Gembloux Agro-Bio Tech
Université de Liège

COMMUNAUTÉ FRANÇAISE DE BELGIQUE

UNIVERSITÉ DE LIÈGE – GEMBLOUX AGRO-BIO TECH

EFFECTIVENESS OF WESTERN LOWLAND GORILLA (*GORILLA GORILLA GORILLA*) SEED DISPERSAL AND PLANT–GORILLA MUTUALISM IN SOUTHEAST CAMEROON

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Dissertation originale présentée en vue de l'obtention du grade de docteur en sciences agronomiques et ingénierie biologique

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Petre, Charles-Albert (2016). *Efficacité de la dispersion des graines par le gorille des plaines de l'ouest (Gorilla gorilla gorilla) et relations plante–gorille mutualistes au sud-est Cameroun*. Thèse de doctorat. Université de Liège–Gembloux Agro-Bio-Tech, 155p.

Résumé

Les frugivores de grande taille jouent un rôle fondamental dans la dynamique forestière et occupent une place déterminante dans les réseaux de dispersion de graines. Cependant, la grande faune est davantage vulnérable aux extinctions locales résultant des perturbations anthropiques grandissantes. Les changements observés dans la structure et la composition du jeune recrû après la disparition des grands frugivores suggèrent une modification sur le long terme de l'écosystème forestier qui pourrait se traduire par une perte de biodiversité et une réduction des services écosystémiques.

Le gorille des plaines de l'ouest (*Gorilla gorilla gorilla* Savage, 1847) est le plus grand des frugivores arboricoles, et il subit malheureusement des réductions populationnelles localement dramatiques. Afin de mieux comprendre les conséquences écologiques de leur disparition, la présente thèse s'attelle à identifier et décrire les différentes composantes de l'efficacité de la dispersion des graines chez une population de gorilles des plaines de l'ouest (site "La Belgique", dans le sud-est du Cameroun).

Cinquante-huit espèces ont été retrouvées dans 1030 fèces collectées pendant 36 mois. Malgré cette diversité, les espèces du genre *Uapaca* (N=5), dont les graines étaient présentes dans les fèces durant 72.2% des mois échantillonnés, contribuaient à elles seules à 36.5% de la quantité totale de graines dispersées durant la période d'étude. Avec un temps moyen de rétention des graines dans le tractus digestif de 50.6 ± 28.1 h et une distance moyenne parcourue quotidiennement de 2 km, les distances de dispersion sont potentiellement très élevées. Cette contribution à la dynamique de métapopulation serait d'autant plus effective que le pouvoir germinatif des graines ne se réduit pas avec le temps de rétention (N=4 spp.), et peut même en être amélioré (N=1 sp.). De façon générale, les graines reçoivent un bon traitement dans le tractus digestif puisque 50% et 41.7% des espèces testées (N=12) possèdaient un pouvoir germinatif après transit inchangé (dont *Uapaca* spp.) et accru, respectivement. Au niveau des sites de déposition des graines, les bousiers (Scarabaeidae coprophages) peuvent toutefois l'altérer en enterrant trop profondément les graines, comme démontré avec une espèce du genre *Uapaca* (73% des graines enfouies se retrouvaient à >10 cm de profondeur où la probabilité d'émergence était nulle). Cet effet négatif des bousiers est cependant moindre pour les graines dispersées dans les sites de nidification, où l'activité des bousiers moins importante résulte en une plus faible proportion de graines enfouies et à de plus faibles profondeurs (8.7 ± 3.9 cm). Les sites de nidification constituent des sites de déposition importants puisque la moitié des fèces y sont produites, et sont caractérisés par une végétation arborée à canopée basse et éparse (ouverture moyenne de 19.1 ± 13.1%) et dont le tempérament héliophile et la classe de diamètre 10–19.9 cm sont surreprésentés, témoignant de perturbations récentes telles que la chute d’arbres émergents. Les conditions lumineuses favorables rencontrées dans ces microhabitats favorisent le recrutement des espèces végétales dispersées, comme démontré avec les espèces du genre *Uapaca*. Les probabilités de recrutement de ces dernières sont davantage accrues lorsque les sites de nidification sont établis sur sol hygromorphe, habitat prépondéramment utilisé pour la nidification en fin de grande saison sèche (50% des sites de nidification rencontrés à cette période étaient construits dans ce type d’habitat). Puisque cette période correspond au pic de dispersion des graines du genre *Uapaca* (moyenne de 31.7 ± 25.5 graines par 100 g de matière fécale ; 38.6% des graines ont été dispersées à cette période), la population de gorilles du site La Belgique réalisent une ‘dispersion dirigée’, faisant de ce disperseur un contributeur particulièrement efficace de la dynamique de population de ce genre. En contrepartie, les fruits du genre *Uapaca* constituent une ressource alimentaire, dites de soudure, contribuant au fitness des gorilles d’une façon non égalée par les fruits des autres espèces, mettant en évidence un cas de mutualisme plante–animale.

Cette thèse confirme donc le rôle capital des larges frugivores dans le façonnement des forêts tropicales et le maintien de leur intégrité. Des actions appropriées de gestion des forêts tropicales doivent être urgemment entreprises pour éviter que ces mammifères clés ne disparaissent.

Mots clés : comportement nidificateur, dispersion dirigée, dispersion secondaire, dynamique forestière, endozoochorie, frugivores de grandes tailles, recrutement de jeunes plants, site de nidification, *Uapaca*.

Petre, Charles-Albert (2016). *Efficacité de la dispersion des graines par le gorille des plaines de l'ouest (Gorilla gorilla gorilla) et relations plante–gorille mutualistes au sud-est Cameroun*. Thèse de doctorat. Université de Liège–Gembloux Agro-Bio-Tech, 155p.

Summary

Large frugivores contribute a notable role in forest dynamics and hence occupy a central position in seed dispersal networks. However, large-bodied vertebrates are disproportionately prone to local extinction caused by increasing human disturbances than are smaller-bodied species. Observed changes in the structure and composition of juvenile plant cohorts following the extirpation of large-bodied seed dispersers constitute evidence for the long-term alteration of the whole tree stand, resulting in a loss of biodiversity and a reduction of ecosystem services.

The western lowland gorilla (*Gorilla gorilla gorilla* Savage, 1847) is the largest arboreal frugivore, facing rapid population depletion in recent years and becoming locally extinct in many parts of its historical range. To understand the likely consequence of their disappearance for the future of Afrotropical forests, this thesis aims at determining the seed dispersal effectiveness of a western lowland gorilla population ("La Belgique" research site, southeast Cameroon).

Seeds of 58 species were identified in 1030 faecal samples collected over 36 months. Despite this diversity of species dispersed, seeds of the genus *Uapaca* (N=5), dispersed in 72.2% of months sampled, represented 36.5% of the total seed load. With a retention time of seeds in the gorilla digestive tract averaging 50.6 ± 28.1 h, and an average daily travel distance of 2 km, the western lowland gorilla may transport seeds over considerably long distances. This contribution to (meta)population dynamics would be effective since seed viability is not reduced by the time seeds are exposed to digestive enzymes (N=4 spp.) and may even be improved (N=1 sp.). Overall, seeds received a good treatment in the mouth and gut as 50% and 41.7% of species tested (N=12 spp.) had a germination success unchanged (including *Uapaca* spp.) or improved, respectively, after gut passage. At the seed deposition site, however, seed viability may be further altered by dung beetles (coprophageous Scarabaeidae) through burial at unsuitable depths, as demonstrated by one species of *Uapaca* (73% of buried seeds were relocated >10 cm deep where the emergence probability dropped to zero). This negative impact is nonetheless lower at sleeping sites where fewer seeds are buried and at shallower depths (mean depth: 8.7 ± 3.9 cm). Sleeping sites are important seed deposition sites as half of the daily faeces production occurs there, and they are characterized by an extant tree stand with a low and sparse canopy (mean openness: 19.1 ± 13.1%) and a relative overrepresentation of light-demanding individuals as well as individuals of small diameter (10–19.9 cm), suggesting recent disturbances such as the fall of emergent trees. The higher amount of light reaching the forest floor in these microhabitats encourages the recruitment of dispersed species, as demonstrated by species of the genus *Uapaca*. For these, recruitment probability is further improved when sleeping sites are established on hygromorphic soils; a habitat type predominantly used at the end of the dry season (50% of sleeping sites discovered during this period were found in this type of habitat). As this period also corresponds to the peak in *Uapaca* seed dispersal quantity (mean of 31.7 ± 25.5 seeds dispersed per 100 g of faecal material; 38.6% of the total *Uapaca* seed load of the whole study period), the gorilla population at La Belgique performs 'directed dispersal' and hence contributes highly effectively to the dynamics of this genus. In return, the fruits of the genus *Uapaca* provide a food resource, known as fallback, that contributes to the fitness of the gorilla population in ways other fruit resources do not, therefore shedding light onto a particular case of plant–animal mutualism.

Using the western lowland gorilla as a model, this thesis supports the unsurpassed role of large-bodied frugivores in shaping tropical forests and ensuring their long-term integrity. Appropriate management actions are urgently needed to cease the ongoing extirpation of such key seed dispersers from tropical forests.

Keywords: directed-dispersal, endozoochory, forest dynamics, large-bodied frugivore, nesting behaviour, secondary dispersal, seedling recruitment, sleeping site, *Uapaca*

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The original work of the the Ph.D dissertation is presented as a succession of the following scientific articles[1] (published or submitted):

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Petre C-A., Tagg N., Haurez B., Beudels-Jamar R., Salah M., Willie J. & Doucet J-L. (submitted). Operational identification of important and fallback fruit resources for a western lowland gorilla population in southeast Cameroon. *International Journal of Primatology*.

Petre C-A., Tagg N., Beudels-Jamar R., Haurez B., Salah M., Spetschinsky V., Willie J. & Doucet J-L., 2015. Quantity and spatial distribution of seeds dispersed by a western lowland gorilla population in south-east Cameroon. *Journal of Tropical Ecology* 31(3): 201–212

Petre C-A., Tagg N., Beudels-Jamar R., Haurez B. & Doucet J-L., 2015. Western lowland gorilla seed dispersal: are seeds adapted to long gut retention times? *Acta Oecologica* 67: 59–65

Petre C-A., Zinque M-H., Tagg N., Beudels-Jamar R., Haurez B., Josso J-F., Moretto P. & Doucet J-L., 2015. Differences in dung beetle activity at western gorilla defecation sites in south-east Cameroon: implications for establishment of *Uapaca* spp. seedlings. *Journal of Tropical Ecology* 31(2): 165–174

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[1] The complete list of scientific production of the Ph.D. candidate is available at the following web link: http://orbi.ulg.ac.be/browse?type=authorulg&rpp=20&value=Petre%2C+Charles-Albert+p036756

Petre C-A., Salah M., Tagg N., Beudels-Jamar R., Haurez B., Willie J. & Doucet J-L. (submitted). Do the western lowland gorilla performs directed-dispersal services at sleeping sites? Insights from southeast Cameroon. *Forest*.

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CHAPTER I.

INTRODUCTION

1. Introduction

1.1. Research context, objective and structure

In tropical forests, the role of animals in shaping the environment is more important than in any other terrestrial biomes as they are the main driver of population dynamics through seed dispersal. For instance, in the Afrotropics, studies report a dependency towards animals ranging from 60 to 85% of the woody species community (Beaune et al. 2013; Doucet 2003; Gillet and Doucet 2012; Holbrook and Smith 2007). Therefore, describing the mechanisms under which tropical forest ecosystems regenerate and maintain their functional integrity is also predicting the future of that ecosystem under the current rate of anthropogenic pressure (Caughlin et al. 2015).

By displacing seeds away from the mother plant, animals improve the per capita recruitment probability by enabling seeds to escape to their specific predators or parasites which are found in higher densities in the vicinity of mother plants where their resources are also encountered in higher densities (Janzen 1970; Connell 1971; Augspurger 1984). In areas where animal populations are reduced or completely extirpated, a much smaller proportion of seeds will escape this distance/density-dependence mortality resulting in a much reduced recruitment probability and consequently a reduced regeneration dynamics.

Among seed dispersal frugivores, large-bodied species are thought to be of greater importance for the population dynamics at the community scale (Vidal et al. 2013). Large-bodied frugivores generally interact with a larger number of plant species, themselves interacting with other frugivores that interact with other plant species and so forth (Donatti et al. 2011). Because large-bodied frugivores are interconnected indirectly to almost all elements of this seed dispersal network, they occupies a central position and their removal from the network will likely impact upon more elements of the network than the one they are directly interacting with (Vidal et al. 2013), hence jeopardising the whole community integrity.

Large-bodied frugivores are also the most vulnerable to local extinction (Cardillo et al. 2005), most often being the first to disappear from an ecosystem under disturbance (e.g. unsustainable hunting pressure, habitat degradation, deforestation). They represent the most valuable targets of hunters, occur in naturally low densities, need large tracks of undisturbed habitats to maintain viable populations and have slow life history traits which makes their demographic recovery capacity slower than the disturbance rate (Davidson et al. 2009).

The western lowland gorilla, which faces major conservation concerns in most part of its distribution range, is the largest arboreal frugivore, potentially occupying a key position within seed dispersal networks it occurs. Yet, its role as seed disperser remains poorly documented. The importance of fruit in the diet of the western lowland gorilla is a recent finding relative to the time-scale of African great ape research. The western lowland gorilla was long assumed to have the same socio-ecological characteristics as the (more studied) mountain gorilla, and was consequently considered a folivorous species and therefore not an important actor in seed dispersal. The first paper documenting the seed dispersal activity of the western lowland gorilla was published in the early 90s (Tutin et al. 1991). Since then, three other studies on western lowland gorilla seed dispersal have been published at the same study site (La Lopé National Park, Gabon; Rogers et al. 1998; Voysey et al. 1999a; Voysey et al. 1999b) and a last one in the Dja Biosphere Reserve, Cameroon (Poulsen et al. 2001).

The goal of the present thesis is therefore to provide new documentation of the seed dispersal activity of the western lowland gorilla by answering a set of research questions developed based on existing evidence and knowledge gaps, and that fit within the general objective of assessing the effectiveness to forest regeneration of a population of western lowland gorillas at La Belgique research site, at the northern periphery of the Dja Biosphere Reserve, southeast Cameroon. Results of this research would contribute to the discussion of what would become tropical forests after the predicted collapse of the remaining large-bodied frugivore populations from most of their range.

I used the hierarchical flowchart produced by Schupp et al. (2010), representing the determinants of seed dispersal effectiveness (SDE), as a baseline from which the present study was structured (Figure 1). The seed dispersal effectiveness of any one frugivore is measured by the number of new adults recruited following seed dispersal activity of that frugivore and corresponds to the product of the quantity of seeds dispersed and the probability that a dispersed seed produces a new adult. Given that the mechanisms regulating the recruitment of new adults of long-lived tropical plants exceed the timeframe considered in this research, the qualitative component of the seed dispersal effectiveness framework can be only partially assessed. However, by answering the research questions I offer a description of all main components or subcomponents of the seed dispersal effectiveness framework, which enables me to thoroughly discuss the ecological role fulfilled by the western lowland gorilla.

Each research question is examined in a separate chapter. These consist of the following:

1) What are the seed-dispersal-related characteristics of the western lowland gorilla and how does it fit with the documented high seed dispersal effectiveness of primates?

   Subsequently to this introductory chapter, before embarking on the description of the components and subcomponents of the seed dispersal effectiveness framework specifics to the western lowland gorilla population studied in this thesis, I present in the second chapter a literature review on the fundamental concepts of seed dispersal and the role fulfilled by animal dispersers in the dynamics of tropical forests, with an emphasis on primates, including a state of the art regarding the seed dispersal activity of western lowland gorillas, and discuss the consequences of animal extirpation on the long-term structure and composition of tropical forests.

   This chapter has been published in the journal *Biotechnology, Agronomy, Society and Environment*.

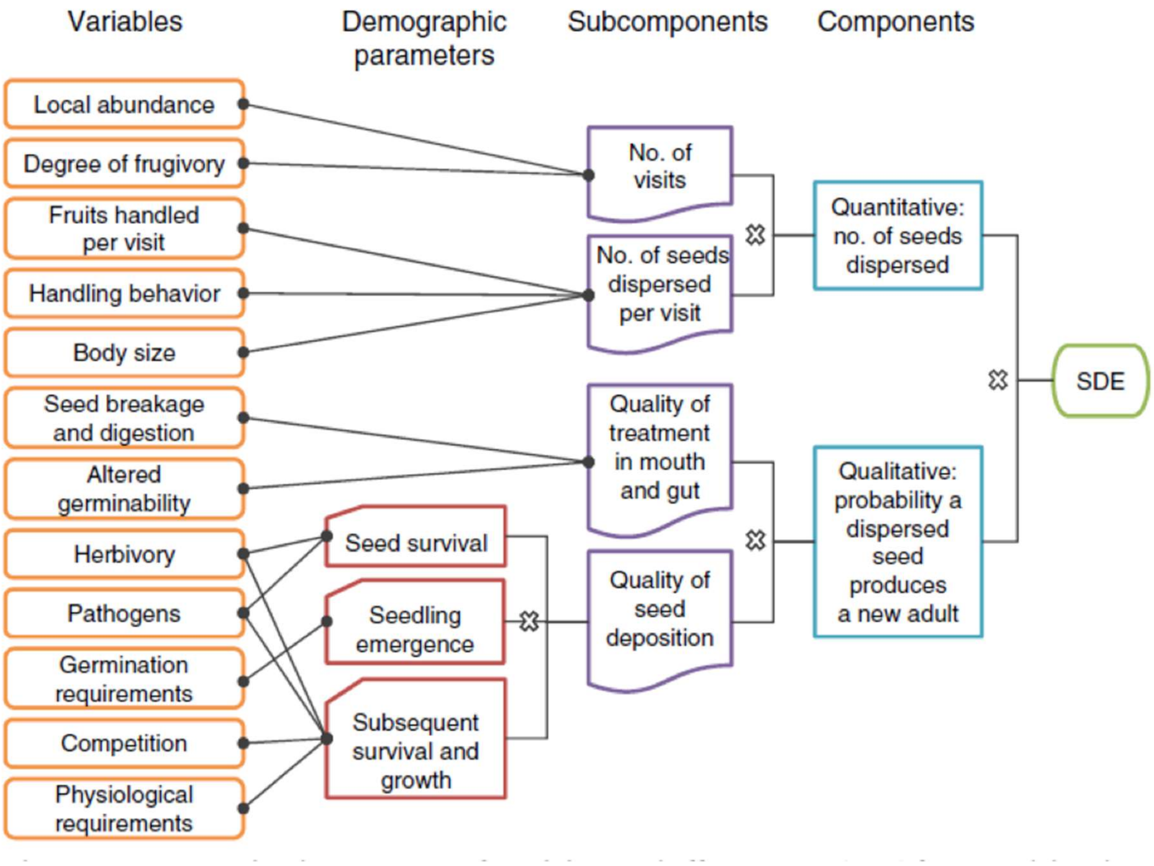


Figure 1. from Schupp et al. (2010), page 336: "A hierarchical flow chart representing the determinants of seed dispersal effectiveness (SDE) for a model endozoochorous seed dispersal system. 'Components' and 'subcomponents' provide the major organizing framework for developing studies and calculating SDE. 'Demographic parameters' represent a simplified life table for determining the 'quality of seed deposition.' 'Variables' are representative measurable variables that are relevant to studies of SDE. Boxes connected by right-angled lines with an 'x' represent factors that are, at least in principle, multiplicative (e.g. the number of visits x the number of seeds dispersed per visit = the number of seeds dispersed). Straight lines with closed circles on the ends indicate that the variable affects the 'subcomponent' or 'demographic parameter,' but not multiplicatively."

2) What is the degree of frugivory of the western lowland gorilla population at La Belgique research site, and which are the most important fruit items?

The most elementary prerequisite for seed dispersal is the incorporation of fruit items in the diet and the more item consumed, the more high the quantitative component of the seed dispersal effectiveness framework is likely to be (Figure 1). In the third chapter, I therefore describe the degree of frugivory of the western lowland gorilla population at La Belgique by providing a list of fruit items consumed. Furthermore, as some plant species are tightly linked to one particular animal for the dispersal of their seeds and, conversely, these plants may be of critical importance for the fitness of the animal dispersers, I apply operational methods to determine important and fallback fruit species, and thus identify species that exhibit the potential to be involved in a mutualistic relationship with gorillas at La Belgique. These results justify the subsequent use of particular species in the investigation of seed dispersal effectiveness in the following chapters. This chapter has been submitted for publication in the journal *International Journal of Primatology*.

3) Among the fruit item consumed, which are the species whose seeds are dispersed by the western lowland gorilla at La Belgique and in which quantity, and what are the environmental characteristics of seed deposition sites?

Depending on the fruit handling behaviour and fruit and seed traits, a frugivore will disperse the seeds of some species but not of others. Furthermore, depending on fruit preferences, fruit availability and seed crops, dispersed species are not likely to be dispersed in the same quantity, which may impact upon the effectiveness of the seed dispersal service they receive from the western lowland gorilla (Figure 1). In the fourth chapter I provide a comprehensive description of the quantitative component of the seed dispersal effectiveness framework through the counting and identification of seeds found in 1030 faecal samples collected during three consecutive years. I also provide preliminary data on the qualitative component by describing the macroscopic physical state of passed seeds (i.e. the variable "Seed breakage and digestion"; Figure 1) and their viability through germination trials. For a subsample of species dispersed, I perform comparative germination trials between gut-passed and hand-cleaned seeds to assess the impact of gut passage on seed viability towards the variable "Altered germinability" and the subcomponent "Quality of treatment in mouth and gut" (Figure 1). Finally, I describe and compare the environmental conditions of the two main types of seed deposition sites (sleeping sites and feeding trails). Based on the physiological requirements of the species dispersed (Hawthorne 1995), the suitability of the seed deposition sites for subsequent seedling survival and growth (Figure 1) is discussed. This chapter has been published in *Journal of Tropical Ecology*.

4) How long are seeds retained in the digestive tract of the western lowland gorilla and does the resulting scarification of the seed coat modify the germination performances of ingested seeds?

The western lowland gorilla is the largest arboreal frugivore (Tutin 1998) and large-bodied species generally have a long digesta retention time (Demment 1983). Hence, the level of scarification of the seed coat by gastrointestinal fluids in the gut of the western lowland gorilla is expected to be more pronounced than in most other frugivores and consequently the modification of germination performances (i.e. the variable "Altered germinability" of the subcomponent "Quality of treatment in mouth and gut" of the SDE framework; Figure 1) might also be of a greater degree (Traveset 1998). In this fifth chapter, I specifically seek to investigate if dispersed seeds are adapted to long gut retention times by performing comparative germination trials between hand-cleaned seeds and seeds having transited for a known amount of time in the digestive tract of captive western lowland gorillas. A reduction in germination performance due to extreme rates of scarification by gastrointestinal fluids would reduce the quality of the seed dispersal service of the western lowland gorilla. Additionally, I aim to disentangle the effects of scarification and deinhibition (i.e. removal of the fruit pulp that may otherwise act as germination inhibitor) resulting from gut passage. The deinhibition effect has too often been overlooked yet it is important to consider when assessing the overall advantage of animal-mediated seed dispersal for plant population dynacmics, and conversely the impact of seed dispersal loss. This chapter, together with the previous chapter, completes the description of the subcomponent "Quality of treatment in mouth and gut" of the SDE framework (Figure 1) and has been published in the journal *Acta Oecologica*.

5) Does the high amount of faecal matter surrounding the dispersed seeds induce high rate of dung beetle-initiated secondary seed dispersal and how this impacts upon seed survival and seedling emergence?

Another consequence of large body-size is that dung beetles and some seed predators use olfactory cues emitted by faeces to locate their food resource (Andresen and Levey 2004; Beaune et al. 2012), and the high volume of faecal matter produced by large-bodied frugivores might indirectly influence the post-deposition fate of seeds deposited in the faeces. In this sixth chapter I therefore aim to describe empirically the impact of the presence of a large amount of faecal matter on dung beetle-mediated seed burial and subsequent seed survival and seedling emergence probabilities. This chapter provides the two first demographic parameters determining the "Quality of seed deposition" (Figure 1) and has been published in the journal *Journal of Tropical Ecology.*

6) Among the seed dispersal characteristics of the western lowland gorilla, what are the determinants of recruitment success of young plant recruits?

Across its range, the western lowland gorilla has been shown to favour habitats with a relatively open canopy in which to construct night nests (e.g., Arnhem et al. 2008; Haurez et al. 2014; Mehlman and Doran 2002; Tutin et al. 1995; Willie et al. 2012), and as light availability is a strong limiting factor in tropical forests (Whitmore 1996), it is hypothesised that seeds dispersed at western lowland gorilla sleeping sites will exhibit a higher probability of producing seedlings that survive and recruit to adulthood than seeds dispersed elsewhere (Wenny 2001). In this seventh chapter, I therefore investigated if the environmental conditions of sleeping sites are more suitable than random sites in the forest for post-dispersal seedling survival and growth. This seventh chapter provides the last demographic parameter determining the "Quality of seed deposition" (Figure 1) and has been submitted for publication in the journal *Forest*.

1.2. Study species

1.2.1. Gorilla taxonomy

« … This province of Mayombe is all woods and groves, so overgrowne that a man may travaile twentie days in the shadow without any sunne or heat… The woods are so covered with baboones, monkies, apes and parrots, that it will feare any man to travaile in them alone. Here are also two kinds of monsters, which are common in these woods, and very dangerous.

The greatest of these two monsters is called Pongo in their language, and the lesser is called Engeco. This Pongo is in all proportion like a man, but that he is more like a giant in stature than a man, for he is very tall, and hath a man's face, hollowed-eyed, with long haire upon his browes…

They sleepe in the trees and build shelters for the raine. They feed upon fruits that they find in the woods, and upon nuts, for they eate no kind of flesh. They cannot speake, and have no understanding more than a beast. The people of the countrie, when they travaile in the woods make fires where they sleepe in the night, and in the morning when they are gone, the Pongoes will come and sit about the fire till it goeth out, for they have no understanding to lay the woods together. They goe many together and kill many negroes that travaile in the woods… Those Pongoes are never taken alive because they are so strong, that ten men cannot hold one of them, but yet they take many of their young one with poisoned arrowes.

The young Pongoes hangeth on his mother's belly with his hands fast clasped about her, so that when the countrie people kill any of the females they take the young one, which hangeth fast upon his mother…. »

Extract of « Purchas his pilgrimes » (Purchas 1625); Chapter III *The strange adventures of Andrew Battell, of Leigh in Essex, sent by the Portugals prisoner to Angola, who lived there and in the adjoining regions neere eighteene yeeres* ; Section VI *Of the Provinces of Bongo, Calongo, Mayombe, Manikesocke, Motimbas : of the Ape Monster Pongo, their Hunting : Idolatries, and divers other observations*

As far as we know, this citation is the very first documentation of the existence of the gorilla. However, the truthfulness of the story of the English adventurer Andrew Battell has been rendered intelligible two centuries after its publication by the discovery made by Dr Thomas Savage that the chimpanzee, known since 1775, was called by the natives of Gabon "Enché-eko", which obviously corresponded to the Battell's "lesser monster", the Engeco (Huxley 1863). The existence of Battell's "lesser monster" being supported, a strong presumption arose that his "greater monster", the Pongo, would sooner or later be discovered. Further piece of evidence came from Edward Bowdich, who reported in 1819 from a mission to Ashantee that natives were recognising a second great ape, called "Ingena", of five feet high and four across the shoulders (i.e. 150 x 120 cm) with a disproportionate paw and one blow of it to be fatal (Bowdich 1819). In 1847, Dr Savage had the good fortune to be hosted unexpectedly by the Reverend

1. *Introduction*

Mr Wilson, on the Gaboon River, who detained in his house a skull of an animal described by natives as monkey-like, remarkable for its size, ferocity and habits (Savage and Wyman 1847). After subsequent further investigations derived from intelligent natives, Dr Savage was induced to believe this skull belonged to a new species of Orang (at that time, all anthropoid primates were called Orang, a Malay word meaning “reasonable being”, given to human and elephant as well, while Utan means “wild” or “from the wood”), called by the natives “Engé-ena”, the long-sought “Pongo” of Battell and the “Ingena” of Bodwich. With the full cooperation of Rev. Wilson and his notable influence on the natives, Dr Savage gathered a large volume of information on this new creature’s habits, and most importantly to science, an ample collection of intact skulls from adult individuals of both sexes as well as other skeleton parts. Dr Savage brought with him to Boston the skulls of two adult males and two adult females, as well as other skeleton remains, to be analysed by the Professor of Anatomy, Jeffries Wyman, of the University of Harvard. The results of Pr Wyman osteological analyses were published in December 1847 in the Boston Journal of Natural History, preceded with a description of the external characters and habits of this new ape species, as learnt from natives, by Dr Savage. Both considered this new species of great ape to be a sister species of the chimpanzee, known at that time as *Troglodytes niger* Geoff. 1812, and therefore ranked it in the genus *Troglodytes*. In seeking for a specific name, Dr. Savage wisely avoided the much misused "Pongo"; but finding in the ancient Periplus of Hanno the word "Gorillae" applied to certain hairy savage people, discovered by the Carthaginian voyager in an island on the West African coast, he attached the specific name "*Gorilla*" to his new ape, though by no means he identified his ape with Hanno's savage hairy people.

