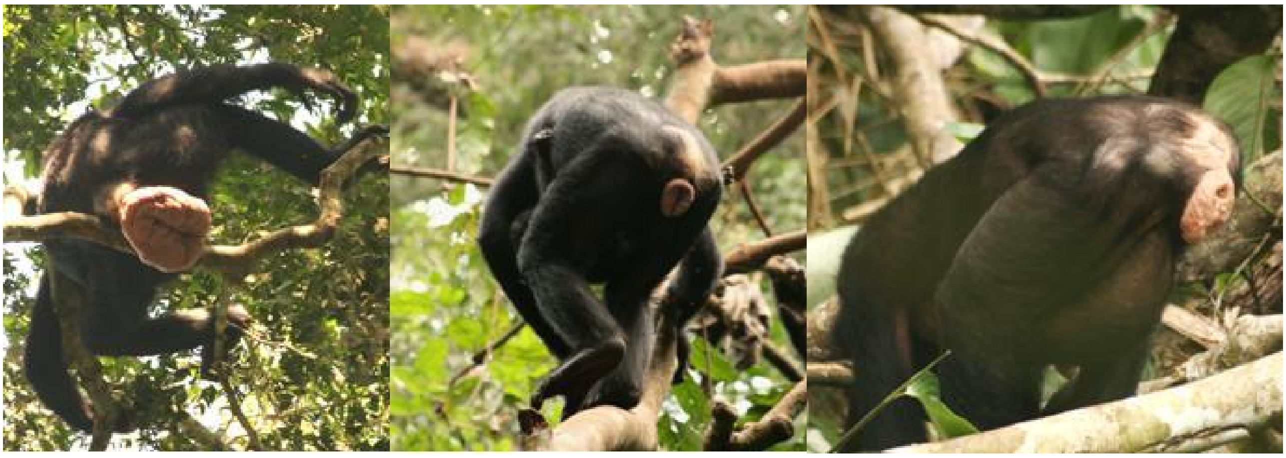

Figure 8 Female bonobos' swellings

Sexual taboos? Homosexuality does not matter…

Bonobos practice public sex (Clay & Zuberbühler 2012) rather than the more secretive sexuality of humans and chimpanzees. Bonobos are bisexual apes and homosexual encounters are common, especially among females (Fruth & Hohmann 2006). Female bonobos engage in a unique sexual behavior also found in humans (tribadism) termed genito-genital (GG) rubbing in which they embrace ventro-ventrally and rub their genital swellings together with rapid sideways movements (Hohmann & Fruth 2000) (Figure 9). Sex seems to be the cement for social bonds. This is why females use it predominantly for their alliance. Sex with high-ranking females could be strategic for subordinates, who can call loudly an audience to acknowledge the scene (Clay & Zuberbühler 2012). Bonobos can have oral, manual and foot sex. They perform multiple positions not found in other non-human primates (such as ventro-ventral or missionary position in humans). Males can be observed mounting other males without intromission, dorso-dorsally rubbing their scrota with sideways movements, or performing face to face ersatz fencing with erect penises. Juveniles can also be involved (de Waal 1997), pers. obs). Bonobos seem to have no limits to the choice of sexual partners with the exception of incest.

Gardener of the forest?

The ecological role of the bonobos has been recently studied at LuiKotale (Beaune 2012). Bonobos are efficient seed dispersers; they spend ≈3.5 hrs/day swallowing the seeds of trees, lianas and herbs of more than 91 species and disperse them at very long distances (0-4.5km). In its entire lifespan, a bonobo should disperse almost 12 million seeds (or 9 tons; excluding seeds <2 mm such as *Ficus* spp). The great majority of the seeds passed through the gut is viable (34/35 tested species). Compared with seeds not passed through the gut, bonobos' seeds germinate faster and at a higher rate. Furthermore, seeds disseminated by endozoochory with bonobos are better able to escape seed predators, thank to dung beetles attracted by bonobos' feces (Beaune *et al.* 2012a). For certain species such as the velvet tamarind, bonobos are germination activator (Beaune *et al.* submitted). In a Congo forest we estimate that 65% of the individual trees in the forest community are disseminated by bonobos. The great majority of the tree species does not recruit and self-replace without seed dispersal (18/19 plant species). Bonobos seem to be tree planters of the Congo forest.

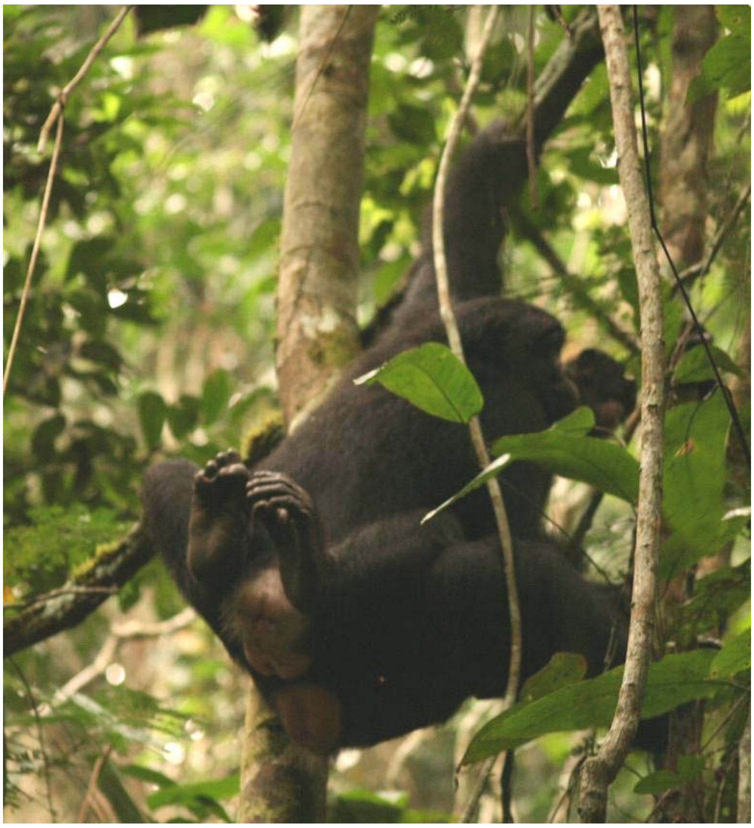

Figure 9 Female-female genito-genital (GG) rubbing

Threatened by extinction

Bonobos are limited to areas south of the Congo River. Their survival depends on the conservation policies and decisions of the one country were they live: the Democratic Republic of Congo. The species' range covers 500,000 km² of the Cuvette Centrale (Thompson, Hohmann & Furuichi 2003). Deforestation in DRC occurs at an average rate of 311,000 ha/year (FAO 2010), but human hunting and bush meat trafficking is the main cause of bonobo extinction (Hart *et al.* 2008b). Bonobo numbers are hard to estimate. They could number between 10,000 and 50,000 but it is also possible that there are fewer than 10,000 (Thompson, Hohmann & Furuichi 2003). Bonobo populations are decreasing and the species is in danger of extinction (IUCN 2012).

Conclusion

Myths… and realities

Bonobos are our closest living relatives…

- ✓ No more than chimpanzees.

Bonobos do not use tools…

- ✓ They do. Sophisticated tools (such as chimpanzees') were not observed in wild populations but bonobos do use and built tools.

Girls' power is within bonobos…

- ✓ Not really. Females' alliance in this matriarchal society allows dominance towards males. But bonobos are rather co-dominant.

Bonobos are peacefull…

- ✓ Yes. Lethal aggression was never reported, although aggressions exist.

Bonobos are the primate sex-champion….

- ✓ No. Bonobos use sex for social issues in various ways and without taboos but no more often than chimpanzees in frequency.

Homosexuality is common in bonobos…

- ✓ Yes. Especially female-female.

Bonobos can disappear…

- ✓ Yes.

The Congo forest

Seed dispersal strategies and the threat of defaunation in a Congo forest

Authors

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Abstract

Seed dispersal mode of plants and primary interactions with animals are studied in the evergreen Afrotropical forest of LuiKotale, at the south-western part of Salonga National Park (DR Congo). We first analysed seed dispersal strategies for a) the plant species inventoried over a decade at the study site and b) the tree community in 12 × 1-ha census plots. Our analyses of dispersal syndromes for 735 identified plant species show that 85% produce fleshy fruits and rely on animals for primary seed dispersal. Trees depending on animals for primary dispersal dominate the tree community (95%), while wind-dispersed and autochorous trees are rare in mixed tropical forests. A list of frugivorous vertebrate species of the ecosystem was established. Among the fruit-eating vertebrate species identified in the ecosystem, forest elephants and bonobos are threatened with extinction (IUCN 2012). Although most of the species listed previously are internationally and regionally protected, ALL the species we observed dispersing seeds are hunted, fished or trapped by humans in the area. With the exception of bush pigs, seed predators, mainly small-sized animals, are generally not targeted by hunters. As a consequence, we expect human pressure on key animal species to impact the plant community. We suggest defaunation to be considered as major conservation problem. Thus, not only for the sake of animal species but also for that of plant species conservation, anti-poaching measures should have priority in both “protected” and unprotected areas. Defaunation could bring a new impoverished era for plants in tropical forests.

Résumé

Dans la forêt tropicale humide de LuiKotale, au sud-ouest du parc national de la Salonga (RD Congo), nous avons analysé a) l’ensemble des stratégies de dispersion des plantes inventoriées dans le site d’étude depuis une décennie, puis b) des plantes recensées dans l’inventaire de la communauté d’arbres sur 12 parcelles de 1 ha. D’après l’analyse des syndromes de dispersion de 735 espèces de plantes identifiées, 85 % produisent des fruits adaptés pour la consommation par des animaux qui dispersent leurs graines. Les arbres dont la dispersion primaire est zoochore dominent la communauté (95%), alors que les arbres autochores et dispersés par le vent sont rare. Nous avons identifié les espèces de vertébrés frugivores de l’écosystème, parmi lesquelles les éléphants de forêts et les bonobos qui sont menacés d’extinction (IUCN 2012). Bien que protégés internationalement, tous ces animaux sont chassés, pêchés ou piégés. Les prédateurs de graines, principalement des petits animaux (rongeurs et oiseaux), ne sont pas des espèces cibles pour la chasse à l’exception des potamochères. La pression humaine devrait affecter la communauté végétale par l’élimination d’espèces clefs de l’écosystème. La défaunation risque d’être la cause d’une nouvelle ère d’appauvrissement spécifique des plantes de forêt tropicale. Cette défaunation doit être considérée comme un problème majeur de conservation. Les mesures anti-braconnage doivent être une priorité dans les zones protégées et « non protégés » et ceci non pas seulement pour la conservation des espèces animal mais aussi pour la conservation des espèces végétales.

Keywords: bush meat; seed dispersal; defaunation; Democratic Republic of the Congo; forest ecology; frugivores; human pressure; seed predators; tropical rainforest; zoochory

Introduction

A critical problem in tropical forest conservation is hunting and poaching for the commercial bush meat trade, and this is particularly true in the Congo Basin (Bowen Jones & Pendry 1999; Wilkie & Carpenter 1999; Fa, Peres & Meeuwig 2002). The Congo Basin is of particular interest investigating the link between defaunation and forest conservation, as it is home to the second largest rainforest block in the world. Almost half of its forests (about 154 million ha) are located in the Democratic Republic of Congo (DRC) (FAO 2010). A total of 60% of the DRC is covered by forest with high biodiversity, but these areas where defaunation is particularly severe are among the least studied in Africa (Bowen-Jones and Pendry 1999; Hart *et al.* 2008). With a total extraction of 4.9 tons of wild mammal meat each year (vs. 0.15 in Neotropical forests (Fa, Peres & Meeuwig 2002)), the rate of exploitation has been judged unsustainable for Afrotropical forests. Causes and consequences of the on-going “bush meat crisis” (Peres & Palacios 2007) are similar across Africa, and where still available, large and medium-sized animals are the most targeted species (Wright *et al.* 2007; Poulsen *et al.* 2009). This impact on animal species and populations has an impact on plants (Terborgh *et al.* 2008): Ecosystems are shaped by animal-plant interactions, and many plant species depend on animals for seed dispersal (Forget *et al.* 2006; Dennis 2007; Forget *et al.* 2011).

To evaluate the impact of hunting on plant species, we need to 1) estimate how many plant species are dependent on animals for seed dispersal; 2) census primary seed dispersers and seed predators; and 3) assess their relative hunting pressure.

1) In tropical areas, zoochory is dominant and seems to outperform other dispersal modes such as barochory (by gravity), hydrochory (by water), anemochory (by wind) or autochory (by ballistic mechanisms) (Gautier-Hion *et al.* 1985; Willson 1993; Jordano 2000; Levey, Silva & Galetti 2002). However, community-scale assessments are rare in the Afrotropics. Studies must therefore assess the abundance and diversity of zoochorous plant species in the ecosystem.

Recent studies indicate that seed dispersal plays a prominent role in recruitment limitation, gene flow, metapopulation dynamics, colonisation potential and plant migration in response to past and future climate change, maintenance of biodiversity, and more (Schupp, Jordano & Gomez 2010). As predicted by models (Muller-Landau 2007) and shown in field surveys (Forget & Jansen 2007; Stoner *et al.* 2007; Wright *et al.* 2007; Terborgh *et al.* 2008; Brodie *et al.* 2009; Vanthomme, Bellé & Forget 2010), defaunation leads to the empty forest syndrome (Redford 1992; Terborgh *et al.* 2008) with noticeable consequences for the structure and dynamics of the habitats concerned. Currently, three not mutually exclusive conclusions are possible concerning the impact of hunting for tropical forest plant communities: (1) Hunting reduces the amount and efficiency of seed dispersal for plant species whose seed dispersal agents include hunted animals (Beckman & Muller-

Landau 2007; Wang *et al.* 2007); (2) Hunting alters the species composition of the seedling and sapling layers (Stoner *et al.* 2007); (3) Selective hunting (*i.e.* pressure on large/medium-sized instead of small animals) leads to differential predation on seeds, with more predation on small seeds (Mendoza & Dirzo 2007). As a consequence of hunting pressure, the tropical forest with plant species disseminated by animals might change with regard to biodiversity, species dominance, survival, demography, and spatial and genetic structure (Wright *et al.* 2007). Although studies have assessed diversity and abundance of plant species in Central African ecosystems such as the Congo Basin (Howe & Smallwood 1982; Idani *et al.* 1994; Boubli *et al.* 2004), certain areas are underexplored and require urgent assessment due to the continuing rapid decline in biodiversity.

2) Plants can interact with many different animals, such as seed predators and/or seed dispersers (Gautier-Hion *et al.* 1985; Jordano, Bascompte & Olesen 2003). Some of these animals are prey for hunters while others are not (or are caught opportunistically). Differential human pressure on fauna could affect plant reproductive parameters. Seed predators (e.g. small rodents) may be less affected by human predation than primary seed dispersers (such as primates, bats, and birds (Wilkie & Carpenter 1999)). Therefore, a census of primary seed dispersers and seed predators is required.

Among the seed predator guild, some species are strictly seed predators (e.g., bush pigs: (Beaune *et al.* 2012b) while others are also secondary dispersers (scatter hoarders, ruminants: (Feer 1995; Vander Wall, Kuhn & Beck 2005; Nyiramana *et al.* 2011; Beaune *et al.* 2012a).

3) The relative hunting pressure on seed predators depends on a variety of factors such as a species' conspicuousness, its arboreality, or body mass. The latter i.e. shows a large variation not only between but also within species (with weights from < 1kg to > 100kg, e.g., bush pig). Within the seed predator community, the seed size panel predated is thought to be linked to seed predator size: the differential predation hypothesis (DPH). The removal of large/medium-sized seed predators such as bush pigs (one of the preferred prey of hunters (Wilkie & Carpenter 1999)) could trigger differential predation on seed species; with large-seeded plants escaping predation with consequences on seed mortality and recruitment (Mendoza & Dirzo 2007).

Here we provide an assessment of seed dispersal strategies within a plant community in a Congo forest. In this study (1) we determine plant strategies and estimate the number of species within a tree community that are dependent on animals for seed dispersal and the relative importance of their abundance/dominance relative to other strategies; (2) we inventory the community of vertebrates interacting with seeds (primary seed dispersers and seed predators) and assess whether or not an animal is hunted by humans; (3) we present the first data on ichthyochory in Africa. Reports on fruit-eating fish are limited although fruits of some trees that inhabit riverine and seasonally inundated forests are already known to be eaten by fish (Hulot 1950; Horn *et al.* 2011).

Methods

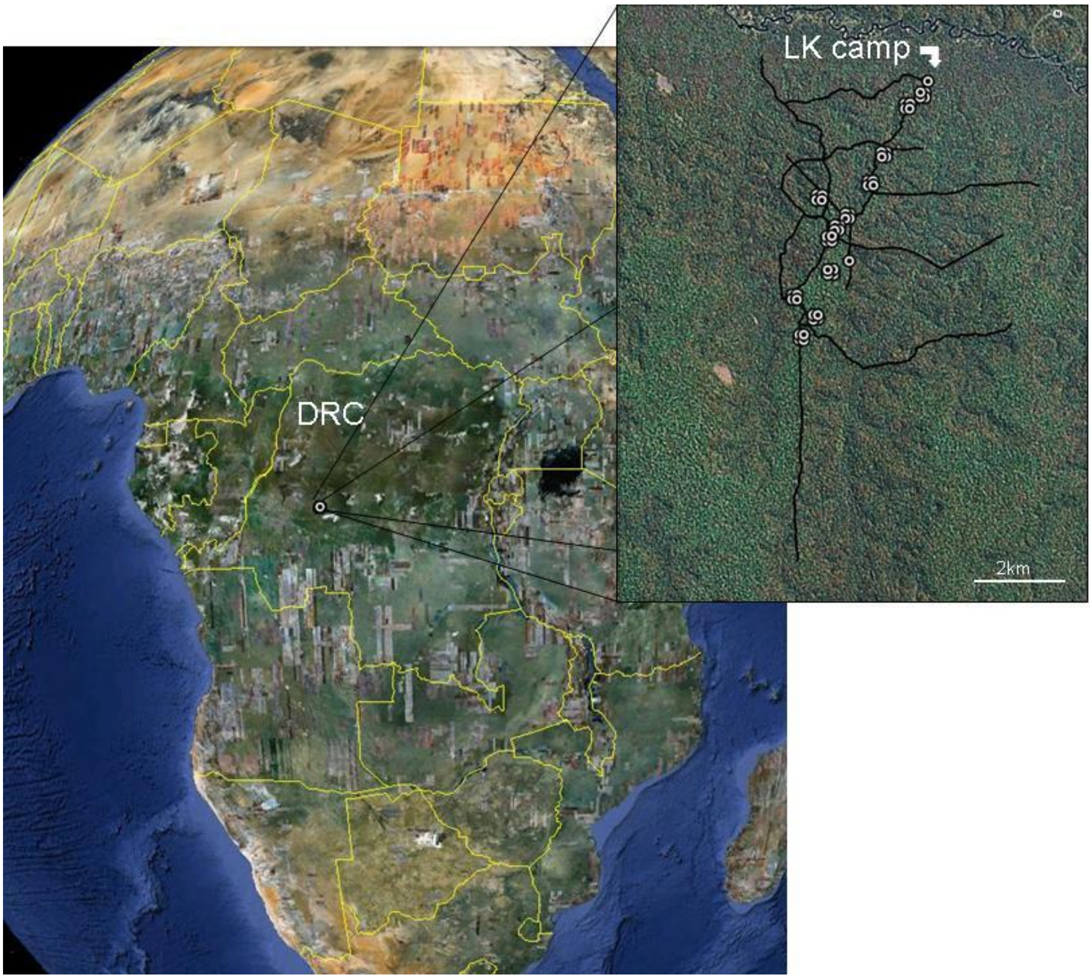


Figure 10 Map of the field site and location of plots (white dots), with main transects shown as black lines.

Study site

The LuiKotale research site (LK) is located within the equatorial rainforest at 2°47' S - 20°21' E, at the south-western fringe of the Salonga National Park (DRC), and in the same continuous forest block as that park. (Figure 10). Classified as a world heritage site, Salonga Naational Park is the largest protected rain forest area in Africa and the second largest protected rainforest in the world (33.346 km², (Grossmann *et al.* 2008). The study site is a primary evergreen tropical lowland rainforest ancestrally owned and used by Lompole village (17 km away). The site covers >60km² with a network trail of 76km. Since 2001, subsistence hunting and harvesting within the site has ceased for the sake of research (Hohmann & Fruth 2003). The climate is equatorial with abundant rainfall (>2000mm/yr), a short dry season in February and a longer one between May and August. Mean temperature at LuiKotale ranges between 21°C and 28°C, with a minimum of 17°C and a maximum of 38°C (2007-2010). Five major vegetation types are distinguished in the site: (1) mixed tropical forest on *terra firme*, (2) monodominant forest dominated by *Monopetalanthus sp.* (3) monodominant primary forest dominated by *Gilbertiodendron dewevrei* (4) temporarily inundated mixed forest (5) permanently inundated mixed forest. Well-drained habitats (1-3) dominate site cover, with 73% of heterogeneous forest composition and 6% of homogeneous composition. Seasonally or permanently flooded habitats (4, 5) represent 17% and 4% of the cover respectively (Mohneke & Fruth 2008).

Plant species & dispersal mode

Between 2002 and 2010, botanical data collection took place as part of the long-term project «The *Cuvette Centrale* as a Reservoir of Medicinal Plants»: Fertile plant material was collected at least in triplicate along natural trails (31 km), standardized transects (8 km), in plots, and opportunistically. Each plant was identified by vernacular name, described, tagged with a unique collection number, and herborised. The dried vouchers were shipped to Kinshasa, taxonomically determined and incorporated into the herbarium of the INERA at Kinshasa University. Duplicates of specimens were shipped to herbaria in Belgium (Jardin National Botanique de Belgique, Meise) and Germany (BSC, Munich) for verification and identification by specialists. By May 2010, the herbarium consisted of 7300 vouchers (Fruth 2011). For the purpose of our study, the dispersal strategies of each inventoried species from LK were categorized through diaspore anatomy and tissue analysis as (1) zoochore (fleshy fruit indicating zoochory by primary dispersers), (2) hydrochore (drift fruit), (3) anemochore (achene or samara) or (4) autochore. (dehiscent tissue). If fruit was unavailable, dispersal strategy was inferred from literature (Gautier-Hion *et al.* 1985; White & Abernethy 1997; Geerinck 2005).

Abundance and diversity of animal-dispersed trees

From February to June 2011, 12 plots of 1 ha (100×100m) were randomly positioned in mixed tropical forest. Within these plots, all trees ≥ 10cm DBH (diameter at breast height) were measured and identified in order to assess the relative importance of zoochorous trees in the community. Plot difference was tested with a Shapiro-Wilk normality test. and tree densities and average DBH were calculated by one-way analysis of variance (ANOVA) (Boubli *et al.* 2004).

The proportional abundance of zoochorous trees found in the plots was compared to the theoretical proportion according to the number of zoochorous species censused on the plots, using a Binomial test (with power analysis of the test specified if H_0 rejected). Analyses were performed using R 2.13 (R Development Core Team 2011).

Vertebrate seed dispersers and predators

Mammals: From January 2010 to June 2011, a list of terrestrial frugivorous mammals was compiled from *ad libitum* direct visual observation and camera traps (Two Wildeview series3 & three Bushnell® Trophy Cam™: Video mode 60s/1s interval/normal sensitivity, were installed for 82 days and nights) at the LK site. The LK site was explored on and off the trail system (>10km/day) and species were recorded opportunistically. To identify seed predators, camera traps were randomly positioned throughout the forest and baited with different seeds (Beaune *et al.* 2012b).

Birds: Frugivorous birds were directly observed from January 2010 to June 2011 and from earlier studies (Surbeck in (Fruth & Hohmann 2005; BirdLife-International 2011).

Fishes: Fishes were captured for market by local fishermen in the Lokoro River and affluents. Catches were brought to scientists for census. Stomach contents were analysed from March to June 2011 in order to find seeds in the bolus.

Animal species were identified and their main interaction with seeds (1-primary seed disperser; 2-seed predator; 3-neutral) inferred from literature, video records and unpublished data observation from the field-site (Gautier-Hion *et al.* 1985; Kingdon 1997; Bourson 2011; Beaune *et al.* 2012a; Beaune *et al.* 2012b). Observed frugivores were considered to be seed dispersal vectors when intact seeds were horizontally moved in space by endo- or ectozoochory. Seed predators were observed destroying seeds (Beaune *et al.* 2012b). Through lack of evidence of secondary dispersal, only primary dispersal was considered. Species status followed the IUCN red list of threatened species (IUCN 2012). The local threat was assigned for each species (poached, hunted or fished) by crosschecking questionnaires from experienced local hunters (n=28), the literature (Wilkie & Carpenter 1999; Poulsen *et al.* 2009) and *ad libitum* observation of catches from January 2010 to June 2011.

Results

How many plant species are zoochorous?

Within the LK area, dispersal syndromes of a total of 735 species were analysed. These included 403 tree, 130 shrub and 202 liana species belonging to 77 plant families. Of these species, 85.0% produce fleshy fruits and are primarily dispersed by animals (zoochory).

Zoochory is the dominant seed dispersal strategy among trees (83.9%), shrubs (97.7%) and lianas (79.2%). Figure 11. The proportion of zoochorous shrubs is significantly higher than for trees and lianas (test of proportion, χ^2=15.65 and 21.51 respectively df=1, p-values$\leq$0.001; power analysis=100%). There was no significant difference in the proportion of trees and lianas dispersed by animals (χ^2=1.70 df=1, p-value=0.2).

Herbaceous species were excluded from this study because it was difficult to distinguish species dispersed by multiple vectors (such as wind+ant, water+fish, etc.). Nevertheless, we identified 123 herbaceous species which may use animals as dispersal vectors (first or secondary).

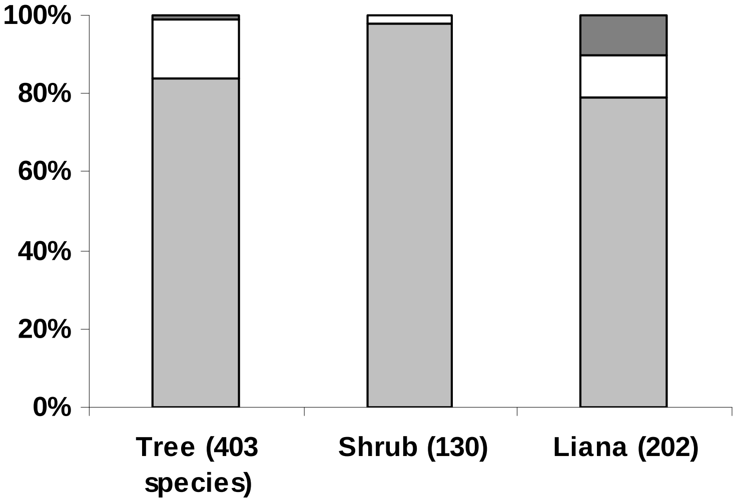


Figure 11 Proportions of species characterized by the different seed-dispersal strategies among tree, shrub and liana species of LK. Grey = animal-dispersed, white = autochorous, black = wind-dispersed.

Abundance and diversity of animal-dispersed trees

All 12 plots were similar in structure (size-class distribution: no significant difference in DBH class size: ANOVA, F = 1.3, p-value = 0.25; normal distribution of tree density: W = 0.93, p-value = 0.43). Within the 12 1-ha plots, zoochorous species accounted for a much greater proportion than did other dispersal strategies. Zoochorous species accounted for a mean of 88.1%, ± SE 0.7, $CI_{95\%}$ = [86.6-89.6%] of all species present in the plots. Autochorous species accounted for a mean of 10.6%, ± 0.7, $CI_{95\%}$= [9.0-12.1%], while wind-dispersed species were nearly absent (0.5%, ± 0.2, $CI_{95\%}$ = [0.0-1.0 %]) (Figure 12). If tree species dispersed by different vectors tend to be equally abundant, then proportions of individual trees dispersed by different vectors should reflect the proportions of species dispersed by these vectors. However, trees belonging to zoochorous species accounted for a higher proportion of all individual trees than that expected under equal abundance of species with different dispersal strategies (p-value < 0.001, power analysis = 100%). A proportion of 95.1% ± 0.7 of all individual trees in the plots belonged to animal-dispersed species ($CI_{95\%}$ = [93.5-96.6%]). Anemochorous and autochorous species account for smaller proportions of all individual trees present in the 12 1-ha plots compared to the proportion of all species that they account for (p-values < 0.001, power analysis = 100%). Among the 25 most dominant species (i.e. from the genera *Dialium*, *Polyalthia*, *Chaetocarpus*, *Drypetes*, *Strombosiopsis*, *Strombosia, Sorindeia*, etc.) representing +78% of individual trees (4098/5234 trees), only one is autochorous: *Scorodophloeus zenkeri*, 23rd in rank with a total of 63 individual trees.

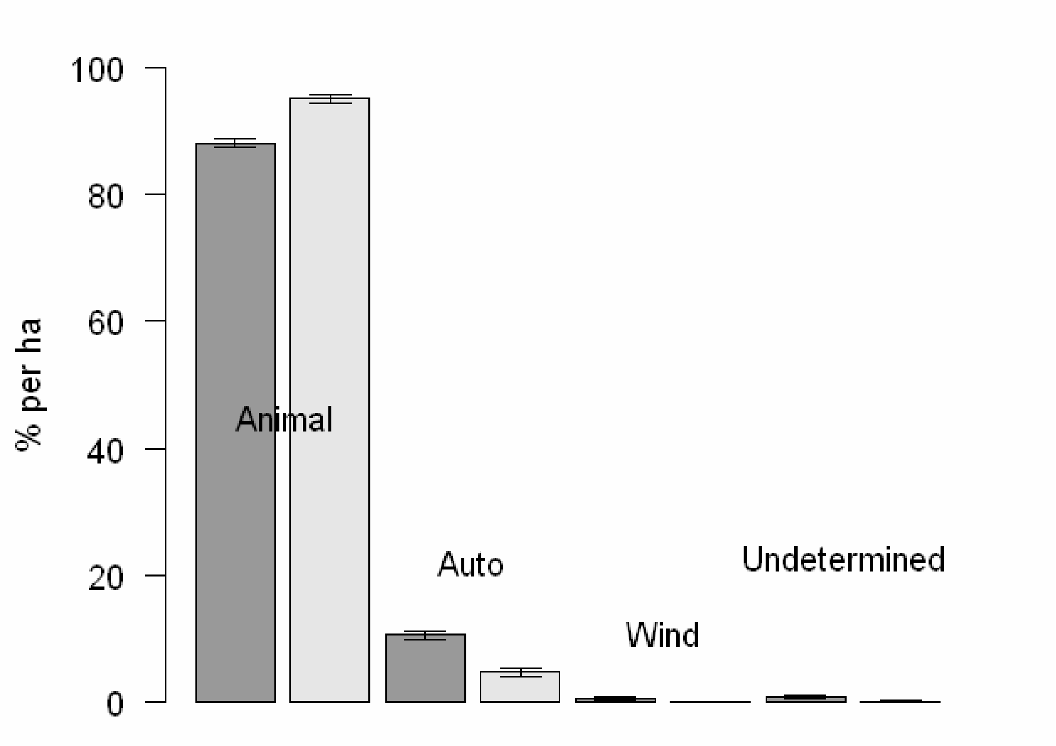


Figure 12 Proportion of different dispersal modes for all species (dark bars), and for all individuals (light bars) present in 12x1-ha plots. Error bars indicate SE.

Vertebrate seed dispersers and predators

Thirty eight non-aquatic vertebrates eating fruit were identified at LK. Some of these fruit-eating species, namely bushbuck (*Tragelaphus scriptus*), common genet (*Genetta genetta*), potto (*Perodicticus potto*), tree hyraxe (*Dendrohyrax dorsalis*), water chevrotain (*Hyemoschus aquaticus*), and west African linsang (*Poiana leightoni*), so far did not show evidence of seed dispersion, and thus were not classified as seed dispersers. Other identified species, namely Afep pigeon (*Columba unicincta*), African green pigeon (*Treron calvus*), Congo peacock (*Afropavo congensis*), crested guineafowl (*Guttera pucherani*), grey parrot (*Psittacus erithacus*), streaky-throated barbet (*Tricholaema flavipunctata*), may both eat and disperse seeds of different plant species. Thus, it was not possible to assign a clear category to these animals. Finally, 31 fruit-eating species (including a non-exhaustive list of fishes) were identified as seed dispersers. All of them are exploited for meat (

Table 2), including threatened species protected by law such as elephants and bonobos. Smaller frugivorous birds and bats which are usually not hunted are probably present but were not recorded. Five vernacular species of fish belonging to five genera (*Xenocharax*, *Distichodus*, *Clarias*, *Malapterurus*, *Schilbe*) were recorded to swallow fruits and seeds. Fruits from the forest gallery are used as bait by local people. Intact seeds of *Parinari congensis*, *Treculia africana*, *Uapaca* sp., etc. have been found in either stomach, intestines, or close to the anus of several fishes (n = 23 content analyses). The last three genera mentioned in Table 1 are catfishes (order Siluriformes) reaching +1m. No amphibians or reptiles were observed to feed on fruits in LK but this cannot be excluded.

The seed predator guild comprises 19 identified species (
Table 3). It is mainly comprised of seed-eater specialists such as rodents and birds (family Estrildidae with *Estrilda paludicola*, *Nigrita bicolour*, *N. canicapillus*, *Spermophaga haematina*). Snare trapping targets specifically the largest terrestrial rodents (Kingdon 1997), such as porcupines (*Atherurus africanus*, 1.5-4kg) or giant pouched rats (*Cricetomys emini*, 1-1.4kg). Squirrels (family Sciuridae**)** and anomalures (*Anomalurus derbianus*) are hunted with weapons when encountered, as are birds (francolin: *Francolinus lathami*). Bush pigs (*Potamochoerus porcus*) with their large body mass (45-115kg) are among hunters' preferred prey ((Wilkie & Carpenter 1999; Poulsen *et al.* 2009). The proportion of seed predator species hunted in their guild is with only 1/3rd as important of the seed disperser species significantly less important (37% to 100%, χ^2=22.4, df = 1, p-value<0.001, power analysis=100%). Yet, unlike the bonobos and the forest elephants, none of the seed predators are threatened by extinction (
Table 2). According to hunters, seed predator species such rodents and passerines are not targeted preys of hunting expeditions, owing to their small size. Most seed predator species are opportunistically shot or trapped, except for *P. porcus*, the largest seed predator, favouring the hypothesis that frugivores are hunted more intensively than seed predators and by that the differential predation hypothesis.

Class	**Familly**	***Species***	**Name**	**Status**	**Population trends**	**Threats**
Mammalia	**Bovidae**	*Cephalophus callipygus*	Peter’s duiker	LC	↓	Hunted
		Cephalophus dorsalis	Bay duiker	LC	↓	Hunted
		Cephalophus monticola	Blue duiker	LC	↕	Hunted
		Cephalophus nigrifrons	Black-fronted duiker	LC	↓	Hunted
		Cephalophus silvicultor	Yellow-backed duiker	LC	↓	Hunted
	Cercopithecidae	*Allenopithecus nigroviridis*	Allen’s swamp monkey	LC	?	Hunted
		Cercocebus chrysogaster	Golden-bellied mangabey	DD	↓	Hunted
		Cercopithecus cephus ascanius	Red-tailed monkey	LC	?	Hunted
		Cercopithecus mona wolfi	Wolf’s monkey	LC	?	Hunted
		Cercopithecus neglectus	De Brazza’s monkey	LC	?	Hunted
		Lophocebus aterrimus	Black mangabey	NT	↓	Hunted
	Hominidae	*Pan paniscus*	Bonobo	E	↓	Poached
	Elephantidae	*Loxodonta africana cyclotis*	Forest elephant	V	↑	Poached
	Pteropodidae	*Epomophorus grandis*	Epauletted fruit bat	DD	?	Hunted
		Hypsignathus monstrosus	Hammer-headed bat	LC	?	Hunted
		Lissonycteris angolensis	Angola fruit bat	LC	↓	Hunted
	Viverridae	*Civettictis civetta*	African civet	LC	?	Hunted
		Nandinia binotata binota	African palm civet	LC	?	Hunted
Aves	**Bucerotidae**	*Bycanistes albotibialis*	White-thighed hornbill	LC	?	Hunted
		Ceratogymna atrata	Black-casqued hornbill	LC	?	Hunted
		Tockus camurus	Red-billed dwarf hornbill	LC	?	Hunted
		Tockus fasciatus	African pied hornbill	LC	?	Hunted
		Tropicranus albocristatus	White-crested hornbill	LC	?	Hunted
	Musophagidae	*Musophaga rossae*	Ross's turaco	LC	?	Hunted
		Tauraco schuettii	Black-billed turaco	LC	?	Hunted
		Corythaeola cristata	Great blue turaco	LC	?	Hunted
Actinoptery	**Citharinidae**	*Distichodus* sp	"Mboto"			Fished
		Xenocharax sp	"Loboli"			Fished
	Clariidae	*Clarias* sp	"Ngolo"			Fished
	Malapteruridae	*Malapterurus* sp	"Nina"			Fished
	Schilbeidae	*Schilbe* sp	"Lolango"			Fished

Table 2 List of fruit-eating vertebrates categorized as seed dispersers in the study site. IUCN status of each species was consulted in June 2011, indicating status of threat as follows: LC: Least Concern, DD: Deficient Data, V: Vulnerable, NT: Near Threatened, E: Endangered, ↕ : stable population trends; ↓ decrease, ? = population trend unknown.

Class	Familly	*Species*	Name	Status	Population Trends	Threats
Mammalia	**Anomaluridae**	*Anomalurus derbianus*	Lord Derby’s Anomalure	LC	?	Hunted
	Hystricidae	*Atherurus africanus*	Brush tailed porcupine	LC	?	Hunted
	Muridae	*Hylomyscus* sp	African wood mouse	LC	?	
		Malacomys sp	Long footed rat	LC	?	
		Mus sp	Common mouse	LC	?	
		Praomys sp	Soft-furred rat	LC	?	
		Stochomys longicaudatus	Target rat	LC	?	
	Nesomydae	*Cricetomys emini*	Giant pouched rat	LC	↕	Hunted
	Sciuridae	*Funisciurus congicus*	Congo rope squirrel	LC	↕	Hunted
		Protoxerus aubinnii	African giant squirrel	DD	?	Hunted
	Suidae	*Potamochoerus porcus*	Bushpig	LC	↓	Hunted
	Estrildidae	*Estrilda paludicola*	Fawn-breasted waxbill	LC	?	
		Nigrita bicolour	Chestnut-breasted nigrita	LC	?	
		Nigrita canicapillus	Grey-headed nigrita	LC	?	
		Spermophaga haematina	Western bluebill	LC	?	
	Phasianidae	*Francolinus lathami*	Forest francolin	LC	?	Hunted
	Ploceidae	*Malimbus nitens*	Blue-billed malimbe	LC	?	
		Malimbus cassini	Cassin's malimbe	LC	?	
		Malimbus rubricollis	Red-headed malimbe	LC	?	

Table 3 List of seed predators in the study site. IUCN status of each species was consulted in June 2011, indicating status of threat as follows: LC: Least Concern, DD: Deficient Data, ↕ : stable population trends; ↓ decrease, ? = population trend unknown.

Discussion

Seeds of most plant species in tropical forests are dispersed by animals, rather than by wind, water or ballistic mechanisms (Jordano, Bascompte & Olesen 2003; Forget *et al.* 2006; Dennis 2007; Forget *et al.* 2011). In the LK forest systems of the Congo Basin, zoochorous species currently dominate plant communities (85% of the referenced plant species in LK areas). More specifically, in the mixed tropical forest we sampled, the abundance of anemochorous and autochorous tree species (4.9%) is lower than expected from the respective proportions of anemochorous and autochorous species in the tree community (11.1%).

Zoochorous tree species are among the dominant trees in this Afrotropical forest, indicating the dominance of this dispersal strategy. However, adaptations for zoochory leads to dependence on animals, so zoochorous plants may become trapped in a coevolutionary dead-end if their partners become extinct (Jordano, Bascompte & Olesen 2003; Muller-Landau 2007; Muller-Landau *et al.* 2008). This is particularly important in tropical forests, where numerous animals, predominantly large vertebrates, are unsustainably overhunted (Wright *et al.* 2007). The importance of the largest seed dispersers in our study site, bonobos and elephants, has already been noted (Yumoto *et al.* 1995; Blake *et al.* 2009), and elephants have been described as the 'megagardeners' of the forest (Campos-Arceiz & Blake 2011). Some of the seed dispersers such as bonobos are endemic, rare, and threatened (Fruth *et al.* 2008) and others such as Allen's swamp monkeys, are insufficiently known (Oates and Groves 2008). Fruiting plants can have several consumers and seed dispersers with functional redundancy. However this does not help when all dispersal vectors are hunted. In the studied ecosystem all primary seed dispersers are hunted, trapped or fished; while seed predators are less impacted. Ecosystem resilience might be compromised.

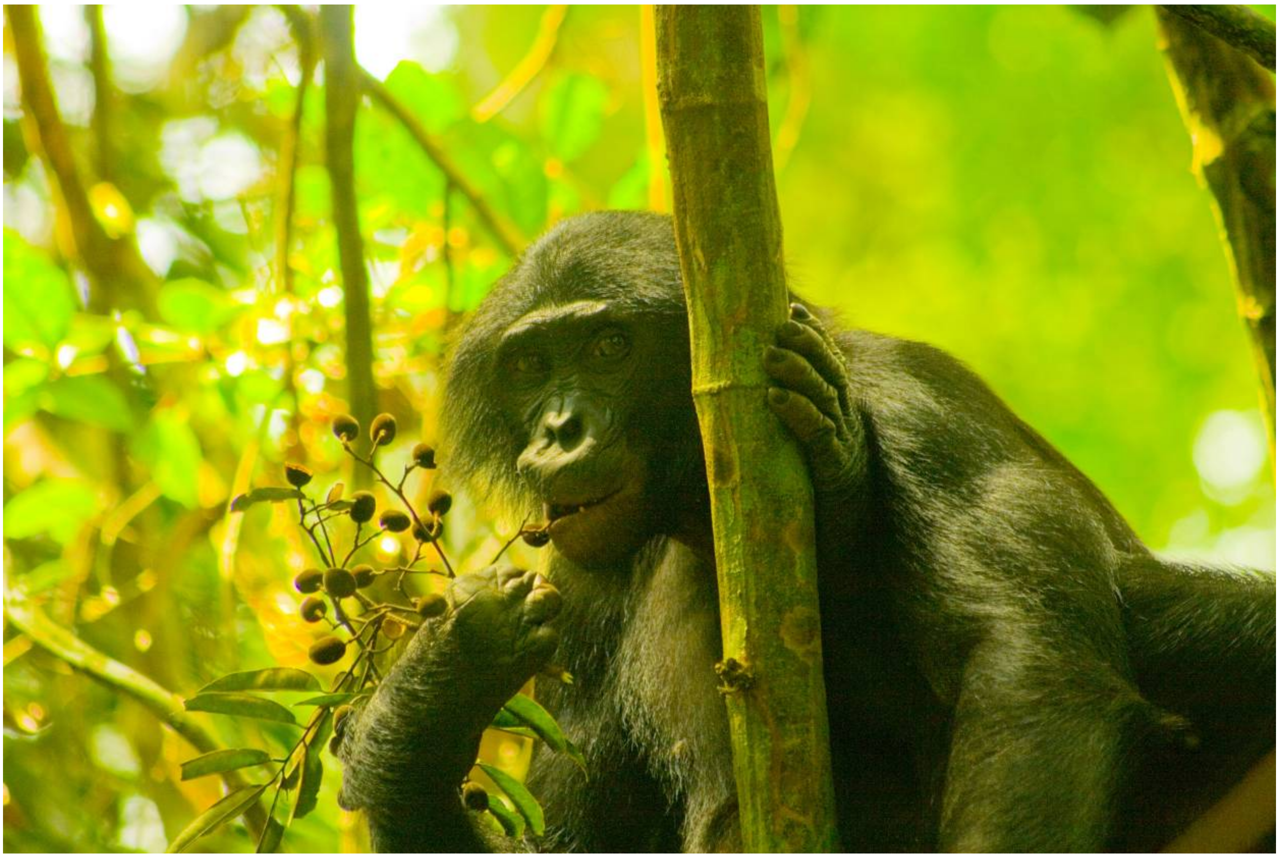
Human pressure on animals providing seed dispersal services and large seed predators such as bush pigs should increase in the future with human demography and population increase (Brashares, Arcese & Sam 2001; Poulsen *et al.* 2009). In central Africa, consumption rates are estimated at 0.16 kg of bushmeat per person per year (Delvingt 1997) and extraction of bushmeat is estimated at 213–248 kg/km^2/yr (Wilkie & Carpenter 1999). Bushmeat demand is increasing steadily as the population increases and cities expand (Poulsen *et al.* 2009). Many parks have failed to prevent poaching, including the adjacent Salonga National Park, where organized poaching is rife (Hart *et al.* 2008). Beyond the survival of animals, the entire ecosystem dominated by plants dependent on animal-mediated seed dispersal is also at risk.