After Savage and Wyman 1847 publications, more gorilla skulls and skeleton parts of different provenance were accumulating in natural history museums of the world, including Le Museum du Jardin des Plantes de Paris which benefited of an entire gorilla specimen, where Pr. de Blainville, Duvernoy and then Geoffroy-Saint-Hilaire could have undergone osteological and anatomical analyses. This latter Pr. Geoffroy-Saint-Hilaire concluded the difference between the two African great apes species was of generic order and proposed the generic name *Gorilla* Geoff. 1852 (Owen 1859).

Along with the exploration of the interior of the African continent, this multiplication of Gorilla material brought to museums lead to the profusion of new species and subspecies in the genus Gorilla, as such that by late 1920’s no less than 15 specific and subspecific names existed (Coolidge 1929). Suspicious that this diversification may have resulted from a great individual variation that exist in the gorilla at the specific level, as observed in the other ape species, Dr. Harold Jefferson Coolidge Jr. revised the genus Gorilla in 1929, based on 26 variables of 213 adult male skulls, from both Western and Eastern Central Africa, held in Museums all over the world. Dr. Coolidge found in all the 26 variables such a uniformity in the measurements that he concluded all specimen analysed belonged to a same and unique species, *Gorilla gorilla* Savage & Wyman 1847. However, a distinction into two groups was evident from the measurements, between the skulls from Western Central Africa provenance (Western Cameroon, Cameroon and Gaboon) and those from Eastern Central Africa (Kivu and Eastern Mountains), which he referred to as the Coast and the Mountain gorillas, respectively. As the type form (i.e. the form that was first described; Groves 2004) was the Coast gorilla and the first-described Mountain gorilla was named *Gorilla beringei* Matschie 1903, following the code for zoological nomenclature Coolidge attributed the name of *Gorilla gorilla gorilla* for the western subspecies and *G. g. beringei* for the eastern subspecies. Dr. Coolidge, however, consented that some naturalists would still consider two additional subspecies, *G. g. diehli* in the mountainous region of western Cameroon, and *G. g. graueri* in the lowlands adjacent to the Mountain gorilla population.

Since Coolidge revision, which posed the basis of the modern taxonomy of the genus gorilla with a maximum of four distinct taxa (two western and two eastern), there is still much of a debate whether there is one or two species of gorillas and on the amount of subspecies associated. In 1961, based on skull morphometric measurements, Vogel suggested to upgrade the two subspecies described by Coolidge to the rank of species (*G. gorilla* and *G. beringei*), both of which comprising two subspecies (*G. g. gorilla* and *G. g. diehli* for the western species, and *G. b. beringei* and *G. b. graueri* for the eastern species). Still on skulls morphometric measurements, though with a much higher sample size (N=747), Groves (1967, 1970) could discern three distinct taxa (*G. g. gorilla, G. g. beringei* and *G. g. graueri*) but in his opinion they did not warrant separation at the species level.

Three decades later, Groves changed his mind and accepted the separation of the genus Gorilla between two species, each of them having two subspecies (Groves 2001a) and this is what remained the most frequently used taxonomy. This new classification arose from a new species concept Groves became an adept of, the Phylogenetic Species Concept (PSC), which defines a species as the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent and that is diagnosably distinct from other such clusters by a unique combination of fixed character states (Cracraft 1983).

The PSC is one of the species concept that have been proposed following the demonstration of the limits of the reference species concept at the time, the Biological Species Concept, which proposes that the species is “a group of actually or potentially interbreeding natural populations which is reproductively isolated from other such group” (Mayr 1963, p19). Although this concept makes perfectly sense in cases of sympatry, as if sympatric taxa maintain their distinctiveness they are obviously not interbreeding and hence constitutes objectively different species, in case of allopatry this concept implies subjectivity as to when one should infer different populations to subspecies of the same species or to distinct species (Groves 2014a). This is the case of western and eastern populations of gorillas that are separated by a 1000km (Groves 1971) (Figure 2). Furthermore, molecular analyses revealed that even sympatric taxa, clearly identified as distinct species, may interbreed (Groves 2014a).

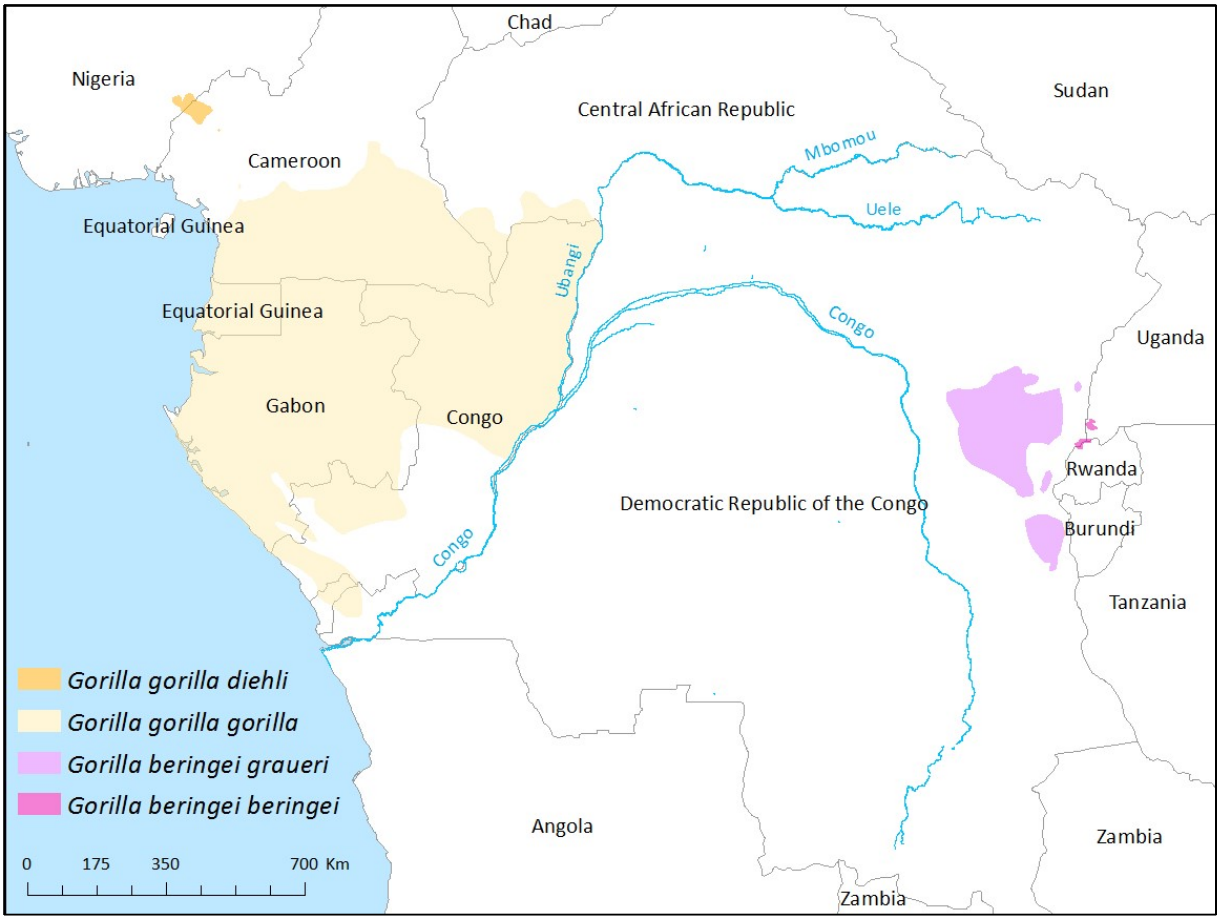


Figure 2. Distribution of the gorilla subspecies

Every "species" is a hypothesis that is ever increasingly challenged by new means of analysis that progress in science may offer (Rylands and Mittermeier 2014). Among the different alternative species concepts ever since proposed (up to 24; Mayden 1997), each have their own part of subjectivity in defining what is and is not a significant difference amongst organisms worthy the species's attribution. All these contemporary species concepts share the fundamental common element that the species is an evolutionary lineage (i.e. primary species criteria), but disagree in adopting different properties acquired by lineages during the course of divergence as secondary defining properties (secondary species criteria; e.g., reproductively incompatible, phenetically distinguishable, ecologically distinct, reciprocally monophyletic, etc) (de Queiroz 2007), which tend to arise at different times during the process of lineage divergence (de Queiroz 2005). In other words, the different species concepts agree on what a species is but differ in how far back we should go along the course of a lineage divergence (Groves 2014a). de Queiroz (2007) proposed that most of the secondary properties emphasized under alternative species concepts should be considered relevant to the issue of species delimitation. Hence, the demonstration that a group of organisms acquired any of those properties constitutes an evidence of lineage separation, and the more properties acquired, the more confident the inference of the existence of separate species is. One may argue, and de Queiroz inferentially does so, that the earliest definitive evidence that a lineage has become separate is that it is diagnosable (has fixed heritable differences from other lineages) (Groves 2014b). Diagnosability is the key concept of the PSC, whereby the distinction between one species and another is absolute; 100% of individuals of each age/sex classes can be distinguished based on fixed character (genetic) difference from every individuals of other species (Groves 2001b). Put another way, there are some genes which are universal (fixed) in one population and absent in the others (Groves 2000). Although the founder of the PSC discarded the subspecies concept, some practitioners of the PSC (including Groves) still use the 75% difference rule of thumb of Mayr (1963) to separate populations or clusters of animals into distinct subspecies (Groves 2001b).

According to Groves, every gorillas are at once distinguishable as an Eastern or Western gorillas; they differ 100% in some of their external character and in the skull and teeth (Groves 2000). Hence, they are distinguishable and therefore constitutes two separate species according to the PSC. In support of this classification, genetic analyses suggest that there is more diversity among gorillas that can be accommodated in single species taxonomy (Anthony et al. 2007; Grubb et al. 2003; Prado-Martinez et al. 2013).

The PSC is however not making the unanimity amongst taxonomists, being criticized to result in taxonomic inflation by upgrading to easily subspecies to the rank of species (e.g. Zachos et al. 2013a). For instance, in 1982 there were 181 species of primates listed in the first edition of the *Mammal Species of the World* (Honacki et al. 1982), while in the 2005 edition, to which Groves applied in his contribution using the PSC, there were 376 species listed (Wilson and Reeder 2005), and in the most recent compilation, *Handbook of the mammals of the world* (Mittermeier et al. 2014), the number of species listed still increased to 488. In response to the criticism of the taxonomy inflation that results from the PSC, Groves and others (e.g. Rylands and Mittermeier 2014) advocate the positive impact this can have on conservation. Indeed, the PSC overcomes the “sub-species” problem in conservation (Gippoliti and Amori 2007); i.e. the disharmonic and non-coherent conservation treatment of below-species diversity by the conservation community for different taxa and in different regions of the planet depending on an animal’s charisma and various national legislations. Given that all gorilla populations are at risk of extinction, the finest split of their taxonomy would obviously contribute to their conservation (through public awareness, political initiatives, fund raising, etc). Note, however, that the counterargument holds true; if endangered species (as defined by the Biological Species Concept) are incorrectly split into several units (under the PSC) and managed as such, for instance in captive breeding or metapopulation management, there could be unnecessary loss of genetic variation and an increased risk of extinction (Zachos et al. 2013b)

1. *Introduction*

The taxonomy of the gorilla used in this thesis is the two-species (the western gorilla *G. gorilla* and the Eastern *G. beringei*) classification of Groves (2001a), each made of two subspecies; the western lowland gorilla (*G. g. gorilla*) and the Cross River gorilla (*G. g. diehli*) for the western species, and the Mountain gorilla (*G. b. beringei*) and the eastern lowland gorilla (*G. b. graueri*) for the eastern species. This choice does not reflect personal position in the debate but rather the consensus view of the members of the IUCN/SSC Primate Specialist Group (Grubb et al. 2003), and therefore the desire of being consistent with most of recent literature. The complete taxonomic classification of the western lowland gorilla is given as follow:

- Class : MAMMALIA
  - Order : PRIMATES
    - Suborder : HAPLORRHINI
      - Infraorder : SIMIIFORMES
        - Superfamily : Hominoidea
          - Family : Hominidae
            - Genus : *Gorilla*
              - Species : *gorilla*
                - Subspecies : *gorilla*

From molecular genetics, it is suggested that these species separated around 0.9–1.6 10^6 y ago, however gene flow between the two nascent species may still have occurred as recently as 80 10^3 y ago (Ackermann and Bishop 2009; Thalmann et al. 2007). This pattern is consistent with the Pleistocene refugia hypothesis for the diversification of forest-dwelling taxa but rivers seemed to have also played a role in shaping gorilla genetic diversity (Anthony et al. 2007). During the Plio-Pleistocene (i.e., 5 10^6–12 10^3 years ago), changes in temperatures and aridity changed the area covered by forests periodically, connecting and isolating repeatedly the western and eastern gorilla populations. During warmer and wetter periods, the extent of the tropical forest was greater than today, extending north of the Congo/Ubangi River and providing a corridor for migration between both populations (Jensen-Seaman 2000). Along these lines, the population of gorillas which may have existed near Bondo, north of the Uele River in the Democratic Republic of the Congo (Figure 2), until the earlier part of the 20th century, for which both cranial morphology and mitochondrial DNA resemble the western lowland gorilla (Meder and Groves 2012), may reflect a relict population from these intermittent forest, and hence gorilla populations, connections (Jensen-Seaman 2000).

1.2.2. Gorilla ecology and social system

Gorillas have a long and voluminous hindgut containing cellulose-digesting ciliates to facilitate the processing of plant food (Chivers and Hladik 1980; Collet et al. 1984). Structural plant parts such as herb stems and tree leaves are consumed year round, in proportions that vary between seasons and altitude. In mountainous habitats, gorillas rely almost exclusively on these items year round, whereas in lowland forests where fruits are much more abundant these items are consumed particularly in periods of fruit scarcity (Doran-Sheehy et al. 2009). The preference for fruits, but with the ability to fall back on plant parts that are more abundant and readily accessible, but of lower nutritional quality, enable gorillas to form cohesive non-territorial groups (Harcourt and Stewart 2007). Intergroup encounters are generally peaceful (Bermejo 2004) and extensive overlaps in the home range of neighbouring groups seem to be common (Arandjelovic et al. 2010).

In both western and eastern lowland gorillas, groups generally comprise one silverback male and several reproductive females (median number=3.5; Harcourt and Stewart 2007) whose access is the sole long-term property of the silverback. In eastern gorillas, multi-male groups are common (up to 61% of social units have two to six silverbacks; Gray et al. 2013) but although females can mate with any silverback, the dominant silverback sires an average of 85% of group offspring (Bradley et al. 2005). Group size averages 8-12 individuals in both western and eastern gorillas (Gatti et al. 2004; Parnell 2002; Magliocca et al. 1999; Gray et al. 2013; Kalpers et al. 2003) but can be as high as 22 in western gorillas and 47 in eastern gorillas (Gray et al. 2013; Kalpers et al. 2003; Magliocca et al. 1999).

1.2.3. Population status

The western lowland gorilla subspecies is the most widespread and abundant of the genus (Figure 2), nonetheless it is highly threatened, being ranked as critically endangered by the International Union for Conservation of Nature (IUCN) (Walsh et al. 2008). Most western lowland gorilla populations are found in one of five countries (southern Cameroon, Equatorial Guinea, Gabon, the Republic of Congo and the southwestern corner of the Central African Republic) with remnant populations existing in the Mayombe forest of Cabinda (Angola) and the Democratic Republic of Congo (Beudels-Jamar et al. 2008). Total population size is estimated at around 100 10^3 individuals (Harcourt 1996).

The reference population size estimation is rather hypothetical and requires an urgent update. Due to the wide range across which gorillas occur, the remoteness and inaccessibility of their habitats and the elusive behaviour of gorillas, techniques used to assess population size traditionally rely on indirect methods, containing several bias factors, which are applied on small scales and extrapolated to wider areas. The most common method consists of walking line transects and counting the night nests created by gorillas in order to obtain a density of nests, which is then converted into a density of gorillas by applying conversion factors of nest production and decay rates (Tutin and Fernandez 1984). Both factors are likely to induce bias in the density calculation as gorillas may sleep on bare ground (Mehlman and Doran 2002), may construct more than one nest per night (Tutin et al. 1995), or may return to previously used nests (Iwata and Ando 2007); and because the rate at which nests decay varies according to the climate (Walsh and White 2005) and the type of vegetation material used (Ancrenaz et al. 2004; Tutin et al. 1995). Few surveys are undertaken using site-specific measurements of nest production and decay rate because of the time constraints they represents. Therefore, such values are borrowed from the few sites that have provided them and researchers commonly acknowledge the limitations of their density assessments.

The reference estimated total population size of 100 10^3 western lowland gorillas has been calculated by multiplying the surface occupied by moist forests within the distribution range of the subspecies in the mid-90s and a somewhat arbitrarily-chosen mean density of 0.25 gorilla/km^2 throughout (Harcourt 1996). This density was chosen because it falls within the limits of mean gorilla densities in suitable habitats as estimated from nest count surveys in Gabon (mean density of 0.18 gorilla/km^2; Tutin and Fernandez 1984) and Congo (mean density of 0.4 gorilla/km^2; Fay and Agnagna 1992). However, since then it has become clear that habitat availability is not a sufficient predictor of population size as commercial hunting and outbreaks of the Ebola virus can dramatically reduce or extirpate gorillas from otherwise suitable areas. For instance, Ebola outbreaks that occurred between October 2002 and January 2004 killed an estimated 90–95% of the gorilla population of the Lossi Sanctuary in Congo (about 5500 gorillas) (Bermejo et al. 2006), and a similar figure (90–97%) has been reported for the gorilla population of Odzala-Kokoua National Park for the period 2003–2004. The effect of poaching on gorillas is more difficult to quantify but it is unanimously regarded as a serious threat (IUCN 2014). Most ethnic groups living in the range of the western lowland gorilla hunt and consume gorilla meat. Together with chimpanzees and bonobos, gorillas are estimated to comprise between 1–4% of the total bushmeat trade in Africa (Eves et al. 2008). Most populations of gorillas are now threatened in the face of hunting due to the widespread network of roads opened by logging companies and other extractive industries (Haurez et al. 2013). There is also medicinal use of some gorilla body parts (Meder 1999). Furthermore, when an adult female gorilla with an infant is killed, the infant is often sold into the pet trade (IUCN 2014), thus having the same effect of removing a potential reproductive individual from the wild population as does poaching. As the worst case scenario, Rizkalla et al. (2007) predicted that the combined effect of Ebola outbreaks and poaching on gorilla populations may be severe enough to eliminate up to 97% of the entire western lowland gorilla population within the next 100 y. A national survey of great apes conducted in Gabon between 1998 and 2002 revealed a catastrophic decline of 56% since the previous national survey of 1981–1983 (Tutin and Fernandez 1984), and the primary cause of this decline was identified as a combination of commercial hunting and Ebola outbreaks (Walsh et al. 2003). In addition to these two drivers of decline identified in Gabon, human-induced habitat loss and degradation also contribute to a loss in suitable environmental conditions for the western lowland gorilla

(Junker et al. 2012) and climate change is expected to strongly exacerbate this loss (Lehmann et al. 2010). Given the unlikely cessation of the drivers of this population decline (hunting, Ebola outbreaks, habitat loss and degradation) and the extremely low reproductive rate of the western lowland gorilla (maximum intrinsic rate of increase of about 3%; Steklis and Gerald-Steklis 2001), a population decline of more than 80% over three generations (i.e. 66 years; D. Caillaud, unpubl. data in Walsh et al. 2008) is expected under this scenario. It was this foreseeable population decline, and not the estimated population size, which led in 2008 to an upgrade of the conservation status of the western lowland gorilla to 'critically endangered' (Walsh et al. 2008).

On a more positive note, another reason to revise the total population size estimate, though with no implications for the conservation status, is the recent confirmation that the large tracts of swamp forests of Northern Congo, previously thought as unsuitable for gorillas (Groves 1971), harbour healthy populations of gorillas in very high densities (5.25 weaned individuals/km²; Rainey et al. 2010). A series of surveys in this region, covering 47,444 km² of swamp forests and surrounding terra firma forests, conducted between 2006 and 2007, estimated that 126 10^3 gorillas were living in this area (95% CI: 90325–161545) (Stokes et al. 2008).

1.3. Study site

We conducted the study in the research site 'La Belgique' at the northern periphery of the Dja Biosphere Reserve, south-east Cameroon (013°07'–013°11'E, 03°23'–03°27'N) (Tagg and Willie 2013; Willie et al. 2012) (Figure 3). This research site has been created in 2001 by the Centre of Research and Conservation of the Royal Zoological Society of Antwerp to undergo researches on the socio-ecology of the sympatric central chimpanzee and western lowland gorilla under the name of Projet Grands Singes (Dupain 2001). The research site covers approximately 40 km² of mixed lowland forest (600–700 m asl), in the transition zone between evergreen and semi-deciduous forests (Letouzey 1968). The site has never been logged but human-made modification of the forest is evident locally by the presence of emergent palm oil trees (*Elaeis guineensis*, Arecaceae), which suggests abandoned village sites, and old cocoa plantations (Petre, personal observation). The upper soil (0-30 cm) contains a high proportion of clay (32.6%), resulting in a poor drainage of rain water (Peh 2009), which has an impact on the composition of the forest notably by enabling hygrophilic species to occur in relatively high densities in terra firma forests (e.g. some *Uapaca* species; Djuikouo et al. 2010; Peh 2009; Table 1). Four main habitat types are recognized at La Belgique (relative abundance values from Willie *et* al. 2012):

(1) Old secondary forest (OSF) with a relatively open understorey and a closed canopy dominated by late-successional tree species (150–200 y old, estimated from annual diameter growth rate of canopy

trees; Bourland 2013, Kouadio 2009) of large diameter and height >25 m. This habitat type represents 38% of the study site.

(2) Young secondary forest (YSF) with dense undergrowth and a discontinuous canopy layer dominated by early-successional trees of smaller diameter and height <25 m; 31% of the study site.

(3) Flooded areas (FA) characterized by a hydromorphic soil and comprising inundated clearings, periodically inundated swamps, and riparian forests; 26% of the study site.

(4) Light gaps (LG) which are open-canopy environments (± 50 m² for branchfall gaps to 600 m² for treefall gaps; Doucet et al. 2009); 5% of the study site.

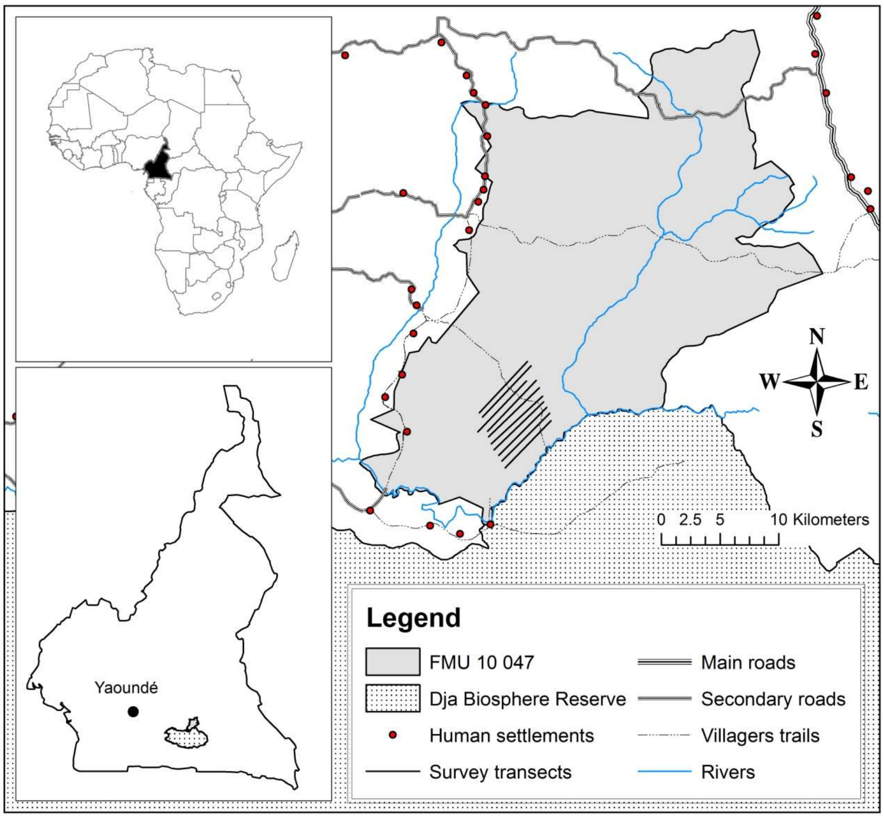


Figure 3. Map showing the localisation of the study site La Belgique, southeast Cameroon, in relation with physical and human features.

Table 1. List of the 15 tree species with highest relative importance (RI) in terra firma forests and inundated forests at La Belgique research site, southeast Cameroon. The relative importance of one species is calculated as the sum of its relative density, dominance and frequency.

Terra firma		Periodically inundated	
Species (Family)	RI	Species (Family)	RI
Petersianthus macrocarpus (Lecythidaceae)	21.1	*Uapaca vanhouttei* (Euphorbiaceae)	47.5
Tabernaemontana crassa (Apocynaceae)	18.7	*Strombosia grandifolia* (Olacaceae)	24.5
Polyalthia suaveolens (Annonaceae)	9.7	*Sarcocephalus pobeguinii* (Rubiaceae)	17.5
Lecaniodiscus cupanioides (Sapindaceae)	9.7	Unidentified species ("Ebim")	14.0
Pentaclethra macrophylla (Fabaceae)	8.7	*Anthonotha lamprophylla* (Fabaceae)	13.8
Plagiostyles africana (Euphorbiaceae)	8.0	*Alstonia boonei* (Apocynaceae)	13.3
Trichilia prieuriana (Meliaceae)	6.4	*Sorindeia grandifolia* (Anacardiaceae)	12.8
Uapaca mole (Euphorbiaceae)	6.2	*Lecaniodiscus cupanioides* (Sapindaceae)	12.6
Strombosia grandifolia (Olacaceae)	6.0	*Lasiodiscus mannii* (Rhamnaceae)	12.5
Sorindeia grandifolia (Anacardiaceae)	5.8	*Uapaca guineensis* (Euphorbiaceae)	10.8
Desbordesia glaucescens (Irvingiaceae)	5.7	*Rinorea* sp. (Violaceae)	9.4
Uapaca acuminata (Euphorbiaceae)	5.5	*Cordia platythyrsa* (Boraginaceae)	8.8
Anonidium mannii (Annonaceae)	5.4	*Trichilia prieuriana* (Meliaceae)	5.0
Annickia chlorantha (Annonaceae)	5.4	*Desplatsia dewevrei* (Tiliaceae)	4.8
Celtis mildbraedii (Ulmaceae)	4.6	*Santiria trimera* (Burseraceae)	4.7

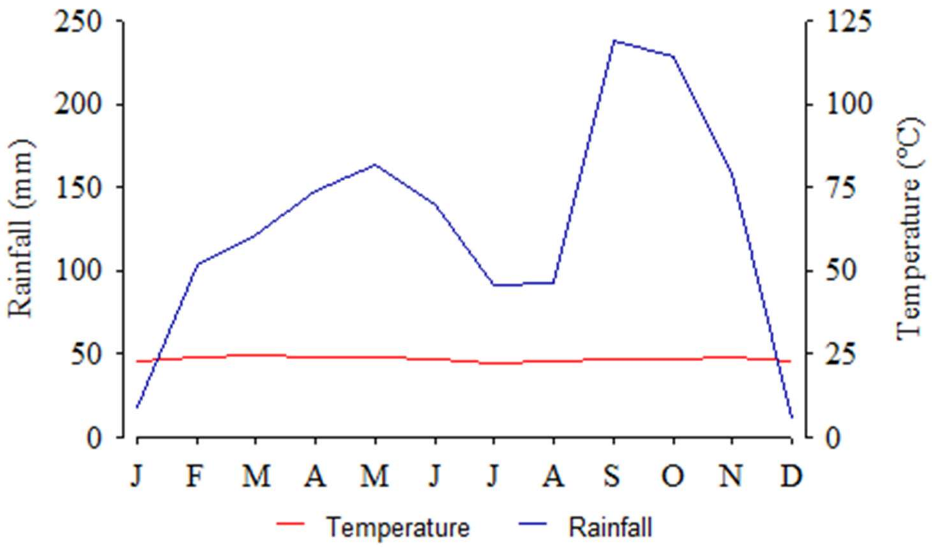


Figure 4. Mean monthly rainfall and temperature at La Belgique research site, southeast Cameroon. Data were recorded between April 2009 and June 2013.

Climatic data recorded in the site between April 2009 and June 2013 correspond to an equatorial climate with a ten-month rainy season and a two-month dry season (December–January) (Figure 4). Mean annual rainfall ranged between 1315–1831 mm and mean minimum and maximum daily temperatures were 19.9°C and 27.1°C, respectively.

The population of western lowland gorillas at La Belgique is not habituated to human presence. Hence, research of their socio-ecology is undergone through indirect observations. This population benefits from the permanent presence of researchers which acts as a deterrent to poachers (Tagg et al. 2015). No killing of gorillas has been reported since the creation of this site (Tagg, personal communication). However, this population of gorillas is at risk of anthrax (*Bacillus anthracis*) outbreaks as it is in this site that in 2004 the first ever reported death by anthrax was documented for gorillas (Leendertz et al. 2006). Since then, another case of a gorilla death following a contimation with spores of *B. anthracis* may well have occurred in 2009 but awaits confirmation (Petre, personal observation; Figure 5). Based on nest count surveys, La Belgique is estimated to hold a density of 0.69 weaned gorillas (PGS, unpublished data), with no significant decline since the creation of this site (Tagg et al. 2011).

Figure 5. Fresh carcasse of an adult female western lowland gorilla found on feeding trails nearby the sleeping site in December 2009 at La Belgique research site, southeast Cameroon.

CHAPTER II.

LITERATURE REVIEW

Role of the western lowland gorilla (Gorilla gorilla gorilla) in seed dispersal in tropical forests and implications of its decline.

Petre C-A., Tagg N., Haurez B., Beudels-Jamar R., Huynen M-C. & Doucet J-L., 2013. *Biotechnology, Agronomy, Society and Environment* 17(3): 517–526

Summary: Patterns of seed dispersal significantly affect plant demography, dynamics and succession. In the tropics, the majority of tree species bear fruits that are adapted to animal-mediated dispersal. Amongst seed dispersers, the contribution of primates is widely recognized by ecologists as incomparable. However, in lowland Afrotropical forests, the specific role of the largest primate species, the western lowland gorilla (*Gorilla gorilla gorilla* Savage and Wyman, 1847), has been overlooked. This is of particular relevance as this species seems to fulfil important criteria for effective dispersal, both quantitatively and qualitatively. One trait makes it potentially unique as seed disperser; the regular deposition of seeds in open canopy environments where light will not be a limiting factor for subsequent seedling growth and survival. The magnitude of which this particular trait contributes to forest dynamics remains unexplored though it could be potentially important. It might no longer be the case, however, as the western lowland gorilla is critically endangered. The loss of the ecological services provided by large-bodied seed dispersers may have considerable impacts on the forests. Through dispersal limitation, population dynamics of plants in forests devoid of large frugivores will be strongly impacted. In the long-term, this may lead to shifts in plant community structure, composition and to reduced tree diversity. Currently, forests of the Congo basin face increasing level of deforestation and degradation which puts already the ecosystem integrity in jeopardy. The additional threat that represents frugivorous wildlife depletion is therefore of forest management concern.

Keywords: seed dispersal, primate, forest dynamics, African forests.

Résumé: La dissémination des graines par les animaux participe significativement à la démographie, dynamique et succession des communautés végétales. En forêts tropicales, la majorité des arbres produisent des fruits adaptés à la consommation et à la dissémination de leurs graines par les animaux. Parmi les différents agents disséminateurs, les primates jouent un rôle inégalable, largement reconnu. Alors que leur rôle fondamental dans la régénération forestière et le maintien de la biodiversité tropicale est accepté, la contribution spécifique du gorille des plaines de l'ouest (*Gorilla gorilla gorilla* Savage and Wyman, 1847), le plus grand des primates des forêts du Bassin du Congo, reste méconnue. Pourtant, cette espèce semble réunir les conditions fondamentales pour qu'une dissémination très efficace se réalise. Il se distingue notamment par une dispersion régulière des graines dans des micro-habitats caractérisées par une forte ouverture de la canopée où la lumière ne sera pas un facteur limitant à la croissance et la survie des jeunes plants. L'influence sur la dynamique forestière que pourrait jouer cet enrichissement en graines dans les ouvertures forestières par le gorille des plaines de l'ouest n'a pas encore été explorée malgré son importance potentielle. Elle pourrait cependant ne plus être active compte tenu des menaces critiques qui pèsent sur la survie des populations de gorilles. La perte des services écologiques rendus par la grande faune disséminatrice de graines pourrait avoir des conséquences considérables sur le futur des forêts. En l'absence de dissémination, la dynamique de population de nombreuses espèces serait impactée. Sur le long terme, cela pourrait conduire à une modification de la structure et composition de la communauté végétale et à un appauvrissement de la diversité. Actuellement, les forêts du bassin du Congo subissent des taux grandissants de déforestation et dégradation qui mettent en péril l'intégrité de l'écosystème. La disparition des frugivores constitue donc une menace additionnelle qui doit être prise en considération dans la gestion des massifs forestiers.

Mots-clés : dissémination des graines, primate, dynamique forestière, forêts africaines.

2.1. Introduction

Plants bearing fleshy fruits are believed to have a mutualistic relationship with their animal consumers: from an evolutionary perspective, plants take advantage of seed dispersal while animals benefit from the nutritive value of the consumed fruit (Kollmann 2000). Frugivore-mediated seed dispersal (i.e. zoochory) can have significant effects on plant demography, dynamics, succession and spatial distribution at all scale (Kollmann 2000; Seidler et al. 2006; Blake et al. 2009; Gillespie et al. 2012).

In the tropics, the majority of tree species bear fruits adapted to animal dispersal. In Neotropical forests, Howe et al. (1982) reported the proportion of animal-dispersed species ranging from 51 to 93% for canopy trees and 77 to 98% for sub-canopy trees. In Paleotropical forests, trees also exhibit adaptations for animal seed dispersal. According to Doucet (2003), about 60% of tree species of Central Gabon are dispersed through endozoochory, and in the Dja region, South-East Cameroon, this value reaches 82% (Letouzey 1985). Despite the importance of seed dispersal in biodiversity maintenance (Janzen 1970; Connell 1971; Harms et al. 2000; Hardesty et al. 2006), mechanisms affecting seed dispersal patterns and recruitment probability of tropical trees remain poorly documented. Furthermore, no generalization intending to predict these parameters for less-known tree species is possible due to the complexity of tropical ecosystems (Müller-Landau et al. 2008).

Fruits and seeds adapted to zoochory vary widely in their shape, size, color, chemical composition, palatability, digestibility and accessibility; therefore they attract and are dispersed by different sets of animal species (Poulsen et al. 2002; Müller-Landau et al. 2008). Behavioral and physiological patterns of frugivorous dispersers, such as activity budget, displacement velocity and distance, retention time and fruit handling, will have consequences on seed viability and spatial patterns of seed deposition (Howe et al. 1982; Lambert et al. 1998; Traveset 1998; Nathan et al. 2008); factors which greatly influence recruitment probability. Seed dispersal, population dynamics and community structure at a given site are thus dependent on the frugivorous community and plant attributes that attract them.

As primates represent a great proportion of the frugivorous biomass in tropical forests (Garber et al. 1998), in general their contribution to seed dispersal has received much attention and they are believed, as a group, to be incomparable dispersers (Poulsen et al. 2001; Lambert 2011). That said, for some frugivorous primate species, documentation of their role as seed disperser is lacking, despite their potential effectiveness. If such potentially effective dispersers disappear from forests, there could be long-term detrimental consequences for natural forest regeneration and dynamics (Terborgh et al. 2008; Blake et al. 2009; Poulsen 2009; Vanthomme et al. 2010). The future of tropical forests is already put in jeopardy by human activities imposing immediate effects on its size, structure and composition, and climate change will further contribute to this (Wright 2010; de Wasseige et al. 2012). Extirpation of effective dispersers constitutes another major threat for the forests that will remain. This may be the case with the "critically endangered" western lowland gorilla (*Gorilla gorilla gorilla* Savage and Wyman, 1847) (Walsh et al. 2008).

Here, we investigate the potential importance and effectiveness of western lowland gorillas as seed dispersers and scrutinize the potential consequences of their removal/extinction for the preservation of the ecosystem integrity. Specifically, the objectives of this review are threefold. First, we aim to describe the advantages and underlying mechanisms of animal-mediated seed dispersal for plant fitness in tropical ecosystems. We then explain the important ecological function of primates as a seed dispersal taxon, summarise what we know about the contribution of the western lowland gorilla and make expectations of its effectiveness. Finally, we discuss the keystone role of large frugivores and the implications of their decline for the future of tropical forests.

For the purpose of this review of the literature we used the database Scopus provided by Gembloux Agro-Bio Tech. The main keywords entered were "seed dispersal", "western lowland gorilla", "primate", "endozoochory", "tropical forest", "regeneration", "forest degradation" and "Congo Basin". Among relevant references, the most recent were selected, with the exception of publications defining ecological concepts, and illustrations from Central African forests were prioritized.

2.2. Endozoochory: advantages and disadvantages

Seed dispersal, regardless of the type of vector, is believed to confer an advantage to the plant through different mechanisms which increase recruitment probability. It reduces the mortality rate caused by sibling competition (Connell 1971), intense predation by granivores and grazers that concentrate their activities where food is abundant (Janzen 1970), and attacks by specific pathogens (Augspurger 1984).

Escape from a density- or distance-dependent mortality is described by the “Escape Hypothesis”, better known as the Janzen-Connell hypothesis (Howe et al. 1982). Seed dispersal also enables colonization of particular habitats that are unpredictable in when they will be created or in their location, such as treefall gaps (Howe et al. 1982). This advantage is explained by the “Colonizing Hypothesis”. In the specific case of endozoochory, the extra costs involved in producing fruits to attract animals is associated with additional evolutionary advantages, known as the “Directed-Dispersal Hypothesis”. This hypothesis considers that non-random movement and habitat preference of some frugivores results in a disproportionate deposition of seeds in sites where specific requirements for seed germination and seedling growth and survival are met (Howe et al. 1982; Wenny 2001). This evolution of plant traits has further consequences that may improve the fate of dispersed seeds; passage through the gut of a frugivore is normally associated with mechanical and chemical abrasion of the seed coat which, in some cases, impacts positively on germination capacity (e.g., Lieberman et al. 1986; Traveset 1998; Valenta et al. 2009). Furthermore, when excreted, these seeds are surrounded by fecal material that protects them from hydric stress and offers a nutrient-rich environment that encourages seedling growth and increases survival probability (Nchanji et al. 2003). Finally, dung beetles are attracted to volatile organic compounds emitted from feces and initiate secondary dispersal which can have a huge impact on seed survival, seed predation, germination success and seedling establishment (Shepherd et al. 1998; Andresen et al. 2004).

Despite the numerous potential advantages of endozoochory, attracting frugivores through fruit production is, however, no guarantee for increased plant fitness through higher recruitment success. Some frugivores do not disperse the seeds from some or all species they feed on, they may break the seeds and kill the embryo when mouth-processing or even masticate the seeds on purpose for nutrient intake (Tutin et al. 1993; Lambert et al. 1998). This results in them being seed predators instead. Passage through the gut does not always enhance germination success or rate of all of the fruit items consumed (Traveset 1998). The level of abrasion of the seed coat and its effect on germination depends on the consumer species and the intrinsic characteristics of seeds, such as thickness and hardness of the seed coat, as well as seed size which affects the gut transit time; smaller seeds are retained for longer periods than larger ones (Traveset 1998). A long retention time can enhance germination rate and success through suppressing seed dormancy or by softening the seed coat and increasing its permeability. However, a retention time that is too long can lead in some cases to total seed digestion or germination inhibition (Lieberman et al. 1986; Traveset 1998). Additionally, the chemical compounds in the feces (e.g. fatty acids and phenols) can sometimes act as germination inhibitors (Valenta et al. 2009) and fecal material can reduce germination success by facilitating fungal and bacterial development (Traveset et al. 2007). Similarly, the fruit pulp may also contain germination inhibitors (Robertson et al. 2006) and the presence of pulp surrounding the seeds also increases the risk of fungal and bacterial development that can be lethal to seeds (Baskin et al. 1998). Therefore, undispersed seeds still surrounded by the fruit pulp, either due to dispersal failure (lack of dispersers' visitation) or as a result of seed processing behavior (spitting of seeds not cleared from pulp), are likely to face a high mortality rate. Furthermore, dung beetle activity can result in seed loss, by excessively deep burial in the soil (Shepherd et al. 1998). Finally, the seed deposition pattern exhibited by large frugivores results in a high density of seeds per fecal clump which, to a certain extent, cancels out the advantage of escaping from density-dependent mortality underneath the crown of the parent (Poulsen et al. 2001; Traveset et al. 2007).

Production of fruit attributes that attract animals represents an energy investment by the plant which would not be cost effective in case of dispersal failure in habitats where animal dispersers are reduced to very low densities or are locally extinct. In general, fruit-bearing plants would have multiple animal dispersers, especially in tropical forests where the frugivore community is highly diverse (Müller-Landau et al. 2008). However, some plants rely on a limited set of dispersers or even a single species and therefore have restricted or no dispersal substitution capacity (Lieberman et al. 1986; Tutin et al. 1991a; Babweteera et al. 2007; Blake et al. 2009). Local extinction of dispersers could therefore lead to important plant population decline through recruitment limitation (Terborgh et al. 2008).

In the tropics, strict one-to-one plant-animal mutualisms occur mainly due to size restriction: big seeds can only be dispersed by large-bodied frugivores with a correspondingly large gut size (Babweteera et al. 2007). The African forest elephant (*Loxodonta cyclotis* Matschie, 1900) is the largest forest dwelling animal on Earth and it has been reported to be the exclusive disperser of at least 13 tree species at Ndoki Forest, Republic of Congo (Blake et al. 2009). Similarly, the western lowland gorilla is the only regular disperser of seeds of *Cola lizae* N. Hallé (Sterculiaceae), endemic to central Gabon, despite the fact that sympatric chimpanzees occasionally swallow and disperse their seeds (Tutin et al. 1991a). Crucially, both species, western lowland gorillas and African forest elephants, are currently facing considerable population decline throughout their range (IUCN 2012).

2.3. Primates as a keystone taxon for tropical forests.

2.3.1. Importance of primates as a seed disperser group: generalities

Among animal seed dispersers in tropical ecosystems, the contribution of primates is thought to be of paramount importance (Poulsen et al. 2001; Lambert 2011). Primates are usually abundant and have a relatively large body size. As most primate species have a high frugivorous diet, they represent a large proportion of the frugivores biomass and are consequently responsible for the removal of a large proportion of the fruit and seed crop (Chapman 1989; Chapman et al. 1998; Garber et al. 1998; Poulsen et al. 2002; Lambert 2011). In such cases, diet overlap is common (e.g.; Chapman 1989; Tutin et al. 1993, 1994; Poulsen et al. 2001, 2002; Lambert 2011), resulting in some degree of redundancy among primates in the seed dispersal service for various plant species. Multi-species dispersal of seeds has a great influence on the seed shadow of the plants concerned (i.e., the spatial distribution of seeds around the parental source; Willson 1993) and subsequently on recruitment probability. Indeed, primates within a community exhibit a variety of feeding strategies, differences in fruit and seed processing, home range size, habitat preference, daily travel distance, gut capacity and retention time of the digesta (Poulsen et al. 2001). As a result, distinct primate species will disperse seeds into different habitat types, at varying distances from the parent plant, and according to a scattered or rather clumped distribution pattern. The probability of encountering suitable conditions for recruitment is therefore higher in case of multi-species seed dispersal (Poulsen et al. 2001).

Contrary to this, some sympatric primate species exhibit diet specialization for certain fruit species, which increases the proportion of seed species in a plant community that is dispersed. For instance, the number of seed species dispersed by each frugivorous primate species in a study site in the Dja Biosphere Reserve, Cameroon, was found to range from 5 to 61, whereas as a whole the primate community dispersed at least 125 seed species through fecal clumps; 77 of them being tree species, which represented 34% of the studied tree flora of the reserve (Poulsen et al. 2001).

These varying dietary, behavioral and ecological characteristics result in a primate community that is diverse yet effective at seed dispersal and therefore able to significantly structure the habitats in which they are found (Poulsen et al. 2001; Lambert 2011).

Primates are thus essential agents of forest dynamics and regeneration, contributing to the maintenance of high biodiversity of tropical ecosystems. As a consequence, their extirpation could significantly impact on recruitment patterns of many plant species (Lambert 2011), which would lead to population collapse and in the long term to a shift in the plant community (Terborgh et al. 2008; Babweteera et al. 2009; Poulsen 2009). It has been argued that large gut-sized birds, such as hornbills, must have a high substitution capacity for primate seed dispersal, by dispersing the same set of seed species. However, hornbills tend to use higher strata of the canopy forest and are attracted by fruits of different colours, feeding more often on reddish fruit species, whereas primates prefer brown and green fruits (Poulsen et al. 2002). Thus, dispersal redundancy between these two taxa is debatable although it seems clear that no one taxon could completely replace the other (Poulsen et al. 2002; Lambert 2011). Moreover, redundancy among species belonging to closely-related taxa is not always high. In the Dja Biosphere Reserve, apes and Cercopithecines (*Cercopithecus*, *Lophocebus* and *Colobus*) exhibit a small overlap in the seed species they disperse, leading to the conclusion that the loss of seed dispersal services by apes could not be completely fulfilled by Cercopithecines (Poulsen et al. 2001).

To highlight the importance of primates for seed dispersal, Lambert (2011) used a powerful approach to demonstrate the ecological necessity of conserving primates for forest dynamics and biodiversity maintenance. She applied the multi-species umbrella concept for ecosystem conservation. An umbrella species is by definition “a species for which its conservation confers protection to a large number of naturally co-occurring species” (Roberge et al. 2004, page 77). The originality of her study was to work at higher taxonomic ranks than the species and to implement in her definition the important mutualism existing among plants and animals. In that way, the conservation of an umbrella taxon will benefit many species, both floral and faunal. Based on species richness within taxa, abundance, sensitivity to human disturbance and visitation rate of fruiting trees, primates proved to be the most fitting “umbrella taxon” compared to birds and squirrels. In terms of seed dispersal and its role in the maintenance of the high biodiversity of tropical forests, conservation efforts targeted towards primates therefore represent an adequate management shortcut in situations where conserving all animal and plant species is economically impossible. Currently, almost half of the world’s primate species face conservation challenges (IUCN 2012). The application of the above management strategy would be therefore highly relevant for the future of many primate species, including the critically endangered western lowland gorilla.

2.3.2. Western lowland gorilla seed dispersal

To our knowledge, the first documentation of western lowland gorilla seed dispersal activity was published two decades ago (Tutin et al. 1991a). Since then, only a handful of studies have provided further information on this topic, and most of them were conducted at the same study site as the initial study in Lopé National Park, Gabon. Nonetheless, improved knowledge of gorilla ecology contributes to the appreciation of its potential quantitative and qualitative effectiveness in seed dispersal, as discussed below.

Quantitative dispersal – In terms of quantitative seed dispersal, the western lowland gorilla is likely to play an important role for the following reasons.

(1) They are regular fruit-eaters, feeding on a diverse set of species. In periods of fruit abundance, fruit consumption accounts for up to 70% of feeding time (Doran-Sheehy et al. 2009). Feeding ecology studies conducted across its range (Ndoki [Congo], Lopé [Gabon], Mondika [Congo and Central African Republic] and Bai Hokou [C.A.R.]) have identified 70 to 115 fruit species in the gorilla diet at each study site (Doran et al., 2002). Fruit remains were found in almost every feces collected over a 7-year period in Lopé (96%, N=4301 feces; Tutin et al. 1993). On average, one fecal clump was found to contain remains of three different fruit species.

(2) With an average body weight reaching 90 and 180 kg for adult females and males respectively (Caldecott et al. 2009), the western lowland gorilla has the largest body size of all primates of the Congo basin. Daily food intake required for metabolism is therefore high and by extension they are responsible for the removal of a large proportion of the fruit/seed crop. In the Dja Biosphere Reserve, Cameroon,

despite the low density of western lowland gorillas compared to the six sympatric primate species (the moustached monkey *Cercopithecus cephus cephus*, the white-nosed guenon *C. nictitans nictitans*, the crowned guenon *C. mona pogonias*, the black-and-white colobus *Colobus guereza occidentalis*, the grey-cheeked mangabey *Lophocebus albigena albigena* and the central chimpanzee *Pan troglodytes troglodytes*), they are assumed to disperse alone almost as many seeds as the rest of the primate community as a whole (Poulsen et al. 2001). With an average of 40.8 intact seeds per fecal unit (SD, ± 262.6), a density of 1.7 weaned individuals km^{-2} [95% IC, 1.0 – 2.9] and 6.7 defecations per day, western lowland gorillas could be dispersing 464.7 seeds day^{-1} km^{-2} [range, 273.4 – 792.7] compared to 664.2 [422.4 – 955.9] for the remaining primate community.

Qualitative dispersal – From a qualitative perspective, western lowland gorillas may also be effective seed dispersers because:

(1) They usually process fruits in the mouth and gut without causing damage to seeds; fruit remains in feces consist mainly of intact and still viable seeds (Tutin et al. 1993; Poulsen et al. 2001; Doran et al. 2002). Many seed species have a high concentration of secondary compounds and gorillas lack the specialization of the digestive tract required to metabolize them (Rogers et al. 1990), resulting in the passing of most seeds through the gut undigested (Williamson et al. 1990). Additionally, the gut size of the gorilla is large enough to allow them to swallow the seeds of most fruit species they feed on. The longest-running study investigating western lowland gorilla seed dispersal identified 70 seed species present in feces samples over a 6-year period, encompassing 76.9% of the fruit species known to feature in its diet at this site (N = 91; Lopé National Park, Gabon: Tutin et al. 1991a; Tutin et al. 1991b). While chimpanzees, the second largest primate of Congo Basin forests, systematically expulse seeds exceeding 4.2 cm^3, seeds up to 7 cm^3 can be found in gorilla feces (Tutin et al. 1994).

Seeds that pass through the western lowland gorilla digestive tract intact conserve their germination capacity. Poulsen et al. (2001) observed a positive effect on germination success of *Uapaca* seeds from passage through the western lowland gorilla gut. Germination success reached 62% after passage through the gut compared to a 26% germination success for seeds manually extracted from fruit pulp. Among the six primate species tested (five Cercopithecines and the central chimpanzee), the western lowland gorilla conferred the highest germination enhancement for *Uapaca* seeds.

(2) Seeds are retained for a long period in the western lowland gorilla digestive tract. In addition to the relationship between digestive tract length and body size, the type of food consumed along with the seeds influences seed transit time. For instance, an increase in the amount of fruit consumed results in shorter retention time of the digesta (Traveset 1998). The diet of the western lowland gorilla, though highly frugivorous, includes non-fruit items such as leaves, pith, shoots, barks and insects year round (Tutin et al. 1993) and in inverse proportion to fruit consumption (Doran-Sheehy et al. 2009). This

mixed diet influenced by seasonality and the large body size of gorillas are responsible for relatively long though variable retention times of seeds in the digestive tract regardless of seed size, ranging from a few hours (< 10 h) to 136 hours, with a mean of 47.1 hours (Remis 2000). By comparison, central chimpanzees have a mean retention time of 23.6 h (Idani 1986) and the one of Cercopithecine species ranges from 21.2 h to 25.4 h (Poulsen et al. 2001). The relatively long retention time of the western lowland gorilla may enhance germination, as demonstrated for *Uapaca* seeds (Poulsen et al. 2001), or may conversely inhibit it (Traveset 1998). Finally, as a consequence of long and variable retention times coupled with long daily path lengths (from < 1 km to 5.3 km; Remis 1997), western lowland gorillas likely provide a complex heterogeneous seed shadow with an extended tail of long distance dispersal. While such an extended seed shadow increases the probability of encountering suitable conditions for seedling recruitment, long distance dispersal also favours maintenance of genetic diversity and rate of range expansion of the plant populations concerned (Kollmann 2000; Hardesty et al. 2006). The dispersal and mating system of individual gorillas further contributes to this; when a male leaves the natal group in search of founding a breeding group, this blackback male may travel very long distances (Douadi et al. 2007).

(3) Seeds dispersed by the western lowland gorilla encounter particular environmental conditions. Western lowland gorillas have a bimodal defecation pattern with half of their feces produced at nest sites and the other half during daily displacement (Todd et al. 2008). Nest sites are not selected randomly and canopy openness seems to be a major determinant. Preference for open canopy areas for nesting, such as tree fall gaps, is a constant feature across the range of the western lowland gorilla (e.g., Tutin et al. 1995; Mehlman et al. 2002; Arnhem et al. 2008; Willie et al. 2012). Seeds dispersed at nest sites are thus likely to encounter microsites with higher light regimes than seeds dispersed during daily displacement. This seems to be particularly profitable for post-dispersal seed fate as pointed out by Tutin et al. (1991a) in Lopé, Gabon. Seeds of *Cola lizae* dispersed at nest sites had higher germination success, seedling establishment and survival rate than seeds dispersed elsewhere; 71.6% of seedlings survived at nest sites after two months compared to 13.2% elsewhere. Although not systematically monitored, *Cola lizae* seeds deposited directly beneath parent trees, either through oral expulsion by primates or from fallen fruits, seemed to face a much higher mortality rate than dispersed seeds. The suitability of gorilla nest sites for post-dispersal seed fate was confirmed for two additional species at the same study site (*Ganophyllum giganteum* [A. Chev.] Hauman [Sapindaceae] and *Uapaca guineensis* Müll.-Arg. [Euphorbiaceae]: Voysey et al. 1999b). Seedling survival and growth of these species were always higher at nest sites after two years than beneath the crown of parent trees or for those scatter-dispersed by other primate species at short distances from the parental source. It seems, therefore, that the western lowland gorilla may be a unique disperser in terms of its "directed dispersal" (i.e. dispersal of seeds in microsites presenting environmental conditions particularly suitable for recruitment: Howe et al. 1982). Although directed-dispersal is thought to be a rare phenomenon, it leads to a much higher probability of

survival to adulthood on a per-seed basis than the other kinds of seed dispersal advantages (Wenny 2001). In this particular situation, the animal species performing directed-dispersal may contribute significantly more to the plant population concerned than all other dispersers. The most explicit example in the tropics comes from male bellbirds perching preferentially in open canopy environment which improves seedling survival of the tree *Ocotea endresiana* Mez [Lauraceae] (Wenny 2001). Regular dispersal of seeds by the western lowland gorilla in open canopy sites is also likely to improve recruitment success of tree species as most of them require at least small canopy gaps to reach adulthood. Interestingly, species requiring a high light regime at seedling stage are most commonly found among timber species (Doucet 2003).

The western lowland gorilla possesses biological and ecological traits required to perform effective seed dispersal. Transportation of many seeds away from the parent plant in open canopy habitats may greatly improve seed and seedling fate of many tropical species, and dispersal of large-seeded species contribute to their spatial distribution. In regards of that, the western lowland gorilla is a good candidate of being a keystone element of the ecosystem, like elephant are considered to be (Blake et al. 2009).

It is worth noting, however, that the western lowland gorilla may also influence its environment by causing damages to recruits of woody species. Although terrestrial herbaceous vegetation composes the majority of gorilla nests, in almost every study site saplings, either bended or broken, are also common nest building material (Tutin et al. 1995; Mehlman et al. 2002; Willie et al. 2012). The western lowland gorilla is also responsible for damages by breaking the shoots for consumption of the soft inner part, young leaves and the apical bud. For example, Kouadio (2009) observed important seedling and sapling destruction in timber plantations. In order to debate on the real contribution of one animal species on the ecosystem dynamics it is important to consider both the positive and negative effects that the animal species exerts. In the present case, lack of empirical information and quantitative data impede balancing both contributions. However, the loss of the seed dispersal service of the western lowland gorilla is believed to have much more negative impact on the forest than do occasional recruit destruction as discussed in the next section.

2.4. Wildlife depletion and the future of tropical forests

In the tropics, the high occurrence of zoochory leads to interdependent dynamics between plants and animals, where disturbance affecting one taxon will have an impact on the other (Sodhi et al. 2009); habitat disturbance may result in a decrease in wildlife density (e.g. Poulsen 2009), and depletion of wildlife may alter regeneration patterns of plant communities (e.g. Terborgh et al. 2008).