This study also highlights the risk of the differential predation hypothesis (Mendoza & Dirzo 2007). While bush pigs are the biggest seed predators of the system, with dramatic effects on the mortality of large and hard protected seeds (Beaune *et al.* 2012b), they suffer greater hunting pressure than small seed predators eating small-seeded species. Large-seeded species such as (*Irvingia gabonensis*, *Mammea africana*, etc.) could benefit from reduced seed predation, This differential could modify plant reproduction and dominance in the forest. Similarly, the disappearance or decline of populations of large frugivores such as elephants and bonobos, which disperse large seeds, seems to alter recruitment of large-seeded plant species (Wang *et al.* 2007; Vanthomme, Bellé & Forget 2010). Of plant species with putative "megafaunal syndromes", many are ecologically disrupted by the loss of megafauna, but some show resilience (Janzen & Martin 1982; Guimarães, Galetti & Jordano 2008; Johnson 2009).

If animal density decreases, animal-dependent plants could be replaced by autochorous and anemochorous species. Although this will be a slow and not immediately detectable process, ultimately a possible scenario in this forest is a radical change in the composition of the dominant species. With this inventory of seed disperser species and pressures on them, we can estimate the proportion of plants potentially affected by their loss as follows: 85% of all plant species, and 88% of tree species (but 95% of individual trees). Thus, hunting is likely to trigger changes in forest structure and composition, as well as in population demography and genetics.

Tree density might stabilise, with autochorous and anemochorous trees occupying vacant space (Chapman & Onderdonk 1998) but biodiversity would decrease as a result (Muller-Landau 2007). More studies determining whether zoochorous plants can reproduce in the absence of animals are urgently required, as are conservation and management plans for these forests. Conservationists have focused on the direct consequences of habitat loss, animal species decline as well as consequences of habitat loss on animal species decline. However, a growing body of literature shows the increasing need to focus in addition on the reverse argument, the consequences of animal species' loss on habitat. In this respect, defaunation has to be considered as major conservation problem (Redford 1992; Terborgh *et al.* 2008). Its consideration is urgent in unprotected areas but even more in "protected" areas, where timber exploitation is banned but poaching still continues due to a lack of law enforcement (Hart *et al.* 2008).

Part I



Seed dispersal by bonobos

Seed dispersal services performed by bonobos (*Pan paniscus)* in tropical forest in the Democratic Republic of Congo

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Abstract

Conservation of Afrotropical 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 by bonobos (*Pan paniscus*) in evergreen lowland tropical rainforest of the Congo Basin. Bonobos are mainly frugivores (66% of all feeding sessions), spending about 3.5 hrs/day swallowing seeds that are transported for an average of 24hours. During the behavioral study (22 months), bonobos dispersed seeds of more than 91 plant species by endozoochory in the gut, carrying them to an average distance of 1.2 km from the parent tree. Seeds passed by bonobos germinated more rapidly, at higher rates and had greater post-dispersal survival than unpassed seeds. Bonobo-dispersed plants account for 40 % of tree species and 65 % of individual trees in the study site. Almost all bonobo-dispersed species investigated (95% of 19 species) are unable to self-recruit without dispersion.

Since bonobos show little functional overlap with other frugivores, loss of their seed dispersal services is likely to affect forest structure and dynamics. Our results justify description of the bonobo as the gardener of the Congo forest.

Keywords Africa, Congo basin, forest ecology, long dispersal distance, seed dispersal, seed rain, seed shadow, zoochory

Résumé

La conservation des forêts d'Afrique tropicale dépend non seulement de la protection des habitats, mais également de la protection des espèces qui la composent telles 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 24hrs 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. Presque toutes les plantes dispersées par les bonobos dont le recrutement a été étudié (95% des 19 espèces) ne peuvent pas autorecruter suffisamment de jeunes individus sans dispersion des graines. 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 comme probable jardinier de la forêt du Congo.

Mots clefs Congo, écologie de forêt, longue distance de dispersion, dispersion de graines, pluie de graines, zoochorie

Introduction

In tropical forests of Africa, Asia, South America, and Australia, between 70.0% and 93.5% of all tree species owe their existence to vertebrate seed dispersal. Fishes, birds, bats and terrestrial mammals are cited as endozoochorous vertebrates responsible for primary seed dispersal, the predominant mode of dispersal in these ecosystems (Janson 1983; Gautier-Hion *et al.* 1985; Jordano 2000). Many tropical plants have evolved fruits that are attractive to only a limited subset of frugivores, with colors, antifeedants, and seed dimensions being adapted to a specific group of dispersers (Fleming 1979). In Africa, Asia, and South America, frugivorous primates are recognized as the most important primary seed dispersers for many fruit-bearing species (Chapman & Onderdonk 1998a; Lambert & Garber 1998; Sato 2011).

Increased rates of successful germination of seeds following passage through the gut have been documented in all great apes, namely chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla gorilla)*, bonobos (*Pan paniscus*), and orang-utans (*Pongo pygmaeus*) (Idani 1986; Wrangham, Chapman & Chapman 1994; Poulsen, Clark & Smith 2001a; Gross-Camp & Kaplin 2011; Nielsen *et al.* 2011). The role of seed dispersal by large primates in forest dynamics and structure has been highlighted in few studies and the impact of their loss by over-hunting on vegetation patterns and plant diversity has become an increasingly urgent question (Nuñez-Iturri & Howe 2007; Peres & Palacios 2007; Wright *et al.* 2007; Nunez-Iturri, Olsson & Howe 2008; Brodie *et al.* 2009). Indeed, there is a general agreement that along with the physical destruction of habitats, the impoverishment of seed disperser communities has a considerable influence on an important ecosystem service, primary seed dispersal, and thus constitutes a major threat for the regeneration of the ecosystem (García & Martínez 2012). In the tropics, many forests are successfully protected from logging, but are insufficiently protected from hunting. For example, Wang and colleagues (2007) were able to show that the extinction of large primates in Cameroonian forests has altered seed deposition patterns of the tree species *Antrocaryon klaineanum*, with the majority of seeds falling beneath the parent trees (Wang *et al.* 2007). In a comparative study of forest regeneration between forests protected and unprotected from primate hunting, Nuñez-Iturri *et al.* (2008) found significant differences in the composition of tree seedling and sapling assemblages. Great apes, the largest primates, are known to ingest a considerable diversity of fruit, including some with large seeds, and are widely involved in their dissemination processes (Lambert & Garber 1998). Thus, their disappearance may disproportionately affect large-seeded tree species (Vanthomme, Bellé & Forget 2010; Gross-Camp & Kaplin 2011).

Despite studies on the diversity of plants dispersed by great apes or the effect of gut passage on seed germination (Idani 1986; Wrangham, Chapman & Chapman 1994; Voysey *et al.*

1999a), our understanding of how great apes contribute to seed dispersal or forest regeneration is limited. For example, seed deposition patterns, considered to be among the crucial components affecting Seed Dispersal Effectiveness (SDE) (Schupp, Jordano & Gomez 2010), have rarely been investigated in the field.

The dispersal kernel (the function that describes the probability of dispersal to different distances from the source (Nathan & Muller-Landau 2000a)), is frequently used as a quantitative descriptor of seed dispersal in plants and is another important factor in plant dissemination; combining information on movements (distances, positions) and gut passage time, that can be measured as either transit time (TT) or mean retention time (MRT) of seeds (Poulsen, Clark & Smith 2001a; Holbrook, Smith & Hardesty 2002; Tsuji, Yangozene & Sakamaki 2010). So far, gut passage time of seeds in primates has been investigated primarily in captivity (for a synopsis see (Lambert 1998)). Ranges in gut passage time within and between species are considerable and depend on various factors at both the individual and environmental levels (Lambert 1998). Individual factors include age, sex, health, reproductive status, hormonal fluctuations, stress, time since last feeding bout, hunger/satiation, and activity level. Environmental factors include temperature, time of day, content of macro-, micronutrients and fiber, and degree of ripeness. Despite the magnitude of influencing factors, local ecological conditions are considered to be crucial in determining dispersal distances (Russo, Portnoy & Augspurger 2006). Additionally in great apes, the general use of large home ranges, extended daily movements, and return to food patches for re-use are expected to strongly influence seed deposition patterns and the probability of dispersal to different distances from short to long (Cain, Milligan & Strand 2000; Bohrer, Nathan & Volis 2005). Long Distance Dispersal (LDD), for example, has been shown to influence survival and genetic patterns of plant species, with ultimate effect on forest structure (Bohrer, Nathan & Volis 2005).

In the Congo basin south of the Congo River, the biggest primate and the only representative of the great ape family is the bonobo (*Pan paniscus* (Schwarz 1929). Population estimation of this threatened species fluctuates between 29,500 and 50,000 animals (Fruth *et al.* 2008. In: IUCN 2012**)**. In the Democratic Republic of Congo (RDC), to which bonobos are endemic, forest fragmentation and the bushmeat traffic seriously undermine their survival. Despite international protection in law, and occasional local taboos, they are still killed in their natural habitats, including protected areas such as the Salonga National Park (Hart *et al.* 2008a). *Pan paniscus* has been studied in the wild since 1979. Previous studies have shown that, with over 83% fruit in their diet, bonobos are important fruit consumers (Kano & Mulavwa 1984), but little is known about their role in seed dispersal. The plants ingested and their potential benefits for the bonobo are comparatively well studied, but the costs or benefits for the ingested plants remain largely unknown (Badrian & Malenky 1984; Kano & Mulavwa 1984). Idani (1986) carried out pioneering work investigating seed dispersal by wild bonobos (Idani 1986), conducting germination experiments on bonobo-passed seeds of 17 fruit-bearing species over 2.5 months. This subject was taken up again only recently by Tsuji *et al.* (Tsuji, Yangozene & Sakamaki 2010) during preliminary investigations over a two-month period. The lack of knowledge concerning the role of *Pan paniscus* in seed dispersal can be explained by the fact that bonobos have predominantly generated interest in anthropology, behavioral ecology and sociobiology (Wrangham 1993; Parish 1996; Hohmann *et al.* 1999; Hohmann & Fruth 2000; Hohmann & Fruth 2003a; Fruth & Hohmann 2006; Surbeck, Mundry & Hohmann 2011), and not in basic tropical ecology with the objective of understanding animals' functions in ecosystems. Our investigations thus have the potential to make an important contribution to a better understanding of the ecological role of this great ape within its natural habitat. The results could be applicable to all other large frugivorous primates. Our investigations have three major goals:

First, we quantify the primary parameters for seed dispersal effectiveness of the bonobos: (1) Are the seeds transported by bonobos and do they remain viable? (2) What is the transit time for seed transport? (3) What is the dispersal curve/kernel and LDD? (4) Is seed germination affected by passage through the bonobo gut? (5) How does gut passage affect post-dispersal survival? 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. How many tree species could be affected by the loss of bonobo seed dispersal services? Third, we compare seed rain resulting from dispersal by bonobos with that produced by other seed dispersers by reviewing the literature. Our hypothesis is that large frugivores such as bonobos disperse to considerable distances seeds of species that are adapted to transport through the gut of this ape and are dispersed by few other animals.

Materials and methods

Ethics Statement

The studied apes are free ranging bonobos observed without invasive methods, constraint, contact or any interaction with the researchers. 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.

Study site

Field work took place between September 2009 and June 2011 at the Max-Planck-Institute research site LuiKotale (LK) (S2°47'- E20°21') that is located within a continuous block of equatorial rainforest at the south-western fringe of Salonga National Park (DR Congo, Figure 1). The study site consists of > 60km² of primary evergreen lowland tropical forest with a trail network of about 76km (Figure 2). The climate is equatorial with abundant rainfall (> 2000mm/year) interrupted by a short, relatively dry season in February and a longer one between May and August. Mean temperature at LuiKotale ranges between 21°C and 28°C with a minimum of 17°C and a maximum of 38°C (2007-2010). Two major habitat types are distinguished: 1-Dry (*Terra firma);* and 2-Wet forest (temporarily and permanently inundated). The dry habitat dominates the area with 73% of mixed and 6% of single-dominant (*Monopetalanthus* sp. or *Gilbertodendron* sp.) primary forest. The wet habitat includes temporarily inundated mixed forest, which covers 17% of the area, permanently inundated mixed forest which covers 4% (Mohneke & Fruth 2008).

Studies investigating bonobo behavior have been ongoing since 2002 with one bonobo community of 25-35 individuals habituated by researchers since 2007 (Hohmann & Fruth 2003c). Bonobos are identifiable by individual physical traits (genital, face, pilosity, color).

Bonobo feeding behavior

From September 2009 to June 2011 behavioral data was recorded for bonobos over 22 months, corresponding to 1879 hrs of observations over 315 days. Bonobos have 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)). 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 behavior) in daily activities and among feeding sessions we analyzed 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 how seeds were processed when they were not consumed (e.g. spitting, handling, and swallowing). Food items were classified into five categories: fruits (including either the whole fruit ingested or the pulp without its seeds), leaves/stem/bark/gum, seeds, animals and other items (honey, mushrooms, soil).

Transit time & dispersal distance

Whenever possible, bonobos were followed daily from nest to nest (approx. 05:30 to 17:30). Daily travel routes of parties were tracked with a GPS (Garmin® 60CSX) using 1 point position /5 minutes for georeferencing. Both bonobo transit time and dispersal distance were calculated from direct observation. Whenever an individual bonobo swallowed a new fruit species not eaten in the previous 36 hours, its seed was considered as a markerseeds and the individual was monitored continuously (not at night) until the seeds of the newly ingested species were found in its feces. The time between ingestion of the markerseeds and appearance of its first seed in the dung was taken as gut transit time (TT). Influences of the sex and seed size on transit time were tested with students t-test and analyses of variance (ANOVA) with all the effects considered as fixed and homoscedasticity tested (Breusch–Pagan test). Seed size was arbitrary categorized as follows: small: < 2mm; medium-sized: 2-10mm; large: > 10mm).

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 markerseeds, 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.

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 7,300 vouchers by May 2010 (Fruth 2011). The dried vouchers were shipped to Kinshasa, taxonomically determined and incorporated into the herbarium of the INERA at Kinshasa University (herbarium code: IUK). Copies of specimens were shipped to herbaria in Belgium (National Botanic Garden of Belgium : code BR, Meise) and Germany (Botanische Staatssammlung München : code M, Munich) for verification and identification by specialists. If unknown, samples were recorded as NID (non identified), and collected for later species identification. All feeding plants (trees, lianas and bushes) 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. When seeds were not ingested but spat in place without primary horizontal dispersal we classified this as frugivory with seed dispersal neutralism (effective dispersal = horizontal displacement). Bonobo-dispersed plant species of the LK community were compared to those of communities from Wamba (Kano & Mulavwa 1984) and Lomako (Badrian & Malenky 1984), the two longest 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 biodiversity and abundance of bonobo-dispersed species within 12 plots of mixed *terra firme* forest. Plots were positioned randomly within the home range of the bonobo community. From February to June 2011 all trees > 10cm DBH (diameter at breast height) were censused in these 12 plots of 1 ha (100×100m) each. *Relative biodiversity* 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 feces were collected at the study site between April 2002 and June 2011 (N = 1152). Feces and seeds therein were weighed (fresh mass); the number of seeds per feces was counted for each species.

To test germination viability of seeds that passed the bonobos' digestive tracts, we extracted seeds from feces collected between January 2010 and June 2011. These seeds were packed in leaves of *Haumania* spp. and depositited in a nursery within the same day. The nursery was an elevated platform (height 170cm) *in situ* under natural canopy cover. It was 200 cm long × 100 cm wide, was filled with natural soil (6cm deep), and was secured with predator-proof table legs. Each seed was marked and observed daily. We recorded emergence of the radicle (germination) (Heß 1999) and viability ratio (proportion of seeds that germinated).

To assess the influence of gut transit on germination, we compared the germination rate of seeds from the same parent and with three different treatment mimicking three dispersal modes, (1) by barochory (*Fruit lot* = seed + diaspore); (2) by seed spitting zoochory (*spitting lot* = diaspore removal); and (3) by swallowing endozoochory (*swallowing lot* = seeds collected after gut passage). Whenever bonobos were observed ingesting new fruit species (see above), mature fruits were directly collected from the respective parent tree (*fruit lot* and *spitting lot*). Ingested seeds (*swallowing lot*) were collected the next day in the feces from identified bonobos. Seeds were marked, alternately positioned in line in the nursey platform (mixing local effects) the evening of collection (D_0), and monitored daily.

To assess actual viability and recruitment of seeds embedded in bonobos' feces *in situ*, 45 feces defecated between January 2010 and May 2011 (and not collected for the above experiments) were monitored from one to 18 months. 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, Clark & Smith 2001a):

$$\text{Seed rain (Seed nb/day/km}^2\text{)} = \text{avg Seed nb/dung pile} \times \text{avg dung pile/day/ind} \times \text{avg bonobo density/km}^2$$

Population density was taken from (Mohneke & Fruth 2008) where it was calculated to be 0.73 bonobos/km². Dung production was calculated on the basis of continuous follows of individual bonobos during which each defecation was recorded. Influences of sex and age (adult, sub-adult) were tested with analyses of variance (ANOVA), with factors considered as fixed effects.

Recruitment under parental trees

To assess seed recruitment under the parental crown, mature trees of 22 species previously observed to fruit (thus excluding males of dioecious species), were investigated between May 2010 and June 2011 following the methodology of (Chapman & Chapman 1995). All seedlings (< 50cm high), saplings (50cm-200cm high), and poles (> 200cm high- < 10cm DBH (Diameter at Breast Height)) were censused in the corresponding fruit-fall zone of trees > 10cm DBH, opportunistically selected in the LK forest. Average numbers of seedlings, saplings and poles were calculated from a minimum of five adult trees/species. We considered a population to be able to self-replace when the average pole production/tree was ≥ 1. For confirmation that a species was able to recruit outside its fruit fall zone, density of its recruits was calculated in the total area censused for all species with exclusion of the conspecific fruit-fall zones.

Functional overlap – the primate community

In addition to bonobo, 41 other species of frugivorous vertebrates occur in LuiKotale, including birds, fruit bats, civets, monkeys and others. 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 qualified and quantified

A total of 133 plant species were recorded in the bonobo diet during the 22-month study period (Table 1). Feeding behavior represented 992 hrs of continuous records (from 1879 hrs of observation). The bonobo group spent 52.8% ± SE. 1.1% of its daily activity engaged in feeding sessions. During these feeding sessions, we recorded fruits of 91 species to be 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 feces, confirming endozoochory.

Among all feeding sessions observed (315 days, average continuous records ≈ 05h 57 min ± 0h 10 min), 54.5% ± 4.4% included the ingestion of fruit with subsequent seed dispersal (i.e., frugivory with seed ingestion and deposition observed, Figure 13), 0.6% ± 0.2% included the ingestion of fruit but deposition of seeds was not confirmed (insufficient data) and 7.3% ±3.0% consisted of the ingestion of fruit but with large seeds that were not swallowed (e.g. *Mammea africana* with average seed size = 324 ± SE. 12 mm, *Anonidium mannii* = 42 ± 2 mm, *Irvingia gabonensis* 55 ± 2 mm) (for each of these species, N ≥ 10). We exceptionally observed transport of these large seeds over distances of about 100 meters by hand or mouth (max = 426 m). Ingestion of food other than fruit such as leaves, terrestrial herbaceous vegetation, flowers, stems, and bark consisted of 30.0% ± 3.3% of the feeding sessions. The remainder could be attributed to granivory (3.4% ± 2.4%), carnivory (squirrels, monkeys: *Procolobus tholloni*, bird chicks, duiker: *Cephalophus* spp.) (0.9% ±0.2%) and other foods (honey, termite soil, digging session for truffles and probably insect larvae, etc. (3.3% ± 0.9%).

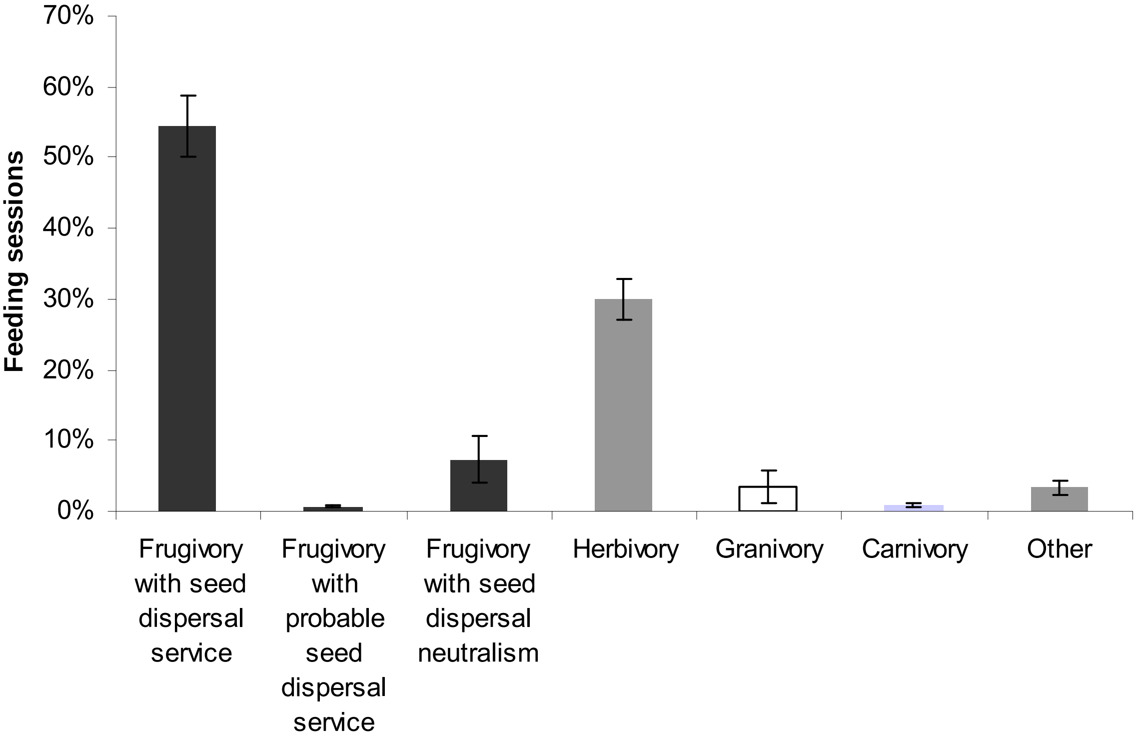

Figure 13 Relative parts of the interactions among the feeding sessions (22 months; 1879 hrs continuous group scans); Error bars indicate SE. Others are honey, mushrooms, soil and unknow.

Seed dispersal by bonobos

Of the 1152 bonobo feces collected between April 2002 and June 2011, 97.8% ± 0.3 contained seeds. Feces weighed on average 93.5 g ± 3.0. Seeds represented 67% ± 2.4 of the feces weight (N = 146). A dung-pile contained on average 1.9 ± 0.1 species of seeds (range = 0-6) with 79.8 ± 7.9 seeds (size > 2 mm. i.e. *Ficus* spp. and *Musanga cecropioides* excluded).

Transit time We recorded 124 markerseeds from ingestion to first deposition. Markerseeds were identified from twelve different genera. These markerseeds were swallowed and defecated by 19 different bonobos, seven males and 12 females. The resulting transit time was 24hrs00min on average ± SE. 9 min; (range: 20 hrs 03 min-28 hrs 17 min). Neither sex nor seed size affected transit time (t = 0.0253, df = 15.285, p = 0.9801; F = 0.382, df = 119, p = 0.683).

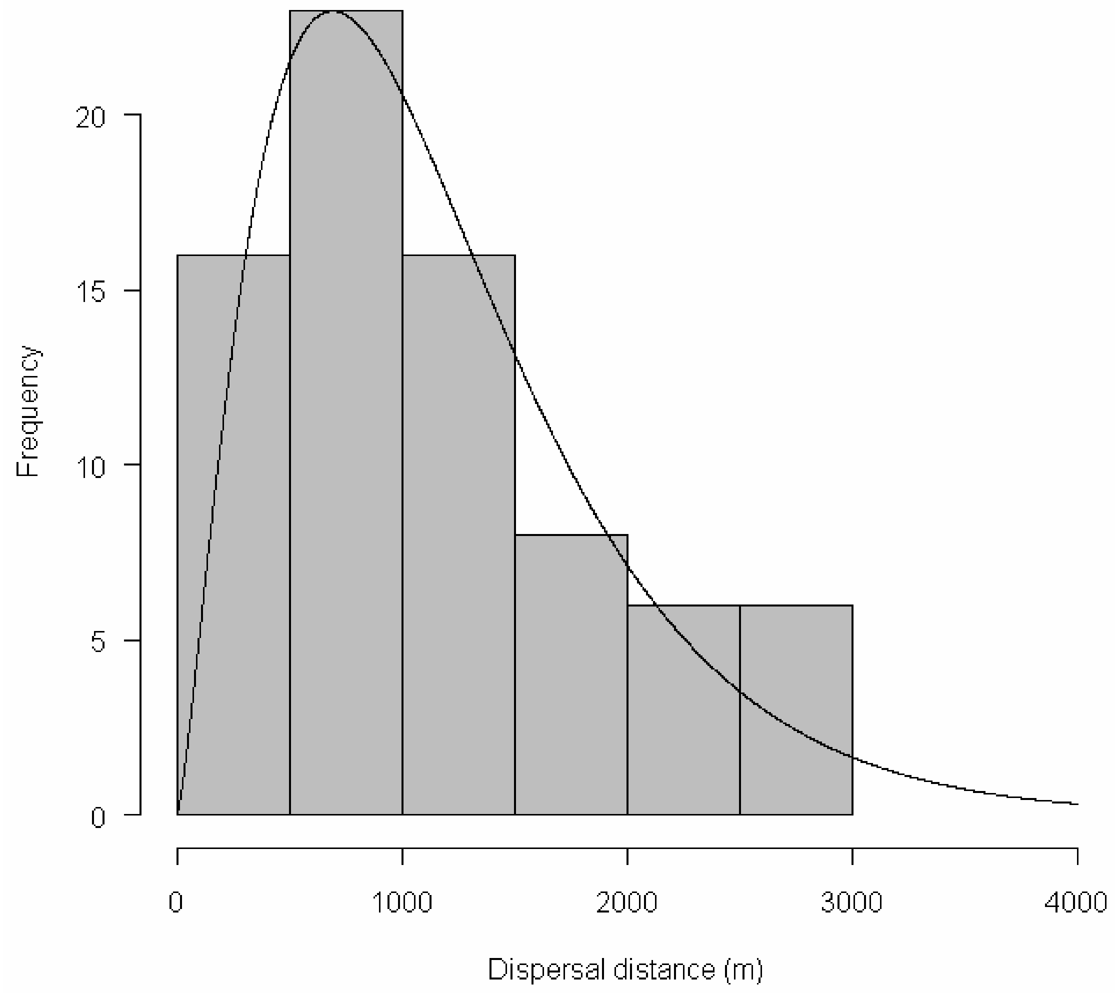

Figure 14 Dispersal distance kernel with fat-tailed dispersal kernel infered by bonobos (N = 75 dispersal events recorded)

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 m ± SE. 88 m ($CI_{95\%}$ [1007 m-1358 m]; range: 0 m-2995 m (
Figure 14). 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; see (Nathan & Muller-Landau 2000a) for the different shapes of dispersal kernels). Bonobos disperse seeds over long distances, with 93.3% of the dispersal events longer than 100 m.

Seed viability/survivorship

Ex-situ (in the nursery): Of the 56 species whose seeds were observed to be swallowed and defecated intact, seeds of 35 species were submitted to a viability census (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). Table 5 shows the 24 genera from 18 families, as well as four tested species that remained unidentified, that were scored as viable.

To assess the effect of fruit manipulation on germination, germination rate of unpassed seeds, as simulation to a situation of spitted seeds (*spitting lot*) was compared to that of seeds from unmanipulated fruit (*fruit lot*). Overall germination rate 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 15).

To assess the role of gut passage on germination, germination rate of unpassed but manipulated seeds, as simulation to a situation of spitted seeds (*spitting lot*) was compared to that of passed seeds (*swallowing lot*). Overall germination rate was higher for passed than for unpassed seeds. Here as well, differences were significant for only four out of eight species with sufficient sample size ($p < 0.05$; power analyses ≥ 99% (Figure 16).

In situ: To assess the viability of seeds in situ, a total of 45 bonobo feces (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 one to 18 months. Of all these dung piles, 67% ± 8 produced seedlings $CI_{95\%}$=[53-81%]. Overall, we identified seedlings of 8 genera. We think it highly likely that feces continued to yield seedlings after monitoring ceased (the shorter monitoring of a dung lasting one month). In an unpublished experiment the T_{50} (= time when 50% of the seedlings germinated) of *Zeyherella longepedicellata* seeds passed in bonobo was equal to 50 days; for *Diospyros* sp., T_{50} = 7 d; for *Guarea laurentii*, 20 d; for *Garcinia* sp., 63 d; and for *Manilkara yangambiensis*, 44 d.

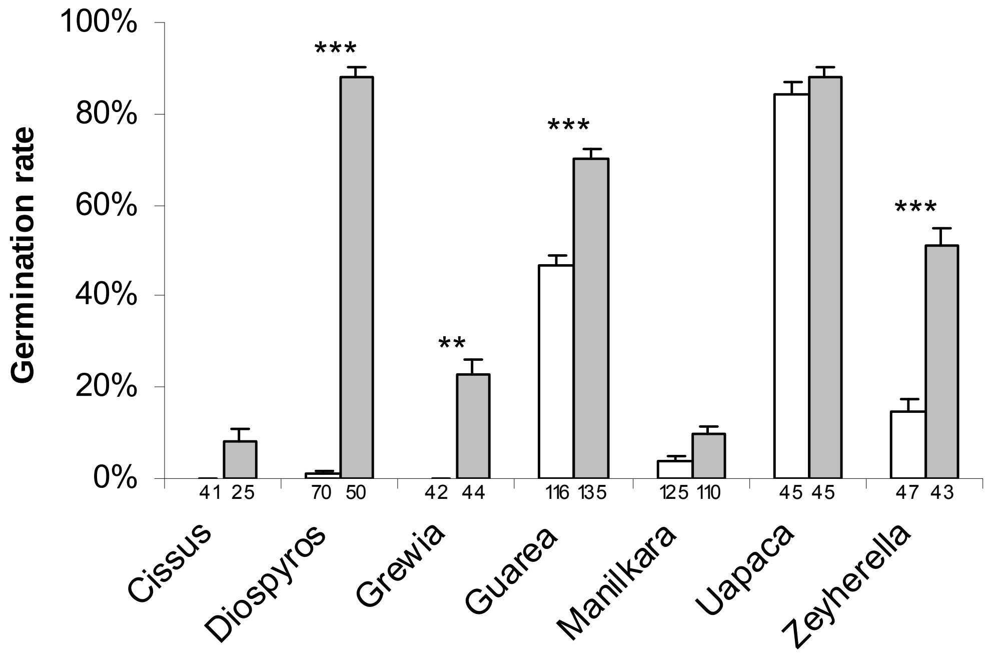

Figure 15 Germination rate of seven species (*Cissus dinklagei*, *Diospyros* sp., *Grewia* sp., *Guarea laurentii*, *Manilkara yangambiensis*, *Uapaca* sp., *Zeyherella longepedicellata*) with (white) and without diaspore (grey bars). ***: $p < 0.001$; **: $p < 0.01$ after *t*-test; Error bars indicate SE. Numbers on the x axis are N.

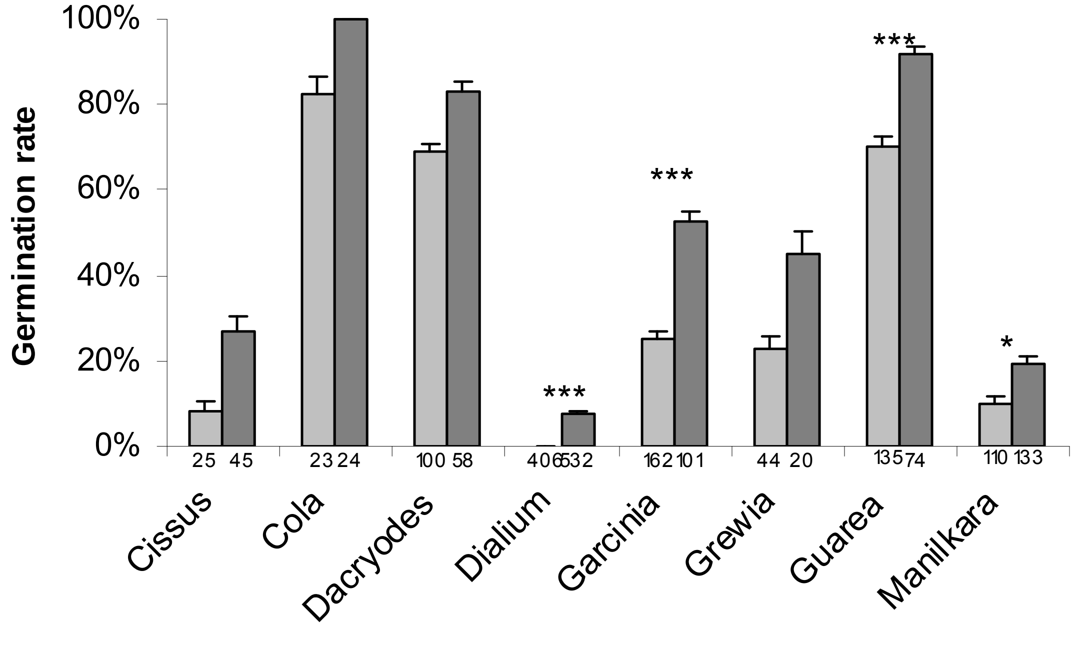

Figure 16 Germination rate of eight species (*Cissus dinklagei*, *Cola gigantea*, *Dacryodes yangambiensis*, *Dialium corbisieri*, *Garcinia ovalifolia*, *Grewia* sp., *Guarea laurentii*, *Manilkara yangambiensis*) comparing passed (dark) and unpassed seeds without diaspore (grey bars). ***: $p < 0.001$, *: $p < 0.05$ after *t*-test. Error bars indicate SE. Numbers on the x axis are N.

Diversity & abundance of trees dispersed by bonobos

Focusing on trees only, we found 5,233 adults in the 12 1-ha plots. A total of 40.1% ± 0.8 of these tree species are dispersed by bonobos via endozoochory through the gut (Figure 17). These account for a total of 64.7% ± 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.

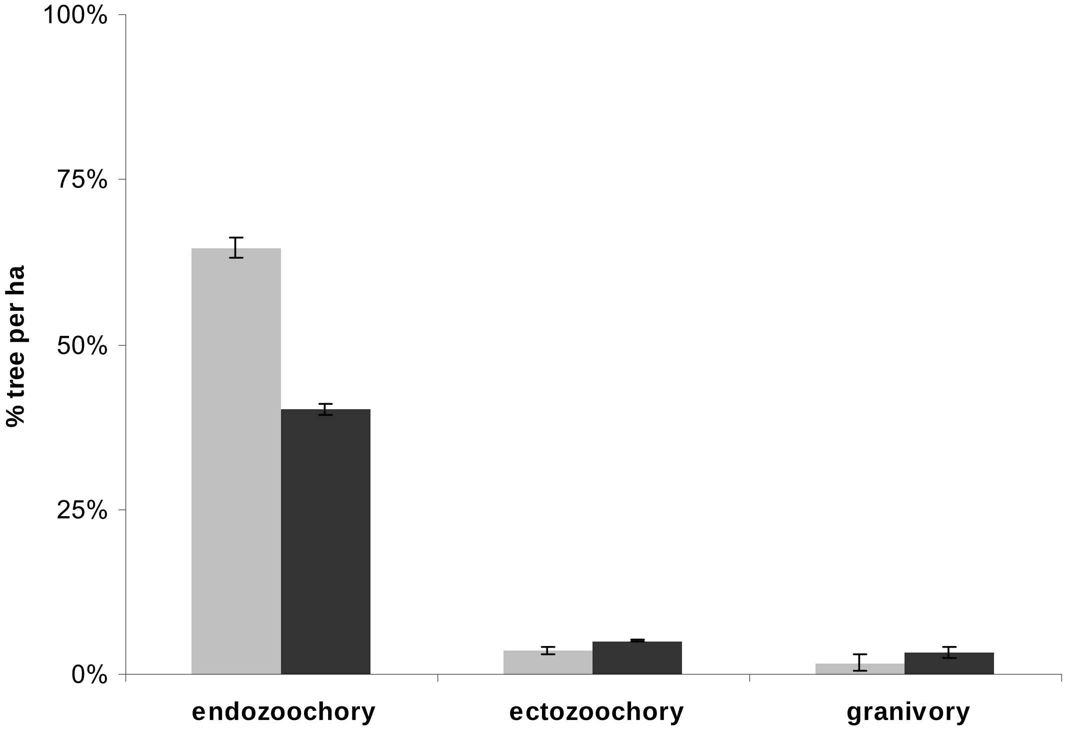

Figure 17 Tree species richness (dark) and abundance (grey) of seeds handled, consumed and dispersed by bonobos. The Y-axis depicts the average proportion of tree species (diversity) or tree individuals (abundance) per hectare (N = 12 1-ha plots). Error bars indicate SE.

Seed rain

To assess defecation interval, we observed 16 individuals, five males and 11 females. A total of 74 defecations were recorded (01/05/10 to 31/05/11), resulting in an average of 7.55 dung piles between dawn and dusk of a day. Thus, the interval of defecation for each individual was on average 1h35 ± 3 min. We detected no effect of sex (t = 0.2438, df = 12.511, p = 0.8113) or of age (adult, sub-adult) (t = -0.3324, df = 4.369, p = 0.7549) on the interval between two defecations. Taking into account bonobo population density, the average seed rain infered by bonobos in the

LuiKotale area is estimated to be 441.1 seeds/day/km². Extrapolating based on their average lifespan in the wild (50-55 yrs), an individual bonobo disperses 9.1 tons of seeds or 11.6 million seeds (not including seeds < 2mm length such as those of *Ficus* spp. and *Musanga cecropioides*).

Recruitment under parental trees

Table 4 shows 19 plant species, including three liana and 16 tree species used for the assessment of self-recruitment under the parent tree. Further, a total of three species considered to be autochorous were included in the assesment (control species), the other 19 are zoochorous. The autochorous species, used as controls, recruited on average more than one pole under the parents, thus fulfilling the criterion for self-replacement. In contrast, the fleshy-fruited species dispersed by bonobo did not recruit enough poles for self-replacement under the parents, except for *Drypetes* sp. (Table 4, Figure 18). While seedlings, saplings and poles were found under other tree species (5.13 ha censused), the majority of endozoochorous species was not able to self-replace without seed dispersal beyond the fruit-fall zone.

Dispersal mode	*Tree species*	*N*	*mean DBH (cm)*	*mean recruitment*		
				seedling	sapling	pole
autochory	*Hymenostegia mundungu*	10	73.7	4.4	4.1	**2.5**
	Scorodophloeus zenkeri	10	48.4	16.3	2	**3.4**
	Strombosiopsis zenkeri	11	35.6	2	2.1	**1.2**
zoochory with *Pan paniscus*	*Anonidium mannii*	10	46.7	0.5	0.6	0.4
	Blighia welwitschii	5	62.8	0	0.2	0.4
	Canarium schweinfurthii	5	109.4	0	0	0
	Cissus dinklagei	5	-	0.8	0	0
	Drypetes sp.	10	30.9	0.7	1.9	**2.6**
	Enantia olivacea	6	15.4	0	1.8	0.8
	Ficus sp.	7	-	0	0	0
	Gambeya lacourtiana	10	92.2	1	0	0
	Grewia oligoneura	6	38.4	0.2	0.3	0.3
	Irvingia gabonensis	54	83.1	1.7	0.0	0
	Irvingia grandifolia	10	110	0	0	0
	Klainedoxa gabonensis	10	124.5	0	0	0
	Landolphia forestiana	5	-	0	0.2	0
	Landolphia sp.	5	-	0	5.6	0.4
	Mammea africana	10	117.6	0.1	0.9	0
	Manilkara yangambiensis	10	40.4	0.6	0.2	0.1
	Pancovia laurentii	10	27	0.1	1	0.5
	Parinari excelsa	10	113.1	19.8	0.1	0.1
	Greenwayodendron (Polyalthia) suaveolens	10	29	0.1	1.6	0.5

Table 4 Mean recruitment under canopy of adults of 22 tree and liana species in LuiKotale, DR Congo.

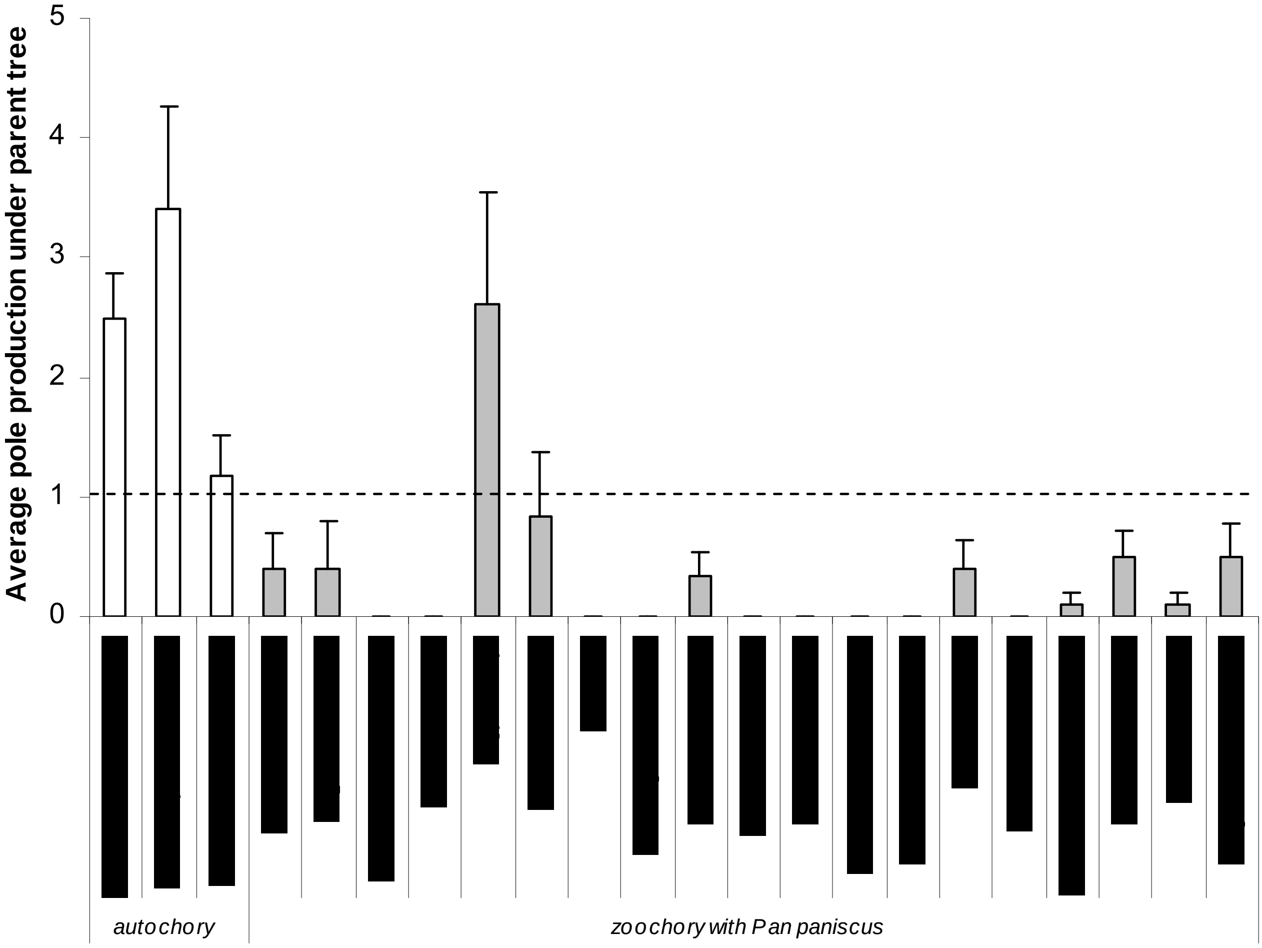

Figure 18 Mean recruitment of pole (<10 cm DBH) under the parent crown for three control species (autochorous) and 19 species dispersed by bonobo. The dotted line is the threshold for self-replacement of the parent. Error bars indicate SE.