Presently, forests of the Congo basin face increasing rates of degradation through increased anthropogenic pressure on natural resources (forest conversion for farming and agriculture, extractive industries, illegal logging, fuel-wood provisioning; de Wasseige et al. 2012). In addition to this, the bushmeat crisis reached a peak due to an increasing human population, together with the improved road network and the easier access to fire-arms (Wright 2010). In summary, forests are declining in size and wildlife is declining in abundance. As frugivores represent most of the tropical wildlife biomass it is not surprising that they are the most harvested taxon, encompassing 82% of the carcasses found on western and central African markets (Fa et al. 2005). The same tendency is observed in the Neotropics, where frugivores of the Amazonian basin, regardless of their size, decline faster in abundance with increasing level of hunting pressure than the other dietary specialization groups (Peres et al. 2007). Only rodents seem to increase in abundance with habitat degradation and large vertebrates' depletion (Malcolm et al. 2000; Poulsen 2009).

Degradation and hunting can lead to local extinctions of frugivores with large-bodied species facing higher risk (Pimm et al. 1988) as 1) they naturally occur at lower densities than smaller species, 2) often rely on large continuous habitat tracts, 3) have slow reproductive rates, 4) give birth to fewer offspring, 5) are more valuable to hunters and 6) cannot adjust to persistent hunting pressure by becoming more behaviorally inconspicuous (Babweteera et al. 2007; Babweteera et al. 2009; Poulsen 2009; Wilkie et al. 2011). Local extirpation of large-bodied frugivores will result in dispersal limitation of large-seeded trees given that remaining smaller-bodied frugivores will not be able to swallow and disperse them (Wang et al. 2007; Blake et al. 2009; Vanthomme et al. 2010). Seeds will then simply fall beneath the crown of the parent plant and risk high density- or distance-dependent mortality (Janzen 1970; Connell 1971; Harms et al. 2000; Seidler et al. 2006; Blake et al. 2009; Poulsen 2009). Without transportation of seeds through the gut of a frugivore, the probability of encountering a favorable site for recruitment is reduced, thus resulting in recruitment limitation (Babweteera et al. 2007). Such altered patterns of tree recruitment could lead in the long-term to shifts in community structure (Seidler et al. 2006; Wright 2010; Wilkie et al. 2011), composition (Poulsen 2009; Wright 2010) and to reduced adult tree diversity (Blake et al. 2009).

Recruitment limitation of large-seeded species will have another disruptive effect on the ecological function of tropical forests. Large seed size is generally associated with shade-tolerant long-lived species because seedlings will rely on seed resources for establishment in a shaded environment, while small seeds are associated with light-demanding, fast-growing and short-lived species (Queenborough et al. 2009). Moreover, seed size is correlated to wood density (Queenborough et al. 2009) which is a good predictor of carbon storage capacity (Ruiz-Jaen et al. 2011). Therefore, recruitment limitation of large-seeded long-lived tree species may result in a plant community shift towards a higher density of small-seeded short-lived tree species (Terborgh et al. 2008; Vanthomme et al. 2010), resulting in turn in a lower rate of carbon sequestration (Kirby et al. 2007).

Like the other two charismatic largest frugivores of Central Africa (elephants and chimpanzees), the western lowland gorilla is at risk of extinction, with hunting pressure and habitat loss/degradation being the most widespread threats (Walsh et al. 2008); a risk which could render the preceding possibilities a reality. Not only large-seeded tree species will be affected by the loss of the service provided by these threatened large frugivores but also zoochorous species which recruit disproportionately better in open canopy sites where gorillas produce most of their feces. If the strong declining trend of these keystone dispersers continues, the effects on the Congo basin ecosystem presented above will be inevitable (Blake et al. 2009). Obviously, survival of tropical forests is compromised first and foremost by much more direct threats imposing immediate effects on them. Satellite image comparisons over time report a net annual deforestation rate in Central Africa of 0.17% per year and an additional 0.09% of dense forest is degraded annually (de Wasseige et al. 2012). Considering all the services provided by forests to humans, such as provisioning of food, timber and non-timber forest products, and carbon sequestration, the loss and degradation of tropical forests is of great concern. In contrast to the external threats, wildlife depletion impacts on the forest from the inside. Although the degradation through dispersal limitation is more subtle with effects that require years before being manifests, consequences on ecosystem goods and services are real. Tree cover alone is therefore not a satisfying measure of the ecosystem health. Instead, equilibrium of the dynamics existing between plants and animals should also be taken into account (Terborgh et al. 2008).

2.5. Conclusion

The effectiveness of primates as seed dispersal agents is widely recognized and the western lowland gorilla should not be excluded. Although poorly documented, an initial review of the physiology and ecology of this African great ape shows that this species fulfills the main requirements for effective seed dispersal, both from the quantitative as well qualitative point of view.

A distinctive trait of the western lowland gorilla which highlights its value as seed disperser, is its specific dispersal-related relationship with at least one tree species, *Cola lizae*, an extremely rare phenomenon which might be prejudicial in case of disperser loss. At present, it is unknown how many such relationships might exist between the western lowland gorilla and other plant species in tropical forests.

By dispersing seeds regularly in treefall gaps, the western lowland gorilla might be an active vector of seed dispersal in light of the directed-dispersal hypotheses (Wenny 2001). Empirical demonstration of this particular advantage on the fitness of species dispersed by the western lowland gorilla would make it a strong candidate for being a keystone species for its ecosystem.

The limited yet revealing information that is available on western lowland gorilla seed dispersal, considered alongside the inherent biological and ecological traits of the gorilla, clearly leads to the suggestion that this ape plays a substantial role in Afrotropical forest dynamics, population structure, and maintenance of biodiversity and ecosystem function. As the western lowland gorilla is critically endangered and needs immediate action to be taken to prevent its extinction, the emphasis on its ecological role within its ecosystem may be used in addition to its flagship status for fund raising and public awareness.

CHAPTER III.

ECOLOGICAL FUNCTION OF DIETARY FRUIT SPECIES

3. Ecological function of dietary fruit species

Operational identification of important and fallback fruit resources for a western lowland gorilla population in southeast Cameroon

Petre C-A., Tagg N., Haurez B., Beudels-Jamar R., Salah M., Willie J. & Doucet J-L. (submitted to *International Journal of Primatology*).

ABSTRACT

The use of fallback foods by animals may be crucial to their adaptation to a changing environment. Fallback foods are those of lower nutritional value, available over extended periods of time and that are mainly consumed in periods of preferred food scarcity. The type of fallback foods consumed has implications for socio-ecology, innovativeness and anatomy. In turn, the availability (in space and time) of fallback foods influences behaviour and is thought to dictate species distribution and abundance. We applied an operational definition of fallback foods to fruits consumed by western lowland gorillas in La Belgique, in the Dja Conservation Complex, whereby a fallback food must be an important item for gorillas and whose consumption is significantly inversely correlated to forest-wide fruit availability. We identified 20 important fruit taxa, among which two fulfilled all the criteria of being classified as a fallback food, namely *Klainedoxa* and *Uapaca* spp. We discuss the particular case of *Uapaca* spp. in the site as ranking first in importance and most appropriately complying to the operational definition and demographic characteristics of a fallback food. This taxon is likely to significantly contribute to the fitness of the western lowland gorilla population, and potentially others, in the Dja complex and requires the appropriate management during logging operations.

3.1. Introduction

Animal feeding ecology is a key component of socio-ecology and hence a thorough understanding is crucial for effective conservation (Steklis and Steklis 2008). Amongst the dietary repertoire of any one animal species, not all food items have the same level of importance or preference (Marshall and Wrangham 2007). Preferred foods are those which are disproportionately selected relative to their availability or provide an especially high rate of energy return (Marshall and Wrangham 2007), whereas important foods are those which comprise a substantial part of the diet at varying time scales (Marshall and Wrangham 2007; Rogers et al. 2004). The availability of preferred food resources generally encompass large variations in space and time (Watts et al. 2012), with more or less prolonged periods of preferred food shortage. Depending on the diet and the environment, animals have different strategies to overcome this lack of food. This can involve migration into areas where food is more abundant, hibernation until the food becomes available or diet modification by 'falling back' on less preferred food (Altmann 2009; van Schaik et al. 1993). These so-called fallback foods (FBF) are typically less accessible, harder to process, or of lower nutritional value (Yamagiwa and Basabose 2009). Given that they enable the maintenance of physiological requirements in times of ecological stress, they are believed to exert ecological, behavioural, anatomical and evolutionary pressures that are not exerted by other food types (Constantino et al. 2009; Harrison and Marshall 2011; Laden and Wrangham 2005; Lambert et al. 2004; Lucas et al. 2009; Marshall et al. 2009). Furthermore, the spatial distribution and availability of such food types influence group size and cohesiveness, innovation for food acquisition (e.g., tool use for honey and insect fishing), and ranging behaviour and socio-ecology (Yamagiwa and Basabose 2009), and as such FBF are suggested to frequently act as the primary limitation of local population densities (Hanya and Chapman 2013; Marshall and Leighton 2006; Watts et al. 2012).

Within the distinction axes importance *vs*. preference, a FBF is typically of high importance (high consumption rate in some periods) but of low preference (not disproportionately used relative to availability) (Marshall and Wrangham 2007). More specifically, a FBF should be available over an extended period of time, being partly ignored when preferred food items are available and increasingly used when preferred food availability decreases, but its increased use should not correlate with increased availability (Marshall and Wrangham 2007). Fallback foods have been further distinguished into staple or filler types (Marshall and Wrangham 2007). Staple FBF are those that can comprise 100% of the diet in periods of preferred food scarcity, whereas filler FBF never do so. Filler FBF are, in this sense, considered a trade-off between preferred foods and staple FBF.

It has been proposed, based on empirical observation, that the western lowland gorilla (*Gorilla gorilla gorilla*) (WLG) adopts a relatively low-quality FBF strategy, with bark, leaves, herbs and dry fibrous fruit as the most common types of FBF (Doran-Sheehy et al. 2009; Harrison and Marshall 2011; Lambert 2007). In this study we used the data of a 3-y faecal analysis (Petre et al. 2015a – see chapter 4) coupled with fruiting phenological records to identify important fruit resources for a population of WLG of southeast Cameroon and specifically assess if some fruit resources act as staple or filler FBF according to the above operational definition. Few studies have reported importance and availability data for great ape food or attempted to assign food items into the right categories of FBF (Marshall et al. 2009), and to our knowledge this is the first to identify FBF fruit resources for the WLG strictly based on its operational definition. This study is also the first to document important fruit items for WLG in southeast Cameroon. Results of such a study may provide a valuable conservation management tool, especially for populations living in logging concessions where extraction activities inevitably result in important food resources being damaged either purposely (exploitable trees) or secondarily (e.g., during road construction) (Marshall et al. 2009).

3.2. Methods

3.2.1. Study site

The study was conducted between September 2009 and August 2012 in the research site 'La Belgique' located in the Dja Conservation Complex at the northern periphery of the Dja Biosphere Reserve, southeast Cameroon (013°07'–013°11' E and 03°23'–03°27' N) (Tagg and Willie 2013; Willie et al. 2012). The research site covers about 40 km^2 of mixed semi-deciduous lowland forest (600–700 m asl) with dense network of watercourses and swamps. Climatic data recorded in the site during the whole study period correspond to an equatorial climate with a ten-month rainy season and a two-month dry season (December–January). During the rainy season, a decrease in rainfall occurs in July and August (mean rainfall of 91 ± 56.6 and 92 ± 64.1mm, respectively); a period that we referred hereafter as the small dry season as opposed to the great dry season of December–January. Mean annual rainfall ranged between 1368–1765 mm and mean minimum and maximum daily temperatures were 19.8°C and 27.2°C, respectively.

3.2.2. Faecal collection and analysis

Throughout the study period, a team of two local trackers sought fresh faeces (<48 hrs old) for 15 consecutive days per month. Opportunistic encounters of faeces at other times outside of these collection periods complemented the sample size. Overall, 1030 fecal samples were collected on feeding trails and at sleeping sites with a monthly mean of 28.6 faeces ± SD 17.1 (range: 2–66). Fecal samples were weighed, washed and sieved, and food remains (leaf fragments, fiber, bark, fruit skin, and seeds) were dried at ambient temperature and separated. Fruit remains were identified to the most accurate taxonomic level. As the focal WLG population is not habituated to human presence, we therefore used the extraction of fruit remains (seeds, skin and undigested pericarp) from faeces as a proxy for quantity of consumption.

3.2.3. Fruit availability index

Based on previous analyses of great ape diet conducted at La Belgique (Djoufack et al. 2007), we monitored the fruiting phenology of 56 tree, seven liana and one strangler epiphyte species known or suspected to be consumed by either sympatric great ape species in the site, the WLG or the central chimpanzee. Where possible, we marked a minimum of 10 adult individuals for each of the 64 species (mean number of individuals per species: 8.6 ± SD 2.72; range: 2–12), and recorded the presence of ripe fruits during the first 10 days of each month. For each species monitored on the phenological circuit, we calculated a monthly Fruit Availability Index as follows (Head et al. 2011):

$$FAI_{ij} = D_j B_j P_{ij}$$

Where D_j denotes the density per hectare of the species *j* in the study site, B_j the mean basal diameter (hectare) of individuals of the species *j* in the study site, and P_j the proportion of individuals of the species *j* on the phenological circuit bearing ripe fruit during the month *i*. Density and basal area values are obtained from 130 botanical plots of 25 x 40 m systematically positioned throughout the study site, at every 500 m along ten 6-km long parallel transects spaced 600 m apart. In each plot, we recorded and identified each tree stems with diameter at breast height ≥ 10 cm and each liana stem of diameter ≥ 5 cm. The list of species monitored for fruiting phenology and their demographic data are given in appendix.

3.2.4. Important fruit

We used previously-described criteria to identify important fruit taxa based on frequency, quantity and duration of the occurrence of fruit remains (seeds, skin and fruit fibers) in fecal samples (Doran et al. 2002). Three categories were recognized in the Doran et al. (2002) study to which we added a fourth category. In order of decreasing importance, the four categories are: 1) species whose remains occur during ≥6 months in high frequency (≥50% of monthly samples); 2) species whose remains are found in ≥6 months in both high and low frequency (≥50% and <50% of monthly samples, respectively); 3) species whose remains occur during <6 months in high frequency; and 4) species whose remains occur in ≥6 months but always in low frequency.

We identified important fruit species on a yearly basis. We then ranked the species in terms of level of importance for the three-year period using two criteria. First, we considered the number of study-years in which the species appeared important (Rogers et al. 2004). And secondly, to differentiate species with equal number of study-year in which they appeared important, we considered the rank of the category to which the species was assigned (with category 1 having the highest weight and category 4 the lowest).

3.2.5. Preferred and Fallback fruits

Preferred foods are, by definition, seasonal foods that, when available, constitute most of the diet. However, preferred foods can be available for a very short and irregular period of time and/or be rare in the environment meaning that an accurate measure of its availability imposes a prohibitive sampling effort (Marshall and Wrangham 2007). As a consequence, inaccurate or incomplete identification of preferred foods may lead to biased results. To circumvent this problem, we instead used important foods in our operational definition of FBF considering that preferred food belong to the important food category.

We used the following operational criteria to identify a fallback food (FBF): 1) food item must be an important food resource; 2) food item must be available when other important fruits are also available (overlap in FAI); 3) food item must experience an increase in consumption when the availability of important fruits decreases, and be partly ignored in periods of important fruit abundance (significant negative relationship); and 4) the observed increase in consumption should not be due to higher availability (lack of significant positive relationship).

3.2.6. Data analysis

We discarded from the dataset the months in which ≤3 faecal samples were analyzed to avoid significant sampling bias (Doran et al. 2002), resulting in 33 monthly values of occurrence of fruit remains in faeces. We worked at the genus level when fruits of congener species are consumed by the WLG, and species level otherwise. This grouping facilitates comparisons between sites where the same genera can be used as fruit food resources but the species may be different (Rogers et al. 2004), and further enable to circumvent the issue of identifying species whose fruit remains are macroscopically similar in feces. We performed correlation tests between monthly percentages of samples containing remains of species *j* and the sum of monthly fruit availability indices of all other important fruit species. We first log-transformed ($\log_{10}(y+1)$) the data in order to linearize the otherwise exponential relationship. A significant negative relationship indicates that the species may serves as FBF. For potential FBF species, we then performed an additional correlation test between the monthly percentages of samples containing remains of that species and its respective monthly FAI. A lack of significant positive relationship confirms that the species serves as FBF. We performed all statistics in Statistica 10 with α level set at 0.05.

3.3. Results

3.3.1. Important species

Fruit remains of 54 taxa were identified in faeces, representing all plant life-forms. Among them, 20 were classified as important components of the diet based on the above criteria (Table I). Of all important species identified, trees represented 75% (15/20), herbs 15% (3/20) and lianas 10% (2/20). Interestingly, the majority of the herb species and all the liana species that feature in the list of important species at La Belgique, also all feature in the top six. All woody taxa providing important fruit resources were monitored on the phenological circuit, except *Dialium pachyphyllum*. Between 10 and 14 taxa were found to be important in each study-year. Five taxa were consistently important each study-year, six others in two of the study-years and 10 in one. The only taxon fulfilling the criteria for assignment to category 1 was *Uapaca* spp. in study-year 2 (Sep 10–Aug 11).

3.3.2. Fallback species

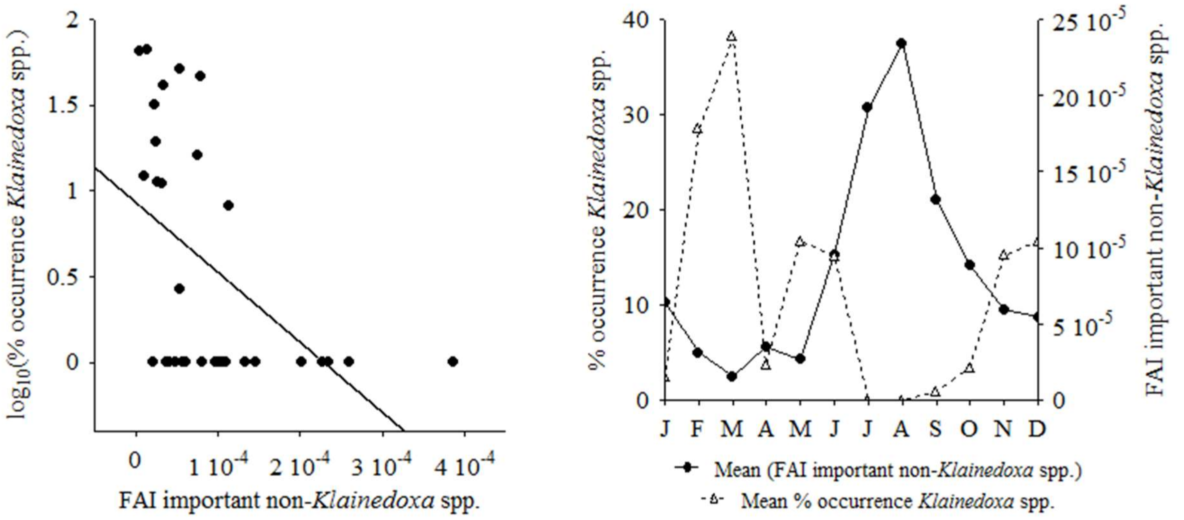
Among the 20 candidates, two taxa exhibited a significant inverse correlation between consumption rate and the availability of all other important fruit taxa, namely *Klainedoxa* spp. (Pearson correlation test:

R=-0.501, P=0.004) and *Uapaca* spp. (Pearson correlation test: R=-0.756, P<0.001) (Figure 1). The consumption rate of the fruits of both taxa was not significantly correlated with their availability (Pearson correlation test: R=-0.147, P=0.431 for *Klainedoxa* spp. and F=0.027, R=0.03, P=0.871 for *Uapaca* spp.), hence revealing both taxa to fulfil the operational criteria of FBF.

Table I. List of 20 important taxa, ranked by level of importance in the western lowland gorilla diet at La Belgique research site, southeast Cameroon, for the period September 2009–August 2012. Importance classification was derived from Doran et al. (2002). H: herb; L: liana; St: strangler; T: tree; n.a.: fruit not available (on phenological circuit); n.c.: fruit not consumed; n.i.: fruit consumed but not important.

		Category				
	Life-form	year 1	year 2	year 3	No. year	Rank
Uapaca spp.	T	II	I	II	3	1
Aframomum spp.	H	III	II	II	3	2
Duboscia spp.	T	II	IV	II	3	3
Landolphia spp.	L	III	II	III	3	4
Cissus dinklagei	L	IV	III	II	3	5
Marantochloa spp.	H	II	n.i.	II	2	6
Tetrapleura tetraptera	T	IV	n.i.	II	2	7
Chrysophyllum spp.	T	n.i.	III	III	2	8
Myrianthus arboreus	T	III	n.i.	IV	2	9
Desplatsia spp.	T	IV	IV	n.i.	2	10
Ficus spp.	T, St	IV	n.i	IV	2	10
Klainedoxa spp.	T	n.i.	n.i	II	1	12
Megaphrynium macrostachyum	H	n.c.	III	n.i.	1	13
Nauclea/Sarcocephalus	T	III	n.c.	n.i.	1	13
Dialium spp.	T	n.a.	III	n.a.	1	13
Celtis spp.	T	III	n.a.	n.a.	1	13
Vitex spp.	T	n.i.	n.i.	III	1	13
Trichoscypha spp.	T	III	n.i.	n.i.	1	13
Sorindeia grandifolia	T	III	n.i.	n.i.	1	13
Duguetia staudtii	T	n.c.	III	n.i.	1	13

Klainedoxa spp.



Uapaca spp.

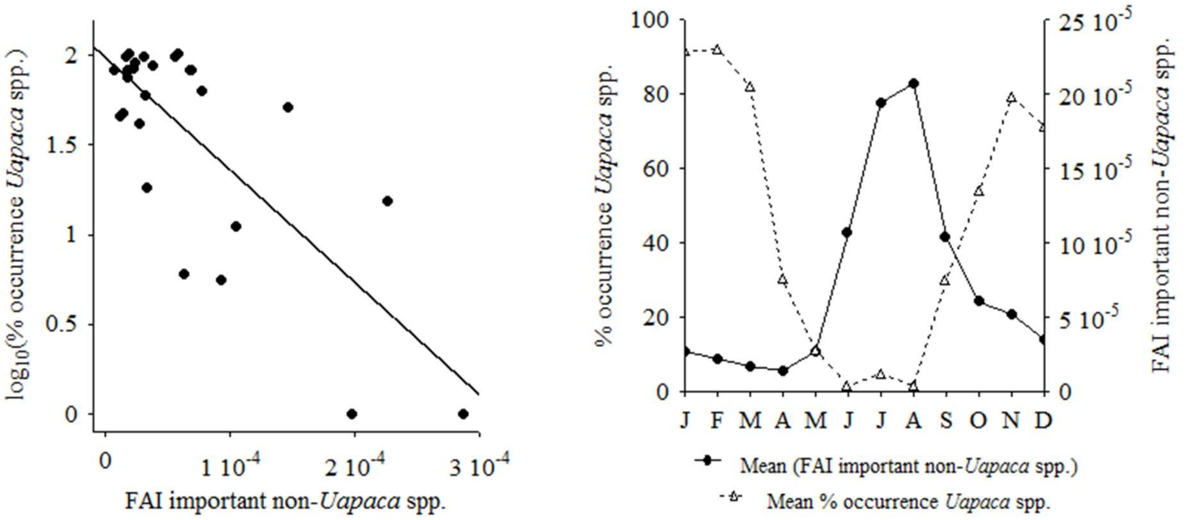


Figure 1. Relationships between the monthly percentage of fallback fruit remains in western lowland gorilla faeces and the monthly fruit availability index of other important species in the diet at La Belgique research site, southeast Cameroon, for the period September 2009–August 2012. Left: Results of the correlation tests. Right: Comparison of mean values for each calendar month.

3.4. Discussion

3.4.1. Important fruits

This study investigated the importance of fruit food at La Belgique in the diet of the western lowland gorilla population under study in the site, to complement existing knowledge on the importance of fruits to gorillas. The main limitation of our study is that we investigated only those fruit species whose consumption can be identified from morphological examination of faeces; our methodology did not allow us to identify fruit resources for which remains do not occur in faeces, such as those whose seeds are too large to be swallowed and/or their pericarp is completely digested in the WLG gut (e.g., *Irvingia gabonensis*, *Baillonella toxisperma*). Furthermore, we did not attempt to operationally define and identify preferred fruit foods in the site, given the difficulties of doing so (as explained in the methods section), and so our operational definition of FBF utilises a measure of important fruit availability instead of preferred fruit availability. Despite these limitations, the results obtained from our study are valuable as they contribute to a fuller understanding of the dietary adaptations of gorillas in times of fruit scarcity.

Twenty fruit taxa of the 54 (37%) identified in the WLG diet at La Belgique represented 'important' dietary components (Table I), and within the list of important fruit taxa, most have already been described as important for other populations of WLG (Rogers et al. 2004). Despite the predominant representation by tree species, all plant life-forms were represented in the importance list, and the majority of herbs and lianas that featured in the list were found in relatively high positions. Interestingly, two herbs occupy the second and third ranks of importance. Collectively referred to as THV, the importance of herbs for the WLG as a non-fruit food resource is widely accepted (Doran-Sheehy et al. 2009; Doran et al. 2002; Nishihara 1995). It has even been advocated that the availability of this taxon dictates the bearing capacity of a site for the WLG (Fay and Agnagna 1992). In agreement with studies in other field sites, herbs are the most commonly-used nesting material in La Belgique (Willie et al. 2014). From our study it appears that THV may also provide some particularly important fruit resources for the WLG, as also demonstrated in other sites (e.g., Rogers et al. 2004).

Two liana taxa occupy the fifth and sixth ranks of importance, *Landolphia* spp. and *Cissus dinklagei*. The importance of lianas in the diet of primates has been reported in many sites for many primate species. For instance, fruits of the water-liana *Cissus dinklagei* contributed to the highest number of feeding events for a troop of *Cercopithecus cephus* at M'passa Reserve, Gabon (Sourd and Gautier-Hion 1986). Fruits of some liana-type species of the genus *Ficus* are such an important dietary component for gibbons (*Hylobates albibarbis*) at Gunung Palung National Park, Indonesia, that local gibbon density is strongly correlated to *Ficus* stem density (Marshall et al. 2009). The diet of the chimpanzee population of Rubondo Island, Tanzania, is composed of mainly (35%) liana fruit species (Moscovice et al. 2007). Our study also acknowledges the importance of lianas as seasonal fruit resources.

3.4.2. Fallback fruits at La Belgique

The fruiting phenology of fallback fruit taxa should contrast with the phenology of forest-wide species in that they lack real seasonality (Marshall and Wrangham 2007). In La Belgique, when peaks of

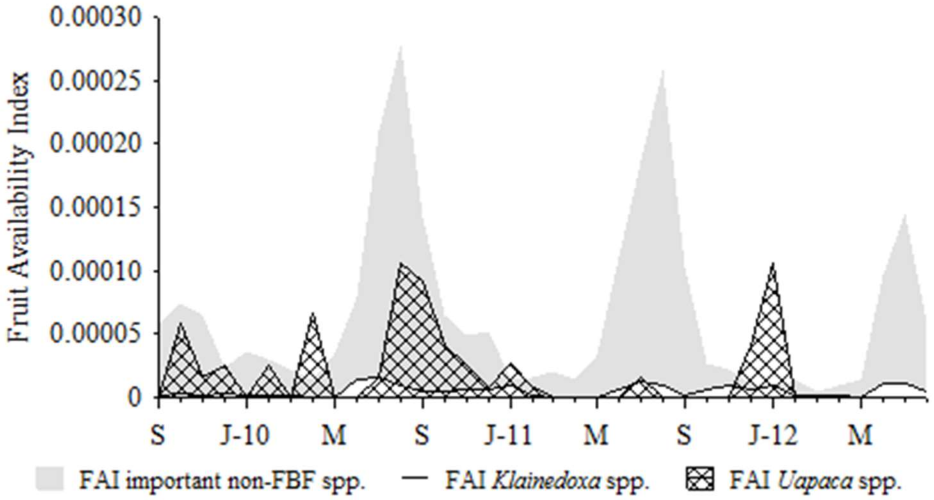


Figure 2. Fruit availability index over the course of the study (September 2009–August 2012) of important non-fallback food and fallback food (FBF) for the western lowland gorilla at La Belgique research site, southeast Cameroon.

important fruit production occurred consistently during the small dry season (July–August) (Figure 2), peaks in the availability of *Uapaca* spp. and *Klainedoxa* spp. follow a different and less regular pattern across seasons and years. The fruits of these two taxa are potentially available in each calendar month as evidenced by remains in faeces and phenological records. This pattern is attributable to the very irregular timing of ripe fruit production within the year for some species (e.g., variance of 60 d around the mean date of ripe fruit production for *Uapaca guineensis* and 42 d for *Klainedoxa* spp. in the Lopé National Park, Gabon; Fourrier 2013), an between species within the same taxon, and the between-year irregularity in the timing of phenophases of both taxa (Fourrier 2013). As such, these fruits are often available when other important fruits are absent or in low abundance. Fruits of *Uapaca* spp., however, provide a more reliable fallback food for the WLG due to the a more regular peak in ripe fruit production in the great dry season (December–January) when fruit availability of forest-wide non-*Uapaca* species is near its lowest.