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*, *Piliocolobus tholloni*; Cercopithecidae: *Lophocebus aterrimus*, *Cercopithecus wolfi*, *Cercopithecus ascanius*, *Cercopithecus neglectus* and *Allenopithecus nigroviridis*. In 16 feces of *C. angolensis* that were investigated, and 124 feces 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 bonobos 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 feces was 0.19 ± 0.06 (N=124). The only species indicating food overlap and dispersal of intact seeds was *Dialium* sp. For *C. wolfi*, we investigated 78 dung piles. Of these, 17.9% contained intact seeds of six different species. On average, each dung pile contained 0.39 ± 0.99 seeds/feces. For C. *ascanius*, we investigated 118 feces, 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 ectozoochory. 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 five months of daily survey, the values of Jaccard's index show that functional overlap between monkeys and bonobos seems to be low. Bonobos 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 bonobos.

Discussion

Here we investigated seed dispersal by bonobos (*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 the trees represent 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 (Table 1), shows that our findings are in line with plant species observed to be consumed in these sites. Kano and Mulavwa (Kano & Mulavwa 1984) reported 113 species for the Wamba site, representing an overlap of 44% at the genus level with our site. Badrian and Malenky (Badrian & Malenky 1984) reported 81 species for Lomako, of which 40% overlap at the genus level with our site. The fact that the overlap at the species level is small (8% and 9% respectively) merits further investigations, 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 feces (98%) contained seeds, which represented over half of the dung's weight, with an average of two different species in each defecation.

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 tegumentary dormancy and endozoochorous processes shaped by co-evolutionary interactions (Howe & Smallwood 1982; Robertson *et al.* 2006; Bradford & Nonogaki 2007). Similar results have been documented for all other great ape species; highlighting their crucial role in regeneration of the forests they inhabit (Poulsen, Clark & Smith 2001; Gross-Camp & Kaplin 2011; Nielsen *et al.* 2011). 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 bonobos fit many crucial criteria characterising efficient dispersers of tree species. Like other large primates, bonobos exploit 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, we have to note that after first seeds found in feces, other seeds can follow after Time of Last Appearance (TLA = 63 h for chimpanzees (Lambert 1998)). Our estimate of dispersal distance is thus likely to underestimate actual dispersal distances. Overall, 93.3% of dispersal events were longer than 100 m. Long dispersal distance (LDD, (Nathan *et al.* 2003) is of critical importance in plant population dynamics (Cain, Milligan & Strand 2000) and in LuiKotale, the majority of zoochorous plants dispersed by bonobos (95% of the investigated species) could not self-recruit without dispersal beyond the parent tree's crown. 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 (Janzen 1970b; Connell 1971; 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 to seeds that remain on the surface (by >50%, (Beaune *et al.* 2012a). Thus, small changes in predation pressures can have a large effect on plant demography (Fenner 2000).

A large gap exists between seed production and the growth of a reproductive adult tree. This gap is not assessed here (secondary/tertiary/quaternary dispersal, post-dispersal mortality, competition, abiotic and biotic factors, etc. (Forget *et al.* 2005; Forget *et al.* 2011). But we assess here the first steps of the seed dispersal loop set in march by 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. But here our system is simplified by the fact that bonobo is the only ape and the only large primate of the area.

If we compare seed rain produced by bonobo with that produced by other Afrotropical primates (Poulsen, Clark & Smith 2001), bonobos outperform them in seed dispersal. Accounting for density, seed rain effected by chimpanzees turns out to be less than that effected by bonobos.

With only 96.5 seeds/day/km² chimpanzees of a Cameroonian site dispersed merely a quarter of what bonobos dispersed in our study site (441.1 seeds/day/km²). Seed rains reported for Gorillas calculated with high density of this ape (1.7 Gorilla/km²) are similar to our results (464.7 seeds/day/km²). The entire arboreal monkey community, with four species of Cercopithecidae, disperses 568 seeds/day/km² (Poulsen, Clark & Smith 2001). The unique and irreplaceable dispersal service provided by bonobo cannot be proved here. However, five months of observation show little functional redundancy for seed dispersal with other primates. 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 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 gardener of the Congo forests.

Conclusion

Pan paniscus is the biggest ape within its geographic range and the second largest frugivore after the elephant. In general, fruit species are dispersed by many frugivorous species (Gross-Camp & Kaplin 2011) such as hornbills, monkeys, and bats. However, for fruit with large seeds, the potential dispersal vectors are scarce, suggesting that the fate of large frugivorous species such as the bonobo may disproportionately affect the regeneration process of these plants (Vanthomme, Bellé & Forget 2010a). Apes with their medium-sized body size category are specialized in a certain seed size range (Forget *et al.* 2007). Moreover, in the LK primate community, very few species that are dispersed by bonobo endozoochory through the gut are also dispersed by monkeys. The overlap in dispersal services seems to be low. Monkeys (mainly *Cercopithecus*) disperse principally by seed spitting zoochory, which is an different mechanism in terms of recruitment (Dominy & Duncan 2005), with different effects on seed fate (Gross-Camp & Kaplin 2011). Finally, a monkey's home ranges and daily travel distances are different in monkeys than in bonobos (several km/days), with consequences for dispersal distances and LDD. In Afrotropical forests, birds and primates consume and disseminate plants located in different canopy strata and exhibit low plant species overlap in the seeds they disperse (Fleming 1979; Clark, Poulsen & Parker 2001; Poulsen *et al.* 2002). In the absence of functional overlap between the bonobo and other dispersers, the extirpation of this primate from the system might lead to an irreplaceable loss of ecosystem services.

With the large size of the bonobo and its peculiar behavior, our hypotheses are verified: bonobos disperse adapted seeds to considerable distance with low functional vector overlap.

Strategies for conserving Congo forests inhabited by bonobos should therefore include strong measures for conserving this key species, which is currently threatened by extinction (IUCN 2012).

interaction	Family	Genus	Species	Life Form	Leaf	Flower	Fruit	Seed	Stem	Sap	Bark	Seed handling	Intact passed seed	viability census germinated /total
seed dispersal	Achariaceae	*Caloncoba*	*welwitschii* [W L]	tree			1					swallow	I	
	Anacardiaceae	*Antrocaryon*	*nannanii*	tree			1					spit	I	
	Anacardiaceae	*Sorindeia*	*zenkeri*	tree			1					swallow	I	
	Anacardiaceae	*Trichoscypha*	*arborescens*	tree			1					swallow	I	
	Anacardiaceae	*Trichoscypha*	*acuminata*	tree			1					swallow		
	Annonaceae	*Anonidium*	*mannii* [W L]	tree			1					handle	I	15/15
	Annonaceae	*Enantia*	*olivacea*	tree			1					swallow		
	Annonaceae	*Enantia*	*pilosa*	tree			1					swallow		
	Annonaceae	*Greenwayodendron*	*suaveolens* [W L]	tree			1					swallow	I	1/4
	Annonaceae	*Isolona*	*bruneelii*	tree			1					swallow	I	
	Annonaceae	*Monanthotaxis*	*myristicifolia*	liana			1					swallow		
	Annonaceae	*Thonnera*	*congolana*	tree			1					swallow	I	5/19
	Annonaceae	*Uvaria*	*acabrida*	liana			1					swallow		
	Annonaceae	*Uvaria*	*acabrida*	tree			1					swallow	I	6/18
	Annonaceae	*Uvaria*	*engleriana*	liana			1					swallow		
	Annonaceae	*Uvariastrum*	*pynaertii*	tree			1					swallow		
	Apocynaceae	*Landolphia*	*forestiana*	liana			1					swallow	I	V
	Apocynaceae	*Landolphia*	*congolensis* [W L]	liana			1					swallow	I	
	Apocynaceae	*Landolphia*	*owariensis* [W]	liana			1					swallow		
	Burseraceae	*Canarium*	*schweinfurthii* [W L]	tree			1					swallow	I	
	Burseraceae	*Dacryodes*	*yangambiensis*	tree			1					swallow	I	69/142
	Burseraceae	*Dacryodes*	sp.	tree			1					swallow		
	Burseraceae	*Dacryodes*	*buettneri*	tree			1					?		
	Burseraceae	*Santiria*	*trimera* [W]	tree			1					swallow		
	Burseraceae			tree			1					swallow		
	Burseraceae			tree			1					swallow		
	Caesalpiniaceae	*Dialium*	*corbisieri* [W L]	tree	1		1					swallow	I	41/542
	Caesalpiniaceae	*Dialium*	sp.	tree	1		1					swallow	I	
	Caesalpiniaceae	*Dialium*	sp.	tree	1		1					swallow	I	
	Caesalpiniaceae	*Dialium*	sp.	tree	?		1					swallow	I	
	Caesalpiniaceae	*Dialium*	sp.	tree	?		1					swallow	I	
	Cecropiaceae	*Musanga*	*cecropioides*	tree	1	1	1					swallow	I	V
	Chrysobalanaceae	*Parinari*	*excelsa* [W L]	tree			1					spit	I	
	Clusiaceae	*Garcinia*	*chromocarpa*	tree			1					swallow		
	Clusiaceae	*Garcinia*	*ovalifolia* [L]	tree			1					swallow	I	52/101
	Clusiaceae	*Mammea*	*africana* [W L]	tree			1					handle	I	
	Cucurbitaceae	*Momordica*	*foetida*	liana		1						swallow	I	0/5
	Ebenaceae	*Diospyros*	sp.	tree			1					swallow	I	V
	Ebenaceae	*Diospyros*	sp.	tree			1					swallow	I	
	Ebenaceae	*Diospyros*	*hoyleana* [L]	tree			1					?		
	Euphorbiaceae	*Drypetes*	sp.	tree			1					?		
	Euphorbiaceae	*Drypetes*	*leonensis*	tree			1					spit	I	
	Euphorbiaceae	*Maesobotrya*	*bertramiana*	tree			1					spit	I	
	Euphorbiaceae	*Phyllanthus*	*muellerianus*	tree			1					?		
	Euphorbiaceae	*Plagiostyles*	*africana*	tree			1					?		
	Guttifereae	*Garcinia*	*punctata* [L]	tree			1					swallow		
	Icacinaceae	*Icacina*	sp.	shrub			1					swallow		
	Irvingiaceae	*Irvingia*	*grandifolia*	tree			1					handle	I	
	Irvingiaceae	*Irvingia*	*gabonensis* [W L]	tree			1					handle	I	5/100

Irvingiaceae	*Irvingia*	sp.	tree			1			handle	I	
Irvingiaceae	*Klainedoxa*	*gabonensis* ^{L}	tree			1			handle	I	
Malvaceae	*Cola*	sp.	shrub			1			swallow		
Malvaceae	*Cola*	*gigantea*	tree			1			swallow	I	24/24
Malvaceae	*Cola*	*bruneelii* ^{W}	shrub			1			swallow	I	
Malvaceae	*Cola*	sp.	shrub			1			swallow	I	
Malvaceae	*Cola*	*clamidandtha*	tree				1		swallow		
Malvaceae	*Cola*	sp.	tree				1		swallow		
Malvaceae	*Grewia*	sp.	tree			1			swallow	I	29/79
Malvaceae	*Grewia*	*pinnatifida* ^{W}	tree			1			swallow	I	13/77
Malvaceae	*Grewia*	sp.	tree			1			swallow	I	15/40
Malvaceae	*Grewia*	sp.	tree			1			swallow	I	9/20
Marantaceae	*Maranthacloa*	*leucantha*	herb			1			swallow		
Melastomataceae	*Dissotis*	*brazzeana*	shrub	1	1	1			?		
Meliaceae	*Guarea*	*laurentii*	tree			1			swallow	I	68/74
Mimosaceae	*Parkia*	*filicoidea*	tree			1			?		
Moraceae	*Ficus*	sp.	liana			1		1	swallow	I	V
Moraceae	*Ficus*	*cyathistipula*	liana			1			swallow	I	V
Moraceae	*Ficus*	*exasperata* ^{L}	liana			1			swallow	I	V
Moraceae	*Ficus*	sp.	liana			1			swallow	I	V
Moraceae	*Ficus*	sp.	liana			1			swallow	I	V
Moraceae	*Ficus*	sp.	liana			1			swallow	I	V
Moraceae	*Morus*	*nigrum*	tree			1			swallow	I	
Myristicaceae	*Pycnanthus*	*angolensis (=kombo)*	tree			1			swallow		
Myristicaceae	*Staudtia*	*kamerunensis*	tree			1			swallow	I	3/67
NID			tree			1			swallow	I	
NID			tree			1			swallow		
NID			tree			1			swallow	I	
NID						1			swallow	I	6/83
NID			tree			1			swallow	I	1/100
NID			tree			1			swallow	I	
NID						1			swallow	I	
NID						1			swallow	I	2/100
NID						1			swallow	I	V
NID			tree			1			swallow		
Olacaceae	*Olax*	sp.	tree			1			swallow	I	
Olacaceae	*Strombosiopsis*	*tetrandra* ^{L}	tree			1			swallow		
Olacaceae	*Strombosiopsis*	*tetrandra* ^{L}	tree			1			spit	I	
Rubiaceae	*Mitragyna*	*stipulosa*	tree			1			swallow	I	V
Rubiaceae			tree		1				swallow		
Sapindaceae	*Blighia*	*welwitschii*	tree			1			swallow		
Sapindaceae	*Chytranthus*	*macrobotrys*	tree			1			swallow		
Sapindaceae	*Eriocoelum*	*microspermum*	tree			1			swallow		
Sapindaceae	*Haplocoelum*	*congolanum*	shrub			1			swallow		
Sapindaceae	*Pancovia*	*laurentii* $^{W L}$	tree			1			swallow	I	54/74
Sapindaceae	*Placodiscus*	*paniculatus*	tree	1		1			swallow	I	V
Sapotaceae	*Autranella*	*congolensis*	tree			1			spit	I	
Sapotaceae	*Gambeya*	*lacourtiana*	tree			1			swallow	I	2/50
Sapotaceae	*Manilkara*	*yangambiensis*	tree			1			swallow	I	30/133
Sapotaceae	*Manilkara*	*malcoleus*	tree			1			swallow		
Sapotaceae	*Manilkara*	*obovata*	tree			1			swallow		
Sapotaceae	*Manilkara*	sp.	tree			1			swallow		
Sapotaceae	*Pachystela*	*bequaertii*	tree			1			?		
Sapotaceae	*Synsepalum*	sp.	tree			1			swallow		

	Sapotaceae	*Zeyherella*	*longepedicellata*	tree			1					swallow	I	V
	Verbenaceae	*Vitex*	sp.	tree			1					swallow		
	Vitaceae	*Cissus*	*dinklagei* ^{W}	liana			1					swallow	I	12/45
	Zingiberaceae	*Aframomum*	sp.	herb			1		1			swallow	I	V
	Zingiberaceae	*Aframomum*	*daniellii*	herb			1					swallow		
	Zingiberaceae	*Aframomum*	sp.	herb			1					swallow	I	
	Zingiberaceae	*Renealmia*	*africana* $^{W L}$	herb			1					swallow	I	
granivory/herbivory	Caesalpiniaceae	*Cynometra*	*alexandri* ^{W}	tree				1						
	Caesalpiniaceae	*Cynometra*	*sessiliflora* ^{L}	tree	1									
	Caesalpiniaceae	*Cynometra*	sp.	tree	1									
	Caesalpiniaceae	*Dialium*	*gossweileri*	tree	1		?							
	Caesalpiniaceae	*Erythrophloeum*	*suaveolus*	tree	1									
	Caesalpiniaceae	*Gilbertiodendron*	*dewevrei* $^{W L}$	tree	1			?						
	Caesalpiniaceae	*Gilbertiodendron*	*ogouense*	tree				1						
	Caesalpiniaceae	*Hymenostegia*	*mundungu*	tree				1						
	Caesalpiniaceae	*Julbernardia*	*seretii*	tree	1									
	Caesalpiniaceae	*Monopetalanthus*	*microphyllus* ^{L}	tree				1						
	Caesalpiniaceae	*Scorodophloeus*	*zenkeri* $^{W L}$	tree	1	1		1						
	Euphorbiaceae	*Manniophyton*	*fulvum* ^{W}	liana	1					1				
	Marantaceae	*Haumania*	*leonardiana*	liana					1					
	Marantaceae	*Haumania*	*liebrechtsiana* $^{W L}$	liana					1					
	Marantaceae	*Megaphrynium*	*macrostachyum* ^{L}	herb	1									
	Melastomataceae	*Ochtocharis*	*ancellandroides*	shrub	1	1								
	Melastomataceae	*Ochtocharis*	*dicellandroides*	shrub	1	1	?							
	Melastomataceae	*Tristemma*	*mauritianum*	shrub	1	1	?							
	Mimosaceae	*Pentaclethra*	*macrophylla* ^{W}	tree		1								
	Mimosaceae	*Piptadeniastrum*	*africanum*	tree				1						
	Moraceae	*Treculia*	*africana* $^{W L}$	tree			1	1						
	NID			epiphyte	1									
	Nymphaeaceae	*Nymphaea*	*lotus*	herb					1					

Table 5 Plants consumed by bonobo 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, unpub data); I = seeds were found intact in feces, V = seeds were tested and found viable in nursery trials but ratio is not posted because census was interrupted. NID = not identified.

The Bonobo-*Dialium* positive interactions

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Abstract

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 south-west of Salonga National Park, DR 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 six 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: 1.25km after 24hrs 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.

Keywords Congo basin, forest ecology, germination activation, plant-animal interaction, seed dispersal, velvet tamarind, zoochory

Résumé

Le mutualisme est une interaction entre des individus de deux espèces qui fournit un avantage sélectif aux deux partenaires. Ici nous présentons un exemple de mutualisme de dispersion de graines entre un animal : le bonobo (*Pan paniscus*) et un arbre : les tamarins africains (genre *Dialium*). Au sud-ouest du parc national de la Salonga, dans la forêt tropicale humide de LuiKotale, sept espèces du genre *Dialium* représentent 29.3% de tous les arbres et sont ainsi le genre dominant de cette forêt. Les fruits de *Dialium* composent une grande proportion du régime alimentaire de ces grands singes. Pendant les six mois de la saison de fructification, plus de la moitié du temps d'alimentation des bonobos est consacré aux fruits de *Dialium*. En outre, les fruits de *Dialium* sont parmi les plus riches des fruits analysés pour les sucres et protéines. Ils sont une source importante de ces nutriments dans le régime des bonobos. Les bonobos ingèrent en contrepartie les fruits avec leurs graines qui sont disséminées via leurs fécès (endozoochorie). Cette endozoochorie affecte la protection tégumentaire des graines qui gonflent et brisent ainsi la dormance germinative. Ainsi, après le passage dans l'intestin, les graines ont un meilleur taux de germination. Les autres espèces de la communauté diurne de primates semblent ne pas avoir le même rôle que les bonobos dans la dispersion de graines de *Dialium*. Nous proposons par conséquent une certaine bonobo-dépendance pour les graines de *Dialium*. Cette interaction plante-animale est un autre exemple d'interdépendance biologique entre deux organismes d'importance majeure dans le bassin du Congo, et place le bonobo comme disperseur efficace de graine pour des arbres du genre *Dialium*.

Mots clefs Activation de la germination, bassin du Congo, bonobo dépendance, coévolution, écologie forestière, interaction plante-animale, zoochorie

Introduction

Seed dispersal mutualism between fruiting trees and frugivores is an important interaction in rainforest ecology (Howe & Smallwood 1982; Lambert & Garber 1998; Nathan & Muller-Landau 2000; Levin *et al.* 2003; Howe & Miriti 2004; Forget *et al.* 2011). 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).

Within tropical rainforests, birds, mammals and to a lesser extent reptiles and even fishes are known to be frugivores and seed dispersers (Asquith, Wright & Clauss 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, Poulsen & Parker 2001) and Ivory Coast (Koné *et al.* 2010) show that seed dispersal services provided by primates are often 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 (Wrangham, Chapman & Chapman 1994; Voysey *et al.* 1999a; Voysey *et al.* 1999b). In a comprehensive study investigating the diurnal primate community in the Dja reserve, Poulsen and colleagues [2001] were able to show 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* (Caesalpinioideae) known worldwide, 16 occur in tropical Africa (Senesse 1995). *Dialium* trees are tall, sometimes more than 40 meters, 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 when in 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, Yangozene & Sakamaki 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 *Pan 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 paper 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 (A) the efficiency of seed dispersal by bonobos, including *Dialium* seed rain and the effects of interactions with bonobos on seed viability and germination, and (B) 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 (C) 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 in *Dialium* seed dispersal. We hypothesise 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 (DR Congo), within the same continuous forest block. The study site comprises > 60 km² of primary evergreen lowland tropical forest with a trail network of 76 km. The climate is equatorial with abundant rainfall (>2,000mm/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 1152 bonobo feces were collected between April 2002 and June 2011 to contribute to the project's long-term data base. These samples were analysed 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 & 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 & breadth) in mm was measured using a slide calliper (0-10cm ± 1µm). Retention time was 24 hours, which is similar to that calculated in the wild bonobo population of LK (24hrs00min ±SE. 9min, 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 36hrs prior to and 24hrs 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, i.e., seeds that were identical in size and shape to fresh seeds, were separated from transformed seeds, i.e., seeds that were visibly swollen (imbibed). All seeds were placed on an elevated platform (1×2m, 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, Herrera & Heymann 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., submitted].

Transit time & dispersal distance

The probability distribution of *Dialium* seeds is based on empirical bonobo movements, georeferenced from 15th of January 2008 to the 21st of September 2011. With bonobo movements after feeding sessions in *Dialium* trees georeferenced and mean transit time of seeds known, a mechanistic model of seed dispersal distance can be calculated (Westcott *et al.* 2005; Tsuji, Yangozene & Sakamaki 2010; Côrtes & Uriarte 2012). Whenever possible, bonobos were followed daily from nest to nest (approx. 05:30 to 17:30). Daily travel routes of parties were tracked with a GPS (Garmin® 60CSX) using 1 point position /5 minutes for georeferencing [Beaune 2012]. Bonobo transit time was calculated from direct observations. Whenever an individual bonobo swallowed a new fruit species not eaten in the previous 36 hours, 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 transit time (TT). Influences of the sex and seed size on transit time were tested with students 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: < 2mm; medium-sized: 2-10mm; large: > 10mm).

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 sub-group 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 lyophilisation. 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, Piliocolobus 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 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 ICCN, and adhere to the legal requirements of the host country, the Democratic Republic of Congo 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 1152 feces analysed from April 2002 to June 2011, 36.1 ± SE 0.0 % contained *Dialium* seeds. Of 416 feces that contained seeds, the number of *Dialium* seeds varied greatly between 1 and 781. The median was 50.0 *Dialium* seeds/feces with an average of 82.9 ± 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 & viability

In the human-gut passage experiment, a total of 112 measured *Dialium* seeds were swallowed, 85 of these were excreted and found 24 hours later. Of these 85 seeds, only five had transformed into bigger seeds (from 1148 to 1502 µm of length, Wilcoxon rank-sum test: W=1, P<0.05; and from 542 to 739µm of breadth: W=0, P<0.05), whereas the remainder of 80 seeds remained unchanged (length: W = 4107.5, P = 0.72; breadth: W = 4244.5, 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 rank-sum test for length (µm): W= 91, P = 0.09). See Figure 19.

None of the control seeds (n= 406) germinated during the eight 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% ± SE 4.7) of these transformed seeds showed radicle emergence becoming visible between 24 and 96 hrs 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% ± 1.3 for seeds that passed through the bonobo digestive tract. This rate was not significantly different from the germination rate of seeds that passed through the human digestive tract (chi squared test = 2.4019, df = 1, P = 0.1212).

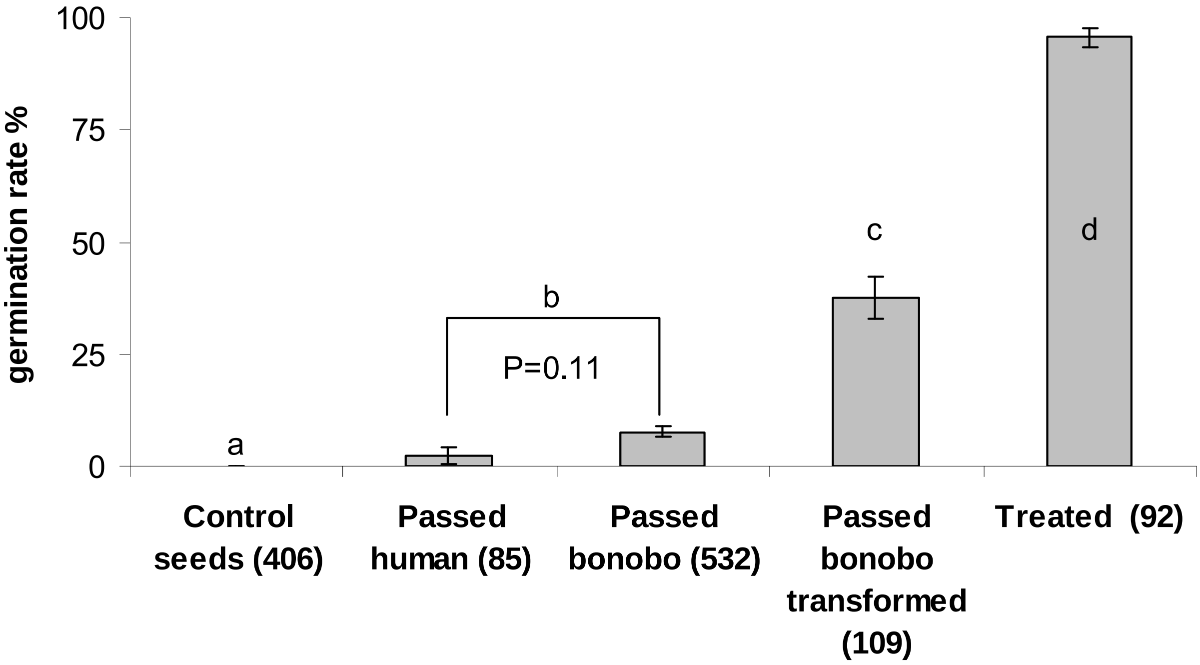

Figure 19 Germination rates of *Dialium* seeds for different preconditions. Columns along X-axes show seeds of different preconditions: Control seeds, passed seed through human and bonobos' digestive tracts, naturally transformed and artificially activated seeds. Number in brackets indicates sample size (N). Error bars indicate SE. Horizontal brackets indicate significance of differences (Multiple pairwise comparisons, binomial test, Power analysis=100%).

Transit time & 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 transit time was 24hrs00min on average ± SE. 9 min; (range: 20 hrs 03 min-28 hrs 17 min). Neither sex nor seed size affected transit time (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, sub-groups (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: 1248 ± 45 m, median= 1115; range = 1-4151 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. Figure 20. 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 % ± 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 % ± 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, 951hrs 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 (Figure 21). 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 centimetres of bark, bonobos ate the leaking sap.

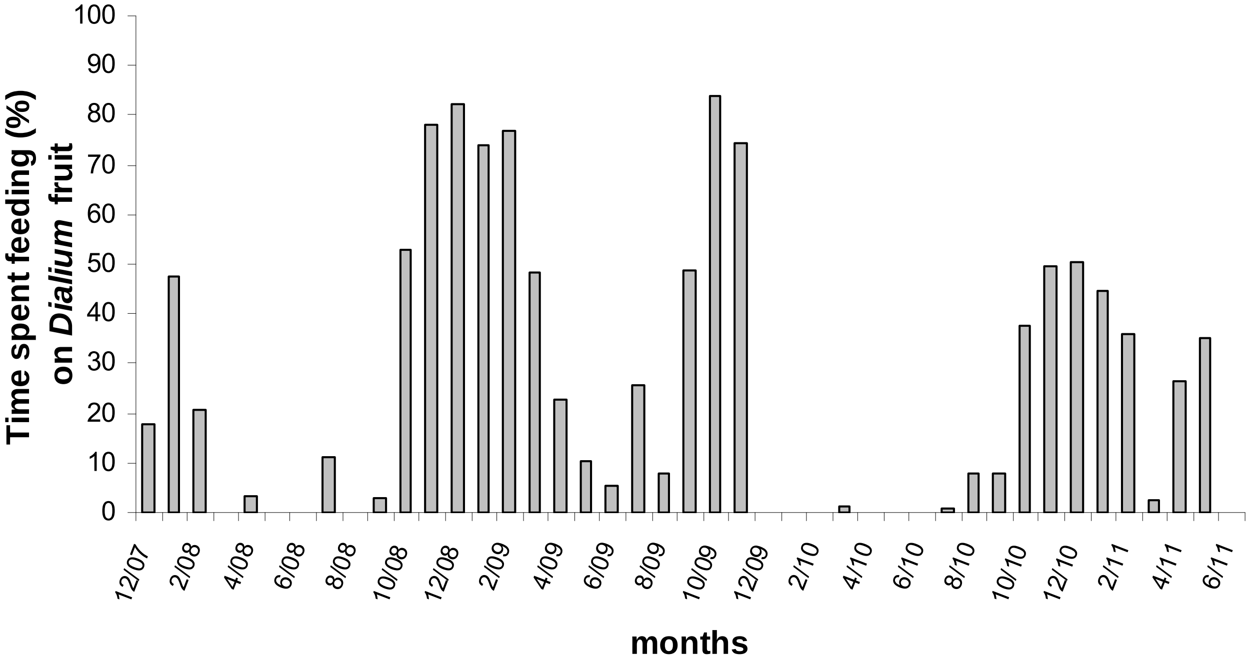

Figure 20 Time spent feeding on *Dialium* fruit. Bars indicate feeding sessions of *Dialium* fruit as proportion of overall time spent feeding for 43 months between December 2007 and June 2011.

Nutritional value of *Dialium* compared to that of other fruits

Table 6 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 to macronutrients such as protein (145.7 mg/g) and sugar (101.4mg/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 (*Cissus dinklagei* and *Greenwayodendron 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: Hominidae: *P. paniscus*; Colobidae: *Colobus angolensis*, *Piliocolobus tholloni*; Cercopithecidae: *Lophocebus aterrimus*, *Cercopithecus wolfi*, *Cercopithecus ascanius*, *Cercopithecus neglectus* and *Allenopithecus nigroviridis*. Based on five months of daily survey: *L.* aterrimus, *C. wolfi*, *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 ± SE. 0.06 (N= 124), *C. wolfi*: 0.39 ± 0.99 (N= 78), *C. ascanius*: 2.80 ± 0.15 (N= 118). *Dialium* seed handling by monkeys is different than that of bonobos. Seeds were mainly dispersed by seed spitting. Whether spit our or passed, *Dialium* seeds resulting from monkey foraging activity never germinated.

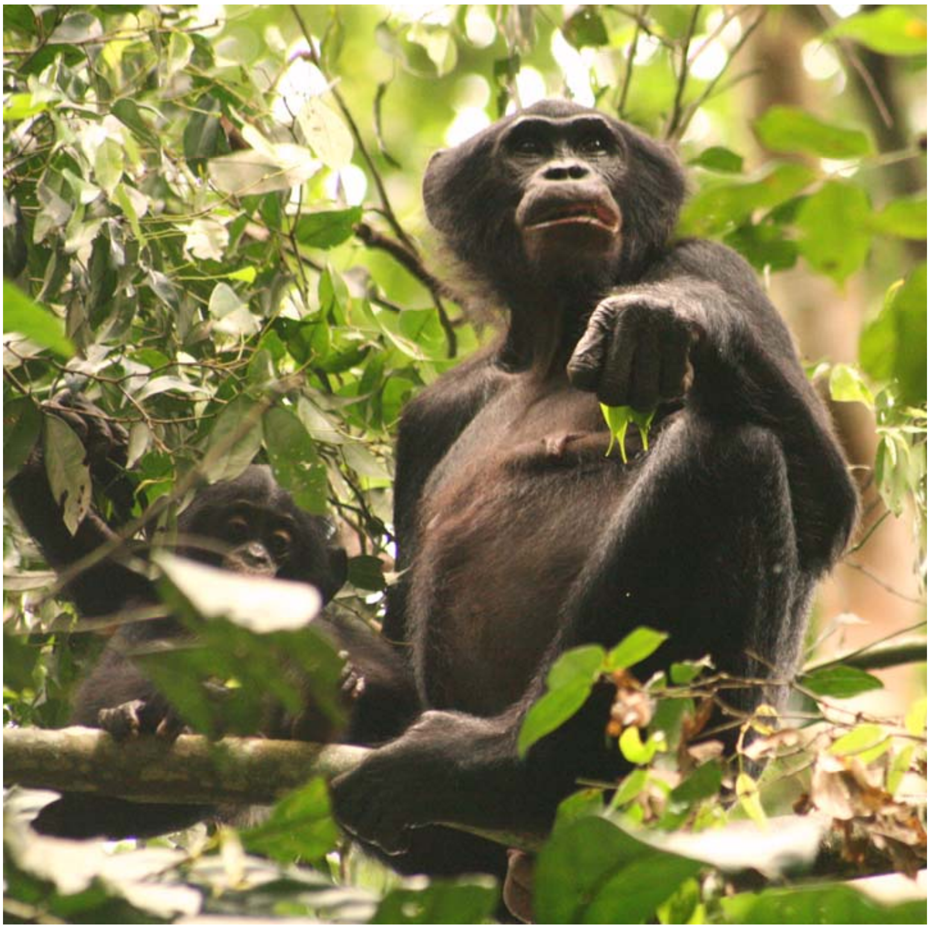

Figure 21 Bonobos eating *Dialium* leaves out of the fruiting season of *Dialium*. LuiKotale, DR Congo.

Discussion

In this study, we investigated ecological interactions between an animal (bonobo, *Pan paniscus*) and a plant (velvet tamarind trees, *Dialium* spp.). Concerning the impact for the tree, we investigated *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 1/3 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 (*Lophocebus aterrimus* and *Cercopithecus 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, which 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, Jamart & Hladik 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. aterrimus*, 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 to 96hrs 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 (Chapman, Chapman & Wrangham 1992; Cochrane 2003; Babweteera, Savill & Brown 2007).

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, Savill & Brown 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 (Fleming 1979; Clark, Poulsen & Parker 2001; 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, Clark & Smith 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 (Lambert & Garber 1998; Gross-Camp, Masozera & Kaplin 2009; Gross-Camp & Kaplin 2011). 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, Jordano & Gomez 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*), which are often found in the company of troupes of monkeys eating fruit and/or seeds that has 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. Secondly, diplocory also occurs: bonobo feces attract dung beetles (*Scarabidae,* tunnellers as *Catharsius* spp.) that bury the seeds and thus hide them from nocturnal predators (Hanski & Cambefort 1991; Feer 1999). 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 (1.25km ±SE. 0.045). Considering this very long dispersal together with home range size and post-dispersal survival, bonobos are more likely to affect the spatial structure of the trees than are sympatric primates (Westcott *et al.* 2005; Seidler & Plotkin 2006; Schupp, Jordano & Gomez 2010). 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; Walsh *et al.* 2003; Hart *et al.* 2008; Tranquilli *et al.* 2012). 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 (Howe 1984; Chapman 1995; Chapman & Onderdonk 1998). In our experiment, none of the 406 seeds that had not gone through the bonobo digestive tract germinated during eight 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% ± SE 2.3 of the tree community in the *terra firme* heterogeneous 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.

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

Table 6 Nutritional values of fruits consumed by bonobos at LuiKotale. Column *Dialium* and *Other fruits* show mean nutritional values or concentration of macronutrients expressed as % of dry matter. Direction of difference indicates > (higher), < (lower), or = (no difference) revealed by application of the Wilcoxon's signed-rank test. Nutritional values of other highly consumed fruits (*Cissus dinklagei* and *Greenwayodendron (Polyalthia) suaveolens*) are presented for comparison.

Undesired consumer: directed deterrence hypothesis with Tannin

How bonobos deal with tannin-rich fruits. Coprophagy and re-ingestion technique for *Canarium schweinfurthii*

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Gottfried Hohmann & Barbara Fruth

Abstract

This note describes the bonobo (*Pan paniscus*) adaptation to process fruits with high tannin level. In the direct deterrence hypothesis, tannin should discourage certain seed dispersers. This is not the case for bonobos that consume and disperse some of these species rich in polyphenol compound. Apes's saliva can neutralize tannin and then bonobo chew *Parinari* and *Musanga* edible pulp. Another original adaptation for *Canarium schweinfurthii* is described. Bonobos of Wamba and Lomako swallow and crunch the pulp. The LuiKotale community performs a peculiar handling technique: bonobos ingest the entire fruit. The next day they check their feces, extract the intact fruit, re-ingest the pulp and spit the seed. We do not know if this treatment 24 hours in the digestive tract affect polyphenols but this softens the pulp and allows endozoochory. This peculiar coprophagy could be a cultural behavior not shared with other group (while present at Wamba). Potentially, bonobo of LuiKotale could use this technique for self-medication with tannin of this fruit. Furthermore this potential LuiKotale's handling technique of eating *Canarium schweinfurthii* fruits implies learning, transmission and concept of anticipation.

Keywords Zoochory, coprophagy, seed dispersal, anticipation concept, directed deterrence hypothesis.

Résumé

Cette note décrit l'adaptation des bonobos (*Pan paniscus*) pour traiter et consommer les fruits hautement concentrés en tannins. La salive des singes peut neutraliser le tannin des fruits de *Parinari* et *Musanga*, les rendant comestibles par mastication. Une adaptation originale pour *Canarium schweinfurthii* est ici décrite. Pour neutraliser les niveaux élevés de tannin de ces fruits, les humains qui consomment *C. schweinfurthii* les font bouillir. Tandis que les chimpanzés et les bonobos de la communauté de Wamba et Lomako rongent la pulpe. La communauté de LuiKotale exécute une technique de traitement particulière : les bonobos ingèrent le fruit entier. Le jour suivant ils vérifient leurs fécès, extraient le fruit intact, re-ingérent la pulpe et crachent la graine. Ceci a pu traiter les composés polyphénolés 24hrs dans le système digestif. Ce comportement de coprophagie particulier semble être un comportement culturel non partagé avec d'autres groupes. Les bonobos pourraient potentiellement utiliser cette technique à des fins d'automédication avec les tannins contenus dans le fruit. En outre, cette technique de consommation complexe des fruits de *Canarium* par la communauté de LuiKotale implique l'apprentissage, la transmission et le concept d'anticipation.

Mots-clés Anticipation, coprophagie, dispersion de graine, hypothèse de dissuasion direct, zoochorie.

Introduction

In the seed dispersal effectiveness (SDE) framework, a plant can have several consumers with different qualities (Schupp, Jordano & Gomez 2010). Plants might be able to 'choose' higher-quality seed dispersal vectors and discourage lower-quality ones. The directed deterrence hypothesis proposed that fruits' secondary compounds or chemical defense mediated by plant secondary metabolites (PSMs) have evolved to discourage damaging vertebrates such as seed predators while not inhibiting helpful frugivores such as seed dispersers (Cipollini & Levey 1997; Levey *et al.* 2006). The secondary chemistry used by plants against animals, such as alkaloids, various glycosides, and saponins, are potentially toxic to consumers (Johns 1999). Others, such as lectins, enzymatic inhibitors and tannins reduce digestion and nutrient availability (Robbins *et al.* 1991). The latter are one of the most well-studied groups and primates seem to have tannin sense (astringency with textural perception, (Dominy *et al.* 2001) and avoid food with the polyphenolic compounds, in both condensed and hydrolysable forms (Oates, Swain & Zantovska 1977; McKey *et al.* 1981; Wrangham & Waterman 1981; Glander 1982). However, apes' saliva contains 'prolinerich' proteins, known as tannin-binding salivary proteins. These proteins allows nutrient assimilation even with tannin presence because of their high affinity with tannin that is neutralised after binding (Lambert 1998).

In southern bank of the Congo tropical forest the sole apes are bonobos (*Pan paniscus*) and are important fruigivores interacting with plants as seed disperser mutualists (Idani 1986; Tsuji, Yangozene & Sakamaki 2010; Beaune 2012). How do bonobos deal with tannin concentrated fruit? Does a concentration threshold exist to repulse these fruit consumers?

In this study, we 1) analyse tannin concentrated fruits among fruits of the forest (potential bonobo food), 2) explore the threshold where bonobo avoid tannin concentrated fruits and 3) describe how bonobos (*Pan paniscus*) are adapted to handle the most tannin concentrated fruits of their diet.

Because complex food processing behaviour can imply local knowledge and transmission (Whiten *et al.* 1999), we give a preliminary comparison of different bonobo communities and their food processing within the community. The ongoing long term field site of LuiKotale provides observations since one decade and allows comparisons with Wamba and Lomako, the two oldest bonobo field sites.

4) We finally analyse the bonobos' handling process and its effect on seed dispersal (either neutral, positive or negative) to test the directed deterrence hypothesis with tannin on bonobos. If bonobos disperse horizontally the seeds by endo or ectozoochory out of the fruit fall zone, (positive effect on seed dispersal), we can say that a bonobo is a seed dispersal vector not repulsed by the plant. If

bonobos eat the fruit without horizontal seed dispersal (neutral effect) or eat the seed (negative), the plant fails for the direct deterrence hypothesis to discourage neutral consumers.

Methods

Study sites

All field sites are situated in the Cuvette centrale (DR Congo), south of the Congo River within the same lowland equatorial rainforest block, that is the home range of *Pan paniscus*. LuiKotale (LK) (S2°47'- E20°21'), Lomako (Loma) (N0°51', E21°5') and Wamba (W) (N0°11', E22°37') are about 400 km apart each (Figure 22). All sites receive rain >2000 mm/yr with average temperature of 24°C. See (Hohmann & Fruth 2003c; Furuichi *et al.* 2008) for more details. In all sites, habituated groups of bonobos were daily observed by research teams. Food species overlap is high across sites (Badrian & Malenky 1984; Kano & Mulavwa 1984; Beaune 2012). We can consider that these bonobo populations share the same genotype and same ecosystem (Eriksson *et al.* 2004).

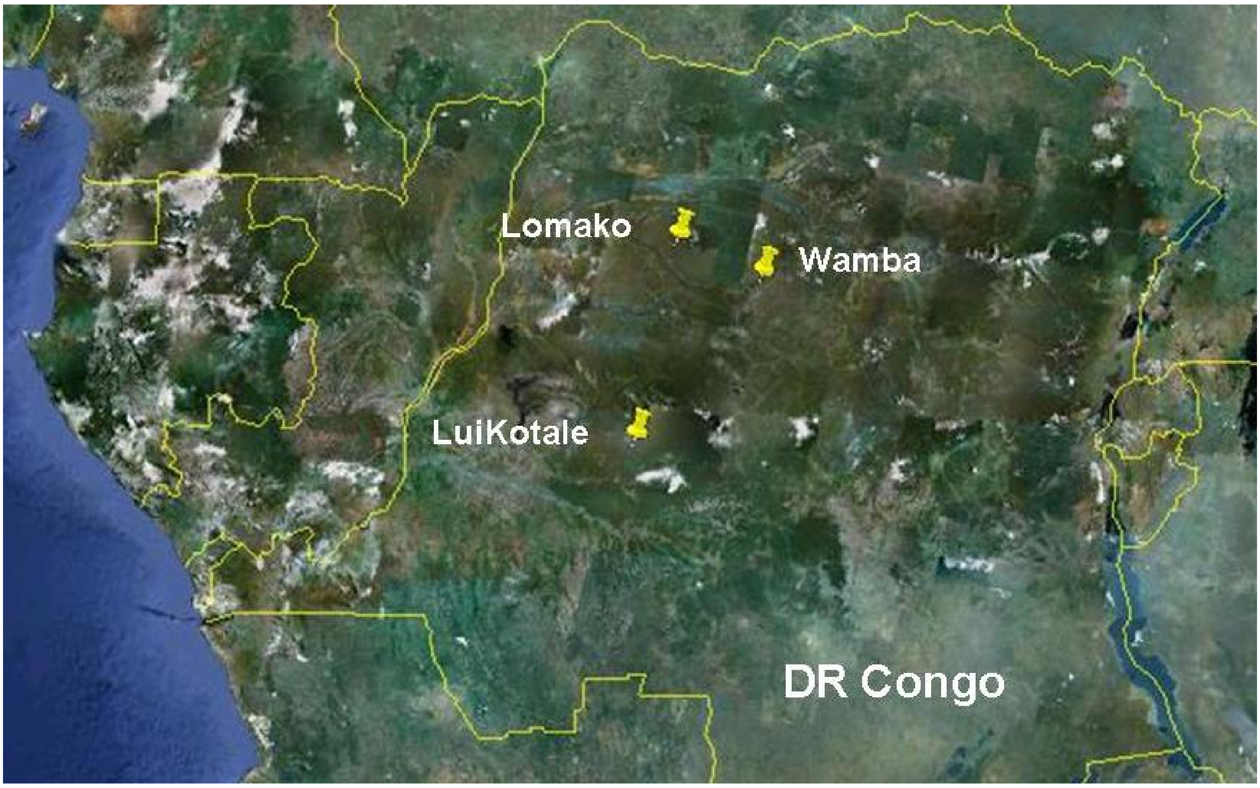


Figure 22 Map of the field sites: LuiKotale (LK) (S2°47'- E20°21'), Lomako (Loma) (N0°51', E21°5') and Wamba (W) (N0°11', E22°37'), Democratic Republic of the Congo

Ethics Statement

The studied apes are free ranging bonobos observed without invasive method, 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 ICCN, and adhere to the legal requirements of the host country, the Democratic Republic of Congo.

Tannins content analysis

Ninety five species of fruit from LuiKotale forest were collected for nutrients analyses (see (Hohmann *et al.* 2006b; Hohmann *et al.* 2010). Analyses of antifeedants such as phenols and tannins were carried out at Hamburg University following the protocol described in Hohmann *et al.* (2006).

Feeding process

From September 2009 to June 2011 behavioral data of LK bonobos was recorded across 22 months corresponding to 1879 hrs of observations or 315 days. Bonobos have a fission-fusion society that is depending on season and time of day the community splits up into smaller foraging subgroups called parties. As parties are largely cohesive going for the same activities, 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). The continuous record stopped with group loss or out of view (Beaune 2012). We analysed interactions (granivory, herbivory, frugivory with or without seed dispersal mutualism) for tannin concentrated fruits. Comparisons with Wamba and Lomako are indicated based on long term observations: Wamba (TS) and Lomako (GH, BF).

Results

Fruits with high tannin

The average percentage of condensed tannin in dry matter of fruit (100 mg) is 4.9 ±SE.1.3% ($CI_{95\%}$ = [2.1-7.7%]). Four species are outliers with significantly higher levels of condensed tannin in the flesh than the other fruits (Wilcoxon signed rank) see Figure 23. *Autranella congolensis* (A.Chev. & De Wild.) (51%; V=0, P<0.001), *Canarium schweinfurthii* (Engl.) (30%; V=6, P<0.001), *Musanga cecropioides* (R.Br.apud Tedlie) (57%; V=53, P<0.001) and *Strombosia glaucescens* (Engl.) (16%; V=58, P<0.001). Another fruit, *Parinari excelsa* (Sabine) is the highest value of the range with 12% of condensed tannin in the flesh. *A.congolensis* fruits are also outliers for total phenol and total tannins with 2.45 and 1.89% respectively. These values are significantly different from the averages total phenol found in fruits: 0.75±1.17%; $CI_{95\%}$ = [0.38-1.12%]; and average total tannin: 0.55± 1.16%; $CI_{95\%}$ = [0.21-0.92%].

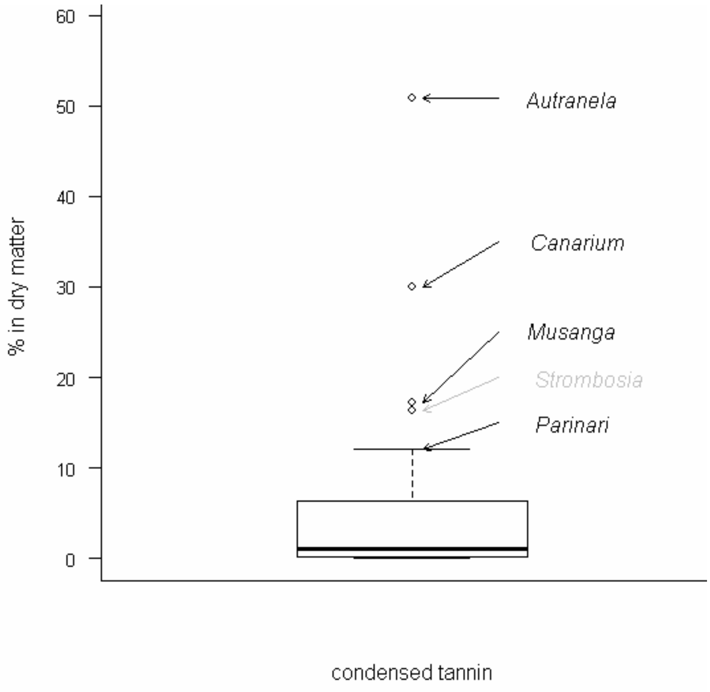


Figure 23 Condensed tannin (% in dry matter) in fruit. Outliers are *Autranella congolensis*, *Canarium schweinfurthii*, *Musanga cecropioides* and *Strombosia glaucescens*. *Parinari excelsa* is the maximum value of the range. *S. glaucescens* fruits are not consumed by bonobos.

Bonobo handling techniques

The following handling processes from LK are based on observations of 992 hrs of feeding sessions. The feeding techniques for dealing with tannins were observed on *Canarium schweinfurthii*, *Musanga cecropioides* and *Parinari excelsia* from January 2009 to June 2011 (DB). *Autranella congolensis* in 2005 (BF). *Strombosia glaucescens* were not observed and is not reported as fruit consumed (Kano & Mulavwa 1984). Nevertheless seed consumption was noticed in Lomako (Badrian & Malenky 1984; Kano & Mulavwa 1984).

Saliva neutralization:

Parinari excelsa: (LK) In June-July 2007 and June-July 2010, 54 feeding sessions were observed with the bonobos on 27 different *P. excelsa* trees. To eat the fruit (44 mm ø, N=10), the bonobos scrape the mesocarp around the seed (35mm ø, N=10) of several fruits and chew the wadges (Figure 24) which is then spat out. Bonobos stay under the crown corresponding to the fruit fall zone. Horizontal seed dispersal is limited comparing to endozoochory, but seeds may be carried at several meters. Apes are not endozoochoric seed disperser of these trees. Consequently, *P. excelsa* failed to discourage this primate in the direct deterrence hypothesis and bonobos are neutral or limited seed dispersers (ectozoochory).

(W): Similar technique (NB: bonobos carry the wadges of the fruits including seeds sometimes about 100 meters).

(Loma): Similar technique.

Autranella congolensis: (LK) feeding session was not observed since 2005 with the last fruiting season of these trees (Fruth unpub data). To eat the fruits (7cm ø, n=10), the bonobos eat the yellow mesocarp around the seed (5.5cm ø, n=10). Chewing behaviour was not reported during this research season but not excludable. Bonobos stay under the crown corresponding to the fruit fall zone. Horizontal dispersal of the seeds is extremely limited when considering dispersal effectiveness. The apes are not endozoochoric seed disperser of these trees. Consequently, *A. congolensis* failed to discourage this primate in the direct deterrence hypothesis and bonobos are neutral/limited seed dispersers.

(W): species absent (Idani *et al.* 1994)

(Loma): Similar technique.

Musanga cecropioides: (LK): From January 2008 to July 2010, 27 feeding sessions were observed on 14 different trees. Bonobos ate the young stem, the flower and fruit. Bonobos chew for several minutes the flat fruit entirely (5-15cm long), that contain thousands of seeds (<2mm ø, n=10). Wadges were swallowed with viable seeds found in dung or occasionally spat out (Fowler pers. com.). Swallowing or spitting behavior is probably linked with ripeness stage of the fruit. The bonobos can be considered as endozoochoric seed disperser for *Musanga* trees.

(W): Similar technique

(Loma): Similar technique

Canarium schweinfurthii: (LK): In July 2007, January 2008, April 2009 & 2010 and February 2011, 14 feeding sessions were observed on 10 different trees. Bonobos swallowed the entire fruits without biting or chewing. The next day, the dung was checked. *C. schweinfurthii* fruits were extracted intact from the dung. After this first passage, bonobos bit the pulp, spat out the seeds and re-ingest the pulp. Independent juvenile bonobos did the same, similarly to all members of the observed parties. Infants observed the mother when she held and checked her own dung. After the second ingestion, the necked seeds of *C. schweinfurthii* are dropped on the ground. Through this local behaviour the bonobo is an endozoochoric disperser of *C. schweinfurthii* at LK.

(W): Bonobos at Wamba first bite or chew the flesh around the seeds, and then eat the pulp if ripen or drop it out without eating if unripen. They may taste the astringency first. Therefore they are not endozoochoric and have limited horizontal dispersal. However the similar technique described in LK was observed (N=???). This feeding technique is not "customary" or "habitual" but just "present" in Wamba population (see the terms in (Whiten *et al.* 2001).

(Loma): Similar to Wamba.

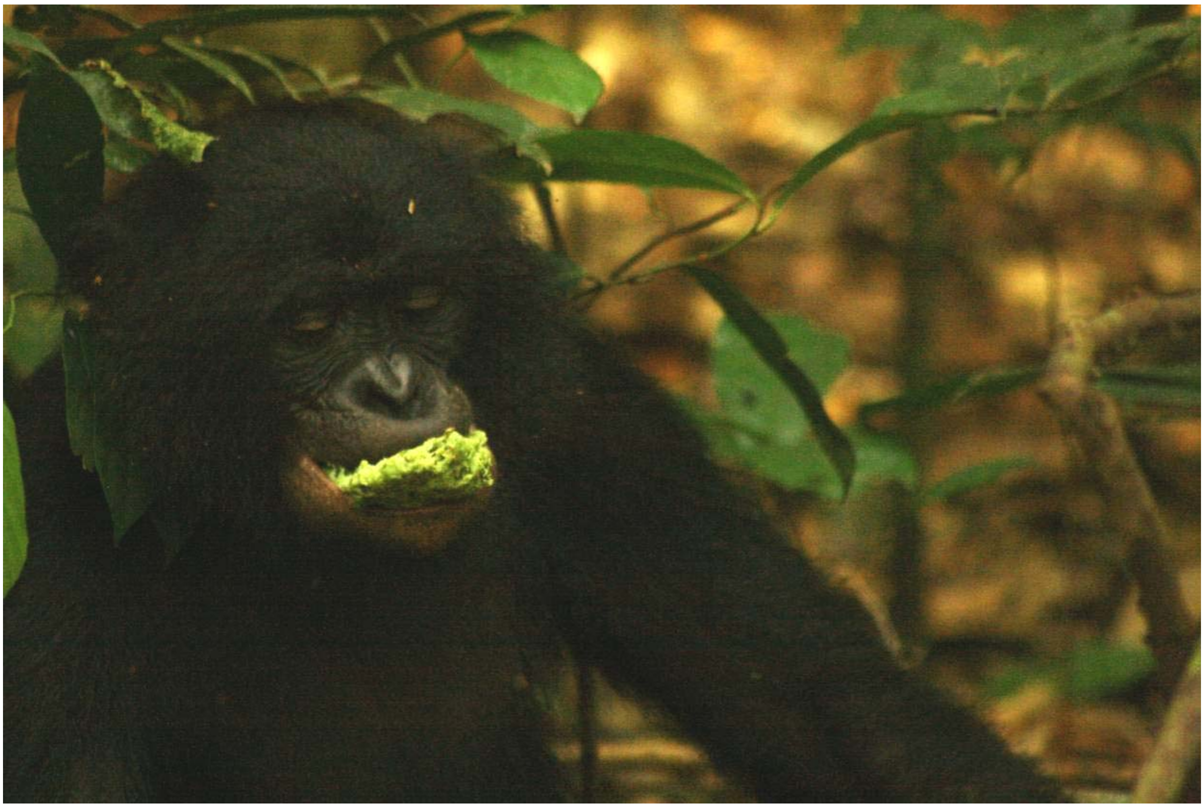


Figure 24 Emile chewing wadges of *Parinari excelsia*. LuiKotale, DR Congo.

Discussion

The directed deterrence hypothesis

The main dispersers of: *Parinari excelsa* and *Autranella congolensis* are elephants (Yumoto *et al.* 1995; White & Abernethy 1997); *Musanga cecropioides*: birds, rodents and primates (Gautier-Hion *et al.* 1985), while *Canarium schweinfurthii* seems to be hornbill dependant

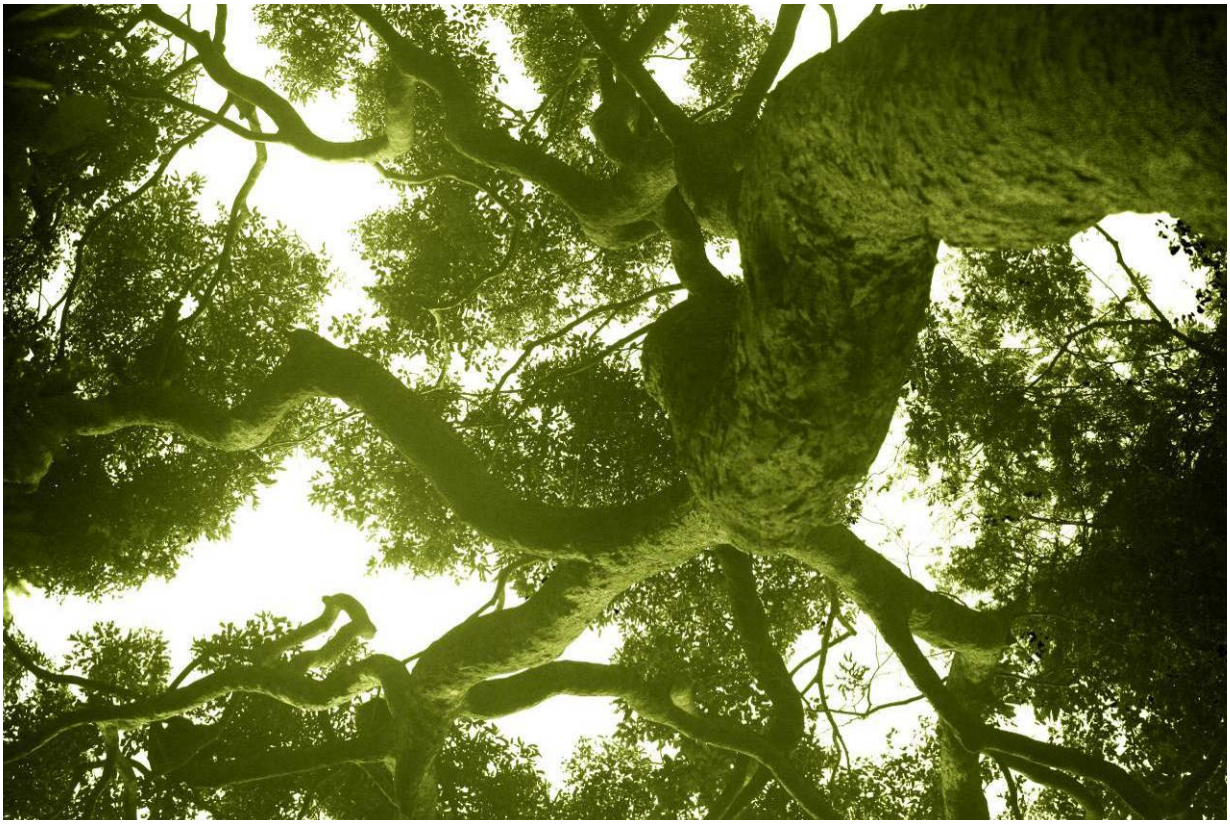
(White & Abernethy 1997). The tannin of this different fruit species could be discouraging enough for seed predators and neutral seed disperser as flesh consumers. However, bonobo adaptability with its apes' saliva and sophisticated handling behavior can eat the fruit and deal with chemical defense. In this study, different seed dispersal interactions are described. Where bonobos avoid *Strombosia glaucescens*, are ectozoochoric with *P. excelsa* and *A. congolensis*, bonobos are alternative endozoochoric partners with birds, rodents and monkeys for *M. cecropioides* or even locally for *C. schweinfurthii*. Seed dispersal in the fruit fall zone with seed spiting can be dangerous for seeds such as *P. excelsa* and *A. congolensis*, due to the density dependant effect and predation of both species by bush pigs (Beaune *et al.* 2012b). While seeds embedded in feces and dispersed by endozoochory (*Musanga cecropioides*) escape seed predators with dung beetles (Beaune *et al.* 2012a) Because bonobos are efficient seed dispersers in term of quality and quantity (Tsuji, Yangozene & Sakamaki 2010; Beaune 2012), the population structure of the *Canarium* from LuiKotale (seed dispersal vectors = Hornbill + bonobo) could be different than Wamba and Lomako's population (seed dispersal vector = Hornbill). For the reason that long dispersal distance and seed dispersal effectiveness are different between these birds and apes (Whitney *et al.* 1998; Holbrook, Smith & Hardesty 2002; Poulsen *et al.* 2002), this should impact populations' biology and structure of *C. schweinfurthii* at LuiKotale, Wamba and Lomako.

The Canarium handling technique

Among 1879 hrs of observation in LuiKotale, other coprophagic behaviours were not observed within the context of *C. schweinfurthii*. Nevertheless, exceptional coprophagy events were observed with juveniles and subadults eating the matrix or picking some *Dialium* seeds (Douglas unpub data, similarly reported at Wamba (Sakamaki 2010) and for juvenile chimps (Krief, Jamart & Hladik 2004). Coprophagy and re-ingestion technique seems to be specifically used to process fruits of *C. schweinfurthii*. This peculiar adaptation to high tannin levels is vivid and original in apes. While humans boil *Canarium* fruit, to soften the flesh and maybe neutralize tannins, bonobos process the fruit for 24hrs in the digestive tract. The fruit still intact could diffuse the antifeedant in the bolus. This uncommon technique was possibly accidentally learnt from rare coprophagy events occurring in bonobos. Then this technical acquisition needed to be transmitted to the group. This re-ingestion behaviour could have emerged in other independent bonobo groups, but is apparently not widespread though populations. As demonstrated with the Wamba and Lomako population which does not process *Canarium* fruit or exceptionally. Could this technique be cultural?

Another explaination is that condensed tannins have antiseptic, antibacterial, antiviral and caustic properties (Robbins *et al.* 1991; Min & Hart 2003). Animal use self-medication (Huffman 2003). Self-medication with leaf folding was reported in free ranging bonobos (Dupain *et al.* 2002). Thus bonobo could possibly use this handling technique to treat parasites or other self-medication with tannin. In the *Canarium* case, bonobos swallow the pill that unfolds its phytochemical properties where they may be required in the intestines. Further investigation are required.

Nevertheless the simplest explanation is that bonobos found an original handling technique to process difficult food. Without tools, bonobo can deal with indigestible food. This processing has neither been described in chimpanzee (*Pan troglodytes*) nor in other primates. Furthermore, cognitive function of prospection seems to be involved. The bonobos have to anticipate a food that they will eat without direct digestion but delayed. 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*.



Example of application in plant conservation

Artificial germination activation of *Dialium corbisieri* by imitation of ecological process

David Beaune, Loïc Bollache, Musuyu D. Muganza, François Bretagnolle,
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Abstract

Species of the genus *Dialium* commonly are trees found in Central African rainforests. They produce tasty sugary fruits, feeding numerous frugivores, but are despite their valuable nutritional value, rarely exploited by humans. Potential reason for this could be the complexity of symbiotic dependence between trees and pollinators, germination activators, and dispersers causing problems in ancestral and contemporary domestication. We investigated *Dialium corbisieri* (Staner-1932) reproduction in DRCongo, Bandundu province. Here we give a key for an artificial activation of germination of these trees ecologically adapted to the digestive system of their ape dispersers: by perforation of the impermeable seed coat protection water assimilation and subsequent activation of germination becomes possible. By this nicking pretreatment germination increases from 0 to 96%, representing an inexpensive and simple treatment to be used under natural conditions and in developing countries. The use of this mechanical activation for forest management, conservation and economical use is discussed.

Keywords *Dialium corbisieri,* African velvet tamarind, seed pre-treatment, germination activation, seed dormancy, endozoochory, domestication.

Résumé

Les espèces du genre *Dialium* sont généralement des arbres trouvés dans les forêts tropicales humides d’Afrique centrale. Ces arbres produisent des fruits sucrés savoureux, qui nourrissent de nombreux frugivores. Mais en dépit de leur importante valeur nutritive, ces espèces sont marginalement exploitées par des humains. La raison potentielle pourrait être la complexité de la dépendance entre les arbres et leurs pollinisateurs, leurs disperseurs de graine et activateurs de germination. Ceci posant des problèmes pour la domestication passée et contemporaine de ces arbres fruitiers. Nous avons ici étudié la reproduction de *Dialium corbisieri* (Staner-1932) en RD Congo, province de Bandundu. Ici nous donnons une clef pour l’activation artificielle de la germination de ces arbres écologiquement adaptés au système digestif des grands singes, leur vecteur de dissémination : la perforation du manteau tégumentaire imperméable permet l’absorption d’eau et l'activation de la germination qui devient possible. Ce traitement par scarification augmente le taux de germination de 0 à 96%. Ce traitement est peu coûteux et simple d’utilisation dans des conditions de terrains et dans les pays en voie de développement.

L'utilisation de cette activation mécanique pour la gestion des forêts, la conservation et un usage économique de l’espèce est discutée.

Mots clefs Activation de la germination, *Dialium corbisieri*, domestication, dormance tégumentaire, endozoochorie, prétraitement de graines, tamarin africain.

Introduction

The family of the Leguminosae got an important ecological role in forests with their ability to directly absorb atmospheric azotes (N_2) and to release it for the rest of the ecosystem (Roggy & Prevost 1999). Of particular interest are *Dialium* species belonging to the sub family of Caesalpinioidae. They dominate parts of the tropical evergreen lowland rainforests of the Central Congo Basin, DRC. Species of this gender are medium sized to very tall trees (up to 40 meters) with a very hard wood, highly valued in timber, and fruit providing an edible pulp (Janick & Paull 2008), p. 391). Some of them are considered of particular interest for their mono-lobed fruit consisting of a slightly flattened seed protected by a hard endocarp, imbedded into a pithy and luscious sweetly sour edible mesocarp and enclosed by a black-brown velvety, thin and brittle exocarp (capsule). Fruits stand erect at the end of branches and ripen over an extended period of the year, usually coinciding with dry seasons. Availability of fruit has been reported between February and May for Nigeria and, between November and July for Gabon (White & Abernethy 1997). These fruits are important for a lot of frugivorous species in rain-forest biocenoses and we can observe a strong interaction between plants and animals (Beaune, unpubl. data). To attract animals as seed dispersers, angiosperm fruit coevolved with fruit-predators adapting to the taste and digestive system of their partners (Thompson 1991; Jordano 1995). Partners include birds, ungulates, monkeys and great apes including Bonobo (*Pan paniscus*) (Hohmann *et al.* 2006b) ; Beaune *et al., in prep*), Chimpanzee (*Pan troglodytes*) and Gorilla (*Gorilla gorilla*) (Kuroda *et al.* 1996; White & Abernethy 1997). *Dialium* seeds are adapted to endozoochory by their strong endocarp (i.e. seed coat dormancy) in order to survive through the frugivorous' gut passage. This potentially avoids or inhibits the ability to self germinate and thus may be considered as displaying dependency to endozoochory.

Dialium fruit are not only of importance to forest dwelling animals, particularly non-human primates, but also to humans. Particularly *Dialium guineense*, known in Africa as Black Velvet Tamarind, is used by people in West and Central Africa. Fruit is popular and traded in Benin and of regular use in Nigeria (Arogba, Ajiboro & Odukwe 1994). It is known to contain high levels of Vitamin C, sugars, essential oils and other nutritive components (Achoba *et al.* 1993; Arogba, Ajiboro & Odukwe 1994; Ude *et al.* 2002; Onwuka & Nwokorie 2006; Essien *et al.* 2007).

However traditional use of *Dialium* fruits across Africa is not widespread, and attempts to enhance cultivation or incite industrialisation so far was constrained by their ecology. In addition, certain *Dialium* species are at risk by habitat loss and registered on the IUCN red list as follows: *D. bipindense* (lower risk/near threatened); *D. cochinchinense* (lower risk/near threatened); *D. excelsum* (endangered); *D. holtzii* (vulnerable); *D. lopense* (lower risk/near threatened); *D. orientale* (lower risk/near threatened); *D. travancoricum* (critically endangered) (IUCN 2010). An increasing risk that has been so far underestimated is the loss of seed dispersers. Commercial hunting and the bush meat trade cause a considerable decline in seed dispersers. Overhunted forests, stigmatized by the empty forest syndrome, become disturbed in the reproduction and dynamic of their current vegetation (Terborgh *et al.* 2008). To conserve and support *Dialium* progeny therefore is not only of interest for the purpose of agriculture but also for the purpose of habitat conservation.

In this study, we propose an artificial activation of the *Dialium corbisieri* seeds, with regard to the natural activation in great apes, trying to mechanically replace what is chemically happening in the apes' digestive tract. *Dialium* seeds recovered from apes' dung are either intact or swollen and show coat removal. The major hypothesis is that strong seed protection (i.e. endocarp or seed coat dormancy) is perforated by mechanical or chemical digestive processes. Consequently, seeds become porous and absorb water. Previous studies tried different chemical (Razanamandranto *et al.* 2004; Tanaka-Oda, Kenzo & Fukuda 2009) or chemical as well as mechanical methods (Todd-Bockarie & Duryea 1993; Sozzi & Chiesa 1995; Razanamandranto *et al.* 2004; Vari *et al.* 2007; Nwaoguala & Osaigbovo 2009; Tanaka-Oda, Kenzo & Fukuda 2009). Both sulphuric acid bath (H_2SO_4) and nicking of seeds appear to be the most effective pre-treatments. However, the chemical effects seem to be similar to the mechanical treatment in that they cause perforation of the seed coat tissue improving water absorption by the embryo. While chemical incitement is expensive, dangerous and needs peculiar equipment for usage in nurseries (Todd-Bockarie & Duryea 1993; Olufunke & Gbadamosi 2009), mechanical treatments are simple, harmless and available to all.

Here we apply a mechanical treatment as a simple and cheap way to test the potential of *Dialium* reproduction in artificial nurseries as replicable procedure for countries containing tropical rainforests.

Material and methods

Study area

The study was carried out from April to May 2009 within the LuiKotale research site (S2°47'- E20°21'), located within the equatorial rainforest, south-west of Salonga national park (Figure 1), Bandundu Province, Democratic Republic of Congo (Hohmann & Fruth 2003c). The climate is equatorial with abundant rainfall (2016 mm for the year 2008; 448 for April and May 2009) and a relatively dry season from February to July. Mean temperature at LuiKotale ranges between 21°C to 28°C with a minimum of 17°C and a maximum of 38°C (n=360 days for 2008). For April and May the range was 21°C to 29.3°C with a minimum of 20°C and a maximum of 33°C.

Sample collection an measurements

We used one species only: *Dialium corbisieri*. For genetic similarity, fruits were collected from the same branch at 25m height. Collection was done the 8th of April 2009 when seeds were fully ripe. Entire fruit were taken back to Lui Kotale camp field laboratory where they were manually opened by breaking the brittle exocarp. Seeds were isolated by manually removing the mesocarp. Seeds were separated into three groups (see below) to undergo a different treatment each. Seed transformation was measured before and after 48h of immersion in water (see below) in order to test the coat permeability and potential water assimilation. For this, seed weight was taken in mg using an electronic balance (KERN-Taschenwaage 0-300mg ± 10µg), seed diameters (length and breadth) were taken in mm using slide calliper (0-10cm ± 1µm).

Groups of seed treatment for activation and monitoring of artificial germination

Group 1: Artificial seed coat perforation: In accordance to the seed enhancement technique (Taylor *et al.* 2008) seed protection was interrupted in 92 seeds by scratching with a knife a piece of endocarp (< 1mm) until the endosperm appeared. These nicked seeds were immersed in rain water for 48h;

Group 2: Intact seed coats: A total of 92 seeds were left with intact endocarp. These intact seeds were immersed in rain water for 48h and served as control for Pw;

Group 3: A total of 100 seeds neither underwent mechanical treatment nor was it immersed in rain water. These seeds were considered being similar to dropped seeds *in natura* such as seeds spread by ectozoochory of monkeys (pers. obs.) and served as overall control group.

All seeds were randomly positioned on a sieve with absorbent paper. For distinction between treatments, each seed was flagged with a bamboo stick next to it. Sieves were kept under the canopy with a grid protection against predators, under *in situ* climatic conditions. Every day at 6:00 hours, all seeds were monitored in order to detect the emergence of the radicle and subsequently hydrated with rain water. Radicle emergence was used rather than flushing of the cotyledons because radicle emergence is considered to be the first sign of germination and thus demonstrates viability of seeds (Heß 1999; Knogge, Herrera & Heymann 2003).

Statistical analysis

After testing the data's normality (Shapiro-Wilk normality test), parametric data of the size and weight were tested by Student's t-test. Germination rate between groups were compared using Binomial test. The power analysis of the tests is specified when a difference is detected. Analyses were performed using R 2.11R (R Development Core Team, 2005) was used for statistical analysis.

Results

Seed transformation

Already after the first hours of immersion, all perforated seeds started to swell. Figure 25a-c shows weight and size dimensions of perforated (n=92) and intact seeds (n=92) before and after 48hours of immersion in rain water.

In terms of weight, perforated seeds were on average twice (× 2.21) as heavy as were intact seeds of the control group. While they weighed 0.27mg±se. 0.01mg on average before, they weighed 0.59mg± 0.01mg on average after immersion, resulting in a highly significant difference (Fig1a: t-test: $t = -31$, $df = 112$, $p<0.001$. power analysis=100%).

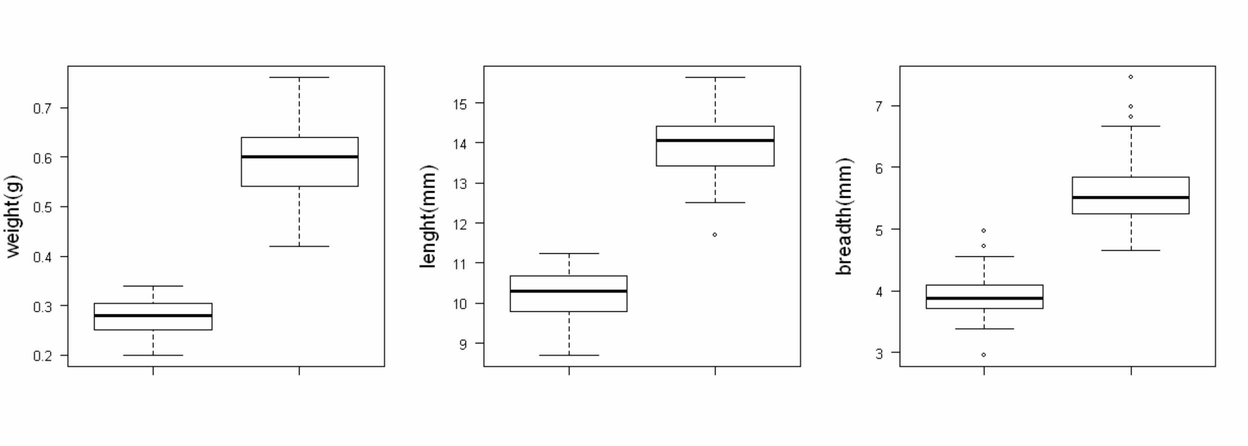


Figure 25 Seeds transformation of intact (left) versus perforated seed coat (right), after 48h of immersion in water. (a): Weight ; (b): Length ; (c): Breadth.

In terms of size, perforated seeds were significantly larger than intact seeds of the control group: This was reflected by increase in length by 1.35 times of perforated seeds in comparison to intact seeds. While length measured 10.28mm± 0.09mm on average before, they measured 13.93mm± 0.09mm on average after immersion (Figure 25b: t-test: t = -28, df = 132, $p<0.001$. power analysis=100%) as well as by increase in breadth by 1.39 times between these two groups of seed treatment. While breadth measured 4.02mm± 0.06mm on average before, they weighed 5.63mm± 0.07mm on average after immersion (Fig 1c: t-test: t = -17, df = 128, $p<0.001$. power analysis=100%).

In summary, all 92 perforated seeds were swollen after 60 hours, there was neither an effect on intact seeds immerged for 48hours in rain water as shown by the control group nor was there any measurable effect on the overall control group without any treatment. (weight: t = -0.7, df = 132, p-value = 0.5; length (t = 1.5, df = 132, p-value = 0.1); breadth: t = 0.2, df = 128, p-value = 0.9).

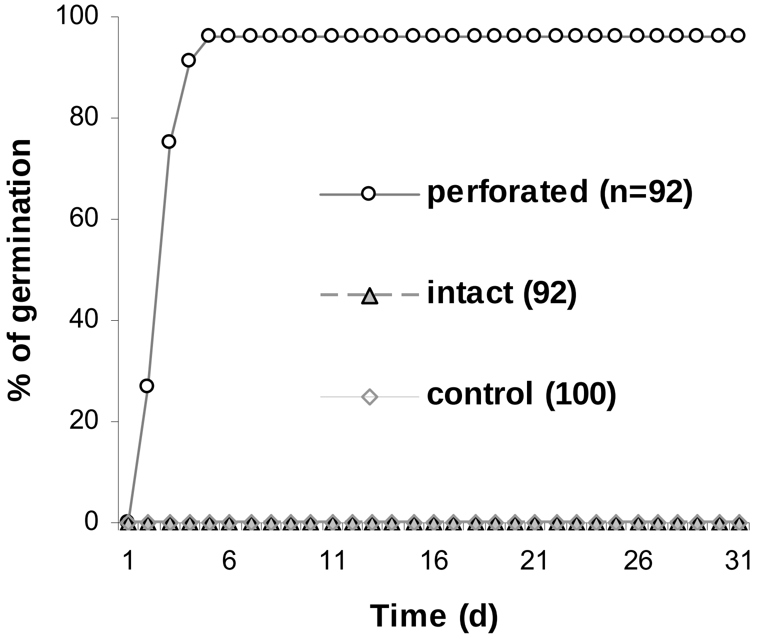


Figure 26 Germination in relation to time in *Dialium corbisieri* according to treatment (perforated seed coat).

Artificial germination activation

Figure 26 shows the results of the monitoring of radicle emergence in 284 seeds divided according to the treatments described above, into three test-groups, Perforated (n=92), Intact (n=92) and Control (n=100). After 24h in nursery, 27% of the treated seeds showed appearance of their radicle. After four days 96% of the perforated seeds germinated whereas all other seeds did not. The proportion of germinated perforated seed is significantly different since the first day ($p<0.001$).

Discussion

As shown in our results, only *Dialium* seeds with seed coat perforation were able to swell and germinate. These results may illustrate a clear adaptation of the seed coat impermeable to rain water on endozoochory. By coat perforation the seeds absorb water and the germination rate is triggered by 0 to 96%. *Dialium corbisieri* recruitment shows dependence of seeds passing a partners'gut to be not condemned to everlasting dormancy in the forest (Beaune *et al., in prep*). In the absence of natural seed dispersers, seed dormancy can be broken by imitation of the natural process, allowing the seed to absorb water, to swell and activate germination. This is what happens with endozoochoric partners as apes: the digestive acid nicks the coat and induces germination. Seeds found in bonobo dung are similar in size and shape to transformed seeds as obtained by artificial seed coat perforation and water immersion (Pw) (pers. obs). However not all frugivores can act as partner for this effect. Cheek pouch monkeys such as crested black mangabeys (*Lophocebus aterrimus*) spit the *Dialium* seeds apparently unharmed onto the ground (pers. obs). Teeth may scratch the coat, but whether or not this is enough to induce water absorption needs to be investigated by focusing on seeds dispersed by ectozoochoric partners. In addition, transit time across the dispersers' gut passage may effect perforation. While bonobo's gut passage time appears to be appropriate, we do not know if the transit time of birds or bats is long enough to perforate *Dialium* seed coats. Moreover, the question remains, whether or not after spiting the seed on the ground, the ambient moisture absorption (versus: digestive bath) is rapid enough to avoid pathogens infection of the dormant seeds. Indeed, fast germination can help to skip seed predators and start the race against seedling pathogens.

This result is a good example for application of ecological processes to ecological and economical management. Pretreatment for tree breeding of *Dialium* species could be of use for both the a) restoration and conservation of natural forests and the b) potential for future nutritional use.

Restoration and conservation

Tree nurseries are used for forest restoration and conservation (Dumroese & Riley 2009). In the restoration of forest impacted by logging, or other ecological catastrophes, fruiting trees are important resources for maintaining or restoring frugivorous populations such as primates, birds, or bats (Dew & Boubli 2005) that consequently, may regain their keystone role in the ecosystem (Terborgh 1986). However in a disturbed system, natural colonisation of these dependant trees could be difficult if populations of animal partners have decreased or partners are already exterminated (Chapman 1995; Chapman & Onderdonk 1998b). Human interventions may be the last solution with *Dialium* nurseries becoming now possible with this artificial method for the breeding of shoots.

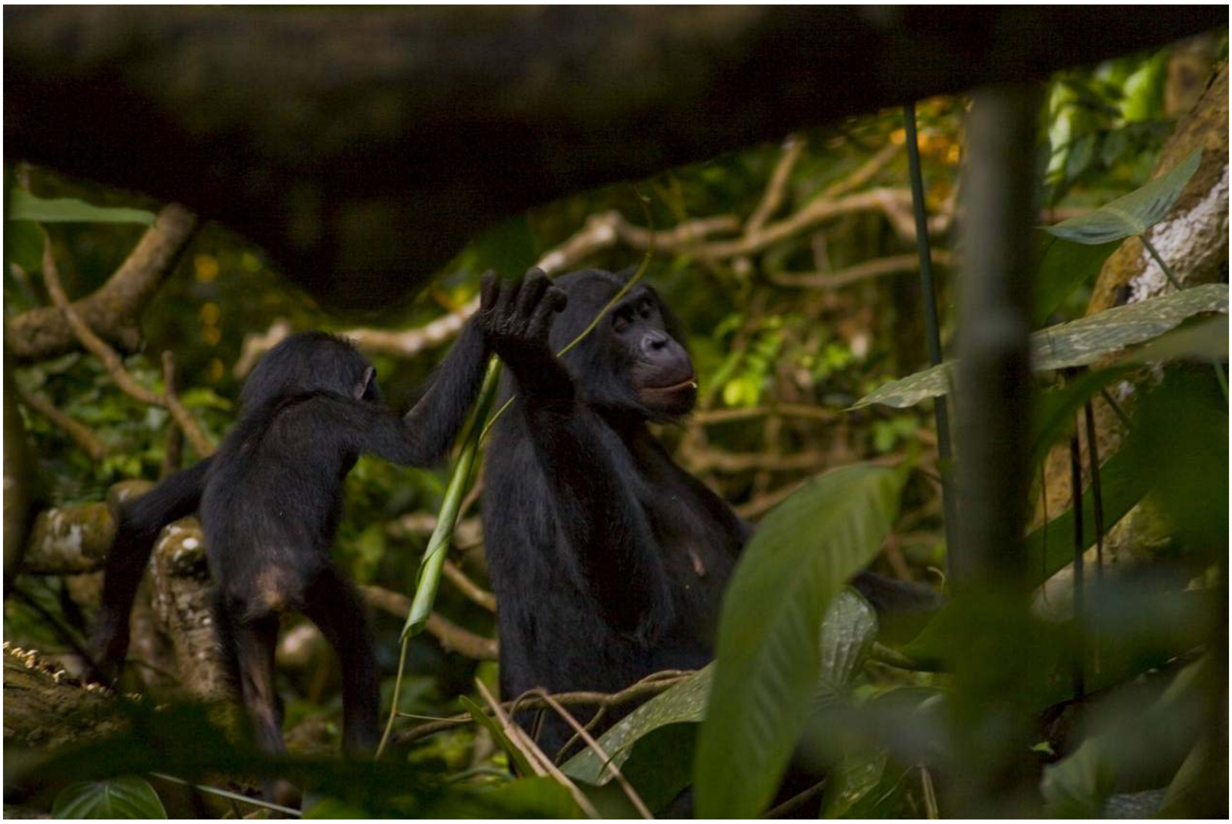
Potential for future nutritional use

Focusing on the larger environments of our study site, indigenous people of the Bolongo area in Bandundu province, south West of the Salonga National Park in DRC, have a profound knowledge of the trees species of their surroundings. Among 56 local people asked during visits to adjacent villages, all knew the “Maku” which is the vernacular name for all *Dialium* trees. The majority of these people distinguishes between two ethnospecies “Maku rouge” and “Maku pembe”, comprising seven species taxonomically described for Lui Kotale study area (Fruth *et al.* unpubl. data): the “Maku rouge” (*Dialium corbisieri* and *D. zenkeri*) and “Maku pembe” (*D. gossweileri, D. kasaiense, D. pachyphyllum, D.angolensis, D. tessmannii*) with reddish and clear bark respectively. With their large naturalist knowledge, “Maku rouge” stays for the consumption of caterpillars feeding on Dialium leaves, as well as for the use of wood in construction or treesap in medicine, fruits of “Maku rouge”, however, despite their highly nutritive value, are not on their menu. In our study area this lack of consumption of *Dialium* fruit by local people, can be easily explained by the availability of fruits of other species that are much easier to access. In contrast, explanations may differ for areas where *Dialium* is part of the human diet such as in Benin. Here, the symbiotic dependence between tree and dispersers, which is a barrier for domestication, may explain the difficulty of this fruit becoming a diet widespread among people inhabiting tropical zones of subsaharian Africa. The system, however, is even more complex: *In addition to* great apes and dung beetles as dispersers (Beaune *et al.* in prep.), *Dialium* trees are highly symbiotic with a lot of partners such as nitrogen fixing bacteria for nitrogen absorption, insects for pollination (Kato *et al.* 2008), or apes for germination activation. All these dependences could be an obstacle for domestication.