Between these two taxa, the fruits of *Uapaca* spp. fulfil the most convincing operational criteria of FBF. In terms of duration, *Uapaca* spp. remains were present in faeces in 26 months (72.2%), of which 16 (44.4%) occurred in >50% of faeces; whereas remains of *Klainedoxa* spp. were present in 15 months (41.7%), and only four (11.1%) occurred in >50% of faeces. *Uapaca* spp. trees are very abundant in La Belgique (Tagg et al. 2013), especially in riverine and swamp forests where as many as 87 stems/ha (dbh > 10 cm) can be found, whereas no more than 3.8 stems/ha of *Klainedoxa* spp. are found in the site (appendix). Furthermore, these two FBF taxa differ in the type of fruit they produce: fruits of *Uapaca* spp. have a fleshy sweet pulp (Rogers et al. 1990; Sourd and Gautier-Hion 1986), whereas fruits of

Klainedoxa spp. are highly fibrous and therefore likely to be less digestible. The nutritional properties of *Uapaca* spp. fruit flesh deserve further investigation in order to understand how they complement the low-quality diet provided by the staple FBF (i.e. non-fruit plant parts; Doran-Sheehy et al. 2009) in periods of ecological stress.

In the Lopé National Park, the fruits of *Uapaca* spp. also constitute a highly important resource for the inhabitant population of WLG (Williamson 1988), being consumed in higher proportion than expected based on their availability (Fourrier 2013). Remains of *Uapaca* spp. fruits (seeds) were present in 33.8% of the 990 faecal samples analyzed over a 7.5-y period (Fourrier 2013), a proportion similar to that observed at La Belgique in the present study. However, in Lopé, *Uapaca* spp. appear to occur in much lower densities, being absent from the top 20 of the most abundant species (Williamson 1988), and they exhibit not two but only one peak of fruit production (Fourrier 2013). Considering this, *Uapaca* spp. fruits may fulfil another, though still important, ecological function for the WLG in Lopé.

Ficus sp. is a well-known fallback resource taxon for most ape species, although no evidence of this exists in the case of gorillas (Harrison and Marshall 2011; Marshall and Wrangham 2007; Yamagiwa and Basabose 2009). Our data support the trend by revealing that figs do not appear to serve as a fallback fruit for the WLG at La Belgique, although they are important fruit items (ranking 10th). It would be interesting to investigate whether the sympatric population of chimpanzees at La Belgique uses figs or *Uapaca* spp. as a fallback resource, as this may allow us to discuss the potential for food partitioning to reduce competition and enable coexistence.

3.4.3. Human disturbance

Like THV, *Uapaca* spp. and *Klainedoxa gabonensis* are light-demanding species, colonizing secondary growth forests (Hawthorne 1995; Meunier et al. 2015). Other non-fallback important fruit species for the WLG at La Belgique have the same regeneration guild. The suitability of secondary forest for the WLG has been widely documented across its range (Dupain et al. 2004; Matthews and Matthews 2004; Stokes et al. 2010). WLG are also found at high density in Marantaceae forests (Bermejo 1999; Fay and Agnagna 1992), where the THV carpet is very dense. Both forest types (secondary and Marantaceae forests) often result from intensive modification of the forest by humans. In Central Africa, the myth of ‘primary forests’ has crumbled in recent decades: widespread archaeo-pedological studies have revealed several waves of human colonisation of forested lands all across the Congo Basin over the last millennia (Oslisly et al. 2013). The Marantaceae forests of northern Congo probably result from palm-oil cultivation and exploitation that took place predominantly 1500 years ago (Gillet 2013). Human disturbance at the origin of secondary forests are more recent, having taken place around 2-7 centuries ago with the use of slash-and-burn practices (Brncic et al. 2007; Gillet 2013; Morin-Rivat et al. 2014 ; Oslisly et al. 2013; van Gemerden et al. 2003).

Past human disturbance of Central African forests has considerably modified the structure and composition, which remains noticeable in the present day (Bourland 2013; van Gemerden et al. 2003). Light-demanding species often dominate the forests. As those human-induced perturbations provided suitable conditions for the WLG, it raises the question as to whether current human disturbance can maintain such habitat suitability. Selective logging operations, accompanied with a wildlife management program, have been shown to provide suitable conditions for the WLG, as inferred by their relatively high densities in logged forests (Clark et al. 2009). If canopy opening as a result of logging operations favours the regeneration of light-demanding species which in turn provide an important food resource for the WLG, we might expect a long-term positive impact of such human disturbance on habitat suitability for gorillas (though, this might not be the case for all forest-dwelling species).

3.4.4. Conclusion and recommendations

In locations where WLG diet has been investigated, at least one species per site has been documented to provide a seasonally important fruit supply for the WLG and these species tend to be among the most common in the forest (*Cola lizae*, Lopé, Gabon, *Anonidium mannii*, Ndoki and Mondika) (Rogers et al. 2004). At La Belgique, *Uapaca* spp. trees are very common. In addition, they rank as the most important fruit resource for gorillas in La Belgique, and are likely to play a particularly important role in WLG fitness. The high densities of *Uapaca* spp. in the Dja complex (Djuikouo et al. 2010; this study), together with the relatively high densities of THV (Willie et al. 2012), may explain the apparently high WLG densities in this region (Dupain et al. 2004). It is worth noting that the importance of *Uapaca* spp. fruits as a food resource has also been documented for cercopithecines in the Dja Biosphere Reserve (Poulsen et al. 2002; Poulsen et al. 2001). The ecological role of *Uapaca* spp. for the entire frugivore community deserves further investigation.

The high density of *Uapaca* spp. trees in swamp forests assigns such a habitat type within the Dja complex as one of high conservation value. As swamps are not disturbed by logging operations, this habitat type may provide a refuge for frugivorous species in logging concessions. We recommend the consideration of swamps in the delimitation of high conservation value zones in the management plan of logging companies seeking certification. An effort should also be made to reduce collateral damage to lianas, particularly those of the genus *Landolphia* and the species *Cissus dinklagei*. For this latter, known as the ‘water liana’, additional measures should be taken to avoid that field workers further contribute to the logging-induced damaging of the liana population by cutting stems to quench their thirst.

Appendix. List of the species monitored for fruiting phenology between September 2009 and August 2012 and species whose fruits were consumed by the western lowland gorilla at La Belgique research site, southeast Cameroon. Density values are given based on 130 botanical plots of 0.1 ha each; TF: Terra Firma; PF: Periodically Inundated (swamp forests and riparian forests); n.a.: not available; H: herb; L: liana; Sh: Shrub; St: strangler; T: tree

					Density (No. stem/ha)	
Family	Species	life-from	No. stems monitored	Consumption	TF	PF
Anacardiaceae	*Antrocaryon klaineanum*	T	4	this study	0.28	0
	Antrocaryon micraster	T	3	Djoufack et al. 2007	0.09	0.48
	Pseudospondias longifolia	T		this study	0.21	0.71
	Sorindeia grandifolia	T	10	this study	10.46	6.67
	Trichoscypha acuminata	T	10	this study	2.31	0
	Trichoscypha oddonii	T	10	this study	0.65	0
Annonaceae	*Annickia chlorantha*	T	11	this study	8.61	0
	Anonidium mannii	T	10	this study	8.15	0.48
	Cleistopholis patens	T	10	this study	0.93	0.48
	Cleistopholis staudtii	T	6		0.74	0
	Duguetia staudtii	T	10	this study	1.11	0.95
	Monodora myristica	T	10	this study	2.96	0
	Polyalthia suaveolens	T	10	this study	17.41	0
	Uvariastrum pierreanum	T		this study	n.a.	n.a.

	Xylopia hypolampra	T	11	this study	1.94	0
	Xylopia rubescens	T	9		0.65	0
	Xylopia staudtii	T	4		1.30	0.48
Apocynaceae	*Landolphia* spp.(ca. 5 species)	L	38	this study	9.26	0
	Rauvolfia sp.	T	2		0.56	0
	Tabernaemontana crassa	T	10	this study	45.56	0
	Tabernaemontana penduliflora	T	10		0.09	0
Arecaceae	Laccosperma secundiflorum	P		this study	n.a.	n.a.
	Raphia spp.	P		this study	0	1.42
Burseraceae	*Canarium schweinfurthii*	T	10	this study	0.28	0.95
	Santiria trimera	T	10	this study	7.13	3.81
Clusiaceae	Garcinia kola	T		this study	n.a.	n.a.
	Mammea africana	T	11	Djoufack et al. 2007	0.83	2.38
	Symphonia globulifera	T	12		0.09	0
Ebenaceae	*Diospyros crassiflora*	T	5		0.59	0
Euphorbiaceae	*Discoglypremna caloneura*	T	7	this study	1.67	0.48
	Uapaca acuminata	T	10	this study	4.72	0
	Uapaca guineensis	T	10	this study	4.44	9.05
	Uapaca mole	T	10	this study	3.98	0.48

	Uapaca pynaertii	T		this study	n.a.	n.a.
	Uapaca vanhouttei	T	9	this study	1.30	28.10
Fabaceae	Dialium pachyphyllum	T		this study	n.a.	n.a.
	Dioclea reflexa	L	4	this study	0.19	0
	Tetrapleura tetraptera	T	10	this study	1.11	0
Flacourtiaceae	*Oncoba crepiniana*	T	10	this study	2.41	1.90
Irvingiaceae	*Irvingia gabonensis*	T	10	this study	1.20	0
	Irvingia grandifolia	T	12	this study	0.56	0.48
	Klainedoxa gabonensis	T	21	this study	3.80	0.48
Leeaceae	*Leea guineensis*	Sh		this study	n.a.	n.a.
Marantaceae	*Halopegia azurea*	H		this study	n.a.	n.a.
	Hypselodelphys scandens	H		this study	n.a.	n.a.
	Marantochloa filipes	H		this study	n.a.	n.a.
	Marantochloa purpurea	H		Djoufack et al. 2007	n.a.	n.a.
	Megaphrynium macrostachyum	H		this study	n.a.	n.a.
	Sarcophrynium brachystachys	H		this study	n.a.	n.a.
Meliaceae	*Leplaea cedrata*	T		this study	0.16	0
Moraceae	*Ficus mucuso*	T	5	this study	0	0
	Ficus sp. (strangler)	St	10	this study	0.37	0

	Milicia excelsa	T	11	this study	0.65	0
	Myrianthus arboreus	T	10	this study	4.54	0
	Treculia africana	T		this study	0.05	0
Myristicaceae	*Coelocaryon preussii*	T	8	Djoufack et al. 2007	0.83	1.43
	Pycnanthus angolensis	T	7	Djoufack et al. 2007	0.46	0
	Staudtia kamerunensis	T	8	Djoufack et al. 2007	1.49	0
Olacaceae	*Heisteria parvifolia*	T	10	this study	3.61	0.48
	Strombosia grandifolia	T	10		9.07	19.52
	Strombosia pustulata	T	11		4.91	0
	Strombosiopsis tetrandra	T	10	Djoufack et al. 2007	2.59	0.48
Pandaceae	*Microdesmis keayana*	Sh		this study	n.a.	n.a.
Passifloraceae	*Barteria fistulosa*	T	9		0.46	0
	Barteria sp.	unk.		this study	n.a.	n.a.
Rubiaceae	*Hallea ledermannii*	T	2		0.09	0
	Nauclea diderrichii	T	10	this study	1.02	0
	Psychotria arnoldiana	Sh		this study	n.a.	n.a.
	Sarcocephalus pobeguinii	T	10	this study	0	8.10
	Tricalysia sp.	T		this study	0.96	0.71
Sapindaceae	*Chytranthus* cf *talbotii*	T		this study	n.a.	n.a.

	Chytranthus setosus	T		this study	n.a.	n.a.
	Lecaniodiscus cupanioides	T		this study	4.39	6.84
Sapotaceae	*Baillonella toxisperma*	T	4	this study	0.19	0
	Chrysophyllum boukokoënse	T		this study	0.26	0.24
	Chrysophyllum lacourtianum	T	10	this study	0.65	0
Tiliaceae	*Desplatsia dewevrei*	T	11	this study	4.63	2.86
	Desplatsia subericarpa	T	10	this study	2.87	1.43
	Duboscia macrocarpa	T	10	this study	1.67	0
	Duboscia viridiflora	T	10	this study	3.33	0
Ulmaceae	*Celtis mildbraedii*	T	10		6.02	0
	Celtis tessmannii	T	11	this study	2.41	0
Verbenaceae	*Vitex rivularis*	T	10	this study	1.39	0
Vitaceae	*Cissus dinklagei*	L	10	this study	4.35	0
Zingiberaceae	*Aframomum arundinaceum*	H		this study	n.a.	n.a.
	Aframomum polyanthum	H		this study	n.a.	n.a.
	Aframomum sp.	H		this study	n.a.	n.a.
	Aframomum sulcatum	H		this study	n.a.	n.a.

CHAPTER IV.

SEED DISPERSAL QUANTITY

Quantity and spatial distribution of seeds dispersed by a western lowland gorilla population in south-east Cameroon.

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ABSTRACT

Understanding the ecological function of large frugivores in tropical forests is important considering their central position in seed-dispersal networks. This study illustrates the seed-dispersal effectiveness of a western lowland gorilla (*Gorilla gorilla gorilla*) population in Cameroon by looking at the interaction of seed quantity, species regeneration traits and the environmental characteristics of the deposition sites (sleeping sites *vs.* feeding trails) in order to discuss the role of gorillas within the ecosystem. The analysis of 1030 faecal samples collected over a 3-y period (September 2009–August 2012) showed that gorillas dispersed a diverse array of species (58 spp. identified), with an average of 289 intact seeds (>5 mm) d^{-1} per individual. Seed damage during mouth and gut processing occurred for 12 spp., generally accounting for <5% of specific seed load. Germination trials suggested that germination success of passed seeds remained unchanged (N = 6 spp.) or improved (N = 5 spp.) after gut passage compared to hand-cleaned seeds, with one exception. Indicator species identification (IndVal method) and General Discriminant Analysis suggested that sleeping sites (N = 36), as a main type of seed deposition site, correspond to regenerating microhabitats and correspondingly degree of canopy openness is one variable discriminating significantly this type of deposition site with random locations in the forest (N = 36) used as a proxy for non-directed seed deposition on feeding trails. With a mean canopy openness of 19%–27%, sleeping sites offer optimal light conditions for the seedling recruitment of non-pioneer light-demanding species, whose seeds encompass 47.4% of the total seed load dispersed over the 3-y period. From this study, it is hypothesized that the gorilla performed directed-dispersal of some light-demanding plant species at sleeping sites, and hence, by being actively implicated in gap-phase dynamics, fulfils a valuable ecological function within its ecosystem.

4.1. Introduction

In interacting plant–frugivore assemblages, species play varying roles in maintenance and dynamics of the composite network. In general, large-bodied frugivores are seen as pivotal components of such seed-dispersal networks because they interact with many plant species, eventually interconnecting the different seed dispersal syndromes (Gautier-Hion et al. 1985). Consequently, their loss can cause cascading disrupting effects within the network, and hence a risk to the ecosystem integrity (Vidal et al. 2013). At plant population level, some frugivores may contribute disproportionately more to recruitment of individuals of a given plant species than other frugivores; i.e. they have a higher seed dispersal effectiveness (Schupp et al. 2010). Likewise, plant species differ in terms of their recruitment probability per seed dispersed by a same frugivore. Differences in quantity of seeds dispersed and in the extent to which gut passage alters seed viability (seed breakage) and germinability (seed scarification) account for differences in seed dispersal effectiveness (Schupp et al. 2010). An arguably greater aspect influencing the seed dispersal effectiveness is the pattern and location of seed deposition (Calviño-Cancela and Martín-Herrero 2009, Schupp et al. 2010) because the characteristics of the seed deposition site will influence seed germination (through seed predation avoidance; Holl and Lulow 1997), seedling establishment (through dung beetle activity; Petre et al. 2015b – see chapter 6), and the likelihood of attaining adulthood (dependent upon whether conditions meet the physiological requirements of the plant species; Agyeman et al. 1999; Norden et al. 2009; Veenendaal et al. 1996). The effectiveness of seed dispersal is therefore dependent upon movement, defecation patterns and habitat preferences of animals on the one hand, and plant-specific ecological niches on the other. When a plant–frugivore system results in most seeds being deposited in sites particularly suitable for recruitment this is referred to as directed dispersal (Howe and Smallwood 1982) and the disperser is considered critical for the population dynamics of the plant species concerned (Wenny 2001).

In the present study, we investigate key determinants of the seed dispersal effectiveness of a western lowland gorilla population (*Gorilla gorilla gorilla*; hereafter referred to as WLG) at a previously unstudied site, in south-east Cameroon. In Congo Basin forests, the WLG is assumed to occupy an important position in the seed-dispersal network (Petre et al. 2013), being the second-largest forest-dwelling species after the elephant and having a diverse frugivorous repertoire. Moreover, in the Lopé National Park, Gabon, where most of the available data on the WLG seed-dispersal activity belong to (Rogers et al. 1998; Tutin et al. 1991; Voysey et al. 1999a,b) post-dispersal seed fate monitoring suggested that the WLG performs directed-dispersal at sleeping sites (Wenny 2001). However, WLG populations are declining in abundance at an alarming rate and consequently the ecological service provided by this ape species may vanish locally with the potential of impacting on the whole seed-dispersal network.

Specifically, our objectives were three-fold: (1) To estimate the quantitative seed dispersal activity of gorillas. We hypothesised that given the diet breadth, gape width and body size of gorillas, a large quantity of seeds belonging to a large variety of species will be found in faeces, but given diet preferences (Doran et al. 2002) a limited set of species will encompass most of the seed load dispersed. (2) To assess the treatment of seeds in the gorilla mouth and gut. We hypothesised that, as with other non-flying mammals, mouth processing and gut passage will not reduce germination performances and may serve to improve them (Traveset 1998). (3) To characterize seed deposition habitats. We hypothesised that sleeping sites exhibit particular environmental characteristics (Voysey et al. 1999b), that are not reliably present at random sites in the forest and which may influence the outcome of seed dispersal.

4.2. Study site

The study was conducted between September 2009 and August 2012 in the research site 'La Belgique' at the northern periphery of the Dja Biosphere Reserve, south-east Cameroon (013°07'–013°11'E, 03°23'–03°27'N). The research site covers approximately 40 km² of mixed lowland forest (600–700 m asl), in the transition zone between evergreen and semi-deciduous forests (Letouzey 1968). Terra firma forests encompass 74% of the study site and are dominated by old secondary forests, whereas flooded areas (inundated clearings, periodically inundated swamps and riparian forests) account for the remaining 26%; Willie et al. 2012) . Climatic data recorded in the site between January 2010 and December 2012 correspond to a humid tropical climate with two rainy seasons (February–June and September–November) interspersed by two dry seasons (monthly rainfall <100 mm; Willie et al. 2014). Mean annual rainfall ranged between 1315–1831 mm and mean minimum and maximum daily temperatures were 19.8°C and 27.2°C, respectively.

4.3. Study species

Western lowland gorilla

The WLG groups present at La Belgique are not habituated to human presence; therefore, seed-dispersal activity was investigated indirectly through faecal analysis. A density of 0.69 individual km^{-2} was estimated based on a standing crop nest count survey conducted in 2008 (Projet Grands Singes, unpubl. data). Genotyping from faecal samples collected at nine WLG sleeping sites distinguished two distinct groups of at least seven and 12 individuals respectively, as well as one solitary male (Martine Peeters, pers. comm.).

Gorilla defecation, and hence seed deposition pattern, is spatially and temporally bimodal with half of all faecal production occurring at sleeping sites where faeces are consequently aggregated, and the other half on feeding trails where they are scatter-dispersed (Todd et al. 2008). Gorillas establish a new sleeping site at a different location most nights (Tutin et al. 1995), but sometimes return to previously used sleeping sites (Iwata and Ando 2007). Gorillas exhibit long daily path lengths (averaging 2 km; Cipolletta 2003) across an extensive home range (Doran-Sheehy et al. 2004), and, unlike elephants, tend not use an established system of permanent trails (Remis 1997, pers. obs.).

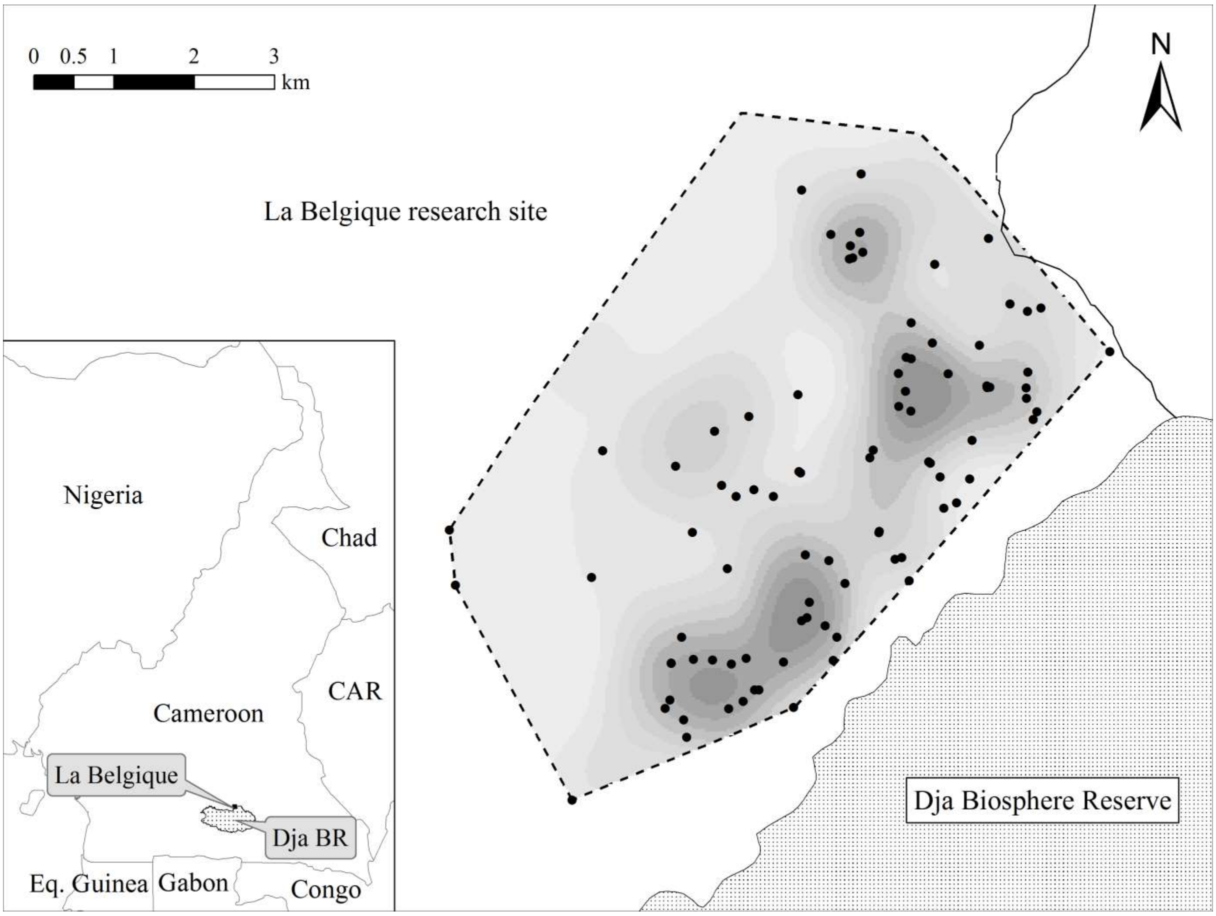

Figure 1. Delimitation and sampling intensity of faecal collection area at La Belgique research site, south-east Cameroon. Dots represent the distribution of the 112 sleeping sites sampled between September 2009 and August 2012, and the level of grey shading correlates with the sampling intensity of feeding trails based on a kernel density function of feeding trail records (N = 1554) where lighter shading indicates lower densities and darker shading higher densities.

4.4. Methods

4.4.1. Faecal collection and analysis

During 15 consecutive d mo^{-1} throughout the study period, we systematically sought recently used gorilla feeding trails (< 48 h old), eventually leading to sleeping sites, to collect fresh faeces. We complemented the sample size with opportunistic encounters of faeces outside of these collection periods. Overall, we collected 1030 faecal samples with a monthly mean ± SD of 28.6 ± 17.1 faeces (range = 2–66), over a 40.3-km^2 area (Figure 1). We weighed, washed and sieved all faecal samples and separated food remains (leaf fragments, fibre, bark, fruit skin and seeds) previously dried at ambient temperature. We identified individual seeds to species level where possible, measured seed dimensions with a calliper and assessed volume using the formula for ellipsoids ($4/3\ \pi$ abc; Williamson 1988). We determined the regeneration guilds of species according to shade tolerance and soil hydromorphy, consisting of pioneer, crypto-pioneer (i.e. species requiring light in early life stages but able to survive in the shade at later ones), non-pioneer light-demanding, shade-bearing and swamp species (J.-L. Doucet pers. comm.; Hawthorne 1995). For each faecal sample, we recorded the number of species and component seeds ≥5 mm. We recorded only presence/absence data for small-seeded species (<5 mm). Although exceeding this threshold, we similarly recorded presence/absence of seeds of *Duboscia* spp. (Tiliaceae; mean seed dimensions 10.4 × 5.5 × 2.7 mm) due to their inconspicuousness; being flat, soft, and generally difficult to distinguish from the fibre and leaf material of the faeces.

4.4.2. Seed treatment in mouth and gut

We scrutinized seeds individually to describe the proportion of intact *vs*. damaged (broken/pierced) seeds found in faecal samples. For abundantly dispersed species, we sowed a subsample of intact seeds (N ≥ 30 seeds when possible) in a field nursery using soil collected from the study site to determine the germination success of passed seeds. For species common in the study site, we compared germination success between gut-passed seeds and those manually depulped from fresh fruits. We used the above-ground emergence of seedling stems to define germination success (Nchanji and Plumptre 2003). We monitored germination on a daily basis for at least 6 mo after sowing, though for species known to exhibit dormancy we monitored them for up to 1 y (*Erythrophleum suaveolens* (Fabaceae), *Marantochloa filipes* (Marantaceae) and *Vitex* cf. *rivularis* (Verbenaceae)). As we did not verify if emergence failure was a result of pre-germination viability loss (for instance through tetrazolium assay) or pre-emergence death (by digging up sown seeds), estimates of germination success are conservative.

4.4.3. Characterization of seed deposition site

In order to characterize seed deposition sites according to the defecation patterns of gorillas, we considered sleeping sites as one type of seed deposition habitat and all other forest locations (potential feeding trails) as another. We thoroughly described the extant vegetation composition and structure in centrally positioned 40 × 40-m plots, subdivided into 100 4 × 4-m grid cells, in 36 sleeping sites and in 36 randomly chosen forest patches (control plots) along the research transects. Within these plots, we recorded (1) canopy openness estimated from hemispherical photographs taken 1 m above the forest floor in 10 randomly chosen grid cells and, in the case of sleeping sites, we took additional photos above each nest because a large proportion of faeces are found in close proximity to nests (Mehlman and Doran 2002; pers. obs.); (2) canopy structure described from presence/absence data (0/1) of foliage in three vertically superimposed zones (2–10 m, 10–20 m and >20 m) at the centre of each grid cell (the sum of all data provided an index of foliage density and connectivity scoring from 0 to 300, where the lower the index value the more sparse and disconnected the canopy, and the higher the index value the more dense and continuous); (3) density of woody stems of diameter at breast height (dbh) >10 cm for trees and >5 cm for lianas; (4) tree dbh structure; (5) basal area; (6) mean tree height; and (7) mean understorey cover described by visually assessing the percentage of the ground covered by herbs, lianas and shrubs separately and all together in each grid cell.