There are two potential ways to successfully domesticate plants: either randomly by trial and error of seed recruitment or by detailed understanding of the complex ecological processes such as shown for *Ficus* requesting a specific wasp for pollination (Murray 1985) and specific manipulations for horticulture thereafter (Kjellberg & Valdeyron 1984).

This example may show the high ecological interdependence of rainforest-species and the problem of domestication of species in these areas despite their great potential for nutritional or economic use. Increase in overall population size of homo sapiens and the related challenge to face nutritional requirements for all, asks for the domestication of new plants by help of modern agriculture paired with scientific knowledge.. As we have shown here, the problem of the activation of germination of *Dialium seeds* can be overcome artificially. Will we find the luscious *Dialium* fruit in our organic supermarket from the African agriculture in 50 years?

Part II



Long-distance dispersal

Can fruit traits control the distance that animals move seeds during dispersal?

David Beaune, François Bretagnolle, Loïc Bollache
& Barbara Fruth

Submitted to Behaviour

Abstract

In an Afrotropical forest, the test hypothesis was that fleshy-fruited plants with interspecific difference in fruit quality affect the behaviour of their seed dispersers, thus affecting seed dispersal distance. From 2007 to 2011, an extensive movement survey was conducted on an important and common seed disperser in Congo forests: the bonobo (*Pan paniscus*), with GPS georeferencing daily movements. Transit times were calculated; dispersal distance was estimated, using 1200 georeferenced dispersal events, and results were compared for species, seasons and years (ANOVA). An exact mechanistic model compared dissemination for eight plant species dispersed by bonobo through its ranging behaviour; the only variant factor being the fruiting species. We tested the trade-off for plants: attracting dispersers by means of fruit quality/quantity versus retaining them in the patch because of the same quality/quantity value that attracted them. Transit time (mean ± SE) is similar among species (24h00 ±00min). Dispersal distance is not affected by year, season or species trait. Although a difference exist for the average feeding time spent per fruiting species, and for the fruit nutrient contents, they are no relation time spends on the feeding patch and the dispersal distance that that follow. The average bonobo dispersal distance is (1332 ± 24 m). Feeding time invested in the patch, fruit quality and abundance had no apparent effect on bonobo ranging behaviour and therefore did not affect dispersal distance.

Keywords African forest, bonobo, Congo Basin, forest structure, long-distance dispersal, mutualism, *Pan paniscus*, seed dispersal, tropical rain forest, zoochory

Résumé

Dans une forêt Afrotropical humide, l'hypothèse testée est que les plantes à fruit avec leurs différences interspécifiques en qualité et quantité affectent différentiellement leur partenaire animal disperseur de graines. Ce qui aurait un impact sur la distance de dispersion. De 2007 à 2011, une analyse des mouvements quotidiens et géoréferencés (GPS) a été conduit sur un disperseur important et commun de graines dans une forêt du Congo : le bonobo (*Pan paniscus*). Les temps de passage ont été calculés; la distance de dispersion a été estimée empiriquement et par modélisation de 1200 événements de dispersion géoréferencés, et des résultats ont été comparés entre espèces de plantes à fruits, entre les saisons et les années (ANOVA). Un modèle mécanistique exact a comparé les distances de dispersion de huit espèces de plantes dispersées par les bonobos : le seul facteur variable étant l'espèce fruitière. Nous avons examiné le compromis évolutif pour ces plantes à fruits : attirer des disperseurs au moyen de fruit qualitativement et quantitativement coûteux sans les retenir à proximité pour permettre la dispersion de leurs graines à bonne distance. Le temps de passage (moyen ±ES) est similaire entre les espèces (24h00 ±00min). La distance de dispersion n'est pas affectée par les variables années, saisonnalité ou espèce. Bien qu'une différence existe pendant le temps d'alimentation moyen passé par espèce fruitière, et pour le contenu nutritif des fruits, ceci ne semble pas affecter la distance parcourue après nourrissage et donc la distance de dispersion des graines. La distance moyenne de dispersion des graines transportées par les bonobos est (1332 ± 24 m). Les temps d'alimentation, la qualité et la quantité des n'ont eu aucun effet apparent sur le comportement de déplacement des bonobos et n'ont donc pas affecté la distance de dispersion des graines de ces espèces.

Mots clefs Bassin du Congo, bonobo, dispersion de graine, distance de dispersion, forêt tropicale humide, mutualism, structure forestière, *Pan paniscus*, zoochory

Introduction

The spatial pattern of seed deposition such as dispersal distance is an aspect of dispersal ecology that have theoretically major consequences on several aspects of plant population dynamics as well as on plant community structure and dynamics (Jordano 1995; Levin *et al.* 2003; Howe & Miriti 2004; Schupp, Jordano & Gomez 2010). However experimental data that quantify real dispersal patterns are scarce, particularly concerning forest species those are dispersed through endozoochory (Clark *et al.* 2005; Russo, Portnoy & Augspurger 2006; McConkey & Chivers 2007; Cousens *et al.* 2010). For zoochoric plants, the spatial distribution of seed deposition (i.e. seed shadows, (Willson 1993) results from the movement and behaviour of animals that feed on the fruit and transport the seeds (Westcott *et al.* 2005). Frugivores can shape plant populations in numerous interactive ways such as spatial configuration of fruiting plants, foraging decisions and the characteristics of the disperser (Jordano *et al.* 2007; Spiegel & Nathan 2007; Carlo & Morales 2008). The behaviour of dispersers after feeding on a fruiting parent plant will influences the shape of the probability distribution of dispersal distance because it will depends on how far the disperser moves away from the source while retaining the seeds (Westcott *et al.* 2005; Russo, Portnoy & Augspurger 2006; Cousens *et al.* 2010). The gut transit time of the seed is another parameter that could potentially affect the probability distribution of dispersal and very few studies showed that this parameter could be affected by seed size and chemical components of the fruit that can increase or decrease seed transport time (Westcott *et al.* 2005). The seed dispersal distances for animals with short gut passage time, such as birds is related to the time spent in fruiting trees (Lenz *et al.* 2010). The quantity and the quality of fruits produced by a plant as well as the level of aggregation of the fruiting plants in a landscape can also affect the probability distribution of seed dispersal (Carlo & Morales 2008). If the food patch can sustain the dispersers for a time superior to the transit time, or if the dispersers frequently come back to the patch, and remain in its vicinity, the amount of seed transported could be high although with low dispersal distance. For example, orang-utans can select large fruiting trees that they repeatedly visit staying around between feeding bouts (Leighton 1993).

Large and medium frugivores, such as elephants or apes disperse numerous plant species (Campos-Arceiz & Blake 2011; Forget *et al.* 2011). In Congo rainforest, bonobo (*Pan paniscus* Schwarz) are efficient seed dispersers that transport seeds of several fruiting species by endozoochory (Idani 1986; Tsuji, Yangozene & Sakamaki 2010). Bonobo in particular have a long gut passage and are wide-ranging animals that forage many fruiting plants during a day although being sometimes able to stay around a big fruiting plant or frequently come back to this patch (own observations).

The hypothesis of the present paper is that plant species with different fruit production strategies can affect their disperser behaviour and, consequently, their seed dispersal distance. Fruiting trees that produce large quantities and/or highly nutritive fruit could attract but maintain the disperser in place, resulting in lower seed dispersal distance. Conversely, trees with limited fruit production could perform in higher dispersal distance although being less attractive.

To test this hypothesis, we first analyzed whether bonobos exhibit variation in the times they spend in fruiting trees. Hence, we compared the difference in fruit quality and quantity provided by the fruiting species with analyse of the fruit nutrient composition, traits and the average feeding duration of the bonobo groups in the fruiting species. Secondly a mechanistic estimation of seed dispersal incorporating transit time for seed and the empirical movement behaviour of a common disperser for several zoochoric plant species is developed here. Many tropical plants have evolved fleshy fruit that are attractive to only a limited subset of frugivores (Fleming 1979). Afrotropical forest frugivores use different canopy strata with low feeding overlap (Fleming 1979; Clark, Poulsen & Parker 2001b; Poulsen *et al.* 2002). Consequently, in certain rainforest of the Congo, bonobo can be considered as main seed disperser for specifics fruiting species selected here, but alternative dispersers among birds, rodents and other primates cannot be excludable.

The long-term project of LuiKotale with a habituated bonobo group which can be daily observed, identified, followed and georefenced allowed us to build empirical seed dispersal estimation. We compared dispersal distances for several tree species with different species traits and fruit production strategies (see Table 1). Those dispersal distances can be used to test whether plants affect frugivore ranging behaviour and thus control their zoochoric partners for seed dispersal distance.

Study species and site

Pan paniscus is restricted to the tropical rain forest of the Democratic Republic of Congo (DRC) on the southern bank of the Congo River. The bonobo is mainly frugivores, feeding on and disseminating hundreds of plant species (Beaune unpubl. data; Tutji *et al.* 2010). Around

40% of the tree species in the forest are dispersed by bonobos (Beaune unpubl. data). Bonobos live in matriarchal groups with fission of subunit groups (parties) during the day while foraging, and fusion in the nesting place before night (Fruth & Hohmann 1993). In the Congo Basin, at the south-west fringe of the Salonga National Park, there is a habituated group of free-ranging bonobos, tracked by research teams at the LuiKotale field site (LK) (Hohmann & Fruth 2003c). Since 2007, groups have been followed from nest to nest and daily travels are georefenced with GPS (Garmin® 60CSX) using one point position per 5 min. Bonobo feeding trees are georefenced when identified during group feeding sessions. The most abundant fruiting species eaten by bonobo (allowing normality with sufficient sample size) were selected and compared (i.e. eight species with dispersal events recorded >30).

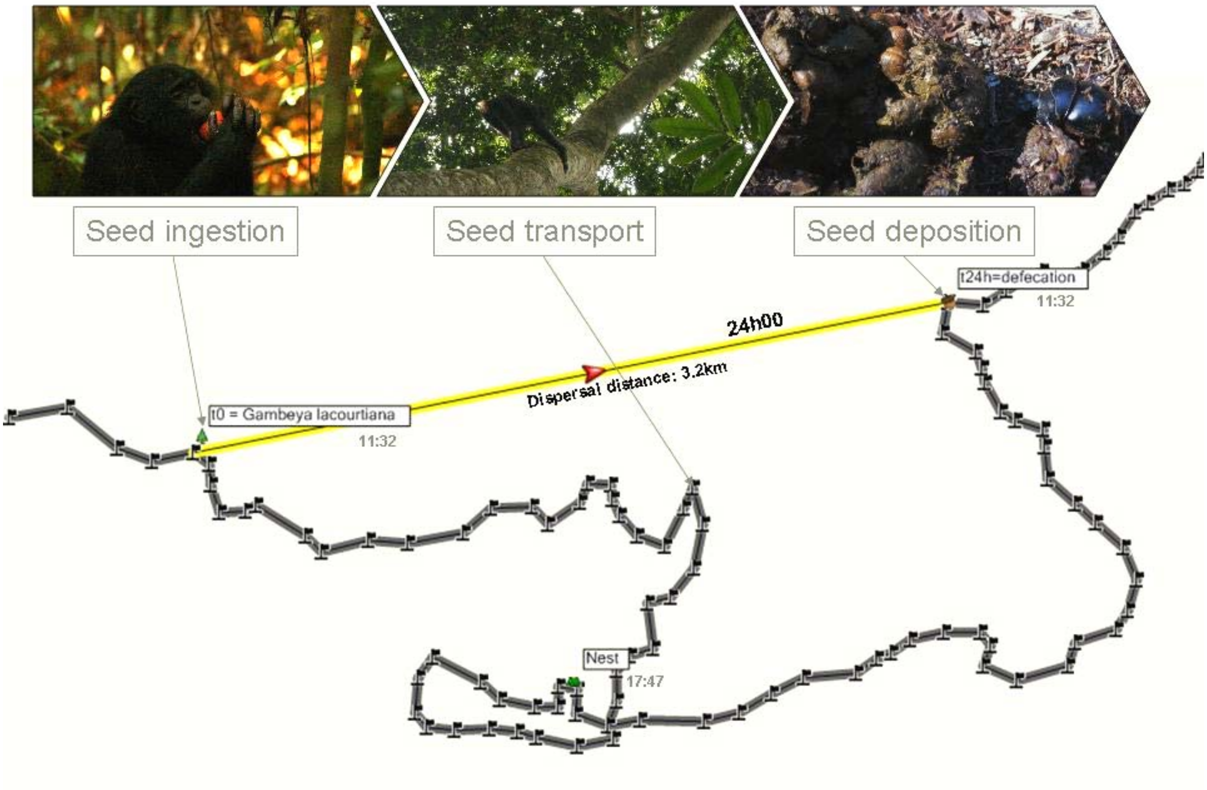


Figure 27 Illustration of the mechanistic seed dispersal estimation with an example of dispersal event (*Gambeya lacourtiana*). Identified bonobo feeding trees are georeferenced during group observations (2007-2011) and bonobo movement daily recorded (dark track log). Theoretical seed deposition site are determined by actual bonobo position (dark track log) after 24 h corresponding to the seed transit time.

Methods

Variation in feeding time session

Feeding duration were estimated by direct observation of the LK bonobo group. From September 2009 to June 2011 behavioral data of bonobos were recorded for 315 days across 22 months of observations. Bonobos are a fission-fusion society that is depending on season and time of day the community splits up into smaller foraging subgroups called parties. As parties are largely cohesive going for the same activities, we considered group activity to be that of the majority of the visible animals during a continuous behavioural records. A total of 573 hours of feeding session with fruiting species was analysed. Among these feeding sessions, the potential correlation of 278 dispersal events linked with feeding duration from 22 different fruiting species was analysed.

Interspecific fruit differences

Fleshy-fruited plant species are different in fruit production and quality (Hohmann *et al.* 2006b; Hohmann *et al.* 2010). The aim of this study is to test whether fruit production and quality affect the probability of seed dispersal distance. We have contrasted medium-sized tree species with relatively low fruit production (i.e. *Polyalthia suavoelens*, *Placodiscus paniculatus*) and large-sized fruiting trees which support and maintain dispersers for longer periods (i.e. *Dialium corbisieri*, *Gambeya lacourtiana*). To estimate the mean fruit abundance of each selected species we have calculated the diameter at breast height (dbh) (Chapman *et al.* 1992). The mean dbh was calculated for the main species, based on a 12-ha plot inventory (Beaune *et al.* In press). One liana, *Cissus dinklagei*, was added to the test and compared with the seven tree species, for a total of eight species analysed. Fruits from LK forest were collected for nutrient analyses (Hohmann *et al.* 2006b; Hohmann *et al.* 2010). Average fruit mass and diameter were measured on at least ten mature fruits.

Dispersal analysis

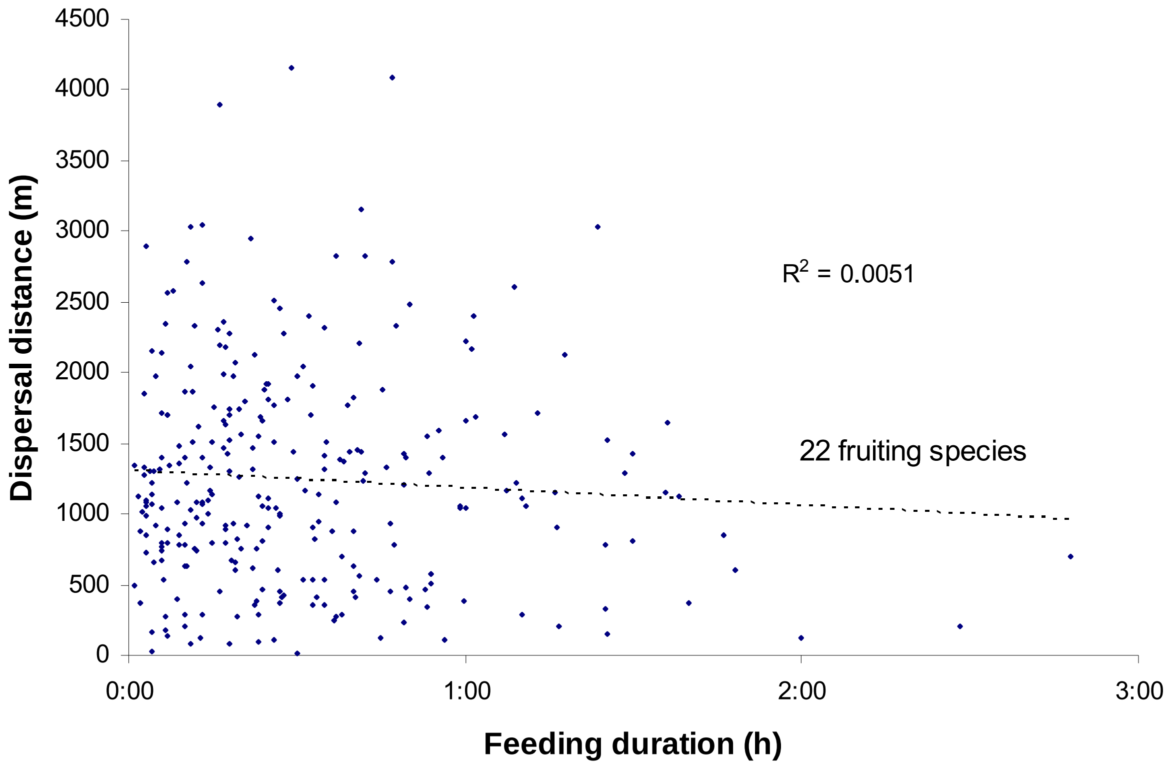
The probability distribution of seeds is based on empirical bonobo movements (Figure 27), georeferenced since 2007. Mean transit time (Tt) was calculated by continuously observing individually identified bonobos from the moment they swallowed seeds of a new species (not previously ingested in the past 36 h), until seed deposition in feces. Theoretical dispersal distance is taken to be the distance between the parent tree on which the bonobo fed and the bonobo's position after mean transit time (Tt). Effect of sex and seed size (categorized as: (1) small <2 mm, (2) large >1 cm and (3) medium (2-10 mm) on Tt were tested with analysis of variance (ANOVA) using R (R Development Core Team 2011), with all the effects considered as fixed. Distances of dispersal with annual, seasonal and species effects were also tested with ANOVA, with all the effects considered as fixed.

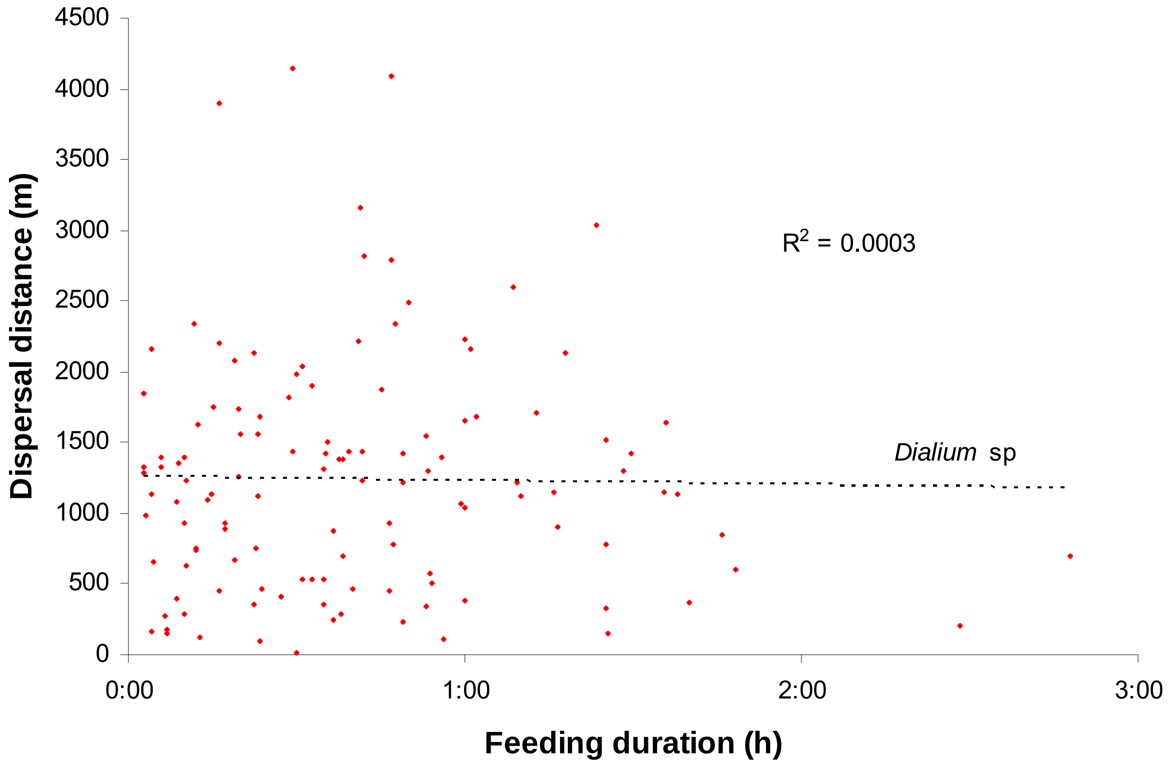
Familly	Species	average feeding session (min)	*n*	Energie kJ/g dry matter	Protein mg/g	Sugar mg/g	mean fruit weight (g)	mean fruit diameter (mm)	average DBH (cm)	*n*
Annonaceae	*Polyalthia suaveolens*	16 ± 3	*75*	18.3	96.9	128.5	3.2 ± 0.2	19.4 ± 0.7	18.3± 0.4	*408*
Caesalpiniaceae	*Dialium* sp	47 ± 3	*230*	16.3	145.7	101.4	0.9 ± 0.1	22.2 ± 0.5	31.3± 1.1	*761*
Moraceae	*Treculia africana*	78 ± 19	*16*	19.8	106.9	17.3	>8000	>800	37± 0	*1*
Sapindaceae	*Pancovia laurentii*	27 ± 5	*58*	14.6	65.5	160.3	15.1 ± 1.2	29.0 ± 1.3	26.7± 1.5	*31*
Sapindaceae	*Placodiscus paniculatus*	46	*1*	16.4	125.9	101.6	2.4 ± 0.1	17.3 ± 0.5	16.7± 0.5	*104*
Sapotaceae	*Gambeya lacourtiana*	16 ± 2	*81*	-	-	-	207.1 ± 28.6	70.7 ± 3.7	96.3± 34.2	*4*
Tiliaceae	*Grewia* sp	27 ± 2	*89*	18.9	80.2	172.4	9.2 ± 0.3	32.9 ± 0.4	22.6± 1.6	*50*
Vitaceae	*Cissus dinklagei*	22 ± 1	*204*	20.4	106.2	119.2	8.3 ± 0.5	26.5 ± 0.6	-	-

Table 7 Main plant species characteristics for feeding ecology (seven tree species, one liana: *Cissus dinklagei*). Average diameter at breast high (dbh) based on 12-ha plots inventory; average foraging session time based on 1879 h of field observation, average fruit weight and largest diameter (n = 10) and mean nutritional value. Values are mean ± SE

Results

Table 7 reports differences in nutritional values, fruit size, weight and dbh for adult trees, and mean feeding duration in fruiting species. There are no correlation between the feeding time spent on a fruiting plant and the dispersal distance infered by the bonobo ranging behaviour (Figure 28).


4500
4000
3500
3000
2500
2000
1500
1000
500
0
Dispersal distance (m)
0:00
1:00
2:00
3:00
Feeding duration (h)
R² = 0.0051
22 fruiting species


4500
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Dispersal distance (m)
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Feeding duration (h)
R² = 0.0003
Dialium sp

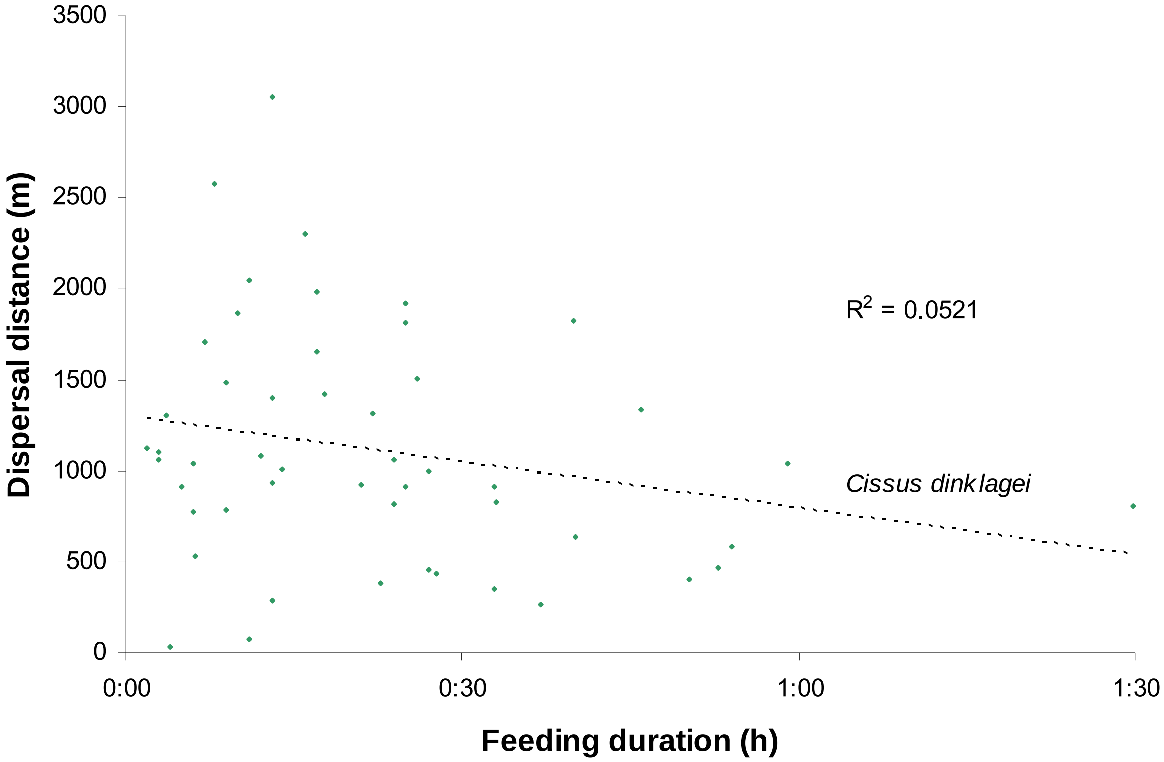

Figure 28 There is no correlation between feeding time spent on the fruiting plant and the dispersal distance by bonobo. For 22 fruiting species analysed as whole (n=278) or other species as *Dialium* sp. (122) or *Cissus dinklagei* (50).

Transit time: 124 transit times (from 13 different genera) from seed ingestion to deposition were recorded, with continuous observation of the dispersers. Mean transit time is 24:00hrs ±SE. 00:09hrs (SD=01:20h; range = 20:03-28:17h). There was no significant effect of seed size (Figure 29; n=61 big, 28 medium, 35 small; $F_{2,119}$ = 0.38; P = 0.68) or bonobos' sex effect (*t* = 0.0253, df = 15.3, P = 0.98) on transit time.

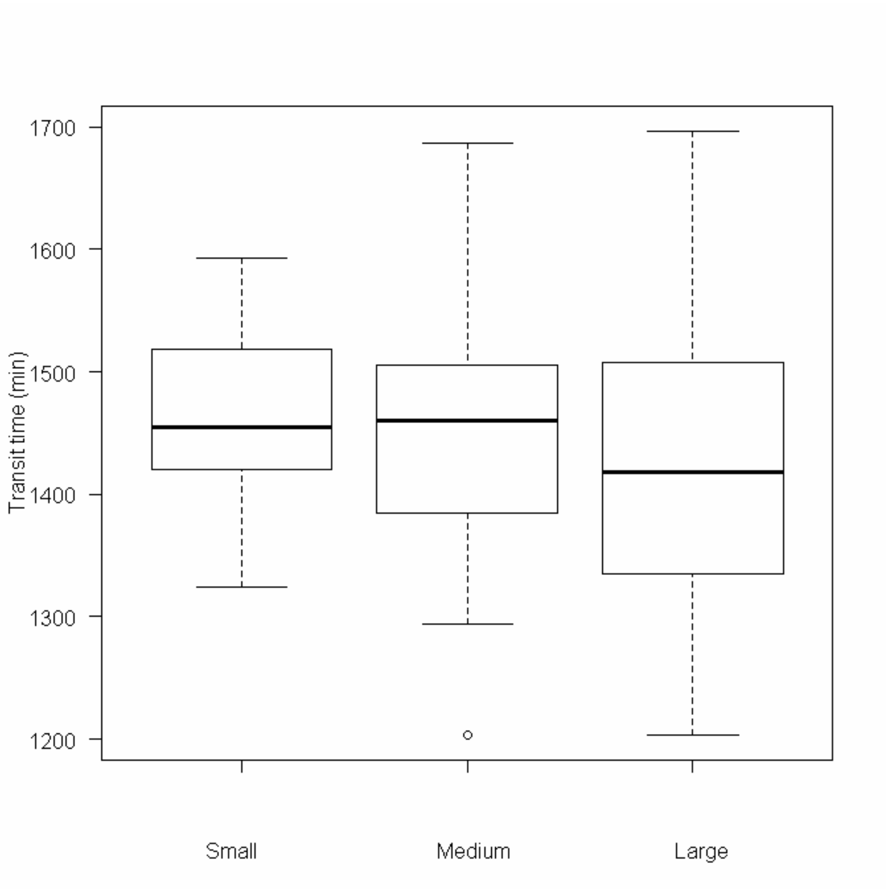

Figure 29 Size effect on the transit time (35 small:<2mm, 28 medium-sized:2-10mm and 61 large seeds:>10mm). No significant effect ($F_{2,119} = 0.38$, P = 0.68). Mean Transit time = 24:00 h.

Based on 1200 bonobo travel distances from the 8th July 2007 to 22nd September 2011, the dispersal curve fitted a unimodal leptokurtic distribution (Figure 30). The average dispersal distance is: 1332 ± 24 m, median= 1198; $CI_{95\%}$ = 1282-1380 m; range = 1-4492 m. This estimation is not significantly different to the actual estimation based on 75 actual seed dispersal events observed ($t = -1.4442$, df = 1273, P = 0.1489). Annual ($F_{4,1195} = 1.87$; P = 0.248) and seasonal effects ($F_{10,1189} = 1.24$; P = 0.26) are not significant. The main species tested (height fruiting species; 890 dispersal events), from large *G. lacourtiana* to medium tree species (*P. paniculatus, P. suaveolens*) (see Table 7 for average dbh) do not significantly affect the dispersal distance by the bonobo ($F_{7,882} = 0.77$; P = 0.61. Figure 31). The hypothesis on interspecific difference in seed dispersal distance is rejected.

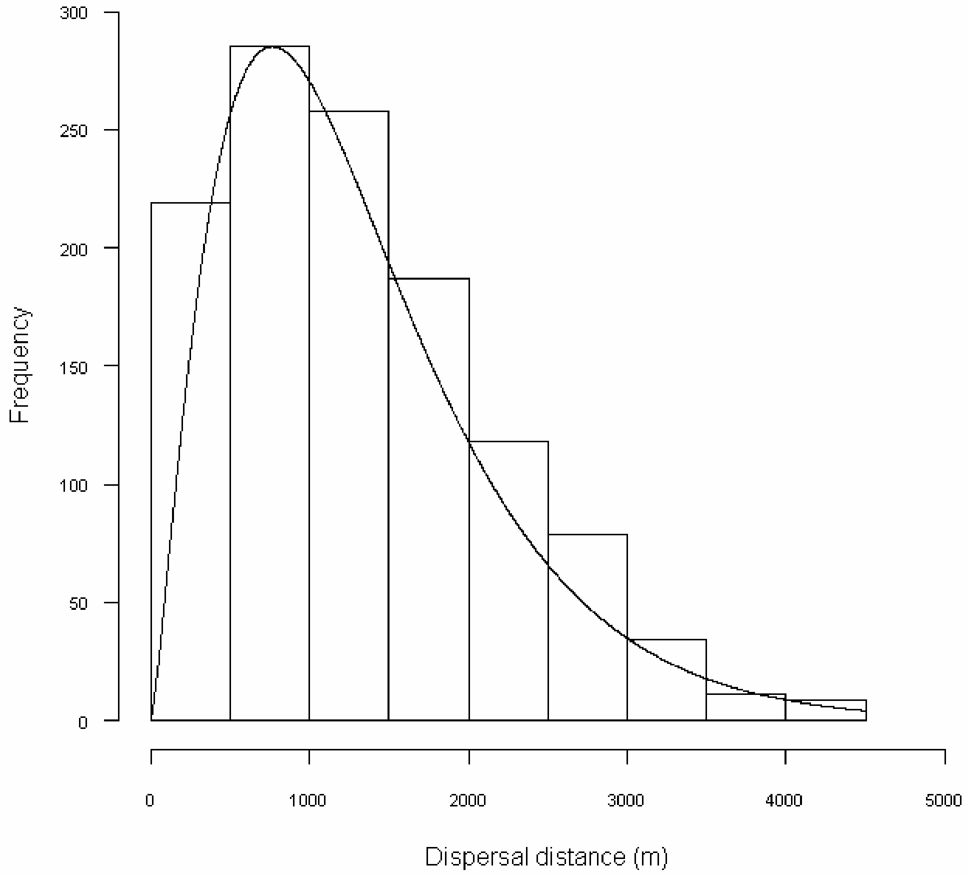

Figure 30 Seed dispersal distribution infered by bonobo based on movement behavior (n = 1200 dispersal events with all plant species) and mean transit time for seed (24:00 h).

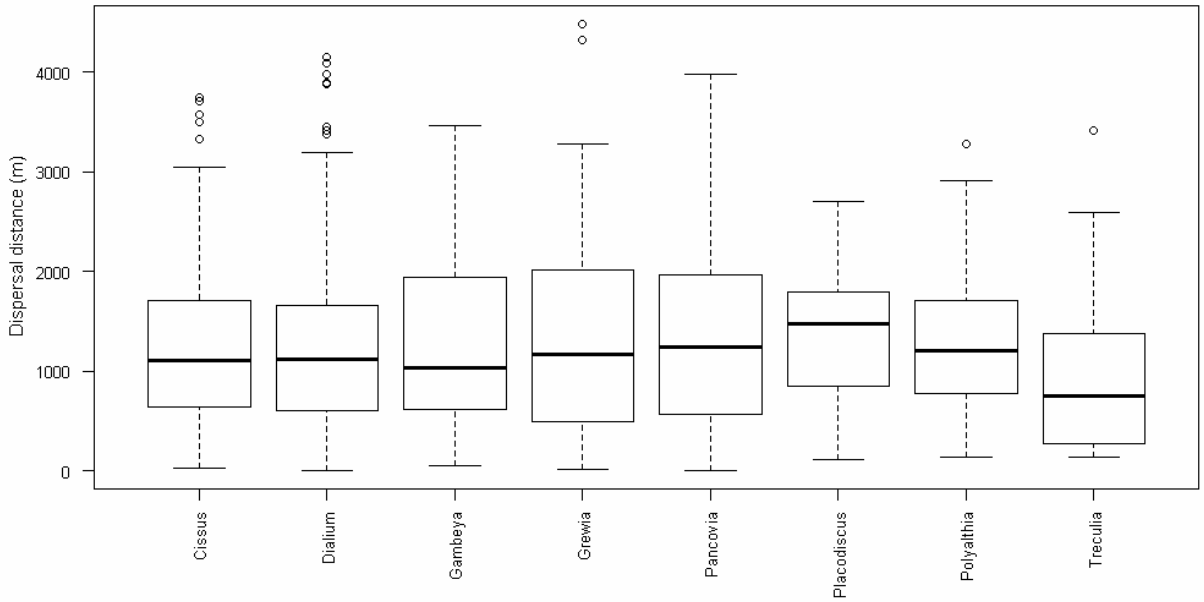

Figure 31 Seed dispersal distances infered by bonobos for eight plant species. (*Cissus dinklagei, Dialium* sp., *Gambeya lacourtiana, Grewia* sp., *Pancovia laurentii, Placodiscus paniculatus, Polyalthia suaveolens, Treculia africana*).

Discussion

Our findings provide the first analysis based on long-term data, of differences in dispersal distance among fleshy-fruited plants disseminated by the same endozoochoric partner. Surprisingly, all the fleshy-fruited species are dispersed at the same average distance, whatever the feeding time on the fruiting plant, their fruit quality and abundance: 1.3 km. Bonobos move at homogenous and regular distances from food patches. This is due to the regular ranging behaviour and consistent travel times of bonobo groups, whatever the year, season or fruiting season. One potential explanation is the stochastic phenology of fruiting species at the site (Fruth *et al.* unpubl. data). This unpredictability could force bonobos to forage permanently for food and then regularly disperse the seeds at long distances. Another unverified hypothesis is differential ripening for these species. With asynchrony in ripe fruit availability, frugivores cannot forage for long sessions in the same area. However, further studies are needed on differential ripening in tropical plants. Surprisingly in our study, seed size does not seem to affect transit time, unlike in other animals, where a shorter gut passage is induced by smaller seed size (Westcott *et al.* 2005). Bonobo physiology and foraging behaviour result in similar dispersal distances for disseminated plants whatever their differences in size, colour, fruit quality and quantity or species traits.

Extensive seed dispersal among communities homogenises species composition, and eventually makes competitive ability dependent on global rather than local abundances, thus facilitating domination by the single most abundant species (Levin *et al.* 2003). This study tends to confirm that finding. Seed dispersal limitation in distance (Muller-Landau *et al.* 2008) does not exist for different plants species sharing the same dispersers.

The assumption in the theoretical dispersal model that animals move randomly in space (Levin *et al.* 2003) is supported by our finding for the distance parameter, which is consistent and without any plant species effect. This is coherent with mechanistic models of zoochoric seed dispersal (Cousens *et al.* 2010).

However we did not explore post-dispersal fate for seed, which surely shapes species distribution (Réjou-Méchain *et al.* 2011). Several studies have shown that the interaction between environmental heterogeneity and the biological characteristics of species can influence distribution patterns at various spatial scales (Muller-Landau 2004; ter Steege *et al.* 2006). Negative density dependence with environmental filtering contributes to community assembly (Paine *et al.* 2012). Nevertheless, it has also been shown that dispersal syndrome predicts spatial distribution, which is relatively dispersed for zoochoric species (Seidler & Plotkin 2006b). For species using large mammals such as the bonobo, we show that seed dispersal is long-distance but without interspecific differences; although interspecific difference in fruit characteristics is wide. Do species dispersed by the same partner share the same distribution pattern? Studies have hypothesised that spatial patterns are highly context dependent but can be predicted by dispersal syndrome (Réjou-Méchain *et al.* 2011) and plant traits (Muller-Landau *et al.* 2008). Our hypothesis goes further with spatial prediction, trait-based generalisation and modelling of seed dispersal in tropical forests, based not on fruit characteristics, but rather on the disperser variable itself (elephant, bonobo, guenon, bat, hornbill, etc.).

To conclude, fruit quantity and quality do not seem to affect disperser behaviour in relation to dispersal distance. Our finding leads to new questions about possible plant adaptations to force zoochoric partners to move constantly within their range.

Part III

Other actors influencing the seed fate

Bush pig (*Potamochoerus porcus*) seed predation of bush mango (*Irvingia gabonensis*) and other plant species in Democratic Republic of Congo

Authors

David Beaune, Loïc Bollache, Barbara Fruth, François Bretagnolle

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Introduction

Bush pigs (otherwise known as Red river hogs, (*Potamochoerus porcus*) are known seed predators in Afrotropical forests (Ghiglieri *et al.* 1982; Whitesides 1985; Blake & Fay 1997; White & Abernethy 1997). Seed predators are key species affecting plant population demographics by influencing the survival of early successional stages, such as seeds and seedlings thereby playing a pivotal role in the regeneration, colonisation ability and spatial distribution of plants (Hulme 1998). While largely omnivorous (Kingdon 1997) bush pigs are also the largest member of the granivore guild in the Democratic Republic of Congo (DRC), and their relative impact on structuring plant communities could be significant. To assess the nature of bush pig seed predation we firstly recorded all plant species predated by bush pigs at the long-term LuiKotale field site, in the DRC, over a period of eighteen months. This new list was used to estimate how many tree species (species richness) and how many trees (abundance) within the tree community are affected by bush pig predation, based on a plot census of heterogeneous primary forest (12-ha plots). We also assessed the role of bush pigs on seed fate in the fruit fall zone, focusing on the bush mango (*Irvingia gabonensis*), an Afrotropical tree of local and western world economic value (White & Abernethy 1997). We estimated seed predation and pathogen infection on seeds in the fruit-fall area and tested the density dependent hypothesis: The density-dependent hypothesis suggests that predation and pathogen levels will be elevated in the vicinity of the parent plant (Janzen 1970b; Connell 1971; Schupp 1992), becoming less prevalent the further one moves away from the parent plant as seeds escape such pressure (Hubbell 1980; Howe & Smallwood 1982). We consequently tested for potential distance effects within 100 m of parent plants to assess the relative impact of bush pigs.

Methods

Study site

The LuiKotale research site (>6000 ha) is located within equatorial rainforest (2°47’ S - 20°21’ E), along the south-west fringe of the Salonga National Park, in DRC (Hohmann & Fruth 2003c). The climate is equatorial with abundant rainfall (>2000 mm/yr), and a relatively dry season from February to July. Mean temperature at LuiKotale ranges between 21°C to 28°C with a minimum of 17°C and a maximum of 38°C (2007-2010). Local people agreed in

2001 to stop all exploitation in the forest (Hohmann & Fruth 2003c). In this hunting-free forest reserve, animals are less wary and more easily observable. A long-term project initiated in 2002 at the site catalogues plant species and allows plant identification (Fruth, 2011).

Seed species predated by bush pigs

Seed predation by bush pigs was recorded by: i) opportunistic observations recorded during 315 days of field work focusing on bonobo feeding behaviour, 1879 hrs from January 2010 to June 2011; ii) camera traps installed to capture medium to large seed predators, randomly positioned in the study site in fruiting places and sites baited with all available seeds of the forest (two Wildview series3 & three Bushnell® Trophy Cam™: Video mode 60s/1s interval/normal sensitivity, set for a total of 82 consecutive days and nights during the study period; Figure 32); and iii) confirmation by trackers and experienced bush pigs hunters from the province. Seed predation of the plant species was identified when seed destruction (crunching sounds) was observed or heard on seed species (identified by direct observation at distance with binocular and/or by collection of seed remains after the observed passage), and there was no seed regurgitation. Bush pig feces were opportunistically collected and analysed (N=8).

Estimation of mean tree number and tree diversity per hectare was made by surveying all adult trees (>10 cm DBH, diameter at breast height) in each of 12 one hectare plots of heterogeneous *terra firme* forest from February to June 2011. The estimated percentage of trees and tree species seed predated by bush pigs were based on the above list of seed species identified as being predated.

Figure 32 Picture of bush pig (*Potamochoerus porcus*) camera trapped in LK, 2011.

Predation under parent trees

Fifty-four fruit-producing adult *Irvingia gabonensis* trees were monitored from January 2010 to June 2011, to calculate the predation rate occurring on seeds under parents by counting the ratio of open endocarps (*i.e.* predated by bush pigs, the only species able to open the endocarp). Unopened seeds with pathogens tracks were also counted to estimate the role of pathogens in seed mortality

To measure survival probability in relation to distance from the parent, we positioned a fruit every 10 m along a 100 m transect in a marked place (square of branches), with care to avoid conspecifics within 200 m. Each transect started at the parent trunk. This experiment started at the end of the fruiting season when all the fruits had fallen (February 6th and 7th, 2010). Five trees were studied, with two transects marked out per tree. For estimating the survival probability, we sampled the remaining fruits five months later on July 6th and 7th, 2010 (when germination occurred in the control nursery where 100 seeds of *I. gabonensis* were observed from the beginning of the season (Beaune unpub. data)). We hypothesise that seed survival would increase with distance from the parent tree with decrease of granivore pressure. Statistical analyses were performed using R (R Development Core Team 2011) for GLM.

Results and discussion

Seed species predated by bush pigs

Twenty-six tree species and two liana species were recorded as being predated by bush pigs in LuiKotale (Table 8). This result is conservative given the brief study and infrequent fruiting periods of some tropical species. Herds of 2-6 animals were observed predating large quantities of seeds beneath the parent trees, within the fruit-fall zone where fruit drop by gravity (barochory). Based on the 12-ha plot census and the conservative list of seed species predated, we estimate that 15.5% ± SE. 0.9 of the tree species are seed predated by bush pigs. These species represent 33.3% ± 1.7 of the trees in the LuiKotale community. Eight feces were collected, undetermined fragments were visible but none of them contained whole seeds. However, given the small sample size we cannot exclude that certain seed species of LuiKotale may pass through the digestive tract and remain viable. While recognised as seed predators, studies from Asia, Australia and Africa have shown that suids also pass seeds intact through the digestive system (Corlett 1998; Castley *et al.* 2001; Westcott *et al.* 2005), and act as important seed dispersers in some habitats (Kerley, McLachlan & Castley 1996). Their role as seed dispersers in other ecosystems within Africa remains to be determined (Geldenhuys 1993; Seufert, Linden & Fischer 2010), but bush pigs can therefore have both beneficial and detrimental functional roles within African landscapes.

Species	**Family**	**tree nb/ha ± SE**
Anonidium mannii	Annonaceae	8,8 ± 1,6
Autranella congolensis	Sapotaceae	0,1 ± 0,1
Colletoecema dewevrei	Rubiaceae	2,6 ± 1
Colletoecema sp.	Rubiaceae	0,1 ± 0,1
Crotonogyne manniana	Euphorbiaceae	0
Dacryodes buettneri	Burseraceae	0,4 ± 0,2
Dialium gossweileri	Caesalpiniaceae	2,1 ± 1,4
Dioscorea praehensilis	Diocoreaceae	N/A (Liana)
Drypetes gossweileri	Euphorbiaceae	8,3 ± 2
Gambeya lacourtiana	Sapotaceae	0,3 ± 0,3
Gilbertiodendron dewevrei	Caesalpiniaceae	0
Gilbertiodendron mayombense	Caesalpiniaceae	0

Guibourtia demeusei	Caesalpiniaceae	0
Irvingia gabonensis	Irvingiaceae	1,7 ± 0,6
Irvingia grandifolia	Irvingiaceae	0,1 ± 0,1
Lasianthera africana	Rubiaceae	2,6 ± 1
Mammea africana	Guttifereae	0,3 ± 0,2
Manilkara yangambiensis	Sapotaceae	0,9 ± 0,3
Parinari excelsa	Chrysobalanaceae	0,3 ± 0,1
Pentaclethra macrophylla	Mimosaceae	0,1 ± 0,1
Pycnanthus marchalianus	Myristicaceae	0,2 ± 0,1
Synsepalum longecuneatum	Sapotaceae	10,1 ± 1
Tetracarpidium conophorum	Euphorbiaceae	N/A (Liana)
Treculia africana	Moraceae	0,1 ± 0,1
Tridesmostemon omphalocarpoides	Sapotaceae	0,1 ± 0,1
Vitex sp.	Verbenaceae	3,4 ± 0,9
Xylopia aethiopica	Annonaceae	0,2 ± 0,2
Zeyherella longepedicellata	Sapotaceae	0,9 ± 0,3

Table 8 Seed species recorded to be predated by *Potamochoerus porcus* in LuiKotale (DR Congo). Tree density is estimated among 12 ha of heterogeneous *terra firme* forest. Tree species such as *Gilbertiodendron* or *Guibourtia* are more abundant in homogenous forests.

Predation under parent trees

Bush pigs have powerful jaws adapted to crush hard food like seeds (Herring 1985). For example, even seeds protected by thick shells, such as *I. gabonensis*, can be crushed. The mean force needed to crack an *Irvingia* shell was calculated to be 2.06 to 3.67 kN (Ogunsina, Koya & Adeosun 2008). This ability to destroy seeds could lead to bush pig mediated density-dependent effects (*sensu* Schupp, 1992), thereby affecting seed survival for many tree species in DR Congo. We calculated that for each adult bush mango monitored (N=54) an average of 54% ± SE. 3 of the seeds present in the fruit fall zone were opened and predated by bush pigs; CI_{95}=[40-67%]. Among remaining unpredated seeds, 76% ± 3 were rotten, reflecting pathogen attacks; CI_{95}=[62-90%]. Figure 33 shows that the probability of seed survival does not increase significantly with distance from the parent tree within a 100 m radius (GLM: $F_{108,-4}$=-4.53; p=0.3392 for distance, no tree effect: F_{105-1}=-1.46; p=0.2274). Within this zone, seed mortality remains high. For all the parent trees, 87% ± 3 of the monitored seeds were predated within a 100 m radius around the trunk. *Irvingia gabonensis* exemplify the high mortality rate in the fruit fall zone where fruit fall beneath the canopy by gravity (barochory) and in the vicinity (at least 100 m). For *I. gabonensis*, intense predation and pathogen effects within 100 m from the parent tree do not appear to conform to the Janzen-Connell model of density-dependent effects. However, the effects on seedling survival remain to be tested. (see appendix 1 : Density dependent effect affecting *Irvingia gabonensis* recruitment)

Bush pigs are important seed predators in LuiKotale, DRC. However, their importance as keystone species within the broader landscape is likely to be affected by a number of anthropogenic factors, primarily hunting as bush pig are a target species in the DRC (Wilkie & Carpenter 1999). The potential impacts of bush pig hunting activities could have direct effects on the dynamics of plant communities (Muller-Landau 2007; Vanthomme, Bellé & Forget 2010a) but are as yet untested.

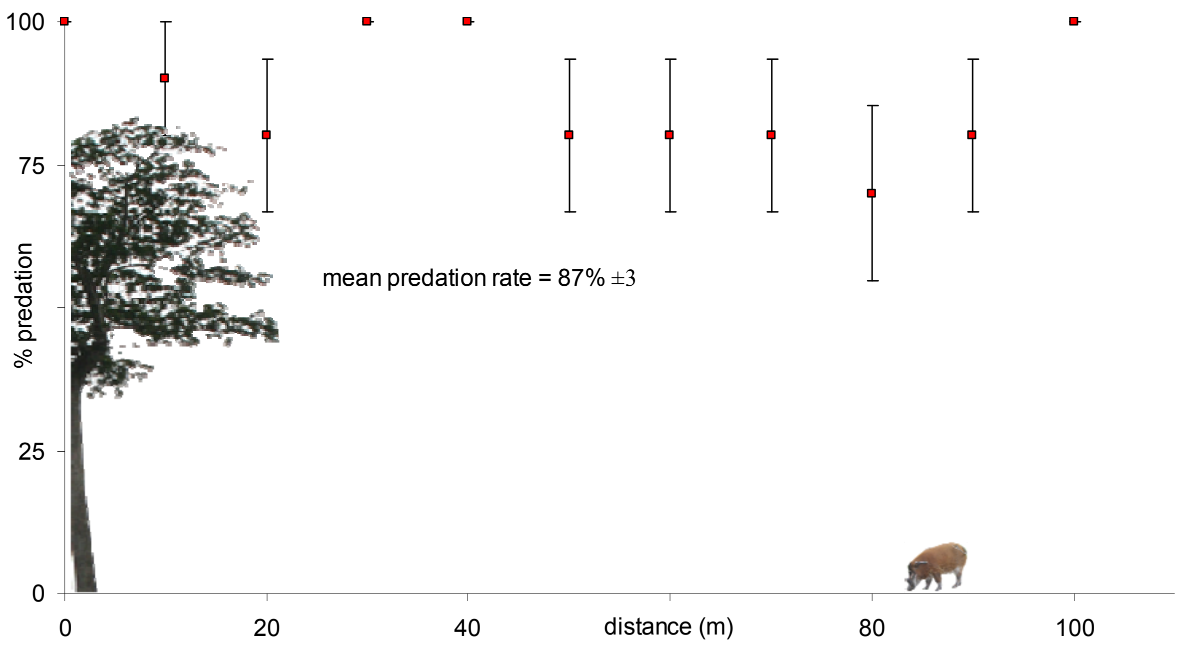

Figure 33 Seed predation rate within a 100 m radius around the parent bush mango (*I. gabonensis*). There was no distance effect (p-value>0.33).

Dung beetles are critical in preventing post-dispersal seed removal by rodents in Congo rain forest

Authors

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Abstract

Seed dispersal with seed deposited by animal in feces attracts dung beetles. In the Congo forest of LuiKotale (DRC), granivores such as the giant pouched rat (*Cricetomys emini*) or porcupine (*Atherurus africanus*) are attracted to bonobo dung in order to forage for seeds. These nocturnal seed predators are preceded by diurnal dung beetles (Scarabaeoidea feeding on feces) while feces are deposited by frugivores during the day, like bonobos (*Pan paniscus*). The largest Scarabaeidae from the genus *Catharsius* bury feces and seeds (≤3.5cm) within two hours of deposition by apes. For three plants species tested, burial effect reduced post dispersal removal and mortality of seeds. This race for dung between granivores and coprophages is probably critical for plant survival and thus demography.

Keywords Congo, *Cricetomys emini,* dung beetle, Scarabaeidae, secondary dispersal, seed predation, zoochory

Résumé

La dispersion de graine via les animaux et leurs fécès attire les bousiers. Dans la forêt du Congo, à LuiKotale (RDC), les granivores tels que le rat géant d'Emin (*Cricetomys emini*) ou le porc-épic (*Atherurus africanus*) sont attirés par les fécès de bonobo afin de trouver des graines. Ces prédateurs nocturnes de graine sont précédés dans leurs recherches de fécès par les coléoptères (Scarabaeoidea coprophage) qui atterrissent sur les fécès déposées par les frugivores comme le bonobo (*Pan paniscus*) pendant le jour. Le plus grand Scarabaeidae du genre *Catharsius* peut ensevelir des graines (≥3.5cm) deux heures après le dépôt par les grands singes. Sur trois espèces de plantes étudiées, l'effet d'enterrement réduit le déplacement post-dispersion des graines par les prédateurs. Cette course pour les crottes entre les granivores et les coprophages est probablement un facteur influent dans les paramètres de survie et la démographie des populations de plantes.

Mots clefs bousiers, dispersion secondaire, *Cricetomys emini*, Scarabaeidae, prédation de graine, zoochory

Dung beetles (Scarabaeidae subfamily Scarabaeinae) are ubiquitous and play an important role in the removal of animal dung and the dispersal of seeds embedded therein. They exhibit a range of dung-acquisition and burying behaviours, from burying dung directly beneath the dung deposit or to rolling dung balls at several metres. Dung beetles act as important agents for secondary seed dispersal and seed survival: the burial of seeds is said to be of advantage against predators and desiccation (Feer 1999; Andresen & Feer 2005; Culot *et al.* 2009). In addition, burial of seeds by dung beetles is considered beneficial as seeds are not only deposited within the range of depths that are favourable for seedling establishment but also among organic fertilizer that is said to increase seedling growth rates (Estrada & Coates-Estrada 1991; Shepherd & Chapman 1998; Andresen 1999; Andresen 2002).

However, post-dispersal seed fate with and without the effects of dung beetles is a challenge and for a better understanding more detailed investigations are required (Vander Wall & Longland 2004); especially in Africa where research is far less developed than in Neotropical systems. Here we explore experimentally under in situ conditions, how dung beetle burial can affect seed removal by predators in an undisturbed forest. Research took place at the LuiKotale research site, Central Congo Basin, Democratic Republic of Congo (DRC). Here, the bonobo (*Pan paniscus* Schwarz) is the primary seed disperser. The giant pouched rat (*Cricetomys emini* Wroughton) is the most common seed predator and dung beetles are secondary dispersers. For the seeds, post-dispersal mortality is affected by seed predators and dung beetles. Thus, seeds embedded in feces could have both, advantages and disadvantages. Advantages as mentioned above, and disadvantages as dung specifically may attract seed predators. In order to assess the impact of seed burial by dung beetles, we tested two hypotheses as follows: (1) Seed predators are attracted by faecal odours; and (2) Seeds buried by dung beetles escape the seed predators. In addition, we investigated dung beetle presence, behaviour and efficiency as well as dung beetle-related seedling establishment.

The LuiKotale research site is located at the south-western fringe of the Salonga National Park, DRC, within evergreen lowland equatorial rain forest (2°47’S, 20°21’E) (Hohmann & Fruth 2003c). The climate is equatorial with abundant rainfall (>2000 mm y^{-1}), and two dry seasons, a short one in February and a longer one between May and August. Mean temperature at LuiKotale ranges between 21°C and 28°C with a minimum of 17°C and a maximum of 38°C (2007-2010).

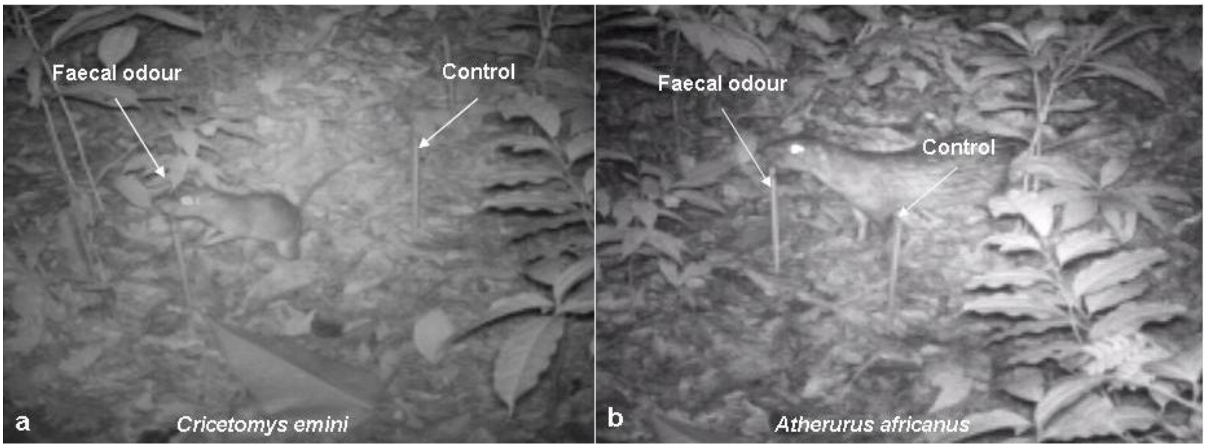

Figure 34 Infrared records on faecal odour attraction: Arrows point at bonobo faecal odour and control stick with giant pouched rat (*Cricetomys emini*) (a) and African brush-tailed porcupine (*Atherurus africanus*) (b) each sniffing at the treated wooden stick.

For the first hypothesis, two sticks from the same wood of 50 cm length, were placed 1 m apart 4 m in front of a camera trap (Wildview series3 & Bushnell® Trophy Cam™: Video mode 60s/1s interval/normal sensitivity) to test faecal olfactory attraction in animals: one stick was covered in fresh bonobo manure (without seeds or faecal material >1 mm; Figure 34) 2 cm of the top end, the other stick was without treatment serving as control. The experiment started at 17h00 and lasted for 24 h. It was run 30 times between January and March 2011 with new sticks each time. Sticks were randomly positioned where giant pouched rats had been observed previously. Only sites visited by predators were analysed. Olfactory attraction was considered when the rat rose on its hind legs and pointed its nose towards the top of the stick (at less than 5 cm) (Figure 34). From these 30 runs, a total of nine showed seed predators. Of these, eight recordings contained giant pouched rats at night. All of the eight videos showed a rat sniffing the stick with faecal odour (Figure 34a). None of the control sticks was sniffed. During their nocturnal activities, giant pouched rats were significantly attracted by bonobo faecal odour (non-parametric Wilcoxon signed rank paired test = 36, P = 0.01; power analysis = 91%, software: R 2.11.). One video recorded an African brush-tailed porcupine (*Atherurus africanus* Gray) sniffing the stick with faecal odour (Figure 34b).

In order to investigate granivore behaviour towards unburied bonobo feces, fresh bonobo feces collected during the day were positioned at night (19h00), 4 m away from a camera trap. The experiment was conducted twice in January 2011 at different sites. Both times fresh bonobo feces were visited by *C. emini* which ate the seeds (19h32 and 02h19). For the second visit, dung beetles had probably started to bury the material because the rat was filmed digging.

For the second hypothesis, we investigated the removal rate of five seeds on the ground compared to five seeds of the same species buried at 5 cm depth with 40 replicates. Seeds of three plant species from three different families, *Cissus dinklagei* Gild & Brandt, Vitaceae; *Polyalthia suaveolens* Engl. & Diels, Annonaceae; *Dialium corbisieri* Staner, Caesalpiniaceae, were extracted manually from several bonobo feces collected the previous day and tested from January to June 2010 and 2011. Seed dimensions were measured for 10 seeds each during their fruiting season between 2010 and 2011 as follows: *C. dinklagei:* weight 0.7 g, length 18 mm, diameter 10 mm; *P.suaveolens:* 0.6 g, 11 mm, 6 mm; and *D. corbisieri*: 0.6 g, 14 mm, 10 mm. Manure was removed manually to mimic dung beetle consumption but not washed to keep faecal odour. This experimental manipulation mimics a situation in which seeds primarily dispersed by bonobos (endozoochory) are secondarily dispersed by dung beetles and represents the two possible outcomes for these seeds: all dung removed by dung beetles but seed not buried vs. all dung removed and seed buried. The seeds of each species (n = 5 buried and n = 5 unburied 15 cm apart) were deposited in the forest and replicated along a transect of 1.2 km length, resulting in three transects. The surface seeds were deposited in a surface depression (2 cm deep, 8 cm diameter, manually created) in order to avoid seed removal by rain. They were checked daily before and after the night (17h00 and 05h00). Presence and scratches of surface seeds were monitored daily, and presence of buried seeds was checked every 30 d by excavation. Seeds were reburied after each control. Camera traps were installed for identifying the seed removers and predators.

Buried seeds remained unaffected by seed predators. After 69 and 78 d of monitoring, 100% of the buried seeds from *P. suaveolens* and *C. dinklagei*, and after 154 d of monitoring, 94% of the buried seeds from D. *corbisieri* were still present (Proportion tests = 217, df = 1, P < 0.001; 154, df = 1, P < 0.001; 172, df = 1, P < 0.001 respectively; power analyses =100%). In contrast, more than half of all surface seeds was removed by nocturnal seed predators: (*P. suaveolens*: 56%; *C. dinklagei*: 58%; and *D. corbisieri*: 74%; Figure 35). All removal events occurred at night.

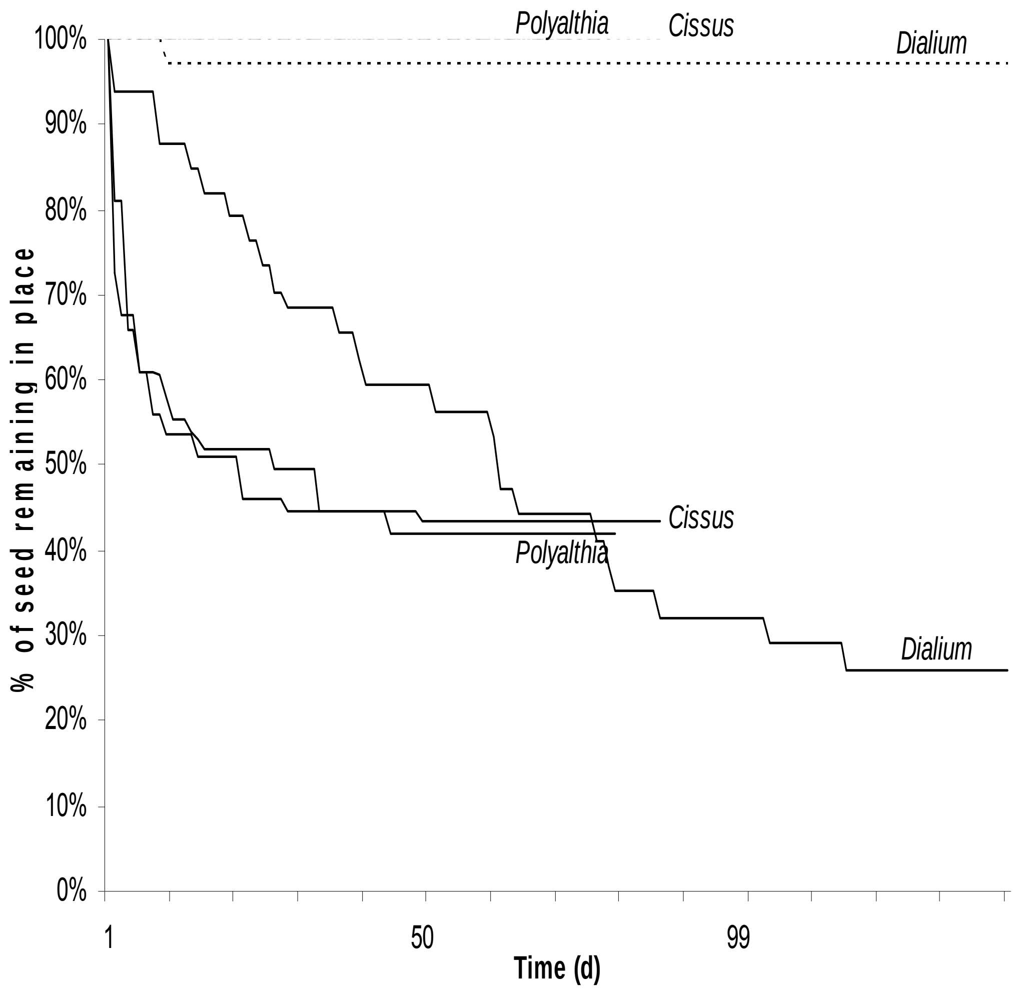

Figure 35 Effect of seed burial on seed predation: Percentage of buried (dotted line) vs. unburied (continuous line) seeds in relation to time of *Cissus dinklagei*, *Polyalthia suaveolens* and *Dialium corbisieri*.

In order to investigate dung beetle presence, behaviour and efficiency, between January 2010 and April 2011 we baited a total of 45 pitfall traps (10 cm diameter, 15 cm depth) with fresh bonobo feces (100 g each) exposing each to nature for 24 h in random places of the forest undergrowth. Of these, 36 were found with several dung beetle species. The biggest identified was possibly *Catharsius gorilla* Thomson (P. Moretto pers. comm.). *Catharsius* sp. was also observed under natural conditions feeding on bonobo feces (n = 45). Freshly deposited bonobo feces were georeferenced and monitored directly or by help of camera-traps. Arrival time, burial time and burial behaviour were recorded. *Catharsius* sp. was able to bury numerous and large seeds (max: 3.5 cm diameter e.g. *Grewia* spp.) in an average depth of 5 cm in large tunnels of 3.5 cm diameter. Mean (± SE) time between bonobo faecal deposition and *Catharsius* sp. arrival was 42 ± 25 min (range = 5-188 min; n = 7). *Catharsius* sp. buried the feces completely (average weight of bonobo feces: 111 ± 76.1 g, n = 407) within an average of 56 ± 10 min (range = 27-89 min; n = 5).

In order to investigate dung beetle related seedling establishment, 45 feces were monitored between March 2010 and June 2011. Of these, 67% ± 7% ($CI_{95\%}$ = 53%-81%) were observed to recruit seedlings between 1 and 18 mo from the beginning of monitoring. The following plant species were identified: *C. dinklagei*, *Dacryodes yangambiensis* Louis ex Troupin, *Ficus* spp, *Grewia* spp, *Guarea laurentii* De Wild, *Landolphia* spp, *Manilkara* sp., *Pancovia laurentii* Gild ex De Wild.

In the forest ecosystem of LuiKotale, the bonobo eats fruits and swallows seeds of hundreds of plant species (unpubl. data). Nocturnal seed predators such as the giant pouched rat or porcupine are attracted by faecal odour likely to indicate seeds dispersed by endozoochory. However, seeds are usually deposited by apes during the day, attracting tunnellers such as species from the genus *Catharsius* in less than 1 h. Seedling establishment is likely to occur in a narrow range of depths (3–10 cm), where seed removal by rodents is low but seedlings can still emerge (Estrada & Coates-Estrada 1991; Shepherd & Chapman 1998).

Deposited feces disappear from the surface in less than 1 h due to tunnellers that can bury seeds of up to 3.5 cm diameter such as seeds of *Grewia* spp, allowing seeds to avoid nocturnal rodents and surface pathogens.

The net outcome of these plant-animal interactions is highly context-specific and deserves attention, particularly in the Afrotropics where related research appears to be underrepresented, further attention. This note, however, allows confirming the following Neotropical findings: dung beetles decrease the probability of seed predation by rodents and favor seedling establishment (Andresen & Levey 2004; Santos-Heredia, Andresen & Zárate 2010; Culot *et al.* 2011; Lawson, Mann & Lewis 2012). However, more emphasis needs to be put on distinguishing rodent seed predation from secondary dispersal. Indeed, seeds removed by granivores such as rodents cannot be considered as 100% predated (Nyiramana *et al.* 2011). A minority could be secondarily dispersed but the majority of the removed seeds is food for seed predators (Crawley 1992). In DRC, dung beetles such as *Catharsius* spp. and other large tunnellers are involved in secondary seed dispersal and thus play a critical role in post-dispersal seed survival.

A bonobo does not replace an elephant

Doom of the elephant-dependent trees in a Congo tropical forest

Authors

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Abstract

In an evergreen lowland rain forest of the *Cuvette Centrale*, DR Congo, at the LuiKotale Max-Planck-Institue research site, forest elephants (*Loxodonta cyclotis*) are close to extinction. Between January 2009 and June 2011 we investigated the influence of elephant decline on sustainability of elephant-dispersed tree populations.

For this, we explored how trees with the megafaunal syndrome reproduce without seed dispersal, what is the recruitment under other tree species, and eventually what are the effects on the population demography and on the spatial structure. We estimated dispersal effectiveness of alternative partners for functional replacement of the elephant.

Overall**,** 18 tree species presenting the megafaunal syndrome were identified. They represent 4.5% of the local tree diversity with a density of 28.2 ±2.7 tree/ha. Seventy-eight percent (14/18) of these tree species are elephant-dependent and do not recruit enough poles for self replacement, neither under the parent nor beneath other tree species. For 12 species populations, the first cohorts were absent in our plots. For species able to recruit, the spatial structures of the young generations are more clumped than adults while they are no difference for control tree species.

The second biggest seed disperser of the forest, the bonobo (*Pan paniscus*), does not replace elephant dispersal effectiveness. Thus, there is no alternative partner for seed dispersal for the majority of the megafaunal trees which are actually elephant dependent.

We discuss the likely consequences of the loss of elephants dispersed tree species and propose alternatives for species survival to bridge the time until efficient conservation strategies take effect.

Keywords Congo basin, defaunation, ecosystem decay, forest ecology, *Loxondota cyclotis*, *Pan paniscus*, poaching, recruitment, seed dispersal

Résumé

Dans une forêt tropicale humide de la *Cuvette centrale* du Congo (RDC), dans le camp de recherche LuiKotale du Max Planck Institut, les éléphants de forêt (*Loxodonta cyclotis*) sont proches de l'extinction. Entre janvier 2009 et juin 2011, nous avons étudié l'influence du déclin des éléphants sur la reproduction et la survie des populations de plantes dont les graines sont dispersées par ces pachydermes.

Pour ceci, nous avons étudié comment les arbres au syndrome de megafaunal se reproduisent sans dispersion de graine, ce qui implique l'étude du recrutement sous les arbres-parents, nous avons étudié le recrutement sous les autres arbres (impliquant une dispersion) et enfin les effets potentiels sur la démographie et la structure spatiale de ces populations d'arbres. Nous avons par ailleurs estimé l'efficacité de dispersion des partenaires alternatifs qui pourraient se substituer au rôle fonctionnel des éléphants.

De façon générale**,** 18 espèces d'arbre présentant le syndrome de megafaunal ont été identifiées. Ces espèces représentent 4.5 % de la diversité locale d'arbre avec une densité de 28.2 ±2.7 arbres/ha. Soixante-dix-huit pour cent (14/18) de ces espèces d'arbre sont éléphant-dépendant et ne recrutent pas assez de jeune pour le remplacement des parents. Le recrutement est insuffisant sous les arbres-parents comme sous les autres espèces d'arbres. Chez 12 espèces, les premières cohortes sont absentes de nos parcelles d'étude. Pour les espèces capables de recruter, les structures spatiales des jeunes générations sont plus groupées que la structure aléatoire, voire uniforme, des adultes.

Le deuxième plus grand disperseur de graine de la forêt : le bonobo (*Pan paniscus*), ne remplace pas les éléphants. Ainsi, il n'existe pas de partenaire alternatif pour la majorité des arbres au syndrome mégafaunale qui sont par conséquent : éléphant-dépendants.

Nous discutons les conséquences probables de la perte d'espèce d'arbre dispersées par les éléphants et proposons des solutions alternatives d'urgence pour la survie des espèces éléphant dépendantes jusqu'à ce que les stratégies efficaces de conservation entrent en vigueur.

Mots clefs Bassin du Congo , braconnage , défaunation , dispersion de graine , écologie forestière , *Loxondota cyclotis*, *Pan paniscus*, recrutement.

Introduction

The elephant is the largest terrestrial animal and one of the last megafauna represented on earth. African Elephants (*Loxodonta cyclotis* Matschie and *L. africana* Cuvier) currently occur in 37 countries in sub-Saharan Africa (Blanc 2007) while extinct from many former ranging areas (Bouché *et al.* 2011), Blanc 2008 in (Bouché *et al.* 2011; IUCN 2012). Rarefaction and possible extinction of elephants in many countries may have implications beyond the loss of the species itself. These large herbivores are known to consume a huge amount of food and interact with many plants, both quantitatively and qualitatively (White, Tutin & Fernandez 1993; Blake *et al.* 2009). Recently Campos-Arceiz & Blake (2011) compiled a food list of 335 elephant dispersed species from 213 genera in 65 families across several African research sites. In Afrotropical forests, many of these plant species are disseminated by forest elephants (*Loxodonta cyclotis*) sometimes at very long dispersal distances (Blake *et al.* 2009), a mutualism that matters to the population dynamics of plants and to the structure of forest tree communities (Cain, Milligan & Strand 2000). Moreover, the rate of seed germination of many forest plant species has been increased significantly after passage of the elephant's gut (reviewed in Campos-Arceiz and Blake, 2011). Therefore, elephants are widely recognized as a keystone species (Western 1989; Power *et al.* 1996), and are qualified as "megagardeners of the forest" (Campos-Arceiz & Blake 2011). Many of the plants the elephants interact with as fruit consumers are generalists and hence dispersed by other animals. To date, obligate relationships have been only demonstrated for *Balanites wilsoniana* (Cochrane 2003; Babweteera, Savill & Brown 2007) but based on different evidences, many other African plant species are suspected to be largely or exclusively elephant dependant in their seed dispersal and regeneration (reviewed in Campos-Arceiz and Blake, 2011) (Cochrane 2003; Babweteera, Savill & Brown 2007). One of the most appealing evidence is based on the traits of the fruits and of the seeds consumed by the elephants that constitute a megafaunal syndrome (Alexandre, 1978, Feer 1995a; Guimarães *et al.* 2008). Following Alexandre (1978) megafaunal fruits have been defined by Guimaraes *et al.* (2008) as the fruits produced by plant species that interact with large bodied frugivore species. These authors have classified these fruits as either big fleshy fruits (4-10cm in diameter) producing big (>2cm) seeds with a hard coat or bigger fleshy fruits (>10cm) producing numerous small seeds. These fruits are generally brown, green or yellow and smelly (Guimaraes *et al.* 2008; Campos-Arceiz and Blake, 2011) . Moreover, the fruits are commonly very noisy when dropping and hitting the soil at maturity, thus likely to be localised acoustically by potential seed-dispersers. Several plant species share these megafaunal syndromes in African forests historically inhabited by elephants. Considering the massive decline of elephant forest populations in Africa these last decades, many authors have suggested that the phenomenon would seriously impact the regeneration process of many plant species in particular those presenting megafaunal syndromes ((Blake *et al.* 2007; Guimarães Jr, Galetti & Jordano 2008; Blake *et al.* 2009; Campos-Arceiz & Blake 2011) although these dramatic predictions are still debated (Campos-Arceiz & Blake 2011). However, it is difficult to evaluate the consequences of the decrease of forest elephant populations in forest ecosystem dynamics because it would necessitate to compare the demography of long generation trees in forests where the elephants are still present with those in forests where they have been extirpated. One approach consists in comparing regeneration and conspecific spatial aggregation patterns of plant species that present megafaunal syndrome at different age classes in forests where elephants have been hunted. Indeed, a strong relationship between dispersion syndromes and spatial aggregation was found among 561 tree species in a 50 ha plot in Malaysia (Seidler & Plotkin 2006b). Barochore and ballistic species with short dispersal distance are more aggregated than species dispersed by large animals and this pattern was found for saplings and adult trees ((Seidler & Plotkin 2006b). Our hypothesis is that in a forest where elephants have been extirpated we should detect either the disappearance of young age classes or a shift in aggregation patterns between old age classes (that have been dispersed by elephants) and young age classes that have been dispersed without elephants for species that present a megafaunal syndrome. These changes should not be detected for barochorous species or for species dispersed by other animals. Hence, if tree species showing the megafaunal syndrome depend on elephants for seed dispersal, one would expect no alternative seed-dispersers and thus a high mortality of seedlings and poles due to the density dependent effect (Janzen 1970b; Connell 1971; Beaune *et al.* 2012b; Paine *et al.* 2012). Very few studies have investigated the consequences of the disappearance of the elephants on the spatial distribution of different age classes of tree species dispersed by these animals. The seedling and the sapling spatial distributions of *Balanites wilsoniana*, a species dependant on elephants for dispersal and germination, differ between forests with and without elephants, with seedlings being more aggregated under adult plants when elephants are absent (Babweteera, Savill & Brown 2007).

In the Salonga National Park (NP) (DR Congo), the largest forested NP in Africa and the second largest on earth, forest elephants have been severely poached for decades (Alers *et al.*

1992; Van Krunkelsven, Bila-Isia & Draulans 2000; Blake *et al.* 2007). Compared to other NP in the Congo Basin, mean forest elephant density of 0.05 individuals km^{-2} in Salonga NP deriving from 1900 remaining individuals is considered being low. In contrast, mean estimated forest elephant densities in the other NP in this area ranged from 0.4 individuals km^{-2} in Nouabalé-Ndoki NP and Dzanga-Sangha NP to 2.9 elephants km^{-2} in the Minkébé NP (Blake *et al.* 2007). Thus, forest African elephant population in Salonga NP can be considered as one of the most limited in the Congo basin with severe potential consequences for the elephant-dependent tree community.

In this paper, we examine the potential impact of a reduced density of forest elephants on the recruitment for several trees species presenting the megafaunal syndrome in the Salonga NP. Overall, we aim to assess the ability of the megafaunal tree community at LuiKotale to reproduce without elephant seed dispersal service.

To test these hypotheses, we compare the spatial distribution of different age classes of tree species (adults, poles, saplings and seedlings) among species with different dispersion syndromes (megafaunal, zoochoric and autochoric), in a forest where elephants have been almost extirpated 30 years ago , still suffer from illegal poaching and are far from having recovered from this serious impact. Moreover we have quantified the recruitment of megafaunal syndrome species under parental trees (without seed dispersal) and other trees; and (2) alternative dispersal partners and their dispersal effectiveness (Schupp 1993; Schupp, Jordano & Gomez 2010) in order to judge ecological redundancy and alternative survival. Here, we focus on the second largest fruit consuming mammal after the elephant and potential dispersal partner, the only great ape of the Cuvette Centrale South of the Congo River, the bonobo (*Pan paniscus* Schwarz); (3) current tree-population demography including recent cohorts born after elephants' disappearance and old cohorts born in the past, when visits of elephants were still regular (before the eighties). For tree-populations with alternative seed-dispersers, we expect different spatial structures of recent generations. For this we (4) compare spatial structure of adults dispersed during the elephant era (potentially long dispersal distances) with that of new recruits not dispersed by elephants (potentially shorter dispersal distances; after the eighties).

Materials and 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 NP, in the same continuous forest block. Salonga NP has a size of 33.346 km², and has been classified as UNESCO world heritage site (Grossmann *et al.* 2008). The study site covers >60km² of primary evergreen lowland tropical forest. This forest traditionally belongs to Lompole village (17 km away) and has been used for hunting, fishing and the collection of forest products. Since 2001 Lompole agreed to stop all exploitation and devote it for the purpose of research (Hohmann & Fruth 2003c). The climate is equatorial with abundant rainfall (>2000mm/yr) and two dry seasons, a short one around February and a longer one between May and August. Mean temperature at LuiKotale ranges between 21°C to 28°C with a minimum of 17°C and a maximum of 38°C (2007-2010). Two major habitat types can be distinguished: 1-Dry (*terra firme* forest) and; 2-Wet (temporarily and permanently inundated forest). The dry habitat dominates with heterogeneous species composition covering 73%, and homogenous species composition (*e.g.Gilbertodendron* spp) covering 6% of the site. The wet habitat consists of heterogeneous forest temporarily (17%) and permanently (4%) inundated (Mohneke & Fruth 2008).

Tree species

Between 2002 and 2010, botanical data collection took place in the frame of the long term project "The *Cuvette Centrale* as Reservoir of Medicinal Plants" (Fruth 2011): Fertile plant material was collected in at least triplicate along natural trails (31 km), standardized transects (8 km), in plots, and opportunistically. It was identified by vernacular name, described, tagged with a unique collection number, and herborized. The dried vouchers were shipped to Kinshasa, taxonomically determined and incorporated into the herbarium of the INERA at Kinshasa University (herbarium code: IUK). Copies of specimens were shipped to herbaria in Belgium (National Botanic Garden of Belgium : BR, Meise) and Germany (Botanische Staatssammlung München : M, Munich) for verification and identification by specialists. By May 2010, the herbarium consisted of 7,300 vouchers. So far, ≥403 tree species from 40 families were identified for LuiKotale (Fruth unpub. data). Among the tree species censused, the diaspores were analysed and dispersal strategies defined as (1)-zoochore (animal dispersed species), (2)-anemochore or (3)-autochore. Species were assigned zoochory when an edible part of the fruit that promotes swallowing or transport of seeds was found. Anemochory (wind dispersal) was assigned when wings or other structures (e.g. plumes) favouring wind transport were found. Finally, autochory was assigned to species that lack any obvious dispersal structure. (Howe & Smallwood 1982). We distinguished the species with megafaunal syndrome following the criteria of (Feer 1995a; Guimarães, Galetti & Jordano 2008). Effective seed dispersal of these species by elephants was confirmed by literature (White, Tutin & Fernandez 1993; Yumoto *et al.* 1995; White & Abernethy 1997; Theuerkauf *et al.* 2000; Nchanji & Plumptre 2003; Morgan & Lee 2007; Blake *et al.* 2009; Campos-Arceiz & Blake 2011). See Table 9.

Family	**Species name**	**vernacular name**	**size (cm) of fruit & seed**		**Mean density (tree/ha)**	**Mean DBH (cm)**	**Bonobo seed handling**	**Human usage**
Anacardiaceae	*Antrocaryon nannanii*	Bokongwende	5ø	4ø	<0.1	97	Dropped	F
Annonaceae	*Anonidium mannii*	Bodzingo	30↔	6↔	8.8	47	Dropped	F, TM
Apocynaceae	*Picralima nitida*	Botolo	17↔	3↔	5.2	19	Fruit not consumed	W
Chrysobalanaceae	*Parinari excelsa*	Bodzilo Mpongo	5ø	3ø	0.3	113	Dropped	W
Euphorbiaceae	*Drypetes gossweileri*	Bopambe	10↔	4↔	8.3	46	Fruit not consumed	TM, W
Guttifereae	*Mammea africana*	Bokodzi	10↔	6↔	0.3	118	Dropped	TM, W
Irvingiaceae	*Irvingia gabonensis*	Boseki	7↔	5↔	1.7	83	Dropped	F
	Irvingia grandifolia	Loote	7↔	5↔	0.1	110	Dropped	TM
	Klainedoxa gabonensis	Boseki ya Moindo	6ø	4↔	2	125	Fruit not consumed	
Mimosaceae	*Tetrapleura tetraptera*	Bolese	16↔	<1ø	<0.1	82	Fruit not consumed	F, TM
Moraceae	*Treculia africana*	Boimbo	35ø	1↔	0.1	60	Swallow/Crunch	F
Rubiaceae	*Massularia acuminata*	Welo	6↔	<1↔	0.8	11	Fruit not consumed	W, TM
	Poga oleosa	*Ememo*	7ø	5ø	<0.1	68	Fruit not consumed	poison
Sapotaceae	*Autranella congolensis*	Bonianga	9↔	6↔	<0.1	185	Dropped	TM, W
	Gambeya lacourtiana	Bopambu	90ø	4↔	0.3	92	Sawallow/spit	F, TM
	Omphalocarpum letestui	Boiliki	14ø	3↔	0.2	69	Fruit not consumed	
	Omphalocarpum procerum	Bosanga	20ø	4↔	<0.1	73	Fruit not consumed	
	Tridesmostemon omphalocarpoides	Boyoko	10ø	3↔	<0.1	27	Fruit not consumed	

Table 9 Elephant-dependent tree species: characteristics show averages of fruit and seed size, species density, trunk diameter in breast-height (DBH). seed-handliong of bonobos as well as current human interests. Fruit-size is average length, seed size is largest width or passage size according to the morphology and passage in a digestive tract, indicated as diameter ø or length ↔ (n=10). Human usage is specified as F (fruit consumption), W (wood), TM (traditional medicine).

Tree population demography

In order to investigate the impact of elephant decline on the actual tree population demography at LuiKotale, we censused all adults trees ≥10cm DBH in 13 plots of 1-ha (100×100m) each, as well as all seedlings (<50cm high), saplings (50cm-200cm high), and poles (>200cm high and <10cm DBH) in 400 subplots of 4m² (2×2m) /ha plot. The plots were randomly positioned in heterogeneous primary forest, haphazardly without previous knowledge of the area. The closest plot pair is separated by 250m and the most distant one by 6km. From February to June 2011, all trees were spatially referenced with compass and hectometer, using the South-Western plot-corner as origin. Tree populations are normally characterized by type III demographic curves because the species produce a huge number of seeds and seedlings but the greatest mortality due to predation and pathogens is experienced early on in life followed by an exponentially decrease of the rates of death (Demetrius 1978; Makana *et al.* 2011). Consequently, with class age cohorts being equivalent to class size cohorts, tree demography is an exponential of Type III curve in viable populations. Our hypothesis is that if the dispersion and the reproduction of a tree species has been impacted by the disappearance of the elephant population we should detect a crash in the youngest cohorts and hence a strong departure from a classical type III curve. In this study we have excluded seedlings (<50cm) from the youngest cohort because of the huge fluctuations observed in the annual factors regulating seedling density such as production, predation, drought, etc. (Beaune, unpub. data). DBH and fruit dimensions have been measured for all species investigated.

Recruitment under parental tree (without seed dispersal) and under non-parental tree (seed dispersal)

To assess the actual recruitment of megafaunal trees elephant dependent for dissemination, both megafaunal and control tree species were chosen from the Max-Planck-projects' long-term inventory of plants and exploration of the realm. As control we included six tree species known to be independent of elephant-dispersal, (a) three autochoric, and (b) three zoochoric. (a) *Scorodophloeus zenkeri* Harms, and *Hymenostegia mundungu* Pellegr, J.Léonard (Caesalpiniaceae with ballistic seed dispersal able to propel seeds 30m away), and *Strombosiopsis zenkeri* Engl. (Olacaceae, with barochory and probable secondary dispersal);(b) *Enantia olivacea* Robyns & Ghesq., *Polyalthia suaveolens* Engl. & Diels (Annonaceae), and *Pancovia laurentii* Gilg ex De Wild. (Sapindaceae), which are dispersed by frugivores still present in LK including primates and birds (Beaune *et al.* in prep).