4.4.4. Data analysis

Except otherwise specified, we performed all statistics in Statistica 10 with α level set at 0.05. Means are given with standard deviation (mean ± 1 SD). We tested differences in germination percentage between gut-passed and manually depulped seeds with a Chi-squared test of independence. We used the following formula to measure the seed-dispersal quantity (Q) for each species each month:

$$Q_i = \sum_{j=1}^{n} (S_{ij} W \gamma_{ij} d_i f)$$

where S_{ij} denotes the mean number of seeds of species j per gram of faeces during month i, W the mean weight of faecal samples, γ_{ij} the frequency of appearance in faecal samples of species j during month i, d_i the number of days within month i, and f the faecal production rate as measured by Todd et al. (2008) (5.57 faeces d^{-1}). The sum of all specific monthly values gives the total seed load dispersed by one WLG individual during the study period. Similarly, we measured the daily seed rain dispersed by the WLG population at La Belgique by multiplying Q (with d set to 1) by the WLG density in the site (Poulsen et al. 2001). We analyzed hemispherical photos of the canopy in the Gap Light Analyzer software 2.0 which calculates the percentage of pixels occupied by sky. We performed a general discriminant analysis (GDA) to investigate if and which environmental variables differ between sleeping sites compared to random areas (control plots) in the forest. We computed a best-subset selection of predictors based on Wilks's Lambda and examined standardized canonical discriminant function coefficients to determine the relative importance of each explanatory variable. Evaluation of model performance was based on the proportion of plots correctly assigned to either sleeping sites or control plots using the defined classification function. We cross-validated the stability of the model by applying to each plot a function derived from all other plots. To test if sleeping sites and control plots differ in terms of botanical composition in addition to structure, and hence belong to different vegetation types, we computed Chao's Abundance-based Sørensen Similarity Index in EstimateS 9.1.0 to compare species assemblages. We computed an index value for each pairwise plot combination between and within types of defecation site as well as between all sleeping site plots combined and all control plots combined. We then tested differences in similarity of botanical composition within defecation site type plot with a Mann-Whitney test. Finally, we calculated an indicator value (IV) in IndVal 2.0 (Dufrêne and Legendre 1997) to identify indicator species of both defecation site types, to further assist in assigning sites to vegetation type. Statistical significance of the resulting IV was evaluated for each species using the Monte Carlo procedure with 999 iterations of individual re-ordering randomization among the two groups.

4.5. Results

4.5.1. Plant species dispersed

Seeds found in WLG faeces varied greatly in shape, size, fruit type, life-form and regeneration guild. Those successfully identified belonged to a minimum of 58 species (some species of the same genus are macroscopically indistinguishable in seed form, e.g. *Landolphia* spp. (Apocynaceae), *Ficus* spp. (Moraceae), and *Uapaca* spp. (Euphorbiaceae)) from 24 families (Appendix 1). The plant life-forms represented were trees (44 spp.; 75.9%), herbs (7 spp.; 12.1%), shrubs (3 spp.; 5.2%), lianas (3 spp.; 5.2%) and strangler epiphytes (1 sp.; 1.7%). Twenty-four of the 50 woody species (non-epiphyte) presented a light-demanding regeneration guild, recruiting either in open-canopied terra firma habitats (21 spp.; 42%) or on hydromorphic soil (3 spp.; 6%), whereas the shade-bearing guild was represented by 22 spp. (44%). The remaining four species were of unknown regeneration guild.

Most species dispersed produce fleshy fruits; however, we also found intact seeds from fibrous fruits (e.g. *Duboscia* spp., *Desplatsia* spp. (Tiliaceae) and *Klainedoxa* sp. (Irvingiaceae)) and pods (*Erythrophleum suaveolens*). Intact seeds measured a maximum length of 53 mm (*Anonidium mannii* (Annonaceae)) and volume of 9 cm^3 (*Trichoscypha oddonii* (Anacardiaceae)). On average, one faecal sample contained seeds of 2.4 ± 1.4 species (range = 0–12), whereas the mean number of species dispersed per month was 10.6 ± 7.6 (range = 0–33; no seeds were found in March 2011 in the two samples analysed).

4.5.2. Seed treatment in mouth and gut

We found damaged seeds for 12 of the 58 identified species in 10.7% of faeces and for unidentified morphotypes in another 1.8% of faeces. In general, damaged seeds accounted for < 5% of the specific seed load (Appendix 1) except for *Desplatsia* spp. and *Heisteria parvifolia* (Olacaceae), which respectively exhibited 15.2% and 49.9% of damage. Finally, we found 7.9% of seeds of *Dialium pachyphyllum* (Fabaceae) in a degraded state, probably partly digested. Seeds remaining intact after gut passage retained a high average germination percentage of 65.8% (Appendix 2). Comparative tests suggested a significant change in germination success of seeds after gut passage for six of the 12 species tested; five exhibited a higher germination success after gut passage and one a lower (Table 1).

Table 1. Results of the germination trials comparing the germination success (%) of gorilla gut-passed seeds to the one of manually depulped seeds of 12 abundant dispersed species. Gut-passed seeds were retrieved in fresh faeces (< 48 h old) of a western lowland gorilla population at La Belgique research site, south-east Cameroon, collected between September 2009 and August 2012. Control seeds were manually depulped from fresh fruits collected at La Belgique. Germination trials were performed in a field nursery.

	Germination percentage (no. seeds sown)		χ^2 test
	Gut passed	Manually depulped	P-value
Chrysophyllum boukokoënse	67.9 (56)	62.5 (56)	NS
Chrysophyllum lacourtianum	85.5 (83)	57.8 (83)	<0.001
Chytranthus setosus	93.8 (16)	87.5 (16)	NS
Duboscia sp.	25.0 (60)	1.5 (63)	<0.001
Ficus sp.	78.7 (300)	0.0 (300)	<0.001
Heisteria parvifolia	79.2 (24)	33.3 (30)	<0.001
Landolphia sp.	53.3 (60)	82.8 (58)	<0.001
Monodora myristica	95.6 (136)	93.5 (108)	NS
Myrianthus arboreus	75.5 (49)	81.3 (48)	NS
Pseudospondia longifolia	83.1 (65)	27.1 (48)	<0.001
Sorindeia grandifolia	73.2 (56)	85.7 (56)	NS
Uapaca sp.	50.7 (75)	49.3 (75)	NS

4.5.3. Seed dispersal quantity

The seeds of *Aframomum* spp. (Zingiberaceae), *Ficus* spp., *Nauclea diderrichii* (Rubiaceae), *Sarcocephalus pobeginii* (Rubiaceae) and *Tricalysia* sp. (Rubiaceae) measured <5 mm, and were therefore not included in the following analyses. Most faeces contained intact seeds. Seedless faeces were mainly collected during the long rainy season (February–June). The monthly weighted mean percentage of seedless faeces for the 3-y sample period was 12.1%.

Faecal samples had a mean weight of 294 ± 202 g and the number of large seeds (> 5 mm) they contained varied greatly (1–727). The period April–May each year (within the long rainy season) was characterized by few seeds per faecal sample (4.8 ± 10.5 per 100 g), whereas the number of seeds dispersed peaked in dry-season periods (July–August and December–January; 61.8 ± 88.9 seeds per 100 g) (Figure 2). Overall, faeces contained an average of 51.8 large seeds, suggesting a quantitative dispersal rate of 289 large seeds d^{-1} per individual and a daily seed rain of 199 seeds d^{-1} km^{-2} at La Belgique (Table 2). The majority of these seeds represented only a few species (Table 3). In particular, species of the genus *Uapaca* accounted for a third of all seeds found in faeces (36.5%).

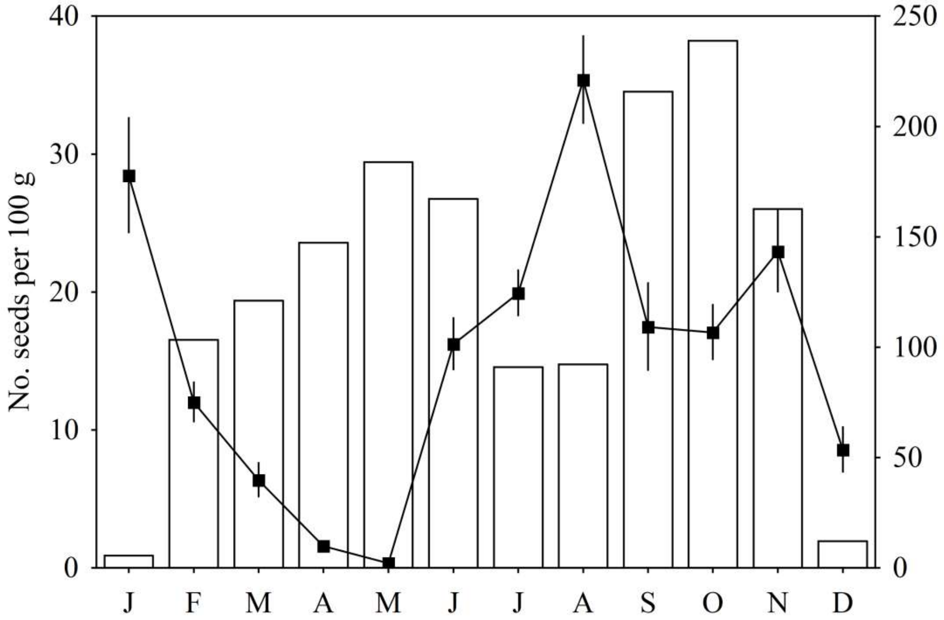

Figure 2. Variation in the quantity of seed dispersal and precipitation across months. Dots and error bars represent the monthly average number of intact seeds (>5 mm) ± SE found in a 100-g sample of faecal material and columns indicate the monthly average rainfall for the period September 2009-August 2012.

Table 2. Overall mean daily seed rain and associated 95% Confidence Interval of a western lowland gorilla population at La Belgique, south-east Cameroon, for the period September 2009–August 2012. Gorilla density values come from unpublished work of Projet Grands Singes. The faeces production rate values were extracted from Todd et al. 2008.

	Density (gorilla km^{-2})	No. faeces d^{-1}	No. seeds (g^{-1} faeces)	Faeces weight (g)	Seed rain (seeds d^{-1} km^{-2})
Mean	0.69	5.57	0.176	294	199
95% CI	0.43–1.09	2.08–12.03	0–0.651	75.5–680	0–5805

Table 3. Estimated seed-dispersal quantity (*Q*) of large seeds (>5 mm) of one western lowland gorilla individual in La Belgique, south-east Cameroon, during 3-y period (September 2009–August 2012) for the ten most abundantly dispersed species. Means are expressed ± SD. For the measurement of the mean occurrence of seeds in faeces, only months in which seeds were found were considered. Life-form: H, herb; L, liana; T, tree. Guild: NPLD, non-pioneer light-demander; P, pioneer; SB, shade-bearer; n.a., not available.

	Life-form	Guild	% months occurrence	Mean occurrence (% faeces)	Mean no. seeds per 100 g of faeces	*Q* (total no. seeds)	Relative quantity (%)
Uapaca spp.	T	NPLD	72.2	57.7 ± 38.6	13.1 ± 19.5	116935	36.5
Landolphia spp.	L	n.a.	38.9	60.2 ± 38.0	12.8 ± 13.0	56419	17.6
Cissus dinklagei	L	P	52.8	24.7 ± 25.2	11.5 ± 16.0	30511	9.5
Celtis tessmannii	T	NPLD	5.6	56 ± 16.7	46.0 ± 25.6	26266	8.2
Dialium pachyphyllum	T	SB	13.9	63.2 ± 24.0	13.5 ± 18.9	17874	5.6
Marantochloa filipes	H	n.a.	61.1	24.2 ± 19.3	5.7 ± 10.5	14,772	4.6
Sorindeia grandifolia	T	SB	13.9	34 ± 16.7	8.8 ± 9.6	8153	2.5
Duguetia staudtii	T	NPLD	13.9	17.7 ± 10.7	9.8 ± 13.0	6853	2.1
Megaphrynium macrostachyum	H	P	19.4	37.3 ± 20.5	3.3 ± 3.6	4462	1.4
Monodora myristica	T	SB	5.6	26.3 ± 7.3	17.2 ± 18.4	4287	1.3
Total top 10						286532	89.4
Total all seed species						320332	

4.5.4. Seed deposition site

The selected best-subset of predictors in our GDA model comprised by decreasing level of relative importance ‘canopy openness’ (standardized canonical discriminant function coefficient: 0.870), ‘canopy structure index’ (-0.634) and ‘DBH class 10-19.9 cm’ (0.405). The coefficients of the classification function for the three variables showed that sleeping sites are characterized by a higher canopy openness (coefficient of 1.07 *vs*. 0.395; mean canopy openness of 19.1% ± 13.1% *vs*. 9.5% ± 4.0%), a less dense and more disrupted canopy (coefficient of 0.094 *vs*. 0.147; mean index of 118 ± 41.4 *vs*. 178 ± 36.9) and a higher relative importance of trees with dbh 10–19.9 cm within the diameter structure of the tree stand (90.7 *vs*. 76.3). Based on these three variables, the model confidently discriminates plot types and explains 73.4% of the observed variance (canonical R = 0.857, Wilks’s Lambda = 0.266, $\chi^2 = 74.8$, df = 3, $P < 0.001$). The percentage of correct classifications for the overall model and the cross-validation is 90.0% in both cases (91.0% and 89.9% for control plots and sleeping sites, respectively). Pairwise plot comparisons of botanical composition between defecation site types lead to a mean Chao's Abundance-based Sørensen Similarity Index of 0.639 ± 0.225. However, once all plots from the same defecation site type were pooled together, the index was remarkably close to 1 (0.978) suggesting that they both belong to the same vegetation formation on a larger scale than the plot size. Furthermore, no significant differences were observed between the mean similarity index within plots of both defecation site types (sleeping sites = 0.669 ± 0.193, control plots = 0.656 ± 0.243; Mann-Whitney: U = 279994, P = 0.602), suggesting that the two types of defecation sites have the same degree of heterogeneity in the composition of extant vegetation. Eleven indicator species were identified in sleeping sites and eight in control plots (Table 4). They are distinguished based on their shade-tolerance guild; indicator species at sleeping sites being dominated by light-demanders, especially pioneers, whereas indicator species at control plots were more shade tolerant.

4.6. Discussion

The first objective of this study was to describe the quantitative component of WLG seed dispersal at community and population levels, to assess the importance of gorilla seed-dispersal activity. During 3 y of investigation, intact seeds from 58 species, varying in fruit and seed traits, were successfully identified in WLG faeces in La Belgique; an amount which falls within the range of findings of previous studies (Head et al. 2011; Nishihara 1995; Poulsen et al. 2001; Tutin et al. 1991). As a result of its large gape width, the WLG ingests seeds of most of the species it consumes (91.1% at Nouabalé-Ndoki NP, Republic of Congo; Nishihara 1995); and tends to spit out seeds exceeding the dimension threshold of 40–50 mm and 7–9 cm^3 (J. Head, unpubl. data; Nishihara 1995; Tutin and Fernandez 1994), a pattern which encompasses all lengths of seeds dispersed by the entire Central African disperser community

Table 4. Indicator plant species listed by decreasing indicator values (IV) of western lowland gorilla sleeping sites (SS) and random areas (control plots; CP) within the home range of the studied population in south-east Cameroon (September 2009–August 2012). Shade-tolerance guilds were extracted from Hawthorne (1995) and J.-L. Doucet: CP, crypto-pioneer; P, pioneer; NPLD, non-pioneer light-demanding; MP: moderate pioneer; SB, shade-bearer; n.a., not available.

Species	Family	Group	IV (%)	Shade tolerance guild
Desplatsia spp.	Tiliaceae	SS	62.4	MP
Markhamia tomentosa	Bignoniaceae	SS	41.7	P
Oncoba crepiniana	Flacourtiaceae	SS	36.3	P
Discoglypremna caloneura	Euphorbiaceae	SS	34.2	P
Glyphaea brevis	Tiliaceae	SS	20. 7	CP
Bridelia micrantha	Euphorbiaceae	SS	20.4	P
Cleistopholis patens	Annonaceae	SS	20.1	P
Barteria fistulosa	Passifloraceae	SS	19.4	P
Unknown sp.	Unknown	SS	16.9	n.a.
Guarea spp.	Meliaceae	SS	14. 9	NPLD
Trichoscypha odonnii	Anacardiaceae	SS	11.1	SB
Polyalthia suaveolens	Annonaceae	CP	53.7	SB
Strombosia spp.	Olacaceae	CP	51.2	SB
Plagiostyles africana	Euphorbiaceae	CP	49.0	NPLD
Anonidium mannii	Annonaceae	CP	44.6	SB
Maesobotrya spp.	Euphorbiaceae	CP	42.1	CP
Heisteria parvifolia	Olacaceae	CP	35.1	SB
Uapaca acuminata	Euphorbiaceae	CP	35.1	NPLD
Antidesma lacinata	Euphorbiaceae	CP	23. 7	CP

(Forget et al. 2007). Therefore, the WLG can be virtually interconnected with almost all species in the seed-dispersal network to which it belongs (Vidal et al. 2013). Quantitatively, the WLG is likely to be an important actor in the regeneration dynamics of some plant species (Table 3). As hypothesized, the WLG seed load is dominated by a few species (three-fourths of all seeds dispersed belonged to five species only), reflecting patterns of seasonal fruit availability and diet preferences. For some of these species, the WLG may contribute disproportionately to dispersal of the seed crop, as was shown for *Ganophyllum giganteum* and *Cola lizae* trees in the Lopé National Park, Gabon (Voysey et al. 1999a). In general, the dispersal service received by a plant is dominated by a limited number of disperser species (Schupp et al. 2010) and a reduction in abundance of these dispersers would have a considerable impact on the plant population dynamics.

At La Belgique, seed damage in the WLG mouth and gut affected a small proportion of species and, with the exception of two species, damaged seeds represented less than 5% of each specific seed load. As expected, scarification of the seed coat in the WLG gut did not negatively affect seed germination: all 21 test species successfully germinated (>75% in the majority of cases), and comparative germination tests with unpassed, manually-depulped seeds revealed a positive or neutral effect of scarification in the gut, with one exception. Furthermore, species exhibiting a neutral effect of scarification on germination success may, however, benefit from the removal of the fruit pulp and skin during gut passage, as their presence may otherwise inhibit germination (Robertson et al. 2006; Samuels and Levey 2005).

Because monitoring the fate of seeds dispersed up to recruitment is time constraining, especially in the case of trees , researchers commonly infer site suitability based on recruitment of early life stages (Tutin et al. 1991; Voysey et al. 1999b; Wenny and Levey 1998). However, processes at play that make a site suitable or unsuitable for a given species are likely to operate beyond this period (Paine and Harms 2009; Schupp 1995). Here, we employed a different approach which identifies the guilds of species more likely to benefit from seed dispersal by the WLG and hence considers their community-wide service rather than population-wide. Sleeping sites are distinguished from random sites in the forest based on the structure and more subtly the composition (i.e. differences in specific relative frequencies and abundances as suggested by the IndVal results; Dufrêne and Legendre 1997) of the extant vegetation stand: in sleeping sites these are characteristic of early-successional habitats, while those of control plots reflect old-growth secondary forests. At sleeping sites, the canopy is disconnected with a sparse foliage allowing the penetration of enough light to enable light-demanding tree species to establish, grow and eventually recruit. There is a higher representation of small diameter individuals (10–19.9 cm dbh) in the tree stand compared to random sites, further highlighting the regenerating phase of the tree stand. Sleeping-site habitats mostly result from recent or past small-scale disturbance, such as treefalls (supported by the presence of fallen trees at various stages of decay in many sleeping sites; pers. obs.); therefore, seed dispersal at sleeping sites is likely to contribute to gap-phase dynamics. The extent of this contribution will depend on the intensity of the original disturbance and the stage of post-disturbance vegetation recovery (i.e. degree of canopy reformation), as well as the shade-tolerance guild of the dispersed species. Species' responses to light availability exhibit a continuum from shade-bearing to light-demanding, and in the case of Afrotropical canopy tree species, optimal seedling performances of shade-bearing species occur at degrees of canopy openness of 10%–16%, those of pioneer species at 27%–44%, and those falling in between representing non-pioneer light-demanding species (Agyeman et al. 1999; Veenendaal et al. 1996). According to this partitioning, with a mean canopy openness of 9.5%, seed dispersal on feeding trails is likely to be more beneficial for shade-bearing species. In contrast, as sleeping sites were found to have a mean canopy openness of 19%, the species most benefitting from the habitat-directed pattern of seed dispersal at sleeping sites by the WLG at La Belgique are likely to be non-pioneer light-demanders. Furthermore, mean canopy openness above nests in particular is 26.9% ± 14.1%, therefore increasing available irradiance levels for a large proportion of seeds dispersed at sleeping sites to encompass the whole range of optimum light conditions of non-pioneer light-demanding species. As nearly half of the seed load dispersed (47.4%) represents non-pioneer light-demanders (e.g. *Uapaca* spp., *Celtis tessmannii* and *Duguetia staudtii*), dispersal at sleeping sites is expected to provide a higher per capita probability of recruitment compared to seeds dispersed on feeding trails. This would suggest directed-dispersal, and corroborates the findings made at Lopé National Park, Gabon, that sleeping sites play a major role in the seed dispersal service provided by gorillas (Voysey et al. 1999b).

To conclude, the WLG exhibits a number of intrinsic characteristics required for effective seed dispersal: they disperse a large quantity of seeds whose germination performances are in most cases either unaltered or enhanced. The spatial defecation pattern of the WLG may contribute to the specificity of its seed dispersal activity and hence to the overall service fulfilled by this disperser compared to others. We demonstrated previously how differing environmental conditions between the two defecation sites may influence short-term post-dispersal seed fate as a result of differing dung beetle activity (Petre et al. 2015b – see chapter 6). Here, we suggest that the respective dispersal services performed at sleeping sites and feeding trails act at different phases of forest dynamics: gap-phase or old-growth stand regeneration, respectively. While virtually all forest-dwelling seed dispersers are likely to contribute to old-growth stand regeneration, a regular contribution to gap-phase dynamics is likely to be more disperser-specific. In the absence of such a contribution, chances are low that seeds of light-demanding zoochorous species will be deposited in open-canopied sites (Babweteera 2012). Therefore, the loss of the seed-dispersal service provided by the WLG at La Belgique is likely to be detrimental to the long-term dynamics of some light-demanding species. Empirical support for this relationship would offer new insights into the central role of large-bodied seed dispersers in tropical forests and how their depletion may impact upon plant regeneration dynamics.

Appendix 1. List of species dispersed by the western lowland gorilla in La Belgique, south-east Cameroon (September 2009–August 2012). Regeneration guilds were extracted from Hawthorne [1995] and J.-L. Doucet: CP, crypto-pioneer; P, pioneer; MP: moderate pioneer; NPLD, non-pioneer light-demanding; SB, shade-bearer; Sw, swamp; n.a., not available. Seed size: mean length of the three axes measured on dispersed seeds with a calliper. Damage: the percentage of seeds found damaged in feces. Nomenclature follows the African Plant Database (available online at http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php).

Family	Species	Life-form	Guild	Seed size (mm)	Damage (%)
Anacardiaceae	*Antrocaryon klaineanum*	T	P	20 × 18 × 11	0
	Pseudospondias longifolia	T	Sw	20 × 12 × 8	0
	Sorindeia grandifolia	T	SB	20 × 10 × 7	0
	Trichoscypha acuminata	T	SB	27 × 16 × 14	0
	Trichoscypha oddonii	T	SB	38 × 22 × 18	0
Annonaceae	*Anonidium mannii*	T	SB	44 × 23 × 13	0.3
	Cleistopholis patens	T	P	17 × 10 × 9	0
	Duguetia staudtii	T	NPLD	12 × 7 × 7	0
	Monodora myristica	T	SB	16 × 10 × 7	0
	Polyalthia suaveolens	T	SB	10 × 10 × 5	0
	Uvariastrum pierreanum	T	SB	20 × 12 × 5	0
Apocynaceae	*Landolphia* spp.	L	n.a.	22 × 14 × 10	4.2
	L. villosa	L			
	L. sp.1	L			
	Tabernaemontana crassa	T	SB	11 × 5 × 3	0
Burseraceae	*Canarium schweinfurthii*	T	NPLD	30 × 15 × 15	0
	Santiria trimera	T	SB	15 × 10 × 5	0
Clusiaceae	*Garcinia kola*	T	SB	22 × 12 × 12	0
Euphorbiaceae	*Discoglypremna caloneura*	T	P	5 × 4 × 4	0
	Uapaca spp.	T	NPLD	15 × 10 × 5	0.9
	U. acuminata	T	NPLD		
	U. guineensis	T	NPLD		
	U. mole	T	Sw		
	U. vanhouttei	T	NPLD		

	Uapaca pynaertii	T	NPLD	35 × 15 × 10	0
Fabaceae	*Dialium pachyphyllum*	T	SB	10 × 8 × 4	7.9
	Erythrophleum suaveolens	T	P	17 × 10 × 6	0
	Tetrapleura tetraptera	T	P	9 × 7 × 4	0
Flacourtiaceae	*Oncoba* sp.	T	P	6 × 4 × 4	0
Irvingiaceae	*Klainedoxa* cf. *gabonensis*	T	NPLD	26 × 17 × 12	3.8
Leeaceae	*Leea guineensis*	S	SB	4 × 3 × 3	0
Marantaceae	*Marantochloa filipes*	H	n.a.	6 × 5 × 4	0.1
	Megaphrynium macrostachyum	H	P	13 × 10 × 7	0.4
	Sarcophrynium brachystachys	H	n.a.	12 × 4 × 4	0
Moraceae	*Ficus mucuso*	T	P	2 × 1 × 1	0
	Ficus sp. (strangler)	E	n.a.	2 × 1 × 1	0
	Myrianthus arboreus	T	CP	16 × 10 × 7	0
Olacaceae	*Heisteria parvifolia*	T	SB	11 × 6 × 6	49.9
Pandaceae	*Microdesmis keayana*	S	SB	5 × 4 × 3	0
Passifloraceae	*Barteria* sp.	T	CP	n.a.	0
Rubiaceae	*Nauclea diderrichii*	T	P	∅ ≤ 1	0
	Psychotria arnoldiana	S	n.a.	9 × 6 × 3	1.2
	Sarcocephalus pobeguinii	T	Sw	∅ ≤ 1	0
	Tricalysia sp.	T	n.a.	4 × 4 × 4	0
Sapindaceae	*Chytranthus* cf. *talbotii*	T	SB	n.a.	0
	Chytranthus setosus	T	SB	15 × 10 × 6	0
	Lecaniodiscus cupanioides	T	SB	12 × 8 × 4	0
Sapotaceae	*Chrysophyllum boukokoense*	T	SB	17 × 9 × 7	0
	Chrysophyllum lacourtianum	T	SB	31 × 16 × 10	0.2
Tiliaceae	*Desplatsia* spp.	T	MP	16 × 7 × 3	15.2
	D. dewevrei	T	MP		
	D. subericarpa	T	MP		
	Duboscia spp.	T	NPLD	10 × 6 × 3	n.a.
	D. macrocarpa	T	NPLD		

	D. viridiflora	T	NPLD		
Ulmaceae	*Celtis tessmannii*	T	NPLD		0
Verbenaceae	*Vitex* cf. *rivularis*	T	NPLD	20 × 15 × 14	0
Vitaceae	*Cissus dinklagei*	L	P	17 × 9 × 6	0
Zingiberaceae	*Aframomum* spp.	H	P	4 × 3 × 2	n.a.
	A. arundinaceum	H	P		
	A. polyanthum	H	Sw		
	A. sulcatum	H	P		
	*A. sp.*1	H	P		

Appendix 2. Germination success (%) of seeds after gut passage in western lowland gorilla at La Belgique, south-east Cameroon (September 2009–August 2012). Seeds were retrieved in fresh faeces (< 48 h old) and sown in a field nursery. Life-form: E, epiphyte; H, herb; L, liana; T, tree. Seed size: L, large (>5mm); S, small (≤5mm).

	Life-form	Seed size	No. seeds sown	Germination success (%)
Duguetia staudtii	T	L	8	100.0
Chytranthus setosus	T	L	16	93.8
Chrysophyllum lacourtianum	T	L	634	93.4
Cissus dinklagei	L	L	45	88.9
Chrysophyllum boukokoense	T	L	40	80.0
Heisteria parvifolia	T	L	59	79.7
Ficus sp.	T or E	S	300	78.7
Pseudospondias longifolia	T	L	129	76.7
Uvariastrum pierreanum	T	L	34	76.5
Marantochloa filipes	H	L	120	75.8
Sorindeia grandifolia	T	L	56	75.0
Monodora myristica	T	L	196	66.3
Desplatsia spp.	T	L	35	62.9
Antrocaryon klaineanum	T	L	75	62.7
Myrianthus arboreus	T	L	79	55.7
Trichoscypha spp.	T	L	8	50.0
Landolphia spp.	L	L	75	49.3
Uapaca spp.	T	L	562	38.6
Erythrophleum suaveolens	T	L	157	35.7
Duboscia spp.	T	L	180	33.9
Vitex cf *welwitschii*	T	L	115	8.7

CHAPTER V.

QUALITY OF SEED TREATMENT IN MOUTH AND GUT

5. *Quality of seed treatment in mouth and gut*

Western lowland gorilla seed dispersal: are seeds adapted to long gut retention times?

Petre C-A., Tagg N., Beudels-Jamar R., Haurez B. & Doucet J-L., 2015. *Acta Oecologica* 67: 59–65.