Between May 2010 and June 2011 a minimum of 10 adult individuals of both megafaunal and control species that were previously observed to produce seeds were censused for actual recruitment under the parental crown (without conspecific within 200m radius) as follows: All seedlings (<50cm high), saplings (50cm-200cm high), and poles (>200cm high and <10cm DBH=Diameter at Breast Height) were counted in the corresponding fruit-fall zone. The surface of the fruit fall zone (=A) was calculated according to $A=r^2\pi$, where r is the measured radius of the crown.

Mean production of seedling, sapling and pole were calculated subsequently (=nb per tree/fruit-fall zone). We considered a population being able to self replace when the average pole production/tree was ≥1. In order to assess actual seed dispersal, the average density of nineteen species-specific seedlings, saplings and poles from twelve families was calculated for each parental and non parental tree species. The average densities calculated under non parental species were compared with adult species densities inferred from 13×1ha-plots (details below). In viable populations pole density should exceed adult density (see demography below). Recruitment abilities were categorized according to (Chapman & Chapman 1995) as follows: 1-Autorecruit (recruits under the parent, characteristic of the autochoric species); 2-Dispersal dependent (no recruit under the parent but high recruits densities (>to adults) under other trees); 3-Polyvalent (able to recruit more than one pole under the parent and other trees); 4-Unable to recruit (insufficient recruits under the parent and other trees (density<to adults').

Bonobos as alternative dispersal partners

Bonobos (*Pan paniscus*) are the biggest frugivores after elephants. Field work with these primates has been ongoing since 2001 (Hohmann & Fruth 2003c). Day-to-day follows of individuals of one habituated community (n=35 mature bonobos) have been conducted since 2007. In order to investigate their role as potential alternative seed disperser, DB observed for 22 months between January 2009 and June 2011, fruit and seed handling of the megafaunal plants using continuous behavioural group observations and *ad libitum* observations (Beaune *et al.* in prep).

Spatial analyses

The spatial distribution of the different cohorts of the megafaunal and control were investigated. For determining the degree of clumping for each species, we calculated Morisita's Index (I_M) within the censused 1-ha quadrates (Morisita 1959). The index corresponds to the scaled probability that two plants randomly selected from the entire population are in the same quadrate. The index varies from 0 to n. In uniform patterns the index varies between 0 and 1, where values >1 indicate clumping, with the distribution being more clumped, the higher the value. When the index value is 1, the distribution of the plants is random irrespective of plot-size or mean density of individuals per plot. Calculations were performed using *PASSaGE* (Pattern Analysis, Spatial Statistics, and Geographic Exegesis; (Rosenberg & Anderson 2008). For control species we expect no difference of spatial structure among generations. Statistical analyses are specified in results. Analyses were performed using R 2.13 (R Development Core Team 2011).

Results

Tree species

Table 9 shows the eighteen tree species from eleven families identified as megafaunal. This megafaunal tree community represents 4.5% of the local tree species diversity. In terms of abundance, the megafaunal tree density represents with 28.2 trees/ha ±2.7, a total of 7.8% ±0.7 of all trees/ha.

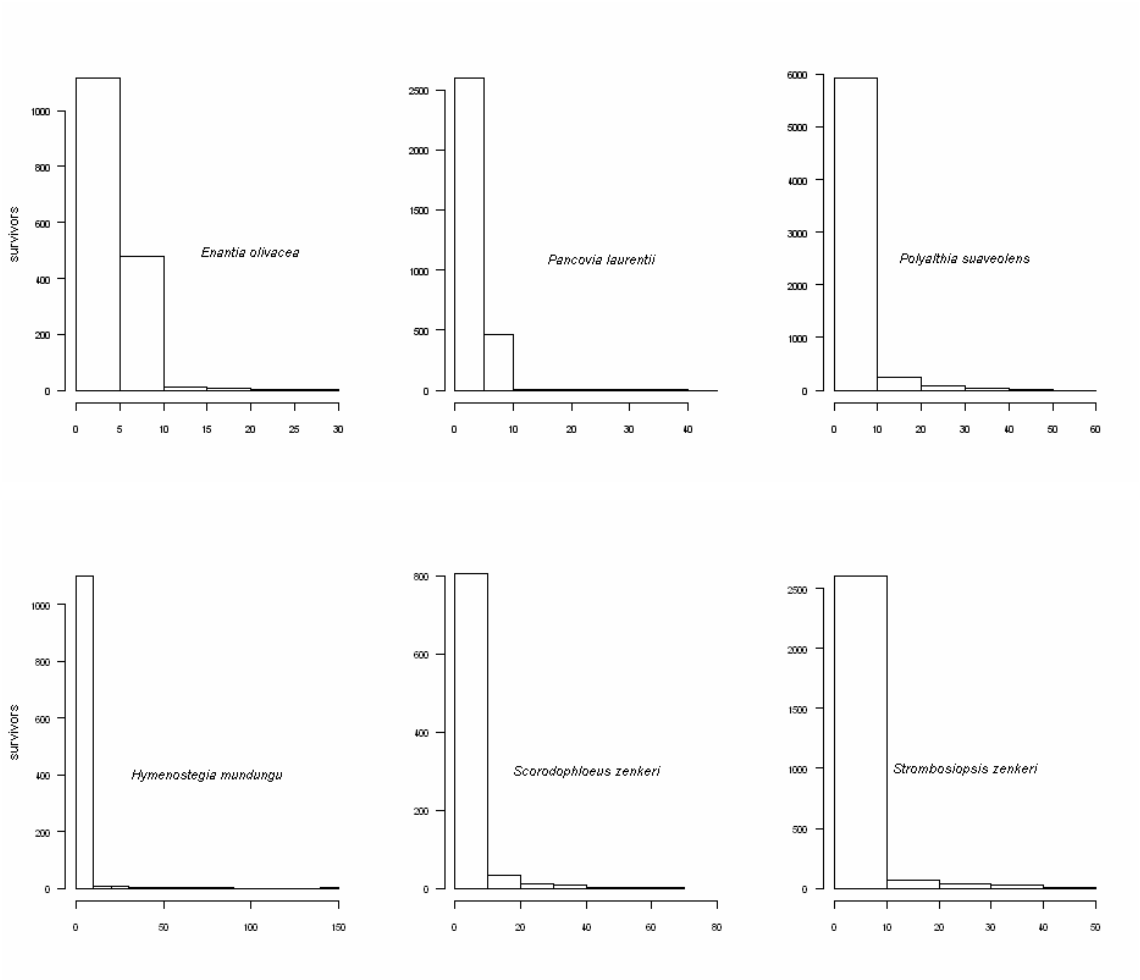
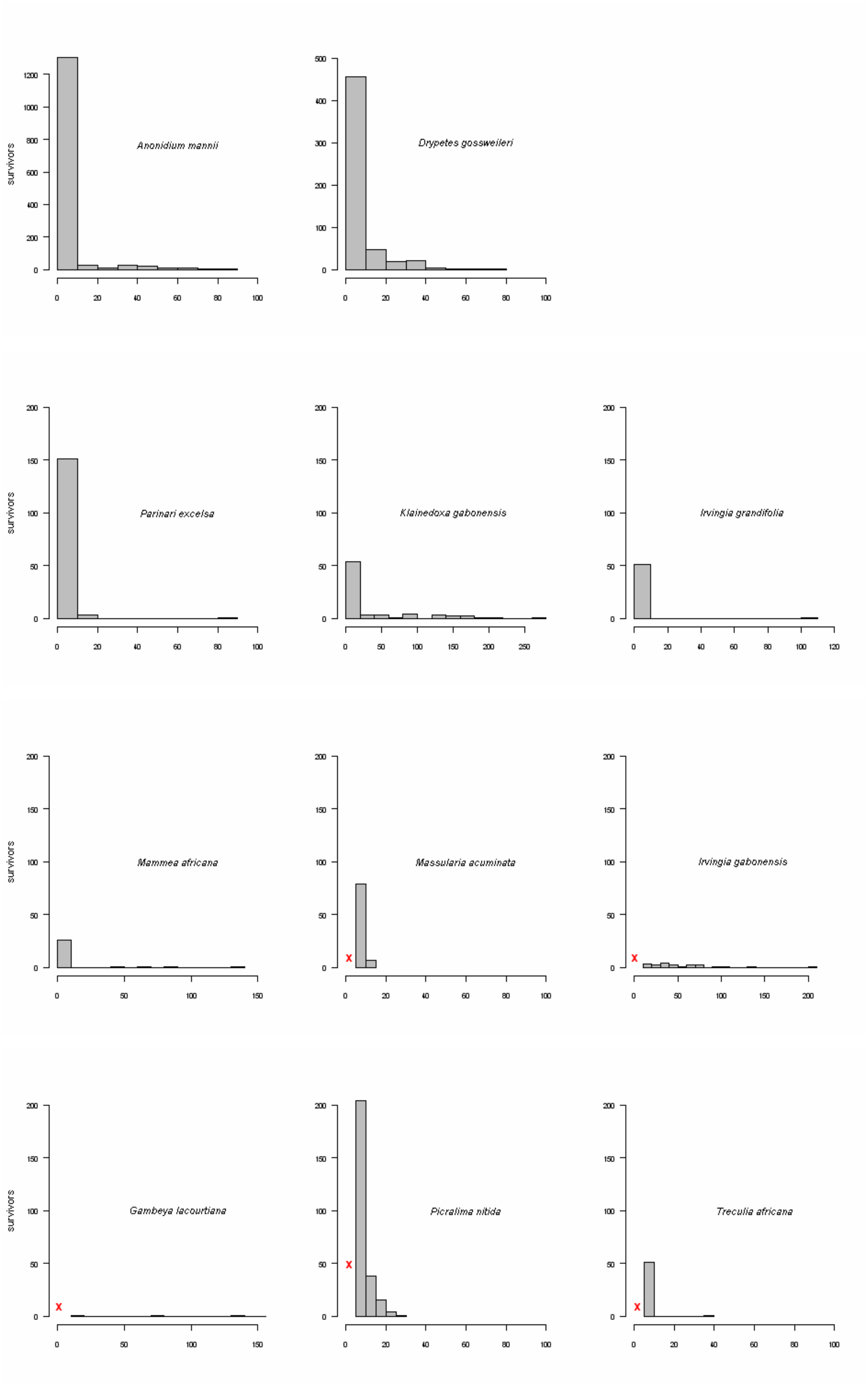


Figure 36 Demography of 6 control tree species censused in 13-ha plots. Y-Axes shows proportion of survivors. X-axes shows cohort size.

Population demography

Control species show demographic curves Type III (Figure 36).

Among the 18 megafaunal species tested at LuiKotale, only two species, *A. mannii* and *D. gossweileri*, follow Type III demographic curve (Figure 37). Four species (*P. excelsa*, *M. africana*, *K. gabonensis*, *I. grandifolia*) show higher numbers of recruits in the first cohort than in the next one, although the fit is not exponential. For the other twelve species the first cohort is absent. No seedlings at all were found for *A. congolensis*, *A. nannanii*, *G. lacourtiana*, *I. grandifolia*, *M. acuminata*, *M. africana*, *O. letestui, O. procerum*, *P. nitida, P. oleosa* and *T. tetraptera* either in the 13-ha plots or in the realm where attention was focused on these species during the study period.


survivors
Anonidium mannii
0
200
400
600
800
1000
1200
0
20
40
60
80
100
Drypetes gossweileri
0
100
200
300
400
500
survivors
Parinari excelsa
Klainedoxa gabonensis
Irvingia grandifolia
0
50
100
150
200
250
120
survivors
Mammea africana
Massularia acuminata
Irvingia gabonensis
x
survivors
Gambeya lacourtiana
Picralima nitida
Treculia africana

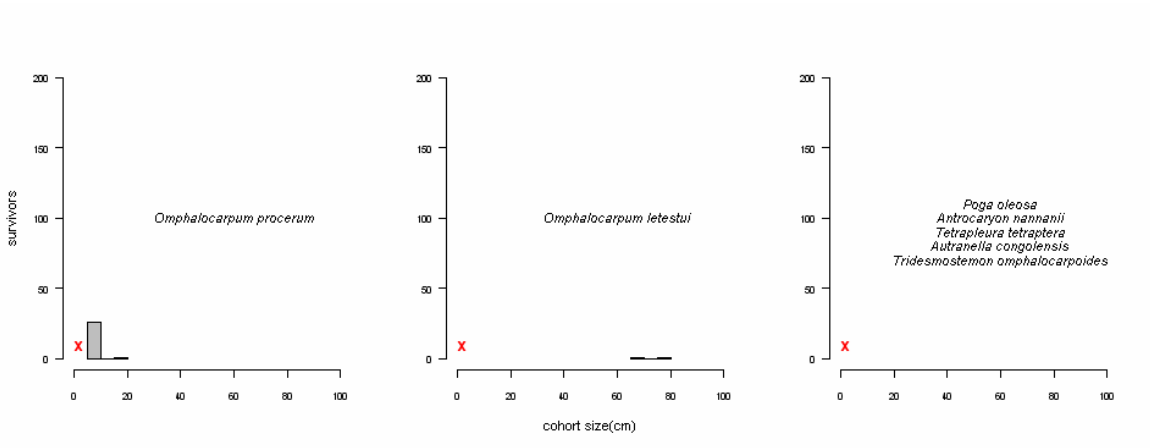


Figure 37 Demography of 18 megafaunal tree species censused in 13-ha plots. Bars indicate cohorts starting with saplings. Red cross shows absence of the first cohort. Y-Axes shows proportion of survivors.

Spatial analyses

Of all 19 control tree-species, three autochoric and three zoochoric were analysed. For megafaunal species, only populations able to recruit with existing cohorts of poles, sapling and poles were analyzed. Consequently, analysis included *A. mannii*, *D. gossweileri*, and *P. excelsa*. Three species, *I. grandifolia*, *K. gabonensis* and *M. africana,* while reported, could not be analysed completely due to a lack of entire cohorts and recruit numbers <2. The spatial patterning is similar among cohorts for the control species with clumped distribution, with I_M >1.8 for autochoric trees and a random distribution for zoochoric trees with a mean I_M =1.2 [1-1.7] (Figure 38). However, the spatial patterning of the megafaunal species varies among cohorts. Young generations tend to be more clumped than adult generations. The spatial patterning of the six adults is similar to the other zoochoric species with a dispersed distribution (uniform and random, I_M range: 0-1.5), while the young cohorts are much more similar to autochoric spatial patterns with clumped distribution (I_M >>1). Our hypothesis is supported: young generations dispersed by alternative seed dispersers are more clumped than adults probably dispersed by elephants during time of highest elephant density.

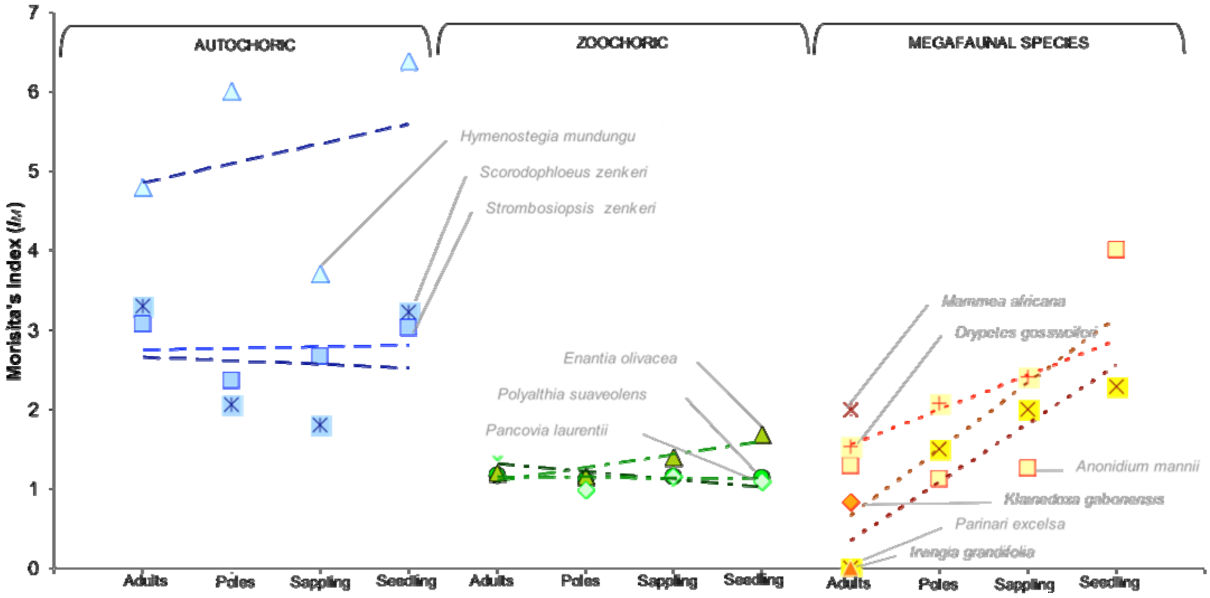


Figure 38 Morisita's index (I_M) of adults, poles, saplings and seedlings of three autochoric (blue), three zoochoric (green) and six megafaunal species (yellow) of 13 one-ha-plots. The index-value is 1 when individuals are randomly dispersed, values greater than one indicate clumping, values between 0 and 1 indicate uniformity.The higher the value, the more clumped the distribution.

Recruitment under parental tree (without seed dispersal) and under non-parental species (seed dispersal)

A total of 302 trees from 37 species were censused (18 megafaunals+19 controls). The cumulative fruit fall zone of these trees represents 5.13 ha, with an average fruit-fall zone for each tree of 207 m² ± SE.19). For eight of the 18 megafaunal species, we were unable to find 10 specimens within the study area. This was the case for *Antrocaryon nannanii* (n=2), *Autranella congolensis* (1), *Omphalocarpum procerum* (6), *Tetrapleura tetraptera* (2), *Treculia africana* (7), *Tridesmostemon omphalocarpoides* (2), *Omphalocarpum letestui* (5), and *Poga oleosa* (2). Both Figure 39 and Table 10, show that none of the megafaunal species can recruit enough poles for self replacement. Sixty seven percent (12/18) of the elephant-dependent tree species did not recruit any pole neither under the parent nor beneath other trees, resulting in the recruitment category 4 (unable to recruit). Only four megafaunal species (*Anonidium mannii*, *Drypetes gossweileri*, *Picralima nitida* and *Treculia africana*) were able to disperse and recruit poles under non parental trees resulting in the recruitment category 2 (dispersal dependent). However for *D. gossweileri* and *P. nitida*, pole recruit densities were significantly lower than the adults' ones (1.2 pole/-ha<<8.3 trees/ha; Wilcoxon signed-rank test: p-value = 0.01 and 0.8 pole/ha <<5.2 trees/ha; p-value <0.01 respectively). Our hypothesis of population viability is challenged by the last two megafaunal species, *A. mannii* and *T. africana,* being the sole dispersal dependent trees that recruit beneath other non parental trees with higher pole densities than adult (falling in category 2: dispersal dependent). However, adult density of *T. africana* is extremely low explaining the extreme difference between adult and pole densities.

Except for *Antrocaryon nannanii,* negative effects of adult megafaunal trees such as growth inhibition of seedlings, saplings and poles within the fruit fall zone can be excluded. Seventeen elephant-dependent tree species censused for recruits from other species beneath their crown, showed an abundance and diversity of other plant species not significantly different from what is found beneath control trees (Wilcoxon rank sum test, p-values>0.05).

Control species in contrast exhibited significantly different patterns. Of 19 species from 12 families, all resulted in the recruitment category 1, 2 or 3. A typical example of autochoric tree-recruitment is illustrated by the control-species *H. mundungu*, *Scorodophloeus zenkeri* and *Strombosiopsis zenkeri*. These species are able to recruit beneath the parental crown on average 2.5 poles/parent ± 0.4; 3.4 ± 0.9; 1.2 ± 0.3 respectively resulting in the recruitment category 1 (autorecruit). A typical example of dispersal dependent tree-recruitment is illustrated by the control species *E olivacea*, *P. suaveolens*, *P.laurentii,* which are dispersed by primates and birds. These were able to disperse and recruit poles under non parental trees resulting in the recruitment category 2 (dispersal dependent).

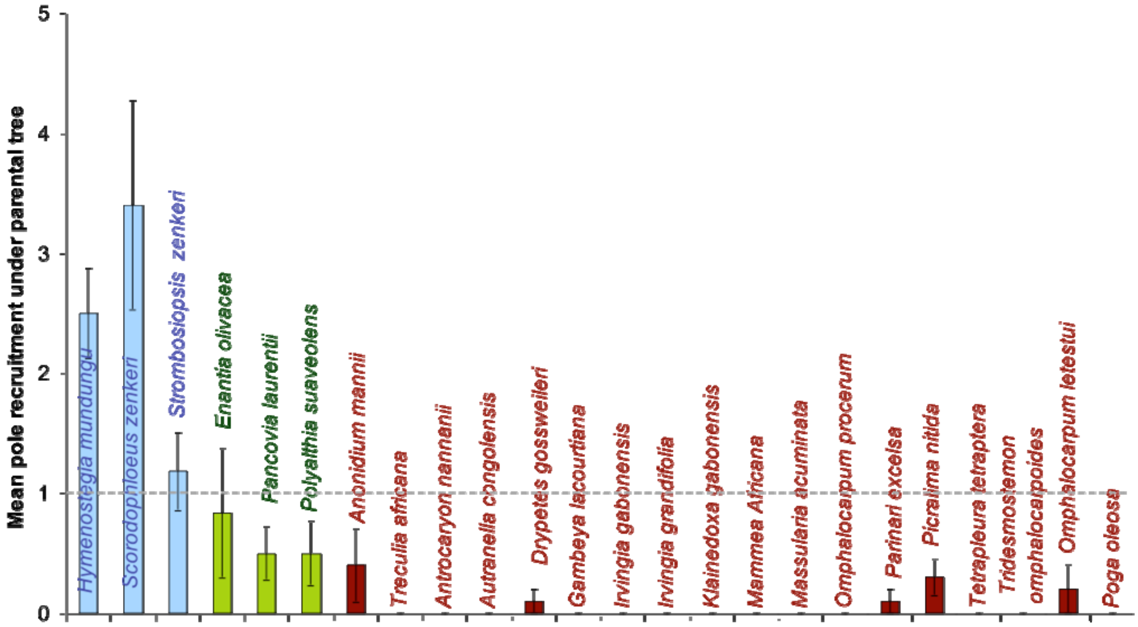


Figure 39 Mean number of poles present (or recruited) under parent tree. For autochoric (blue), zoochoric alternative partners (green) and zoochoric megafaunal partners tree species (red). The dotted line is the theoretical value of pole recruitment necessary for self replacement of the parent tree. Y-error lines in bars indicate standard errors.

The Bonobo as an alternative partner

Table 9 presents the megafaunal fruits that have been observed to be consumed by bonobos at LuiKotale. Of the 18 species identified as megafaunal, nine are consumed by this second largest frugivore. Bonobos consumed fruits of *A. mannii* in 1.6% ±0.2 of the feeding sessions (based on 1879 hrs of continuous group observation), *A. nannanii* (0.2% ±0.7), *I. gabonensis* (2.3% ±0.2) & *grandifolia* (<0.1%), *M. africana* (0.4% ±1.1) and *P. excelsa* (2.5% ±0.3). *A. congolensis* consumptions were observed in 2007. These big size fruits are usually consumed within or beneath the crown. Fruits become available by bonobos' harvest or dropping by gravity when ripe. Depending on the species, the fibrous mesocarp is chewed and swallowed, or the juice extracted fabricating wadges and the fibrous remainders or the seeds dropped on the spot with no differences from dispersal induced by barochory (no horizontal movement). Sometimes individuals took one or more fruits (species: *I. gabonensis*, *M. africana*, *A. mannii*), transporting them in their mouth and/or hands to eat while travelling, documenting seed dispersal by ectozoochory. From our observations, seeds were transported in the 100 m radius zone, with a maximum considered to be exceptional, where a bush mango was carried for 426 m from the parent tree. Only *G. lacourtiana* (2.3% ±0.2 of the feeding sessions) seeds were observed to be swallowed and found in feces and also spat. The size of this species seems to be the limit for bonobo endozoochory with its ovoid shape (3cm long and 1cm wide). The bonobo could be considered as a partner for endozoochoric seed dispersal of *G. lacourtiana*. Bonobos were observed eating *T. africana* in flower, unripe and ripe including the soft seeds (2.6% ±4.5). The bonobo is not considered as a dispersal partner for these trees. Nevertheless, the megafaunal community is part of the bonobo diet representing 11.8% ± 0.1 of their feeding sessions.

Bonobos were not observed interacting with the other megafaunal species which do not seem to be attractive for a primate. *T. tetraptera,* observed to be eaten by black mangabeys (*Lophocebus aterrimus* Oudemans) in LK, are an exception.

	Recruitment	**Species**	**average recruitment under parent tree**			**recruitment density/ha under other trees**
			seedlings	**saplings**	**poles**	**poles**
Control	**Polyvalent**	*Hymenostegia mundungu*	4.4	4.1	2.5	11.8>**
		Scorodophloeus zenkeri	16.3	2	3.4	25.0 >**
		Strombosiopsis zenkeri	2	2.1	1.2	1.3>**
	Dispersal dependent	*Enantia olivacea*	0	1.8	0.8	7.6>**
		Pancovia laurentii	0.1	1	0.5	34.4>**
		Polyalthia suaveolens	0.1	1.6	0.5	96.4 >**
Megafaunal species		*Anonidium mannii*	0.5	0.6	0.4	27.7 >**
		Treculia africana	0.1	-	-	1.4 >***
	Unable to recruit = **Elephant dependent**	*Antrocaryon nannanii*	3	4.5	-	-
		Autranella congolensis	-	-	-	-
		Drypetes gossweileri	-	0.2	0.1	1.2 <*
		Gambeya lacourtiana	1	-	-	-
		Irvingia gabonensis	1.7	0	-	-
		Irvingia grandifolia	-	-	-	-
		Klainedoxa gabonensis	-	-	-	-
		Mammea africana	0.1	0.9	-	-
		Massularia acuminata	-	-	-	-
		Omphalocarpum procerum	0.2	-	-	-
		Parinari excelsa	19.8	0.1	0.1	-
		Picralima nitida	-	-	0.3	0.8 <**
		Tetrapleura tetraptera	2	-	-	-
		Tridesmostemon omphalocarpoides	1.5	-	-	-
		Omphalocarpum letestui	0.6	-	0.2	-
		Poga oleosa	-	-	-	-

Table 10 Recruitment of the megafaunal & control species, with mean pole recruitment under the parent trees and density under other species. Poles density is compared with adults (from the 13-ha plots) using Wilcoxon signed rank test (> =poles density> adults density (and reverse with <); *:p-value<0.05, **:<0.01, ***<0.001)

Discussion

Here we analyzed 18 species of the megafaunal community to test the megafaunal tree population's ability to survive without elephants in an evergreen lowland rainforest of the *Cuvette Centrale*. Without seed dispersal none of the 18 studied megafaunal species can recruit enough poles for self replacement. Twelve of those species did not recruit poles under other species, resulting in the recruitment category 4 (unable to recruit). These results can be explained by the density dependent effect also named the Janzel-Connel effect, where the seed mortality is correlated with seed density which attracts predators and pathogens (Janzen 1970b; Connell 1971; Beaune *et al.* 2012b). In the absence of an endozoochoric partner such as the elephant, this "putting all your eggs in one basket" adaptation is likely to turn out as a maladaptation, unless a tree-species has alternative dispersal partners or mechanisms. Within the megafaunal community we found four species with recruits beneath non parental trees demonstrating alternative seed dispersal. However their pole density was lower than the current adults' density found in the forest except for one species: *A. mannii*.

With demographic analysis, six species seem to be resilient without elephants: *A. mannii*, *D. gossweileri*, *I. grandifolia*, *P. excelsa* and *K. gabonensis*. But only *A. mannii and D. gossweileri* show an exponential demography characteristic of trees. These species are likely to be dispersed by other agents that are efficient enough to allow a high recruitment of the first cohort. Duiker species are known to disperse several large-seeded plants in African tropics (Gautier-Hion *et al.* 1985; Feer 1995b). And scatter-hoarding rodents such as *Cricetomys emini* for example can be secondary dispersers for some plants usually dispersed by megafauna. In our site, this nocturnal rodent was observed and camera trapped catching seeds >3cm. As demonstrated with *Cricetomys kivuensis* in an afromontane forest (Nyiramana *et al.* 2011), this genus transports and buries seeds for later consumption. Part of these seeds can germinate due to superabundant reserves, obliviousness or death of the animal. The 12 other described species currently seem to not recruit sufficiently to maintain their population and could be qualified as elephant-dependent. Therefore, elephant decrease affects the largest proportion of megafaunal-tree reproduction, not yet visible in the grown-up forest, however already visible in the understory looking at several generations of recruits.

For resilient species able to recruit without elephants, the spatial patterning could change. New generations of megafaunal species are distributed differently from the adults. The spatial pattern of the young cohort is more similar to autochoric species (clumped) while the adult pattern is more similar to animal-dispersed species (random). Even if secondary dispersers such as rodents allow certain megafaunal species to recruit, the next population would be clumped with consequences for inter-populational genetic exchange (Hamrick & Trapnell 2011) and increased mortality due to density effects (Burkey 1994). In addition to seed dispersal, absence of gut passage could affect germination success. As (Nchanji & Plumptre 2003) showed, unpassed seeds revealed both a longer germination time and a lower growth rate compared to seeds passed in elephants.

These results illustrate that megafaunal species cannot rely on barochory for recruitment. However, even if it was possible to recruit in the surrounding area of the adult trees as for *A. mannii*, *D. gossweileri*, *P. excelsa*, etc. , this dispersal pattern would be different and problematic for range expansion, genetic structure and metapopulation dynamics (Levin *et al.* 2003). In the megafaunal community, we can conclude that all the species, except *A. mannii*, seem to be elephant-dependent. In summary, our results show that the first step in population dynamics is compromised without elephants, with weaker or even non-existent self recruitment for the elephant-dependent species.

In the southern area of the Congo River, bonobos, the second biggest frugivores, are unable to replace elephants as seed dispersers, as the seeds are too large to be swallowed. They may contribute in some cases to dispersal outside the fruit fall zone by short distance ectozoochoric transport, similar to what can be dispersed by rodents (Forget & Wall 2001). For *I. gabonensis*, *M. africana*, *A. mannii*, bonobos can be considered as a poor disperser, dispersing over much shorter distances than elephants and omitting passage through their digestive tract.

Unfortunately for the elephant-dependent tree community, elephants have vanished from numerous forests. Healthy adult trees producing fruits remain in structurally intact in forests, empty of elephants and often of other large/medium fauna (Wilkie & Carpenter 1999). This so called empty forest syndrome (Redford 1992; Terborgh *et al.* 2008) occurs everywhere in overhunted forests giving the illusion that plant communities are still fine despite the lack of animals. Since recruitment and population dynamics of trees take longer than animal dynamics and go beyond human life time, ignorance to the change is widespread. Several studies described the first changes in recruitment due to changes in seed dispersal (Asquith, Wright & Clauss 1997; Chapman & Onderdonk 1998a; Andresen & Laurance 2007; Babweteera, Savill & Brown 2007; Muller-Landau 2007; Wright *et al.* 2007; Terborgh *et al.*

2008; Vanthomme, Bellé & Forget 2010a), and recent models of forest defaunation show alteration of plant reproduction, with changes after each generation and clear consequences for the future of our forests (Muller-Landau 2007). This study closes the loop by demonstrating the decline or absence of the last cohort likely to have been produced during the decades of elephant massacres (after the 1980s). The doom of the large dispersal vector might trigger a radical change in the forest composition, probably with a new era for the wind and ballistic dispersed trees (Beaune *et al.* in prep).

Looking closely at the primate-*Irvingia* seed dispersal commensalism, however, it's not only the tree species that is on the losing side. Numerous primate species include fruits of *Irvingia* in their diet. Certain populations use it massively during the fructification season as shown with drill (*Mandrillus leucophaeus*) (Astaras, Muhlenberg & Waltert 2008), bonobos and chimpanzees (see. Annex 2). *Irvingia* is only one of many elephant dependent tree species that highlight the cascade effect that is likely to occur with elephant extinction: first on the direct mutualists, such as the elephant-dependent trees, second on their consumers, third on all species depending on the consumers for endo- and ectozoochory, et cetera. However, this will take at least a tree lifespan's time. At Gashaka for example, a study site in Nigeria, where elephants have been extinct for more than 50 years, chimpanzees still eat bush mangos (Fowler personal communication), as do bonobos in some areas in DRC such as at Wamba and other sites (see appendix 1).

Taking into consideration that some of these trees, already on the 1st level of this cascade, are valuable for humans with respect to supplies such as nutrition, medicine construction material and economic aspects (Table 9), the following steps have to be included in conservation management plans. There are several strategies to investigate.

1) artificial nurseries in National Parks, scientific stations, forest concessions and other places where elephant preservation is not ensured in order to bridge the time till effective conservation measures allow the elephant to rebuild viable populations; 2) law enforcement; 3) reintroduction.

The park, classified as a World Heritage Site in Danger since 1999, may soon turn into another 33,346 km² of empty forest.

We invite all partners to join and contribute of the creation list of the species which cannot reproduce without their endangered partners (contact authors). In order to create a web red list of the species that needs artificial reproductive assistance for conservation in their ecosystem.

Species	location	elephant local status
P. paniscus	LuiKotale, DRC[1]	poached
P. paniscus	Lomako, DRC[2]	poached
P. paniscus	Wamba, DRC[3]	extinct
P. troglodytes verus	Conkouati Douli, Congo[4]	preserved
P. troglodytes verus	Gashaka, Nigeria[5]	extinct
P. troglodytes verus	Tai, Ivory Coast[6]	poached
P. troglodytes verus	Lopé, Gabon[7]	poached
G. gorilla gorilla	Lopé, Gabon	poached

Table 11 Examples of great ape populations eating bush mango and local elephant status (ref: 1: this study, 2: (Hohmann and Fruth 2000), 3: (Kano and Mulavwa 1984); Furuichi pers. comm. , 4: Renaud & Jamart pers. comm., unpub. data., 5: Boesch comm. pers., 6: (White and Abernethy 1997))

Conclusion

The most visible threat on tropical forest is habitat loss with deforestation. From 1990 to 2010 the world lost 135 million ha of forest area, including 75 million ha for Africa only (FAO 2010). However another serious problem although less visible is defaunation with the empty forest syndrome (Redford 1992; Terborgh *et al.* 2008, Figure 40). Defaunation affect all large/medium animals in tropics, including apes in Africa (Bowen-Jones & Pendry 1999). In DRC, at the southern bank of the Congo River, bonobos are the largest primates and sole representing of apes.

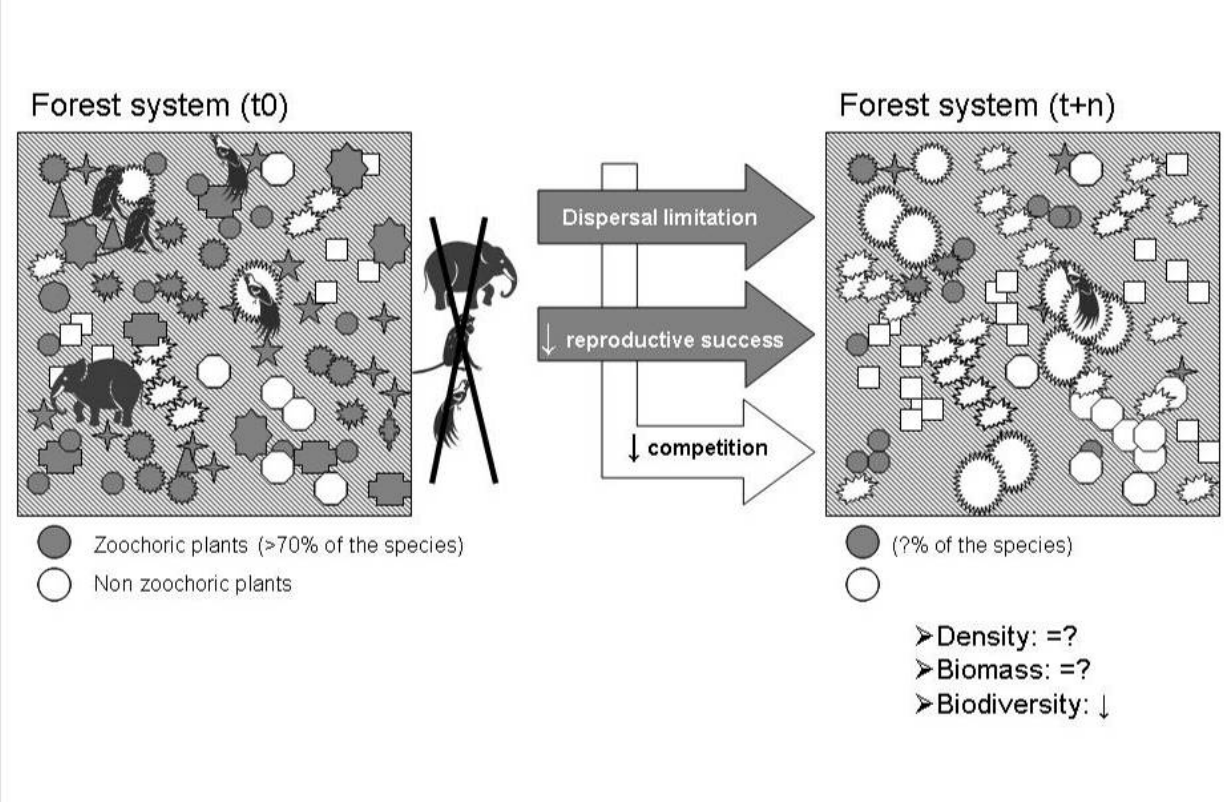


Figure 40 Empty forest syndrome and the possible effect on the plant community scenario.

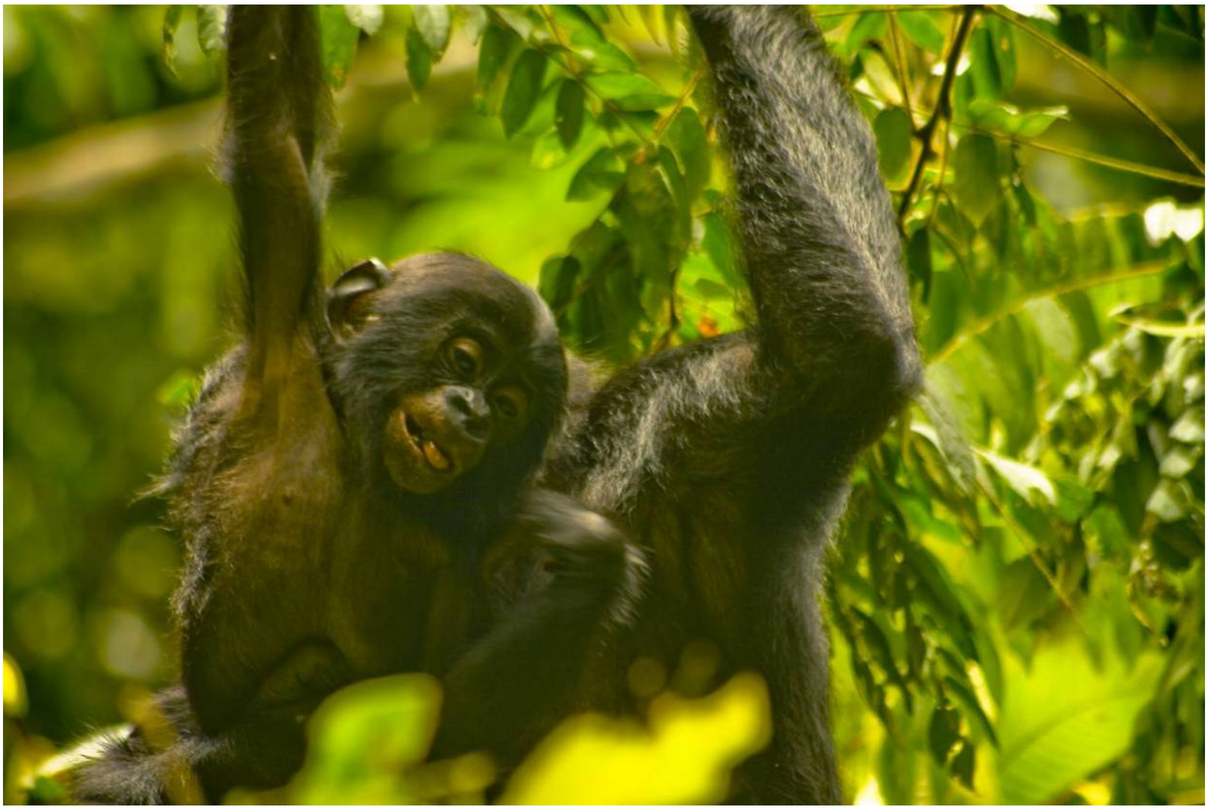
The ecological role of the bonobo project shows that bonobos are important seed disperser (Part I). They provide seed dispersal service to the majority of the fruiting plants (probably more than a hundred of plant species; 65% of the trees). All these plants are adapted to the bonobo endozoochory showing probable coevolution process with the apes. One of these adaptations is the seed coat adapted to the apes' gut passage and the need to be scarified to activate or improve germination. As demonstrated with the *Dialium* mutualism, both partners take advantage of the interaction. By imitation of these ecological processes we can artificially trigger the germination of *Dialium corbisieri* as probably the great majority of the Congo trees.

In this ecological story, numerous animals interact in the seed fate. For primary seed dispersal, very low functional overlap occurs with bonobo and other primates. After deposition: rodents, birds, Suidae and others can affect post dispersal survival (Part II). But endozoochory with bonobo imply dung effect which attract secondary dispersers (dung beetle) such as *Catharsius* that burrow the seeds and improve survival rate (Andresen & Feer 2005). Granivores are both seed predators and can act as secondary/tertiary seed dispersers (Forget & Milleron 1991; Forget 1996; Forget *et al.* 2005; Forget & Cuiljpers 2008; Nyiramana *et al.* 2011). However, while bonobos have crucial role in seed dispersers, bonobos do not replace elephant ecological service for species with megafaunal syndrome and by consequent elephant dependant. We show in this Congo forest specialized dispersal (Nathan *et al.* 2008) for certain plants with elephant as vector.

The bonobo seed dispersal induce long dispersal events at an average distance >1km; thus probably affecting populations' structure. It is surprising to see that a fruit character does not affect the behavior of their dispersal vector. Differential dispersal distance does not exist for plant species sharing the same vector: bonobo (Part III).

To conclude, bonobo are important animals of the forest providing irreplaceable ecological service. Unfortunately, bonobo are threatened of extinction (IUCN 2012) and their fate does not improve with time. They are threatened by bushmeat trafficking (Hart *et al.* 2008a; Reinartz *et al.* 2008) which growth with human demography. The forest might change unless bonobo efforts for conservation are not seriously managed.

See appendix for few organizations involved in bonobo conservation.