Abstract

The degree of seed scarification in the frugivore gut, itself partly dependent on gut retention time, is a key component in determining the extent to which gut passage alters germination performances. Another potential benefit of gut passage arises as a result of the removal of fruit pulp which otherwise may act as a germination inhibitor. Using experiments designed to disentangle the respective effects of pulp removal (germination deinhibition) and seed scarification, with gut retention time as an explanatory variable, we investigated the effect of gut passage on germination performances (percentage and latency) of five tropical tree species dispersed by the western lowland gorilla (*Gorilla g. gorilla*). The percentage of seeds germinating after gut passage increased for three species, respectively, through the effects of scarification only, deinhibition only and scarification and deinhibition combined. A negative scarification effect was observed for one species, and no effect of gut passage for another. Passage through the gut led to a decrease in germination latency of three species, as a result of the depulping of seeds. However, seed scarification resulted in germination delays for another species. The gut retention time of the five species averaged 39–56h and had no effect on intra-specific germination performances except for one species whose germination probability increased as gut retention time increased. As gut retention time often correlates with dispersal distance, the fact that gut retention time *per se* does not reduce seed viability of these tropical tree species may have positive implications for their population dynamics and maintenance of genetic diversity. If no detrimental effect of gut retention time on germination performance is a general trait among tropical species, the extirpation of large frugivores with long gut retention time, such as the western lowland gorilla, would likely have negative long-term implications for tropical forests.

Keywords: deinhibition effect, endozoochory, *Gorilla gorilla gorilla*, gut passage, long-distance dispersal, seed scarification

5.1. Introduction

In tropical forests, animals play an important role in seed dispersal as the proportion of plant species producing fruits that are consumed by frugivores ranges between 50–95% (Beaune et al. 2013; Gillet and Doucet 2012; Howe and Smallwood 1982). In addition to the advantages for plant fitness of displacing seeds away from the parent tree (i.e. escape, colonisation and directed-dispersal hypotheses; Howe and Smallwood 1982), mechanisms at work at the earliest stages of endozoochory may also influence plant fitness. Passage through the digestive tract of frugivores may influence germination performance, through chemical and mechanical abrasion of the seed coat or endocarp (known as the 'scarification effect') (Traveset and Verdú 2002), and/or by removing fruit pulp from the seeds which may otherwise act as a germination inhibitor (known as the 'deinhibition effect') and facilitate growth of pathogens (Traveset et al. 2007). Most studies that attempt to assess the impact of gut passage on germination, however, lack treatments to control for the deinhibition effect of pulp removal (Samuels and Levey 2005). It has been shown amongst the avian disperser group, for which enough studies testing both effects simultaneously are available in the literature, that the deinhibition effect acts significantly more frequently than the scarification effect (Robertson et al. 2006). Consequently, not testing the deinhibition effect may result in under-appreciation of the real benefit plants receive from frugivores for seed germination.

Passage through the gut of non-flying mammals appears to enhance germination performance less frequently than has been recorded for birds, but the effect of deinhibition is generally not understood (Traveset and Verdú 2002). Alternatively, differences between birds and non-flying mammals in the frequency of germination enhancement induced by gut passage may be explained by differences in gut retention time, and hence the extent to which seeds are scarified. Non-flying mammal seed dispersers generally exhibit a notably longer gut retention time compared to birds. This leads to the hypothesis that a scarification threshold exists, rarely reached in birds, above which its effect on germination is cancelled out or may even become detrimental (Traveset and Verdú 2002). This is supported by evidence that germination success decreases as avian gut retention time increases within single plant-frugivore systems (Charalambidou et al. 2003; Murray et al. 1994; Wongsriphuek et al. 2008), and that among three frugivore taxa (birds, lizards and non-flying mammals) dispersing the same plant species, seeds passing through the mammal gut and thus being retained for longer, germinated in lower proportions compared to the other two taxa (Nogales et al. 2005). To date, no evidence exists of decreasing germination success with increasing gut retention time from single plant-frugivore systems involving non-flying mammals, though such evidence is required to confirm this hypothesis (Traveset et al. 2007).

The objective of our study was to test the impact of gut passage on seed germination of tropical trees dispersed by a large mammal with a long gut retention time, the western lowland gorilla (*Gorilla gorilla gorilla* Savage & Wyman 1847; hereafter referred to as WLG). Specifically, we tested the effects of scarification, deinhibition and gut retention time on the germination of seeds of five tree species, the fruits of which are consumed and the seeds dispersed by a wide variety of frugivores (Blake 2002; Chapman and Chapman 1996; Clark et al. 2001; Feer 1995; Petre et al. 2015a; Poulsen et al. 2001). The gut retention time of the WLG features among the longest within the sympatric frugivore community (averaging 50h: Caton 1999; Remis 2000; Remis and Dierenfeld 2004), surpassing that of elephants (20–40h; Campos-Arceiz and Blake 2011), and therefore we expect a degree of seed scarification, and subsequent potential changes in germination, that would not be evident with other sympatric frugivores.

We tested the following research questions: (1) Does a deinhibition effect occur in the five species tested? (2) Does germination performance (percentage and latency) change as gut retention time increases? With respect to (2), we subsequently discuss if the WLG can perform effective long distance dispersal.

Table 1. Characteristics of the tree species collected at 'La Belgique' research site (southeast Cameroon) and fed to captive western lowland gorillas of the Limbé Wildlife Center (southwest Cameroon) to test the effect of gut passage on germination patterns.

Species	Fruit type	Fruit skin	Seed coat	Seed size (mm)
Anacardiaceae				
Antrocaryon klaineanum Pierre	Fleshy; 3–4 seeds	Thick; resistant	Nut-like; hard; thick	20 x 18 x 11
Pseudospondias longifolia Engl.	Fleshy; one seed	Thin; soft	Nut-like; hard; thick	20 x 12 x 8
Pseudospondias microcarpa (A. Rich.) Engl.	Fleshy; one seed	Thin; soft	Nut-like; hard; thick	11 x 6 x 5
Trichoscypha acuminata Engl.	Fleshy; one seed	Thin; soft	Membranous; soft; thin	37 x 21 x 17
Moraceae				
Myrianthus arboreus P. Beauv.	Fleshy; one seed [a]	Thick; resistant	Nut-like; hard; thick	16 x 10 x 7

[a] Drupe-like infructescence of about one hundred fruits each

5.2. Materials and methods

5.2.1. Study locations

During the peak fruiting seasons of 2009–2011 (June–September), we collected fresh fruits of five species (Table 1) at 'La Belgique' research site, southeast Cameroon (Dupain et al. 2003), that are known to be important in the diet of the WLG in this site and others. We transported these fruits to the Limbé Wildlife Center, southwest Cameroon, and offered them for consumption by a captive WLG group. The captive group comprised one silverback male, two adult females, one sub-adult female and one four-year-old juvenile, thus representing a structure and composition commonly seen in wild groups (Parnell 2002). The group was housed in an approximately 600 squared m outdoor enclosure by day, and a sheltered cage comprising three main interconnected compartments and two central satellite areas by night.

5.2.2. Seed germination treatments

We used the experimental design suggested by Samuel and Levey (2005) comprising three types of treatments, to disentangle the scarification and deinhibition effects of gut passage (gut passed seeds, manually depulped seeds and seeds within intact fruits). We repeated the treatments one to five times for each species over the course of the study.

The seeds of each specific germination trial replicate originated from fruits we collected on the same day and from a same individual tree. We did so to avoid seed age and genetic effects, respectively, on germination performance, and thereby allowing reliable comparisons between treatments. Each replicate involved fruits collected under a new individual tree at the research site La Belgique, some within the same fruiting season (16–31d apart) and others during subsequent ones.

For each tree sampled, we divided the fruit crop into three batches of equal size, destined for the three germination treatments. We fed gorillas with the first batch of fruit crop during a single feeding session and kept the other two batches in a dry, ventilated and shaded room for later use (see below). Feeding sessions took place either in the morning (8h00–8h30) or late afternoon (16h30–17h00). We collected all faeces produced by the captive WLG group on at least two occasions each day (8h30–9h30 and 17h00–18h00). We immediately washed faeces in a meshed-sieve and extracted and counted all seeds (treatment 1: gut passed). On the same day, we retrieved an equal number of seeds of the relevant species from the second batch of fruit stock and removed the pulp (treatment 2: manually depulped). We air-dried both groups of seeds, passed and manually depulped, and then stored them for an equal amount of time (3–11 days, depending on the retrieval date within a feeding-seed collection session) in paper envelopes in dry and dark conditions to avoid any effect of length of exposure to air on germination performance. We ceased faecal collection when we found no more seeds in three consecutive sessions (i.e., ≥24h). As it was not possible to record the exact time of all defecation events, nor the individual responsible, we pooled all faeces together for each collection session and measured gut retention time (RT) as follows:

$$\mathrm{RT} = \frac{(\mathrm{T}_{out} - \mathrm{T}_{in})}{2} - \mathrm{T}_f$$

where T_{out} denotes the time the group exited the day or night enclosure, T_{in} the time the group returned to the same enclosure and T_f the time the group was fed. Results presented in this study therefore reflect the mean gut retention time exhibited by this captive group of WLG.

We sowed passed and manually-depulped seeds of each fruit species in a field nursery at the La Belgique research station. We sowed seeds individually in perforated polyethylene nursery bags filled with soil collected from a single location in the research site, to avoid an effect of edaphic composition on germination performance (Robertson et al. 2006; Traveset and Verdú 2002). From the third batch of the initial fruit crop, we selected intact fruits that presented no signs of rotting or skin damage (i.e., holes and fissures) for the deinhibition effect control treatment (treatment 3: intact fruit), amounting the same number of fruits as were implicated in passed and manually depulped treatments. We placed fruits individually on the surface of soil-filled nursery bags. For each germination trial replicate, we installed seeds and fruits of all three treatments for each species the same day, and we monitored each nursery bag on a daily basis for three months, then every 15 days for up to six months. When rain was scarce, we watered bags on a regular basis. We identified seed germination from the above-ground emergence of the hypocotyledonous stem (Nchanji and Plumptre 2003).

5.2.3. Data analysis

Significant differences in germinability (i.e. the percentage of germinated seeds) between seeds passed through the gut and those manually depulped indicate a scarification effect, whereas significant differences between seeds manually depulped and left within intact fruits indicate a deinhibition effect (Samuels and Levey 2005). We analyzed differences in germinability between fruit species and seed treatments with generalized linear models using binomial error distributions and logit link functions. Germination success constituted the response variable, whereas fruit species and seed treatment constituted the categorical explanatory variables (fixed factors). The overall model indicated a significant species by treatment interaction (χ^2 Wald=106.1, df=8, P<0.001); consequently, we tested the influence of seed treatment separately for each fruit species.

In a second analysis, using the dataset of gut-passed seeds only, we tested the influence of gut retention time on seed germination success, using gut retention time (h) as a continuous explanatory variable, and fruit species as the fixed factor. Since the effect of gut retention time on germinability is not necessarily linear, we also tested a second and third order polynomial factor of gut retention time in the model (Figuerola et al., 2010). Because the interaction with fruit species was significant (χ^2 Wald=37.159, df=4, P<0.001), we tested the impact of gut retention time on germinability for each fruit species individually.

We tested differences in germination latency (i.e. number of days from sowing to emergence of hypocotyledonous stems) between treatments with a one-way ANOVA, and pairwise comparisons were tested with the Scheffé post-hoc test. Finally, we performed regression tests between germination latency and gut retention time for each species.

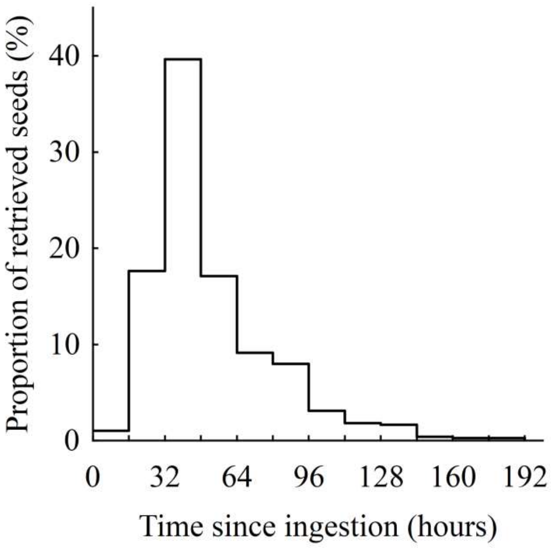

Figure 1. Western lowland gorilla gut retention time: percentage of retrieved seeds over time. The graph shows the gut passage rate of five seed species pooled together (*Antrocaryon Klaineanum*, *Myrianthus arboreus*, *Pseudospondias longifolia*, *Pseudospondias microcarpa*, *Trichoscypha acuminata*) in a captive group of five individuals housed in the Limbé Wildlife Center, southwest Cameroon.

Table 2. Retention time characteristics of the seeds of five tree species passed through the gut of captive western lowland gorillas at the Limbé Wildlife Center (southwest Cameroon) used to test the effect of gut passage on germination patterns

Species	No. seeds ([a])	TT	T_{50}	MRT ± SD
Antrocaryon klaineanum	127 (4)	16	43.5	46.7 ± 21.9
Myrianthus arboreus	229 (5)	8	44	55.7 ± 35.1
Pseudospondias longifolia	147 (2)	8	55.8	52.9 ± 26.4
Pseudospondias microcarpa	148 (1)	20	32	39.2 ± 16.5
Trichoscypha acuminata	126 (3)	8	56	55.9 ± 28.4
All species	777	8	44	50.6 ± 28.1

[a] : number of feeding replicates (each one corresponded to fruits that originated from a different parent tree sampled); TT: transit time, or time of first appearance; T_{50}: median retention time; MRT: mean retention time

5.3. Results

5.3.1. Gut retention time

Gut retention time information for the five species are presented in Table 2. On average, all seed species were retained in the digestive tract for 50.6h ± 28.2, ranging from less than 8 to 188h. The peak of the seed excretion curve occurred during the retention time frame 32–48h, where 39.6% of seeds were retrieved from faeces (Fig. 1).

5.3.2. Germination success

Gut retention time had a significant positive effect on seed germinability for *Myrianthus arboreus* (χ^2 Wald=3.95, df=1, P=0.047), where seed germinability increased as gut retention time increased. The coefficient of the regression slope was positive for all other species except *Trichoscypha acuminata*, but none were significant.

Of the five fruit species, four displayed significant differences in germinability between treatments (Table 3). We found a deinhibition effect for *Antrocaryon klaineanum* and *M. arboreus* as seeds that remained within intact fruits exhibited a significantly lower germination percentage compared to manually-depulped seeds (χ^2 Wald=8.8, df=1, P=0.003 and χ^2 Wald=5.6, df=1, P=0.018, respectively), and passed seeds (χ^2 Wald=9.5, df=1, P=0.002 and χ^2 Wald=21.6, df=1, P<0.001, respectively). We found a positive scarification effect for *M. arboreus* and *Pseudospondias microcarpa* as gut passed seeds exhibited a higher germinability than manually-depulped seeds (χ^2 Wald=6.9, df=1, P=0.009, and χ^2 Wald=46.5, df=1, P<0.001, respectively). In contrast, however, *Pseudospondias longifolia* exhibited a negative scarification effect on germinability (χ^2 Wald=24.5, df=1, P<0.001). Gut passage had no effect on the germinability of *T. acuminata*.

5.3.3. Germination latency

Gut retention time had no effect on seed germination latency for the five tree species. However, we observed significant differences in germination latency between treatments for *M. arboreus*, *P. longifolia*, and *T. acuminata* (Table 4). In the case of *M. arboreus* and *T. acuminata*, seeds left within intact fruits exhibited a significantly longer germination latency compared to seeds that were passed (Scheffé post-hoc tests: P=0.042 for *M. arboreus*, P<0.001 for *P. microcarpa* and P=0.012 for *T. acuminata*) and manually depulped (Scheffé post-hoc tests: P=0.003 for *M. arboreus* and P<0.001 for the other two species). In the case of *P. longifolia*, seeds left within intact fruits exhibited a significantly shorter germination latency compared to seeds that were manually depulped (Scheffé post-hoc test:

P=0.036) but not those passed in the gut. Because only one seed of *P. microcarpa* germinated within intact fruits, we could not perform the statistical test.

Table 3. Results of the generalized linear models performed to test the impact of seed treatment (western lowland gorilla gut passed, manually depulped and within intact fruits) on germinability of the five tree species tested.

Species	No. sowing replicate [a]	Germination percentage			df	χ^2 Wald	P-value	Effect
		Gut passed	Manually depulped	Intact fruit				
Antrocaryon klaineanum	5	68.7	68.7	37.8	2	11.2	0.004	D
Myrianthus arboreus	5	67.0	49.6	32.5	2	21.9	<0.001	D, S+
Pseudospondias longifolia	2	22.2	75.5	73.9	2	27.8	<0.001	S-
Pseudospondias microcarpa	1	85.5	10.3	1.8	2	61.3	<0.001	S+
Trichoscypha acuminata	3	81.3	84.3	90.0	2	1.9	0.396	N

Effect : D, deinhibition ; S-, negative scarification; S+, positive scarification; N, neutral

[a] Each sowing replicate corresponded to seeds that originated from a different parent tree sampled

Table 4. Impact of seed treatment (western lowland gorilla gut passed, manually depulped and within intact fruits) on germination latency expressed in days.

	Gut passed	Manually depulped	Intact fruit	DF	F	P-value
Antrocaryon klaineanum	40.9 ± 18.6	40.9 ± 14.8	48.1 ± 16.3	2	1.01	0.337
Myrianthus arboreus	26.4 ± 7.9	24.6 ± 6.6	30.6 ± 7.9	2	6.0	0.003
Pseudospondias longifolia	19.2 ± 4.9	16.4 ± 5.4	20.2 ± 4.5	2	3.81	0.027
Pseudospondias microcarpa	22.1 ± 6.0	22.8 ± 1.6	67 [a]	-	-	0.154
Trichoscypha acuminata	40.3 ± 17.5	36.1 ± 17.1	49.6 ± 12.7	2	10.6	<0.001

[a] only one seed germinated and therefore we excluded this treatment from the comparison test, and the statistics reported refer to the student t test (t=-1.449).

5.4. Discussion

5.4.1. Limitations of the study

Firstly, as a result of controlling for genetics, seeds used in the germination trials originated from a restricted number of parent trees. Since individuals exhibit differences in seed viability, the values of germination performance presented for each species may not be representative of the species in general. However, since the proportion of seeds originating from any given sampled parent tree was consistent between treatments, the observed differences in germinability between treatments are still relevant. Secondly, as we collected faeces only twice a day, the time that seeds spent in faecal material before collection potentially varied from a few minutes to 16h. This may have affected germination performances, for instance through enhanced hydration or exposure to an abrasive chemical component of the manure. However, any influence on our results would reflect natural conditions as seeds may remain in faecal material for any length of time before being washed out by rain or decomposed by dung beetles. Furthermore, as this potential bias concerns gut passed seeds of all retention time frames, it is unlikely to have markedly influenced the results of the impact of gut retention time, and does not challenge the following discussion on the ecological advantage of gut passage in the WLG. Thirdly, as a result of our study protocol, seeds passing faster through the gut will have spent a longer time exposed to the air before sowing, thus potentially leading to a decrease in viability. This may account for the trend of enhanced seed germinability with increasing time spent in the WLG gut, as observed in four species, though not significantly in three of them. If so, a significant negative effect of gut retention time on seed germinability might have been observed for *Trichoscypha abut* given the model provided a negative coefficient of the regression slope for this species.

5.4.2. Gut scarification and deinhibition effects

Our study confirmed that seeds are retained for very long periods of time in the digestive tract of the WLG and therefore the level of scarification of the seed coat might reach levels not attained in other sympatric frugivores. This potentially high scarification level was observed to improve the germinability of two species, but to reduce it in another, with the remaining two species being unaffected. Surprisingly, change in germinability was a function of the time seeds spent in the gut for only one of the three species. A larger sample size might be necessary to detect significant changes over time in the two remaining species. We observed a deinhibition effect in two species, one of which exhibited only this benefit of gut passage, and therefore our study confirms that the lack of appropriate sowing treatments could result in an under-appreciation of the effect of passage through a frugivore gut.

The differing responses to passage through the WLG gut of the five species tested highlight the complexity of plant-frugivore systems and the resulting difficulty in making generalizations (Traveset 1998; Traveset et al. 2007). Furthermore, this supports evidence that changes in germinability through scarification and deinhibition are mainly determined by intrinsic traits of the seed species dispersed rather than by morphological and/or physiological traits of the frugivore disperser (Traveset et al. 2007).

It has been shown that phylogenetic relatedness among plant species is a crucial aspect that must be considered when interpreting gut passage effect (Verdu and Traveset 2004), as species sharing a common ancestry are likely to respond similarly to gut passage (Traveset 1998). From our study, it is difficult to draw firm conclusions about a phylogenetic effect given the small sample size; however, it is worth noting that four of the five species belong to the same family (Anacardiaceae), with two congeneric species (*P. microcarpa* and *P. longifolia*), and together they exhibited all three possible responses to scarification: neutral (*A. klaineanum* and *T. acuminata*), positive (*P. microcarpa*) and negative (*P. longifolia*). Because gut retention time did not significantly affect these four related species, inter-specific differences in germinability were not likely to have been caused by differences in gut retention time *per se*. Rather, this variation is likely due to inter-specific differences in the rate at which seed coat scarification by gastrointestinal fluids translates into an increased permeability, thus enhancing germinability, or the removal of much of the protective endocarp damaging the embryo (Traveset 1998). It would be expected for thinly and softly coated seeds to experience higher scarification, altering germinability (positively or negatively) more strongly than hard and thick coated seeds (Tewksbury et al. 2008; Traveset and Verdú 2002; Venier et al. 2012). However, we did not observe this pattern here as the thinnest and softest coated seed species (*T. acuminata*) of the four related species exhibited no change in germinability after gut passage, whereas the germinability of two out of the other three, which all have relatively thick seed coats, was negatively (*P. longifolia*) and positively (*P. microcarpa*) affected. We suggest to repeat this study including the examination of seed mass, water content, permeability, seed coat thickness, texture and resistance before and after passage through the WLG gut (Traveset et al. 2008), to shed light on the underlying mechanisms explaining the different responses observed between these related species.

Germination inhibition, which prevents early germination when the fruit is still attached to the tree (Evenari 1949), can result from either the presence of secondary compounds in the fruit pulp or structural and compositional properties of the fruit pulp and/or skin impeding gas and water uptake necessary to initiate the germination process (Mayer and Poljakoff-Mayber 1982). For plant species presenting such characteristics, the removal of both the skin and the pulp in the frugivore mouth and gut therefore liberates the seed from these impervious effects, thus enabling germination. In the present study, the species for which gut passage induced a deinhibition effect also share the trait of a resistant and thick fruit skin. It is therefore probable that fruit skin properties may play a role in the germination inhibition observed in these species. To confirm this we recommend an additional treatment in further germination trials consisting of seeds discarded from the skin but still embedded in the pulp.

5.4.3. Germination latency

A difference in germination latency was only found between seeds left within intact fruits and those depulped (either manually or in the gut), suggesting that the fruit pulp and/or skin induce a germination delay. In theory, a seed that germinates faster than conspecifics of the same age will have a higher rate of survival as a result of being exposed to predation, microbial or fungal attacks for a shorter period of time and having an enhanced competitive ability for space and resources (Moore 2001). However, depulping in the gut reduces exposure time only by a few days (<10 days) and seeds left within intact fruits (i.e. non-dispersed seeds) and those depulped in the mammal gut become spatially separated, and so they are not in competition for space and resources. Furthermore, the fact that mechanical and chemical actions taking place in the digestive tract had no effect on germination latency could further preclude an evolutionary adaptation to improve nutrient uptake from the faecal matrix. Therefore, it seems unlikely that germination latency reduction in this context should have a significant effect on the fitness of the species tested.

5.4.4. Implications for effective long-distance dispersal

The fact that seed germinability is not negatively affected by the time for which seeds are retained in the digestive tract of the WLG has positive implications for the role of this frugivore in plant dynamics, at least in the case of the five species studied here. Because home range size of a given mammal species strongly correlates with its body mass (Blake et al. 2009; Haskell et al. 2002) and because large-bodied species often travel long distances each day (Carbone et al. 2005) the dispersal distance provided by large frugivores with long gut retention times is potentially very long. The home range of a WLG group ranges about 5–20 squared km and daily travel distances average 2 km but can exceed 5 km (Remis 1997). As half of the seed load dispersed by the WLG is retained in the gut for more than 44h, we argue that the dispersal distance of these seeds is measurable at the kilometre scale. In general, most seeds in a plant community are dispersed no further than a few tens of meters (Willson 1993), especially those of large size (Muller-Landau et al. 2008) such as the ones tested in this study. Therefore, any dispersal event at longer distances leading to successful recruitment is of great relevance for the spatial dynamics of a plant population (Guimaraes et al. 2008; Spiegel and Nathan 2007). Furthermore, as a result of most seeds being dispersed at short distances, genetic ‘neighbourhoods’ of related individuals exist for many plant species (Willson and Traveset (2000) and references therein). This potential long-distance dispersal performed by the WLG would contribute to the maintenance of genetic diversity of plant populations by encouraging gene flow between these so-called ‘neighbourhoods’. An absence of this specific type of long distance disperser of viable seeds could result in individual plants having a more clumped distribution with an associated risk of population fragmentation and genetic erosion in the long-term (Harrison et al. 2013). This is especially true for large-seeded animal-dispersed fruit species which rely exclusively on large frugivores for seed dispersal (Guimaraes et al. 2008).

5.5. Conclusion

With regards to our research questions, we have shown that gut passage may improve seed germinability of tropical trees through a deinhibition effect and that the benefit of gut passage of one species (*A. klaineanum*) would not have been detected had this influence been overlooked. We detected no, or a positive, effect of gut retention time on germination performances of the five species tested; therefore our study lends no support for the hypothesis that long gut retention times account for the lower rate of germination improvement after gut passage observed in mammals compared to birds. We were unable to associate the different responses to gut passage to seed characteristics, such as coat type and thickness, and we suggest that fruit skin properties may play a role in germination inhibition. However, given the small number of species tested, our results and conclusions are preliminary and we highly recommend a repetition of this study with a more exhaustive set of species and encompassing a wider range of fruit (skin and pulp) and seed (size, coat) traits, and, if possible, by precisely measuring how these traits are modified in the WLG gut. Where appropriate, we suggest an additional treatment consisting of the seed embedded in the pulp but devoid of fruit skin.

For those species that are not harmed in the WLG gut, the long gut retention time and large home range and daily travel distance of the WLG offer a potentially effective long-distance dispersal; a phenomenon which adds to the potential effectiveness of the seed dispersal service it provides (Petre et al. 2013). The WLG is critically endangered and faces extirpation in many parts of its range (Junker et al. 2012). This threat is experienced by most large-bodied species (Cardillo et al. 2005), including other frugivores that are also likely to be providing effective long distance dispersal (i.e. forest elephants; Blake et al. 2009). If removed from an area, the resulting loss of seed dispersal services is likely to have negative implications for the long-term dynamics and maintenance of biodiversity of the forest; a consideration supported by various studies investigating regeneration patterns of defaunated forests (Effiom et al. 2013; Harrison et al. 2013; Kurten 2013; Terborgh et al. 2008; Vanthomme et al. 2010). As suggested by Trakhtenbrot et al. (2005), these important long-distance dispersal traits should be taken into consideration when evaluating the ecological functions of animal species to guide conservation management decisions.

CHAPTER VI.

QUALITY OF SEED DEPOSITION

I. SEED SURVIVAL

Differences in dung beetle activity at western gorilla defecation sites in south-east Cameroon: implications for establishment of Uapaca spp. seedlings

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ABSTRACT

For endozoochorous seed dispersal systems, the extant dung beetle assemblage at seed deposition sites may influence site suitability as burial activity may change the probability that seeds germinate and seedlings establish. This study tested if the different conditions of the two main seed-deposition habitats of a western lowland gorilla population of south-east Cameroon (sleeping sites and old secondary forest) influenced dung beetle assemblages and consequently the seed relocation patterns. In March 2012, in both habitats, burial patterns (proportion and depth) were described in eight stations based on two 300-g experimental faeces with known number of *Uapaca* spp. seeds (N = 75) left for 48 h, and beetle assemblages were described based on one 48h-dung-baited pitfall trapping in five of these stations. To assess the impact of burial pattern on seedling emergence, *Uapaca* seedling emergence trials were performed in a nursery (75 seeds per depth treatment). Assemblage at sleeping sites had a higher species richness (non-significant) and was significantly more abundant than in old secondary forests. Conversely, significantly more seeds were buried in old secondary forests than sleeping sites and at significantly greater depths (mean: 14.9 cm *vs*. 8.7 cm). As trials suggested that burial depth ≥7 cm prevented *Uapaca* seedling emergence, dung beetles are assumed to induce seed loss more strongly in old secondary forests than sleeping sites (20.5% *vs*. 6.7% of initial seed crop). The demonstration that dung beetles may exert a negative influence on seed fate overall, and that the degree to which this occurs may vary depending on habitat, highlights the complexity in determining the suitability of deposition sites for recruitment.