Synthèse

L'étude des derniers grands singes découverts par la science est récente ; et l'intérêt porté à *Pan paniscus* ne cesse de croître depuis ses quelques décades d'existence scienifique. Figure 41. Or très peu de sujets concernent le rôle écologique de cette espèce (cf : *Pan paniscus myths and realities*) gravement menacée d'extinction par le braconnage, les maladies humano-simiennes et la dégradation de l'habitat (Dudley *et al.* 2002; Hart *et al.* 2008a; IUCN 2012; Tranquilli *et al.* 2012) : (*Deforestation throughout the ape's range*). Les bonobos peuplent une vaste partie des forêts du bassin du Congo, et ce, depuis plusieurs millions d'années. Quels sont les risques de la disparition annoncée de ces grands singes sur l'écosystème ? Jusque-là les réponses restèrent incertaines. Les arguments en faveur de la conservation des bonobos étaient principalement d'origines philosophiques, morales (avec la proximité filiale que nous autres humains partageons avec les bonobos, et scientifiques (pour comprendre nos origines communes d'il y a 5 à 6 millions d'années (Cavalieri & Singer 1993). Évidemment, le caractère frugivore des bonobos n'a pas échappé aux écologistes et leur rôle dans la dispersion de graines a été souligné (Caldecott & Miles 2005; Tsuji, Yangozene & Sakamaki 2010). Cependant, la quantification de la dispersion de graine, l'efficacité (viabilité, distance de dispersion, etc.), la diversification et la complexité des interactions écologiques des bonobos n'a pas été étudiée. L'histoire écologique des bonobos avec leur milieu est une ébauche. Grâce à la communauté habituée de bonobo à LuiKotale, le projet 'rôle écologique des bonobos' apporte des réponses.

Nous avons vue dans la partie introductive (*Seed dispersal strategies and the threat of defaunation in a Congo forest*) que dans la forêt mixe de LuiKotale la grande majorité des plantes utilise les animaux comme vecteur de dispersion de leurs graines. L'inventaire quasi exhaustif des plantes de l'écosystème a permis une estimation de la part des plantes zoochores de 88 % dans la communauté végétale. Peu d'études ont permis une telle estimation dans un écosystème Afrotropical (Gautier-Hion *et al.* 1985). De plus, cette partie montre bien le problème de pression de chasse humaine qui vise essentiellement les animaux de grandes tailles et les frugivores disperseurs de graine. Cette défaunation sélective pourrait défavoriser la majorité des plantes à fruits dispersées par les bonobos, éléphants, cercopithèques et autres coq congolais. Mais pour cela il est nécessaire de quantifier la dispersion de graine des vecteurs tels que les bonobos : l'objet de la présente thèse.

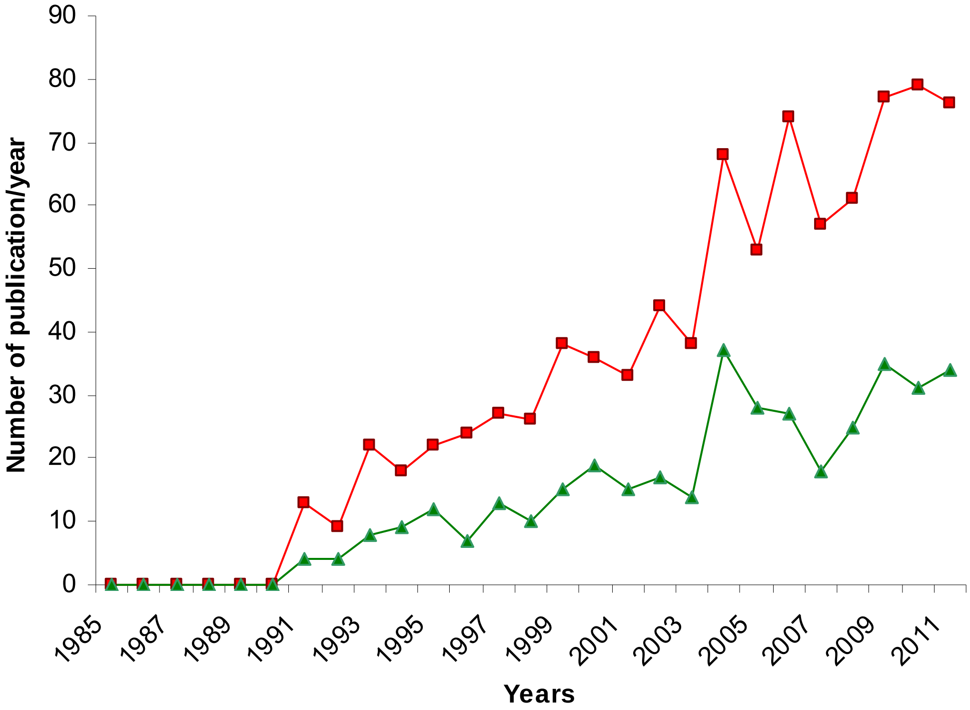


Figure 41 Nombre de publications scientifiques par année contenant le terme « *Pan paniscus* » référencé par ISI Web of Knowledge THOMSON REUTERS, dans le titre (vert) et dans le sujet (rouge).

L'écologie de la dispersion des graines est une science jeune mais vigoureuse (Forget *et al.* 2011). Ces travaux ne sont pas révolutionnaires dans le domaine. Mais ils apportent une vision large, proche de l'exhaustivité, des interactions de *Pan paniscus* avec les autres espèces de l'écosystème : plantes à fruits, compétiteurs, granivores, disperseurs secondaires et alternatifs de graines, etc. Les études des interactions plante-animal concernent souvent un modèle à deux espèces (Jordano 2000; Jordano, Bascompte & Olesen 2003b). Néanmoins, les observations en milieux naturelles, la discrétion, la rareté des espèces ou la difficulté du terrain d'étude permettent rarement d'aller au-delà de la description d'un mutualisme entre les deux espèces (Schupp, Jordano & Gomez 2010). Or les interactions avec d'autres espèces, la quantification de ces interactions, et les paramètres de l'efficacité des bénéfices réciproques sont essentiels à la compréhension des interactions écologiques. Dans la partie I (*Bonobo (Pan paniscus) seed dispersal service in tropical forest in the Democratic Republic of Congo*), nous pouvons estimer avec combien d'espèces de plantes les bonobos agissent comme vecteurs de dispersion des graines : 91 espèces. Grâce à l'inventaire botanique effectué sur le site d'étude (Fruth 2011), nous pouvons estimer à 40 % les nombres d'espèces d'arbres dont les graines sont dispersées par les bonobos. Par ailleurs des données inédites sur la biologie de l'espèce, le comportement alimentaire et de déplacement ont été étudié. Ainsi, les différents paramètres permettent d'estimer la pluie de graines induites par un bonobo au cours de sa vie : 11,6 millions de graines dispersées. La zoochorie récemment décrite chez les bonobos (Hohmann & Fruth 2008; Surbeck & Hohmann 2008; Surbeck *et al.* 2009) peut être ici quantifiée dans le régime alimentaire grâce à 1879 heures d'observations comportementales : 0.9 %. Avec les analyses fécales, nous pouvons noter le biais induit par l'utilisation seule des fèces dans les études d'écologie alimentaire chez les primates et le risque de conclusions inexactes (McGrew *et al.* 2007; Hofreiter *et al.* 2010; Hohmann *et al.* 2010).

Déterminer quels sont les interactions plantes-bonobos est une chose, mais il faut déterminer l'exclusivité de ces interactions : d'autres disperseurs peuvent ils remplacer les bonobos ou les plantes peuvent-elles tout simplement se passer de disperseurs ? Dans cette première partie, nous constatons que la grande majorité des arbres dispersés par les bonobos ne peuvent recruter de nouvelles plantules sans dispersion. Par ailleurs, la redondance fonctionnelle avec les autres singes de la communauté de primates semble faible aux vues des résultats préliminaires d'une étude de 5 mois de terrains (Bourson 2011).

Le second chapitre de la première partie (*Bonobo-Dialium mutualism*) se concentre plus spécifiquement sur le couple d'espèces : Bonobo et arbres du genre *Dialium* afin d'estimer quantitativement et qualitativement les interactions plante-animal. Cette étude montre que pour le grand singe, les fruits de *Dialium* sont une ressource importante de nourritures, au cours de l'année et en termes de nutriments. Pour l'arbre, les graines sont dispersées efficacement (selon les critères d'efficacité de dispersion (Schupp, Jordano & Gomez 2010)) et le passage des graines dans le tube digestif des bonobos briserait la dormance tégumentaire et activerait ainsi la germination. Ce constat permettrait l'activation artificielle des graines de *Dialium* par imitation du processus écologique. Les applications en biologie de la conservation sont intéressantes et prometteuses (*Artificial germination activation of Dialium corbisieri by imitation of ecological process*).

L'étude du comportement des bonobos ne fut pas en reste dans ce projet. Le comportement animal et ses effets sur la pluie de graines, et donc la biologie des plantes, sont avérés (Lambert & Garber 1998; Robertson *et al.* 2006; Russo, Portnoy & Augspurger 2006; Kitamura *et al.* 2008). Le troisième chapitre de la partie III (*How bonobos deal with tannin* *concentrated fruits. Re-ingestion technique for Canarium schweinfurthii*) montre que les bonobos grâce à un comportement élaboré (ingestion et re-ingestion des fruits de *Canarium schweinfurthii*) peuvent être des vecteurs de dispersions malgré la haute teneur en tannins qui écartent certains consommateurs : mais pas les bonobos de LuiKotale. En effet, malgré la présence des arbres sur leur territoire, il est intéressant de noter que ces fruits de *Canarium schweinfurthii* ne sont pas consommés par la communauté de Lomako ou consommés de manière différente (wadge technique) par les bonobos de la communauté de Wamba. Cette recherche en cours pourrait être la première description d'une culture chez les bonobos vivant en liberté (voir(Hohmann & Fruth 2003a), pour une revue sur la culture chez les bonobos).

Le comportement de déplacement alimentaire d'un animal influence la dispersion des graines qu'ils transportent (Russo, Portnoy & Augspurger 2006; Nathan *et al.* 2008). Ici il est surprenant de constater que la qualité et la quantité des fruits consommés par les bonobos ne semble pas influencer la distance de dispersion des graines, toutes dispersés 24heures en moyenne après ingestion, à 1.3 km en moyenne de l'arbre-parent. Ce fait assez étonnant ne va pas en faveur de la limitation de recrutement des différences espèces dans la forêt comme moteur de maintien de la biodiversité (McEuen & Curran 2004; Muller-Landau *et al.* 2008). En effet, nos analyses préliminaires en écologie spatiale (données non publiées, en collaboration avec le Dr B. Borgy (INRA)) semblent montrer qu'il n'existe pas d'agrégation spatiale particulière des arbres à fruits. Les arbres dispersés par les bonobos auraient une structure homogène dans la forêt. Mais le fossé entre la déposition d'une graine et sa survie à l'âge adulte est grand et restera difficile à combler (Balcomb & Chapman 2003; Vander Wall *et al.* 2005; Schupp, Jordano & Gomez 2010). Les perspectives de recherche sont donc nombreuses : survie post dispersion des plantules ; influence du microsite ; écologie spatiale avec analyse d'associations interspécifiques (les espèces dispersées par le même vecteur sont-elles associées spatialement ?) ; le rôle des rongeurs dans la dispersion secondaire ; etc. D'autres perspectives de recherche sont à envisager : l'étude de forêt jumelle avec et sans bonobos (forêt de Lompole avec population de bonobo éteinte) ; quantification de la défaunation avec recensement des prises ; défaunation diffreretielle ; carte mentale de déplacement des bonobos ; icthyochory dans le bassin du Congo et effet de la pêche ; zoochory des singes ripisylves (singes de Brazza : *Cercopithecus neglectus* ; singes des marais : *Allenopithecus nigroviridis*) ; effet du passage des graines dans le tube digestif des éléphants de forêts ; etc.

Les interactions biotiques impliquant deux espèces sont rares dans les forêts tropicales (Gautier-Hion *et al.* 1985). Ce projet explora naturellement les interactions avec d'autres disperseurs (éléphants de forêt, cercopithèques, etc.), les disperseurs secondaires (bousiers) et les prédateurs (Cricétomes, potamochères, etc.). Pour les graines, le premier chapitre de la troisième partie montre que les potamochères sont d'importants prédateurs de graines à LuiKotale et doivent être des espèces clefs pour la reproduction d'un tiers des arbres de la communauté de LuiKotale. (*Bush pig (Potamochoerus porcus) seed predation of bush mango (Irvingia gabonensis) and other plant species in Democratic Republic of Congo*). Les rongeurs, bien que probable disperseurs secondaires à LuiKotale comme dans d'autres forêts (Forget *et al.* 2005; Forget *et al.* 2006; Nyiramana *et al.* 2011) sont des prédateurs de graines pour beaucoup de plantes. Or nous avons montré que la zoochory induite par les bonobos attire les bousiers qui dans leur course aux matières fécales (NB : qui attirent aussi les rongeurs) enterreront les graines et leur permettent d'échapper aux rongeurs de manière efficace (deux fois plus (*Dung beetles are critical in preventing post-dispersal seed removal by rodents in Congo rain forest*). Finalement, la présence de nombreux fruits présentant le syndrome mégafaunale (Feer 1995a; Guimarães, Galetti & Jordano 2008) à LuiKotale, attira l'étude des éléphants et les effets de leur disparition sur les populations de plantes ancestralement dispersées. Ce dernier chapitre (*Doom of the elephant-dependent trees in a Congo tropical forest*) montre que la majorité des espèces végétales présentant le syndrome mégafaunale, sont en fait éléphants dépendants : ces arbres ne recrutent plus assez de jeunes pour permettre la viabilité de leur population sans les irremplaçables éléphants de forêt. Les bonobos ne remplacent pas les éléphants. Serait-ce une crise écologique similaire qui menace les plantes dispersées par les derniers bonobos si ces derniers venaient à disparaître ?

De nouveaux et solides arguments viennent s'ajouter pour la préservation de *Pan paniscus*, actuellement menacé d'extinction (IUCN 2012). Mais les mesures de conservation des bonobos vont au-delà de la conservation de ces grands singes : il en va de la conservation de l'ensemble de ces forêts du bassin du Congo.

List of abbreviations

ANOVA:	ANAlysis of Variance
CI:	Confidence interval
CNRS:	Centre National de la Recherche Scientifique
DBH:	Diameter at Breast Height
DPH :	Differential Predation Hypothesis
df:	degree of freedom
FRA :	Forest Ressources Assessment
FAO :	Food and Agriculture Organization
GPS :	Global Positioning System
ha :	Hectare (100 m by 100 m)
ICCN:	Institut Congolais pour la Conservation de la Nature
IUCN:	International Union for Conservation of Nature
LDD:	Long Dispersal Distance
LK:	LuiKotale
MPI:	Max Planck Institute
MTT:	Mean Transit Time
N:	Sample size (number)
P:	P-value
RDC:	Democratic Republic of Congo
SE:	Standard error
TT:	Transit Time
UB:	University of Burgundy/ Université de Bourgogne

Glossary

Some of the definitions are based on (Wang & Smith 2002; Vander Wall & Longland 2004; Nathan *et al.* 2008)

Abundance: the number of individuals in a species that are found in a given area; abundance is often measured by population size or population density.

Anemochory: seed dispersal by wind.

Arboreal: tree-living; referring to animals that are adapted to life in the trees.

Ballistic dispersal: abiotic dispersal by mechanical ejection of a seed from a fruit (does not work as weapon).

Biodiversity: a term used to describe the diversity of important ecological entities that span multiple spatial scales, from genes to species to communities.

Bonobology: studies of bonobos.

Coprophagy: feeding on excrement. Not tasty for most of the human.

Defaunation: extirpation of the medium/large animals from the system, often by overhunting.

Density-dependent: of or referring to a factor that causes birth rates, death rates, or dispersal rates to change as the density of the population changes.

Diaspore: any propagative structure of a plant, especially one that is easily dispersed, such as a seed.

Dispersal kernel: a probability density function characterizing the spatial distribution of dispersal units originating from a common source. The 'dispersal distance kernel' describes the probability of seed deposition at a certain distance, whereas the ‘dispersal density kernel’ describes the same probability per unit area. We use the former type throughout this review.

Dispersal limitation: recruitment limitation resulting from the failure of seeds to arrive at favorable sites.

Dispersal vector: an agent transporting seeds or other dispersal units. Dispersal vectors can be biotic (e.g. birds) or abiotic (e.g. wind). (A spacecraft is biotic).

Displays: visual messages, or body language, used by primates and other animals primarily to communicate anger, fear, and other basic emotions.

Diurnal: being awake and active during the daylight hours but sleeping during the nighttime. Most of the apes are diurnal exept certain night workers, insomniacs, perverts or students.

Dominance hierarchy: a group of individuals arranged in rank order. In some non-human primate species, each community has a distinct male and female dominance hierarchy. Every individual is ranked relative to all other community members of the same gender. In the case of rhesus macaque females, rank is determined by the relative rank of their mothers. Depending on the species, male ranking may be similarly determined by the mother's rank or it may be earned in competition with other males. Individuals who are higher in the dominance hierarchy usually have greater access to food, sex, and other desirable things.

Ecological interaction: the relation between species that live together in a community; specifically, the effect an individual of one species may exert on an individual of another species.

Ecological niches: specific micro-habitats in nature to which populations or organisms adapt. They are usually seen in terms of being food getting opportunities in the environment.

Ecosystem services: the beneficial outcomes, for the natural environment, or for people, that results from ecosystem functions. Some examples of ecosystem services are seed dispersal, support of the food chain, harvesting of animals or plants, clean water, or scenic views.

Egalitarian: (Primatology) lack of hierarchy or pecking order. Resources likely to be obtained by whoever gets there first, rather than any social order.

Endozoochory: seed dispersal by vertebrates that ingest fruit and either regurgitate or defecate seeds unharmed.

Estrus: the period of time when female animals are sexually excited and receptive to mating. Estrus occurs around the time of ovulation in many species.

Ethogram: The behavioral repertoire of a species.

Fat-tailed dispersal kernel: a highly leptokurtic dispersal kernel, indicating relatively high levels of LDD, formally defined as a kernel with a tail that drops off more slowly than that of any negative exponential kernel.

Fission-Fusion: Chimp-like social structure where small groups go off together for periods of time but then join up again later.

Foraging group: a group of animals that seek food together. In the case of non-human primates, this group may consist of all community members or only some of them.

Free-ranging population: a non-captive group of primates or other animals that is living in its natural habitat, largely free from constraints imposed by humans.

Frugivore: any animal that eats fruit.

Frugivory: consumption of fruits by animals. In this context, a broad definition is used whereby frugivory need not involve ingestion and encompasses all seeds removed from the plant by animals, including seeds in cheek pouches of primates or attached to coats by burs.

Fruiting/flowering phenology: the timing of the production of flowers and fruits.

Gene flow: the transfer of alleles from one population to another via the movement of individuals or gametes.

Granivore: any animal that eats seeds.

Great apes: the gorillas, common chimpanzees, and bonobos of Africa and the orangutans of Southeast Asia. These species are referred to as great apes because they are the largest apes.

Grooming: carefully picking through hair looking for insects, twigs, and other debris.

Guild: a subset of the species in a community that use the same resources, whether or not they are taxonomically related.

Habitat fragmentation: the breaking up of once continuous habitat into a complex matrix of spatially isolated habitat patches amid a human-dominated landscape.

Habitat loss: conversion of an ecosystem to another use by human activities

Habituation: The process where animals cease to change their behaviour because of the presence of human observers.

Haplochory: seed dispersal by a single dispersal vector.

Hydrochory: seed dispersal by water.

Janzen–Connell hypothesis: postulates that a main benefit of seed dispersal is that it allows seeds and seedlings to escape the high density-dependent mortality owing to pathogens, seed predators, and/or herbivory that can occur directly under the parent plant.

Keystone species: a strongly interacting species that has a large effect on energy flow and on community structure and composition disproportionate to its abundance or biomass.

Kurtosis: descriptor of the shape of a probability distribution, measure of the "peakedness" of the probability distribution of a real-valued random variable.

Mutualism: A form of symbiosis in which both species benefit.

Non-equilibrium seed dispersal system: a seed dispersal system in which the relationships between the animal species and plant species vary either in time and/or space. The relative importance of the various subprocesses and constituent factors can also vary seasonally, yearly or spatially.

Nonstandard dispersal vector: a dispersal vector different from the one that can be inferred from the phenotypic characters of the plant.

Olfactory: the sense of smell.

Party: subgroup of bonobo after fission of the main group. No link with dancefloor or BBQ.

Philopatry: (Primatology) Where an individual stays in the natal group.

Polychory: seed dispersal by multiple dispersal vectors.

Primatology: the study of primates and their behavioral patterns.

Recruitment limitation: the failure of a species to establish in all sites that are favorable to its growth and survival.

Quadrat: a sampling area (or volume) of any size or shape.

Scatter hoarding: a primary or secondary dispersal process by which an animal deposits food resources (often seeds) in caches for later use. Unrecovered cached seeds are candidates for germination.

Secondary dispersal: process by which seeds that are already on the ground are moved to other locations; this dispersal is often mediated by ground-dwelling mammals (e.g. rodents, tapirs, and forest antelopes) and insects (e.g. ants and dung beetles).

Seed deposition/placement: process by which seeds carried by dispersal agents are dropped in new locations.

Seed dispersal cycle: a succession of processes whereby fruits produced by a plant are removed by animals that disperse the seeds, some of which might germinate to seedlings and recruit to adult plants, influencing the fruit availability of the next .

Seed dispersal: movement of seeds away from parent plants, usually by animal agents or by wind, water, or intrinsic explosive mechanisms. Directed dispersal occurs when seeds are deposited disproportionately in favorable locations.

Seed predation: action on seeds that renders those seeds nonviable for germination. Often this predation occurs through ingestion by animals or by infestation of pathogens.

Seed rain: the pattern of seedfall to the ground. (more poetic than dung rain, isn't it).

Seed shadow: the area on the ground where the seeds of a single tree either fall to the ground or are placed by dispersers.

Seed: in a strict sense, the fertilized ovule of spermatophytes consisting of embryo, endosperm and testa. We follow here the typical use of this term in the plant dispersal literature as a synonym for a reproductive propagule.

Sexual dimorphism: referring to anatomical differences between males and females of the same species. Primate males are usually significantly larger and more muscular than females. Humans are also sexually dimorphic (usually).

Skewness: describe asymmetry from the normal distribution in a set of statistical data. Skewness can come in the form of "negative skewness" or "positive skewness", depending on whether data points are skewed to the left (negative skew) or to the right (positive skew) of the data average.

Subadult: the stage of maturation in which animals are beyond infancy and early childhood but are not yet fully grown.

Specialized dispersal: a dispersal system in which the plant exhibits phenotypic characters that are interpreted as adaptations for dispersal by a particular vector. This vector is also called the 'standard dispersal vector.'

Terrestrial: referring to animals that spend most of their time on the ground rather than in the air, water, or trees.

Type I survivorship curve: a survivorship curve in which newborns, juveniles, and young adults all have high survival rates and death rates do not begin to increase greatly until old age (e.g : modern human).

Type II survivorship curve: a survivorship curve in which individuals experience a constant chance of surviving from one age to the next throughout their lives (e.g : bacteria).

Type III survivorship curve: a survivorship curve in which individuals die at very high rates when they are young, but those that reach adulthood survive well later in life (e.g : tree).

Waypoint: a coordinate that is input into a navigation device, such as a GPS receiver, representing a position that a vessel, aircarft, vehicle or person has to navigate to, with the aid of GPS (and/or any other position fixing device).

Appendix

Density-dependent effects affecting elephant seed-dispersed tree recruitment (*Irvingia gabonensis*) in Congo Forest

Authors

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Published in Pachyderm

Several species are known to be important for local wildlife, rural communities (White & Abernethy 1997) and even the “western world”. However little is know about the ecology of these species and biodiversity crisis could change the population survival. Among these, the bush mango (*Irvingia gabonensis*), widespread in West and Central Africa, is of major importance for rural communities (Atangana *et al.* 2001; Leakey *et al.* 2005). Recently, the plant is used as a slimming supplement in western world. Elephants are widely recognised as the most important *Irvingia* seed dispersers in Africa (Theuerkauf *et al.* 2000; Nchanji & Plumptre 2003; Morgan & Lee 2007). In this study we focus on this species as the example to illustrate seed fate without dispersion and thus density dependence effect affecting tree recruitment.

Here we conduct investigation on this megafaunal tree population’s ability to survive without elephants in the evergreen lowland rainforest of the Max-Planck research site, LuiKotale, on the South-Western fringe of the Salonga National Park, DRCongo. In and around Salonga National Park, elephants (*Loxondota cyclotis*) have been severely poached for decades (Van Krunkelsven, Bila-Isia & Draulans 2000; Blake *et al.* 2007), and poaching has increased with increasing availability of automatic weapons (AK47) and ammunition after war. The current nationwide elephant population is said to have declined by as much as two-thirds to that of the 1990’s and the remainder are said to survive in fragmented subpopulations (Alers *et al.* 1992). Across 10 years of continuous presence at the research site at LuiKotale, the pressure on the species became evident when leftovers from massacres were documented.

Overall, we aim to assess the ability of the *I. gabonensis* tree community at LuiKotale to reproduce without elephant dispersal. If megafaunal trees depend on elephants for seed dispersal, one would expect no alternative seed-dispersers and thus a high mortality of seedlings and poles due to the density dependent effect (Paine *et al.* 2012).

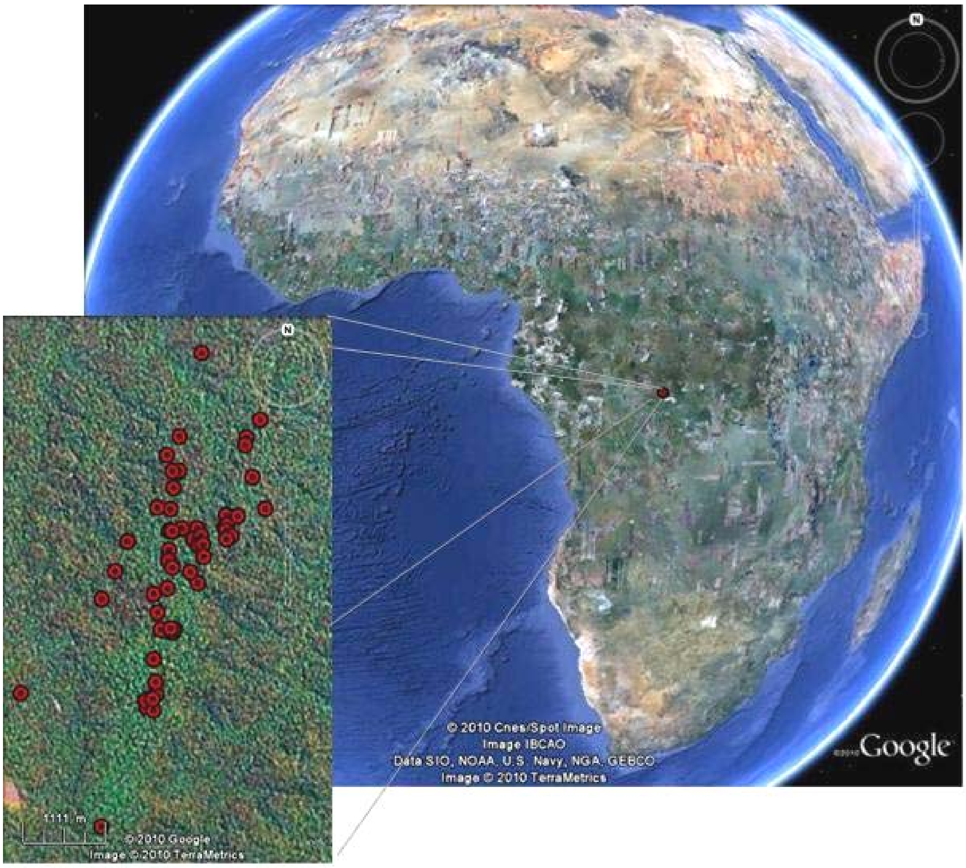

Figure 42 Sampling area. Red spots representing adult trees

Methods

To investigate the density dependent effect on seed survival of this elephant-dependent tree, we focused on all adult trees of *Irvingia gabonensis* inventoried since 2007 (LK-research-site data base: all feeding trees within the bonobo-communities' range, observed to be used by *Pan paniscus* are geo-referenced (Figure 42) that produced ripe fruits during the survey from January 2010 to June 2011. We i) counted (1) seeds, (2) seedlings, (3) saplings, and (4) poles in the fruit fall zone of each individual,. and ii) judged the state of each of the 4 stages of growth, assessing pathogens and folivory by visual inspection (absence/presence of traces).

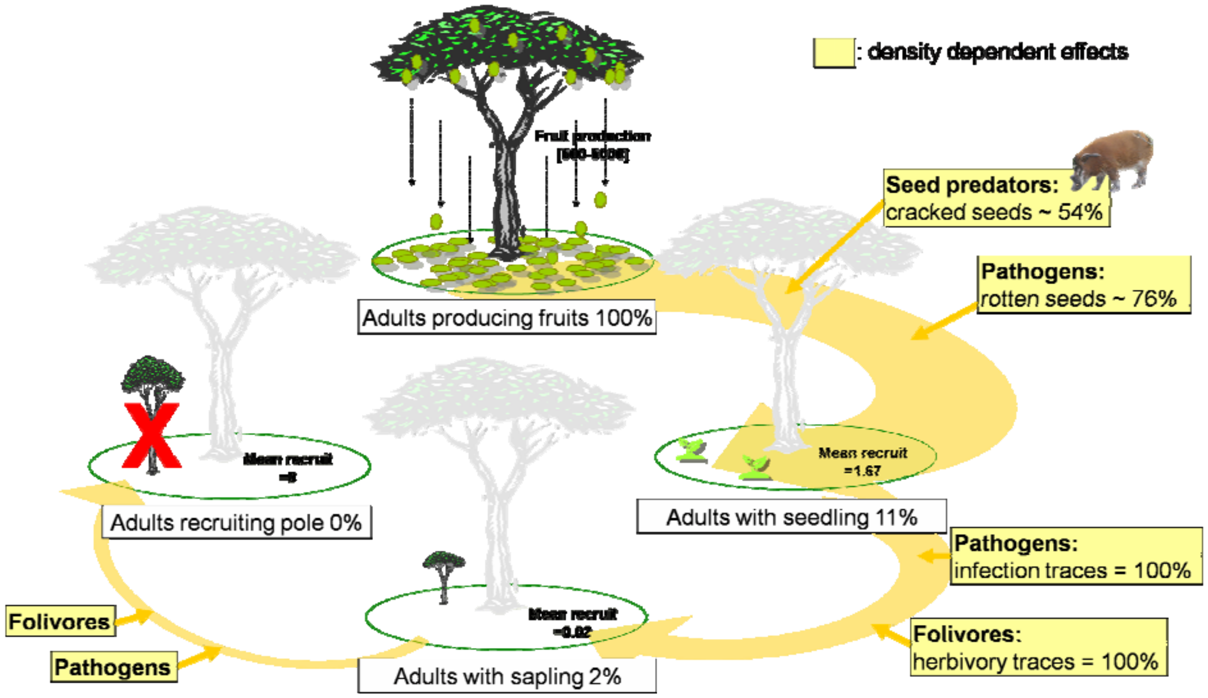

Figure 43 The density dependent effect of *Irvingia gabonensis*. No recruitment under the parental trees (n=54)

Results

We investigated 54 adult trees of *Irvingia gabonensis* (83.1cm± SE. 0.7 DBH) producing ripe fruit. Figure 43 shows the presence and state of (1) seeds, (2) seedlings (Figure 44), (3) saplings, and (4) poles.

1) Seeds: Seeds were present within all fruit fall zones. Seeds revealed a loss rate of 54% ± SE 3 due to seed predation and among the unopened seeds, 76% ± 4 were rotten or showed signs of pathogen attacks. Red river hogs (*Potamochoerus porcus*) in herds of 2-6 animals were found responsible for predating on large quantities of seeds cracking the endocarps.

2) Seedlings: Only 6 of the 54 trees (11%) showed seedling recruitment. Of these, all 90 seedlings were infested by pathogens or showed traces of folivory whereas some other surrounding seedling species and the *Irvingia* of the nursery did not (unpub. data). Although these adult trees reproduced, no established offspring (*i.e.* producing fruit) was found beneath the adults' crowns. A total of 48% (n=26) of the fruit fall zones clearly showed tracks of animals' road leading to the feeding place.

3) Saplings: A single sapling recruit (<2m high) was found below an adult crown.

4) Poles: No pole was found below an adult crown.

Figure 44 Seedling and adult tree of *Irvingia gabonensis*

Conclusion

Our results showed a high mortality for *Irvingia* seeds and recruits on all levels with a loss of 1) seeds, 54% due to predation and 76% due to pathogens; and 2) seedlings , 100% due to predation and pathogens. These results can be explained by the density dependent effect also named the Janzel-Connel effect (Janzen 1970b; Connell 1971; Burkey 1994) where the mortality of seeds, eggs, or other immobile organisms is correlated with their density which attracts predators and pathogens. In the absence of an endozoochoric partner such as the elephant, this “putting all your eggs in one basket” adaptation is likely to turn out as a maladaptation, unless a tree-species has alternative dispersal partners or mechanisms.

In the southern area of the Congo River, bonobos, the second biggest frugivores, are unable to replace elephants as seed dispersers, as the seeds are too large to be swallowed. They may contribute in some cases to dispersal outside the fruit fall zone by short distance ectozoochoric transport, similar to what can be dispersed by rodents (Forget & Wall 2001). For *I. gabonensis*, bonobos can be considered as a poor disperser, dispersing over much shorter distances than elephants and omitting passage through their digestive tract.

Daily differences in bonobo activities: More sex in the morning?

Authors

David Beaune, Pamela Heidi Douglas
& Gottfried Hohmann

Abstract

This technical note for field primatologists demonstrates that behavioral activities are not consistent throughout the day. In LuiKotale (DR Congo), a habituated group of bonobo (*Pan paniscus*) was continuously followed in 2010 and 2011 (38 and 124 entire days of analyzable data) for comparison of the morning and afternoon activities (midday=11 :30). While group size, number of females, and feeding activity are similar, bonobos travel more in the afternoon. Furthermore sexual activities show differences: bonobos copulate more in the morning and homosexual interaction between females (GG rubbing) seems to be consistent between morning and afternoon. This fact highlights the risk of bias in studies based on number of hours observation. Preliminary observation during entire days is a prerequisite for generalization of a behavior with bonobos and probably, other primates and animals.

Introduction

In behavioural studies, and particularly with primates, following free-ranging groups is always an adventure. Habituation is an important stage, allowing scientists to follow animal groups and collect relatively undisturbed behaviours. Often in remote areas with sampling effort limitations, continuous data collection embracing twelve hours of daily activities is challenging and unbalanced data can result from these logistical constraints. In primatology literature, observation hours are sometimes indicated without precision of time consistency, accepting the hypothesis that behaviours are similar and consistent throughout the day. However, if daily activities are not regular throughout the day, and if observations are mainly taken during a certain window of time, results will be biased: minored or majored. This note tests this last hypothesis: no difference between morning and afternoon behavioural activities; in a habituated group of wild bonobos in LuiKotale MPI field station (Hohmann & Fruth 2008; Surbeck & Hohmann 2008; Fowler & Hohmann 2010; Oelze *et al.* 2011). Morning and afternoon activity budgets are compared through an examination of the following: 1) feeding session; 2) travel (average speed); 3) group size; and 4) copulation rate. Since 2007, several observers followed standardised methods of behavioural observation during bonobo daily activities (between 5:30 AM and 5:30 PM).

Materials and methods

The study was carried out at the LuiKotale research site (S2°47'- E20°21'), located within the equatorial rainforest, South West of Salonga National Park (DRCongo) (Mohneke & Fruth 2008). Field work with bonobos has been conducted since 2001 (Hohmann & Fruth 2003c) with one habituated community of 35 bonobos (the Bompusa community) on a realm range of 60km² crossed by 76km of trails for access. Parties of bonobos were followed and observed on a daily basis. However, during fieldwork, logistical limitations reduced the data length on certain days and observations were stopped when the bonobos were lost. Only continuous observations from nest to nest were compared. In this equatorial area, sunrise varies minimally over the year, and bonobo activity can be split at midday, *i.e.*, 11:30 AM.

For feeding activity, continuous feeding group scan observations (Altmann 1974) were used. For travel activity, GPS Garmin® 60CSX with track log (1 georeference/5mins) recorded the bonobo position and average speed. Parametric data were tested by Student's paired t-test. The power analysis of the tests is specified when a difference is detected. Analyses were performed using R 2.11 (R Development Core Team 2005).

Results

Feeding session

Fifty-one complete days were analysed and do not show a significant difference in bonobo feeding activity, which represents more than half of the daily activities (*i.e.* 51%, see Figure 45.1). Paired t-test (t = -1.4899, df = 50, p-value = 0.14).

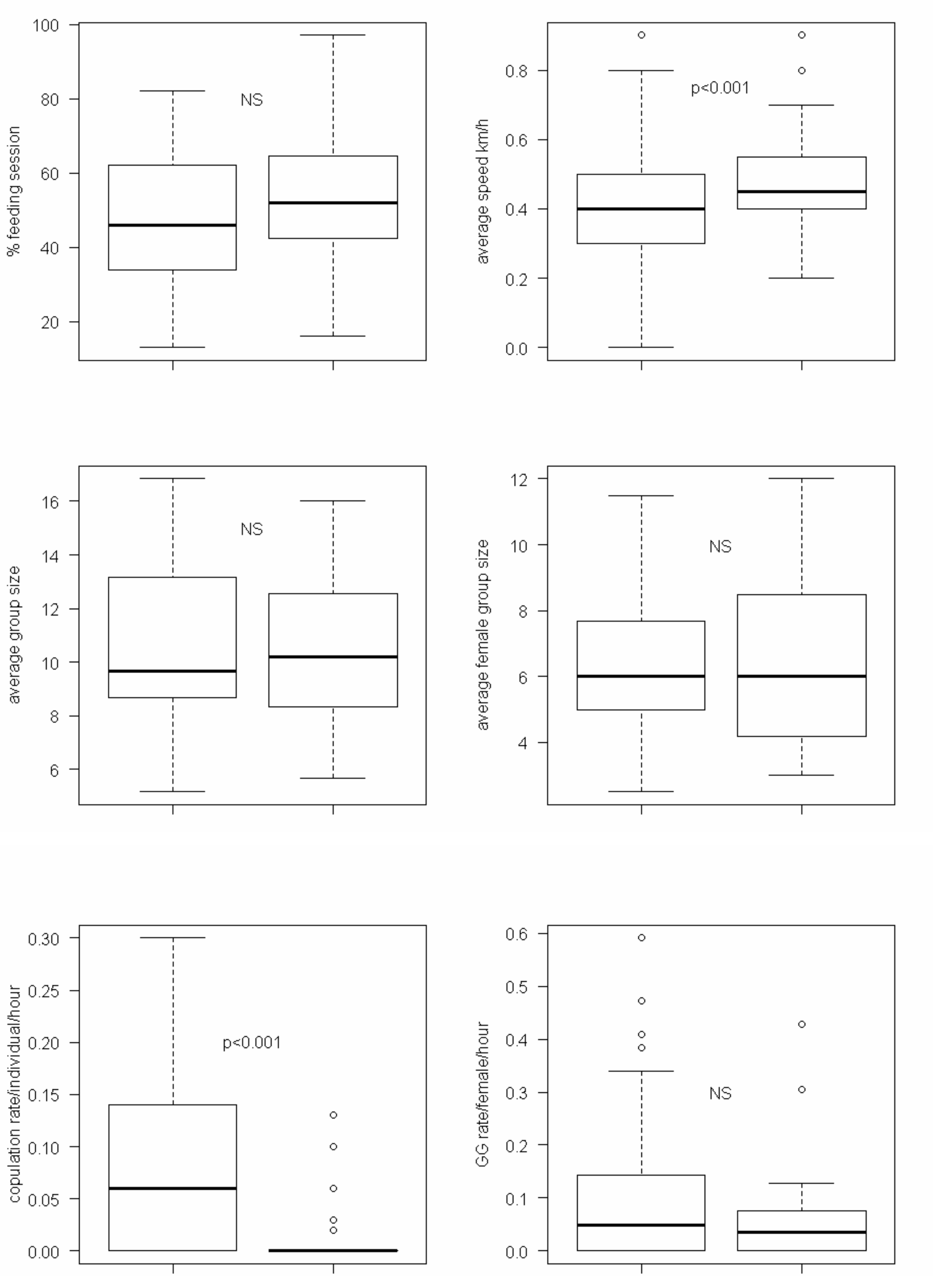

Figure 45 AM (left) and PM (right) comparison, 1. feeding activity, 2. average speed, 3. group size, 4.female composition, 5. copulation rate, 6.GG rubbing rate,. NS= non significant difference.

Travel (average speed)

A hundred and twenty four complete days were analysed and average speed is significantly different (Figure 45.2) (t = -3.7832, df = 123, p-value = 0.001, test power=90%).

Bonobo travel

15% (+0.07km/h) more in afternoon than in morning; from 0.40±0.17km/h in the morning to 0.46±0.16km/h in the afternoon.

Group size

Forty complete days were analysed and do not show any difference in group size with an average of 9 individuals per group. (Fig1.3) Paired t-test: (t = 0.0058, df = 39, p-value = 0.99). The proportion of females does not change neither during between morning and afternoon (Figure 45.4) (t = -0.1441, df = 38, p-value = 0.89)

Copulation rate

Forty complete days were analysed and show a significant difference in copulation rate between morning and afternoon (Figure 45.5).

Paired t-test: t = 4.3071, df = 39, p-value < 0.001; test power=90%). The mean difference is 0.05 copulation/ind/hrs from AM to PM. The copulation peak occurs during the first hours of daily activities.

GG rate

Thirty eight complete days were analysed and do not show significant difference in GG rate between morning and afternoon (Figure 45.6).

(t = 1.6792, df = 37, p-value = 0.1015)

Conclusion

Certain bonobo daily activities vary, such as travel or social activities. These data lead to two conclusions: First, we logically cannot announce a behavioural rate, percentage or average based solely on behavioural hours collection. Authors should assess the consistency of the behaviour over the day before making comparisons such as those between bonobos and chimpanzees because if the behaviour varies over the day, just recording hours of observation does not give an accurate representation of the rate of the behaviour. An example might concern the numerous debates about copulation rate comparison between bonobos and chimpanzees (Takahata, Ihobe & Idani 1999; Hashimoto & Furuichi 2006) or among apes population). We can remark that some of these rates are based on observation hours without precision of daily consistency.

For the LK bonobo, the Bompousa community show a clear unbalanced copulation rate and a calculation of the copulation rate based on the morning observation would be overestimated and lead to numerous false hypothesis regarding the literature's rates (0.11, 0.13, 0.18, 0.19 copulation/hours, (Stevens, Vervaecke & Elsacker 2008).

Secondly, behaviourists could improve their data collection effort by focusing their observations in the best behavioural window regarding their need. If the study concerns comparison (inter individual, inter communities) for example, researchers can focus on the best time period where maximal activities needed occurs. This time window has to be validated by preliminary daily collection. Similarly, if the behaviour of interest does not show daily change, researchers can acquire data hours without daily time constraint.

Few organizations for bonobo conservation

Bonobo Alive

http://www.bonobo-alive.org
Bonobo Alive is an organisation initiated by bonobo researchers dedicated to the protection of wild bonobos and their habitat in the south-western part of Salonga National Park, DR Congo.

The Bonobo Conservation Initiative

http://www.bonobo.org/
(BCI) is dedicated to ensuring the survival of the bonobo (*Pan paniscus*) and its tropical forest habitat in the Congo Basin. By working with indigenous Congolese people through cooperative conservation and community development programs, as well as on the national and international levels, BCI is establishing new protected areas and leading efforts to safeguard bonobos wherever they are found.

Lola ya Bonobo

http://www.friendsofbonobos.org/

http://www.lolayabonobo.org/

Founded by Claudine Andre in 1994, Lola ya Bonobo is the sanctuary of the NGO, Les Amis des Bonobos du Congo (ABC). Since 2002, the sanctuary has been located at Les Petites Chutes de la Lukaya, just outside of Kinshasa in the Democratic Republic of Congo.

And also:

http://mboumontour.org

http://www.worldwildlife.org/species/finder/bonobo/bonobo.html

http://www.awf.org/section/wildlife/bonobos

http://www.awely.org/fr/programmes/casquettes-vertes/republique-democratique-du-congo

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