6.1. Introduction

The pattern of seed transportation (abiotically *vs*. biotically) and deposition (regurgitated *vs*. defecated, singly *vs*. in clumps), and the deposition site characteristics are crucially important aspects influencing the likelihood that a dispersed seed survives germination and produces a seedling that successfully establishes and meets appropriate environmental conditions for recruitment (Schupp et al. 2010). When seeds are dispersed through the digestive tract of frugivores (i.e. endozoochorously), the faecal matrix in which seeds are excreted will attract both rodents and dung beetles (Andresen 1999; Beaune et al. 2012a) that may act as predators (rodents) and/or seed dispersers (rodents and dung beetles) and hence affect the post-dispersal fate of seeds (Chambers and MacMahon 1994; Vander Wall and Longland 2004; Vander Wall et al. 2005). In particular, the depth at which seeds are relocated underground by burrowing dung beetles (i.e. ball-rollers and tunnellers), and less frequently by scatter-hoarding rodents, is a determinant parameter as it will influence both the probability of seed detection by granivores and seedling emergence success (Shepherd and Chapman 1998). In the specific case of dung beetles, the pattern of seed relocation, and hence the impact on post-dispersal seed and seedling fate, will partly depend on the composition of the dung beetle assemblage colonising faeces, which in turn can be influenced by intrinsic and extrinsic attributes of the frugivore dispersing the seeds, such as the timing of faeces deposition, the spatial defecation pattern, the volume and physico-chemical properties of the faecal matter, habitat and season (Andresen 2002; Hanski 1989; Hosaka et al. 2014). It is therefore important to study the impact of seed deposition pattern on the burial activity of dung beetles when assessing the effectiveness of dispersal events initiated by frugivores.

This study tested the influence of seed deposition habitat on dung beetle assemblages and the resulting secondary dispersal patterns using an Afrotropical system, involving seeds most commonly dispersed by the western lowland gorilla (*Gorilla gorilla gorilla*) in a site in south-east Cameroon. A 3-y investigation of the gorilla in this study site demonstrated that a third of all seeds dispersed belong to the genus *Uapaca* (Euphorbiaceae), and, as a result of gorilla defecation pattern (Todd et al. 2008) and site-specific habitat preference, most of these seeds encounter either open-canopied conditions at sleeping sites (canopy gaps and young secondary forests) or shaded conditions on feeding trails (old secondary forest). As the degree of canopy openness is known to affect the composition of dung beetle assemblages (Bicknell et al. 2014; Hosaka et al. 2014), we hypothesised the following: (1) The different environmental conditions at sleeping sites and old secondary forests will translate into differences in dung beetle assemblages, and subsequently into (2) differences in the proportion of seeds dispersed by dung beetles, dispersal distances and burial depths, which (3) eventually will result in differing secondary dispersal services. Furthermore, based on published findings on seed burial depths, we hypothesised that (4) most seeds will be buried at shallow depths at which seedling emergence probability will remain high, leading to an improvement in the post-dispersal fate of *Uapaca* seeds by dung beetles.

6.2. Study site

We conducted the study in the research site ‘La Belgique’ at the northern periphery of the Dja Biosphere Reserve, south-east Cameroon (013°07’–013°11’E, 03°23’–03°27’N) (Tagg and Willie 2013, Willie et al. 2012). The research site covers approximately 40 km² of mixed lowland forest (600–700 m asl), in the transition zone between evergreen and semi-deciduous forests (Letouzey 1968). Climatic data recorded in the site between January 2010 and December 2012 correspond to a humid tropical climate with two rainy seasons (February–June and September–November) interspaced by dry seasons (monthly rainfall <100 mm; Willie et al. 2014). Mean annual rainfall ranged between 1315–1831 mm and mean minimum and maximum daily temperatures were 19.8°C and 27.2°C, respectively. The site is dominated by old secondary forests and comprises a dense network of watercourses and swamps (Willie et al. 2012).

6.3. Study species

6.3.1. Western lowland gorilla

The western lowland gorilla is the second largest frugivore of the Congo Basin forests, contributing to the seed dispersal of many species and in large quantities (Petre et al. 2013). The gorilla defecation pattern and hence seed deposition is bimodal with half of faeces produced at sleeping sites mostly early in the morning and the other half along the feeding trails during the day (Todd et al. 2008). Gorillas use an extensive home range, travelling long distances daily, and each night they construct a new sleeping site at a different location (Tutin et al. 1995), resulting in a widespread seed shadow. Most gorilla nests are constructed on the ground in open-canopied environments where herbaceous terrestrial vegetation flourishes (Willie et al. 2012) and repeated use of the same sleeping site is uncommon (but see Iwata and Ando 2007). At La Belgique, however, evidence of previous use by gorillas exists for about a quarter of sleeping sites (Petre, unpubl. data).

6.3.2. *Uapaca* spp.

At La Belgique, there are five species of *Uapaca* (*U. acuminata*, *U. guineensis*, *U. mole*, *U. pynaertii* and *U. vanhouttei*). With the exception of *U. pynaertii*, all species exhibit similar shaped and sized seeds (slightly elongated, mean dimensions 15 × 10 × 5 mm, mean weight 0.42 g; Petre, unpubl. data), and are therefore morphologically indistinguishable in gorilla faeces. *Uapaca* trees occur at high density in the research site (18.2 stems ha^{-1}; Willie, unpubl. data). The fruiting phenology is asynchronous, with fruits potentially available every month of the year (Petre, pers. obs.). Between November and March, when other fruit species are scarce, mast fruiting of *Uapaca* spp. may occur and intact *Uapaca* seeds are found in large quantities in most gorilla faeces (mast fruiting periods 2009–2012: mean ± SD = 71.5 ± 108 per faeces, mean weight of faeces ± SD = 294 ± 201 g; Petre, unpubl. data).

6.4. Methods

6.4.1. Experimental design

In March 2012, we carried out dung beetle trapping in five gorilla sleeping sites and five patches of old secondary forest , followed 4-7 d later by secondary-dispersal experiments in these same experimental stations and an additional three of each type (totalling eight per habitat type). We used gorilla sleeping sites located 6-12 mo before the present study thereby ensuring that the emergence and dispersal of adult dung beetles from gorilla faeces had already occurred to avoid interference with the experiments (Hanski 1989; Scholtz et al. 2009). We selected patches of old secondary forest along permanent survey transects within the home range of the gorilla groups known to not have been used as sleeping sites for at least 3 y prior to this study. The distance between any two neighbouring experimental stations ranged between 111 and 688 m (thus maximizing independence; Larsen and Forsyth 2005). All experimental samples comprised 300 g (equating to the mean weight of natural deposits; Petre et al. unpubl. data) of fresh (<24 h old) gorilla faeces collected from the research site, installed between 08h00 and 10h00, maintained for 48 h and protected from rain by a plastic sheet positioned 1 m above.

6.4.2. Dung beetle assemblage

We carried out a single session of dung beetle trapping in the five sleeping sites and five old-secondary-forest patches in which we installed one faeces-baited pitfall trap, comprising the experimental faeces hung in a nylon stocking above a 5-l plastic bucket, one-third-filled with soapy water, and buried flush with the ground surface. We preserved trapped insects in 90% ethanol solution for later identification by Philippe Moretto and Jean-François Josso (Association Catharsius). Voucher specimens are available for consultation at the Royal Belgian Institute of Natural Sciences, Belgium.

6.4.3. Secondary seed dispersal experiments

In each station, we placed two semi-spherical experimental faecal samples 20 m apart, each mixed with 75 marked seeds of *Uapaca* previously collected from gorilla faeces in the site, and marked with a flag at their centre. After 48 h, we visually assessed the proportion of dung removed by dung beetles using a scale with 10% intervals. While looking for seeds remaining on the forest floor, we collected all ground litter present in a 1-m² area around each faecal sample and weighed them. We then counted the number of experimental seeds remaining on the forest floor and measured individual distances to the flag and assigned seeds to the following categories: 'seed not relocated' (<5 cm from the flag, generally still covered by dung) and 'seed relocated on the soil surface' (≥5 cm from flag and cleaned of dung). When fewer than 75 seeds were counted, we dug up the soil, layer by layer, within a 30-cm radius around the flag (Andresen 2001) and recovered buried seeds. If seeds were still missing we searched for surface mounds in a 1-m radius around the flag indicating the entrance of a ball-roller burrow eventually conducting to buried seeds. We recorded the burial depth and horizontal distance to the flag for each recovered seed. Once the experiments had ended, we took five soil samples with an auger (2.8 cm diameter and 12 cm long) just outside the periphery of the 30-cm-radius search area of each experimental samples, and immediately stored them in labelled zip-loc plastic bags for transport to the laboratory of Gembloux Agro-Bio Tech (University of Liège) at the Pallisco logging company sawmill at Mindourou, Cameroon, for analysis. We spread the soil samples on a metallic plate, extracted and discarded all root fragments, and placed them to dry in an oven at 105°C. We weighed soil content every 2 h until the weight stabilised, and calculated the soil bulk density (g cm^{-3}) (ratio between dry mass and volume of the soil sample) as a proxy for the degree of soil compaction.

6.4.4. Seedling emergence

To determine the impact of burial depth on seedling emergence probability, we performed trials with seeds of *Uapaca vanhouttei* in an unfenced field nursery at the forest edge of the clearing which houses the La Belgique research camp. We extracted the seeds from ripe fruits recently fallen from a single fruiting tree to avoid genetic influence on germination performances. In March 2012, we sowed 50 depulped seeds at each of the following depths: soil surface (0 cm), 1, 3, 5 and 10 cm (Andresen and Levey 2004), in perforated plastic nursery bags (one seed per bag) filled with manually compacted soil collected from the study site. Results from this germination trial revealed that seedling emergence could only occur for seeds deposited at the soil surface and buried at 1 cm. However, it did not consider the potential fertilising effect of the faecal matter buried by dung beetles together with the seeds. Therefore, we later repeated this trial (March 2014) using depulped seeds from the same fruiting tree that we embedded in approximately 5 g of faecal matter prior to sowing. We also added a sixth depth treatment of 2 cm and sowed 75 seeds per depth treatment instead of 50. We regularly weeded and watered bags and monitored seedling emergence (above-ground appearance of hypocotyledonous stems) daily for 4 mo.

6.4.5. Data analysis

Except otherwise specified, we performed all statistics in Statistica 10 with α level set at 0.05. Means are given with standard deviation (mean ± 1 SD). We applied an arcsine-square-root transformation of values expressed in proportions in order to use parametric tests. We controlled for the homoscedasticity of data with the Levene test.

Dung beetle assemblage. - We computed diversity estimates in EstimateS 9.1.0. We measured estimated species richness (S_{est}) and associated 95% confidence interval (CI), using Chao 1 estimator (S_{chao1}) (Chao 1984, 1987), on individual-based abundance matrices from 1000 runs of randomized sampling order, and considered the smallest number of individuals caught in one habitat (309 in old secondary forest) as the reference sampling level for comparison between habitats. A significant difference ($P < 0.05$) is obtained when the 95% CI do not overlap. We used Chao's Abundance-based Sørensen Similarity Index, which takes into account potential undersampling bias and is therefore more conservative, to compare species assemblages. We performed a Chi-squared tests of independence to test for differences in the proportion of individuals belonging to each dung-processing guild between the two habitat types. We measured body size of each individual caught, accurate to the nearest 0.5 mm, using callipers and compared the mean body size of the dung beetle assemblages of each habitat type with the Mann-Whitney test. We then performed Chi-squared tests of independence to test for differences in the proportion of individuals with respectively a higher and smaller body size than the mean length of *Uapaca* seeds (i.e. 15 mm) between the two habitat types.

Secondary-dispersal experiments. – We investigated the effect of habitat type on seed burial with a Multivariate General Linear Model, using as the response variables proportions of: seeds buried, seeds relocated on the soil surface, seeds not relocated and seeds not recovered. We included habitat type as the categorical predictor (fixed effect) and proportion of dung removed, soil compaction index and ground litter mass as continuous predictors (covariates).

We tested differences in secondary-dispersal distances between habitat types using General Linear Models. We distinguished two categories of dispersal distance (dependent variables), according to the vertical and horizontal plane, resulting in two models. In both models, we included the same predictors as above, to which we added as a fourth continuous predictor the proportion of seeds relocated vertically or horizontally depending on the model.

Seedling emergence. – We performed a Cochran's test of linear trend to look for differences in the proportion of seedlings that successfully emerged between burial depths.

6.5. Results

6.5.1. Dung beetle assemblage

We collected a total of 870 dung beetles (family Scarabaeidae) from 41 species (22 genera, six tribes; Appendix 1) in pitfall traps. Four species (*Catharsius gorilla*, *C. gorilloides*, *Onthophagus fuscidorsis*, *Pedaria oblonga*) accounted for >60% of all individuals caught, and 27 spp. each contributed only <1%.

We found the majority of dung beetles to have been trapped at sleeping sites (N = 561; 64.5%), with an average of 112 ± 35 individuals caught per pitfall trap compared to 62 ± 23 individuals caught per pitfall trap in old secondary forests. All but two of the 41 species were represented at sleeping sites whereas only 24 species were recorded from old-secondary-forest traps. Despite this difference in observed species richness, estimated species richness at sleeping sites (S_{chao1} = 46.2; 95% CI = 40.6–71.3) was not significantly different to that of old secondary forest (S_{chao1} = 33.3; 95% CI = 25.9–68.8). For both habitats, species accumulation curves were far from reaching the asymptote, suggesting that other species would have been found with an increase in sampling effort.

The two habitat types shared 22 species in common. Because the dominant species were the same in the two habitats and the 19 species found in only one type of habitat were represented by only few individuals (≤6), the estimated Chao's Abundance-based Sørensen Similarity Index was remarkably close to 1 (0.993), suggesting that even an increased sampling effort would have resulted in very similar assemblages.

Overall, tunnellers dominated the trap-caught dung beetle community accounting for 78.0% of individual beetles (N = 622) and 71.5% of species (N = 32) caught, respectively; whereas ball-rollers accounted for 8.2% of beetles (N = 71) and 9.8% of species (N = 4) caught. Kleptoparasites (i.e. dung beetles parasitising faecal material previously buried by tunnellers and ball-rollers) and dwellers (i.e. dung beetles processing faecal matter within the dung pile without transporting it) accounted for the remaining 19.9% (N = 173) and 0.5% (N = 4) of individuals and 7.3% (N = 3) and 5.9% (N = 2) of species caught, respectively. There was a significant difference in the proportion of individual tunnellers *vs*. ball-rollers between the two habitat types ($\chi^2 = 6.2$, df = 1, $P < 0.02$). Ball-rollers accounted for a higher proportion of beetles caught in old secondary forests (13.9%; N = 38) compared to sleeping sites (8.0%; N = 33), and conversely tunnellers were represented by a lower proportion of beetles in old secondary forests (81.6%; N = 236) compared to sleeping sites (92.0%; N = 381).

Individual dung beetle body size varied from 3.0 mm (*Caccobius elephantinus*; tunneller) to 40.0 mm (*Heliocopris eryx*; tunneller) (mean = 10.4 ± 7.7 mm). Mean ball-roller species (N = 4) body size varied between 4.3 and 6.8 mm; and tunneller species (N = 32) between 3.25 and 39.0 mm (Appendix 1). We found the dung beetle assemblage mean body size to be significantly larger at sleeping sites than old secondary forests (11.3 mm *vs.* 8.9 mm; Mann-Whitney test: U = 50907, P = 0.009), and proportionally the assemblage at sleeping site contained significantly more large-bodied beetles in comparison to that found in old secondary forests (26.6% (111 individuals) caught at sleeping sites *vs*. 14.1% (39) in old secondary forests: $\chi^2 = 12.6$, df = 1, $P < 0.01$).

6.5.2. Secondary dispersal experiments

Dung beetles processed all experimental faecal samples within 48 h in sleeping sites, whereas four samples remained intact in old secondary forests. For processed samples, the proportion of dung removed was not significantly different between secondary forest (median 90%) and sleeping sites (85%) (Mann-Whitney test: U = 98, P = 0.812), and was a good overall predictor of the fate of seeds 48 h post deposition (Table 1). However, the habitat specific pattern within each fate category was significantly different from each other (Wilk's lambda = 0.463, F = 5.79, df = 4, P = 0.003). Of the 12 processed faecal samples in old secondary forest, the percentage of seeds buried was 25.8%, seeds relocated on the soil surface 19.8%, seeds not relocated 48.7% and seeds not recovered 5.6%. The respective pattern of seed fate for the 16 faecal samples at sleeping sites was significantly different (Wilk's lambda = 0.463, F = 5.79, df = 4, P = 0.003): 9.3%, 39.0%, 46.3% and 5.3% of seeds. Univariate results indicated that old secondary forest had a significantly higher proportion of seeds buried, and sleeping sites a significantly higher proportion of seeds relocated on the soil surface (Table 1). The proportion of seeds not relocated and not recovered were similar between the two habitats; for the former, the degree of soil compaction and ground litter mass exerted significant positive influences (Table 1).

Table 1. Results of the General Linear Model testing the effects of the habitat type (sleeping sites and old secondary forests) and environmental variables on the short-term fate (48h post deposition) of *Uapaca* sp. seeds contained in 300 g of western lowland gorilla faecal material at La Belgique research site, south-east Cameroon, in March 2012. The model compared the proportion of seeds experiencing each of the four categories of fate: seeds buried by dung beetles, seeds relocated on the soil surface by dung beetles, seeds not relocated and seeds not recovered. The level for the categorical predictor 'Habitat type' is old secondary forest. Therefore a positive parameter indicates a higher proportion compared to sleeping site, and inversely a negative parameter indicates a smaller proportion.

	Buried			Relocated on the soil surface			Not relocated			Not recovered		
	Parameter	F	P	Parameter	F	P	Parameter	F	P	Parameter	F	P
Intercept	0.417	1.28	0.269	0.547	3.96	0.059	0.551	3.06	0.094	0.289	1.06	0.313
Ground litter	-0.0001	0.979	0.333	-0.0002	3.98	0.058	0.0002	4.37	0.048	0.0001	1.25	0.275
Soil compaction	-0.046	0.562	0.461	-0.049	1.14	0.297	0.114	4.64	0.042	-0.063	1.80	0.192
% dung removed	0.288	7.26	0.013	0.352	19.5	<0.001	-0.526	33.1	<0.001	0.158	3.78	0.064
Habitat type	0.126	9.64	0.005	-0.13	18.3	<0.001	-0.008	0.06	0.814	0.003	0.009	0.924

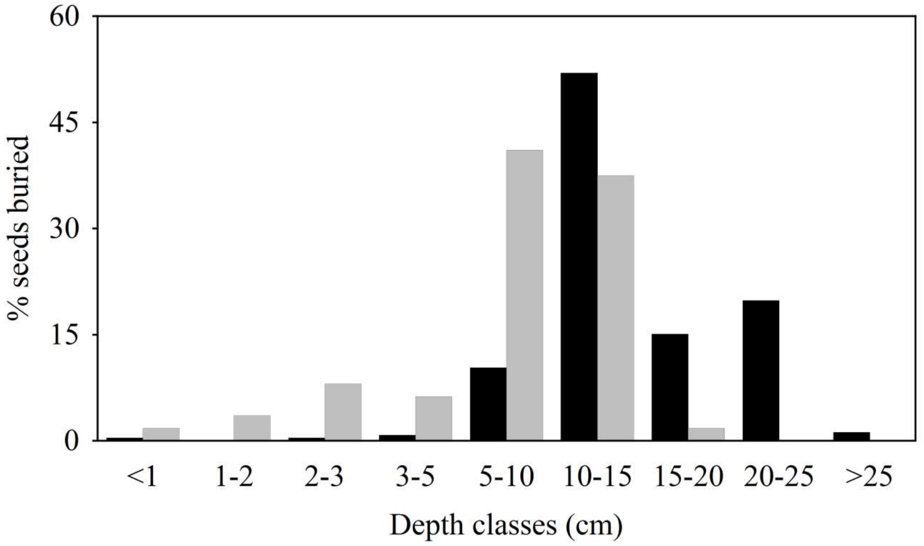

Figure 1. Percentage of *Uapaca* seeds contained in western lowland gorilla faeces buried by dung beetles at the different depth classes (<1, 1–2, 2–3, 3–5, 5–10, 10–15, 15–20, 20–25 and >25 cm) in old secondary forests (black columns) (12 experimental faecal samples processed by dung beetles; N = 252 seeds buried out of 900 seeds) and gorilla sleeping sites (grey columns) (16 experimental faecal samples processed by dung beetles; N = 112 seeds buried out of 1200 seeds), at La Belgique research site, south-east Cameroon (March 2012).

Overall, secondary-dispersal distances differed significantly between habitat types (Wilk's lambda = 0.625: F = 5.09, df = 2, P = 0.019). Seeds vertically relocated by dung beetles were buried at greater depths in old secondary forests (mean = 14.9 ± 4.9 cm; median = 13.8 cm; range = 0.5–26.5 cm) than at sleeping sites (mean = 8.7 ± 3.9 cm; median = 9.1 cm; range = 0.8–15 cm) (Figure 1), and burial depth co-varied positively and significantly with the proportion of dung removed and seeds buried (Table 2). Seeds dispersed horizontally were relocated further from the original source in old secondary forests (mean = 7.8 ± 6.8 cm; median = 6.4 cm; range = 0.1–37.7 cm) than at sleeping sites (mean = 3.7 ± 4.0 cm; median = 2.5 cm; range = 0.1–28.5 cm), but horizontal distances did not co-vary significantly with any of the predictors (Table 2).

Table 2. Results of the General Linear Models testing the effects of the habitat type (sleeping sites and old secondary forests) and environmental variables on the secondary dispersal distances on the vertical and horizontal planes of *Uapaca* sp. seeds contained in 300 g of western lowland gorilla faecal material at La Belgique research site, south-east Cameroon, in March 2012, and subjected to dung beetle activity during 48 h. The level for the categorical predictor 'Habitat type' is old secondary forest. Therefore a positive parameter indicates a higher proportion compared to sleeping site, and inversely a negative parameter indicates a smaller proportion.

	Vertical distance			Horizontal distance		
	Parameter	F	P	Parameter	F	P
Intercept	15.0	8.37	0.009	1.71	0.091	0.766
Ground litter	-0.003	2.08	0.164	0.003	2.26	0.148
Soil compaction	-0.272	0.097	0.758	0.069	0.006	0.938
% dung removed	-3.74	4.70	0.042	0.750	0.211	0.651
% seed buried	7.41	6.50	0.019			
% seed relocated horizontally				1.29	0.219	0.645
Habitat type	1.74	6.82	0.016	2.06	22.8	<0.001

6.5.3. Emergence probability

In the 2014 trials, seeds placed on the soil surface experienced a high level of predation by rodents with 57 (76%) of the initial 75 seeds being removed. Therefore, this depth was not included in the Cochran's test of linear trend testing the effect of burial depth on emergence probability.

Burial depth exerted a significant influence on emergence probability (Cochran test: $Q = 104$, $df = 4$, $P < 0.001$), with seedling emergence probabilities 74.7%, 66.7%, 58.7%, 30.7% and 0% for depth treatments 1, 2, 3, 5 and 10 cm, respectively (Figure 2). The equation of the second-order-polynomial-adjustment regression slope fitting the emergence probability values obtained (Figure 2) suggests that an emergence probability of zero would have been found at a depth of 7 cm (at 6 cm the probability would have been 13.2%).

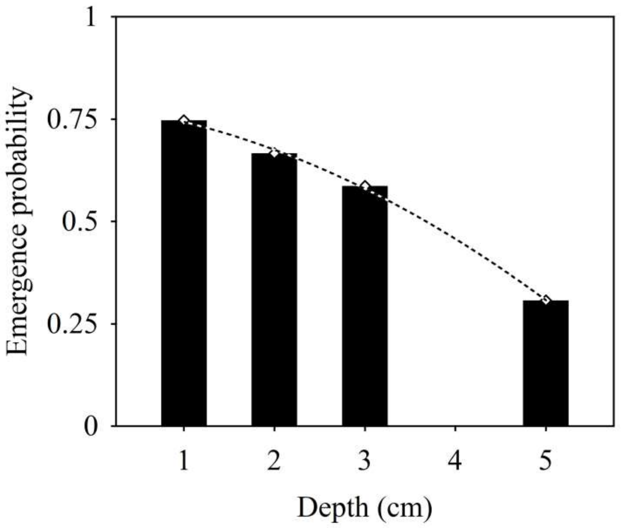

Figure 2. The impact of burial depth on the emergence probability of *Uapaca vanhouttei* seedlings nursed in a field nursery (March–July 2014) at La Belgique, south-east Cameroon. The depth 4 cm was not tested. Emergence probabilities are represented by black bars and the dashed line indicates the regression curve fitting the observed emergence probabilities with a second order polynomial adjustment ($y = 0.784 - 0.0271x - 0.0136x^2$).

6.6. Discussion

6.6.1. Dung beetle assemblages and secondary dispersal patterns

We did not find a significant influence of habitat type on dung beetle species richness and composition. In both habitat types, the dung beetle assemblage was characterized by a small number of abundant species and a greater number of rare ones, resulting in large, overlapping, 95% CI for the estimated species richness of the two habitats. A greater sampling effort might have reduced the effect of such unbalanced distribution of individuals among species on diversity estimates and eventually resulted in significant differences and the identification of species specialized to either habitat. However, these species, if they exist, are not likely to be abundant enough to exert a strong influence on the secondary-dispersal activities in either habitat type as all of the 19 species caught in only one habitat type (17 spp. in sleeping sites and 2 spp. in old-secondary-forest patches) each accounted for less than 1% of the total number of individuals caught in each habitat. Furthermore, only four species of these 19 exhibited a mean body size large enough to enable active dispersal of *Uapaca* seeds (i.e. body-size equal to or larger than seed size; Feer 1999). Of the 22 shared species, another seven have a sufficiently large body-size to be involved in the *Uapaca* seed-burial events we observed in our secondary-dispersal experiments. Together, these 11 large-bodied dung beetle species, all tunnellers, represented only 17.6% of the total number of individuals caught, and this relatively low abundance is likely to be the reason for the small proportion of buried seeds we observed (15.2%). Furthermore, the fact that ball-rollers caught in the traps were less than half the size of *Uapaca* seeds suggests that seeds not recovered were not likely to have been transported beyond the 1-m search radius but more likely to have been removed by rodents.

The more abundant large-bodied dung beetle community observed at sleeping sites predicts more intense activity and a subsequently enhanced secondary dispersal in this habitat type. However, we observed large-bodied tunnellers to bury more seeds in old secondary forests and at greater vertical and horizontal distances. When competition is fierce, dung beetles reduce the amount of faecal matter they buried (Scholtz et al. 2009), resulting in a lower probability that a large seed such as *Uapaca* spp. would be also transported. Additionally, since we installed the experimental faeces in the morning, if the large-bodied tunnellers are nocturnal beetles as is often the case (Andresen 2002; Slade et al. 2007), diurnal beetles would have broken the faecal clump into pieces more actively at sleeping sites than in old secondary forests, reducing the volume of matter still containing seeds that the large-bodied tunnellers could process (Hosaka et al. 2014). Finally, it is reasonable to suspect that with an increased competition at sleeping sites, tunnellers allocated less time to tunnel construction resulting in shallower tunnels and hence smaller secondary-dispersal distances. Dung beetle abundance, rather than composition, may explain the observed differences in seed relocation patterns.

6.6.2. Post-secondary dispersal seed fate

Our study provides evidence of a potentially high rate of rodent predation of *Uapaca* spp. seeds from the forest floor (up to 5.4% of seeds within 48 h in secondary-dispersal experiments and 76% of ‘soil-surface seeds within 4 mo in the field nursery trials); therefore, we suggest that seed burial by dung beetles may play an important role in the short-term post-dispersal fate of *Uapaca* spp. seeds in this site. Furthermore, the associated burial of faecal matter during seed burial serves to improve the fertility of the available growing substrate (Nichols et al. 2008; Scholtz et al. 2009), which may ultimately improve the vigour of the seedlings and the depth at which emergence is possible, as suggested by the discrepancy in the emergence probabilities between our 2012 and 2014 trials. However, this fertilising effect would not facilitate emergence beyond a certain depth. In our 2014 trials, the emergence probability decreased almost linearly with burial depth to 3–4 cm and then experienced a sharper decline to a depth between 5 and 10 cm, beyond which the emergence of seedlings is completely prevented (estimated by regression to be 7 cm). As burial depths >5 cm greatly inhibit the emergence probability of *Uapaca* seedlings, and detection by rodents has been shown in other studies to be zero or very low for seeds buried at such depths (Andresen 1999; Estrada and Coates-Estrada 1991; Shepherd and Chapman 1998), we suggest an optimum burial depth (Shepherd and Chapman 1998) between 1 and 5 cm. However, we observed only a small proportion of *Uapaca* seeds being buried by dung beetles at depths <5 cm (7.1%), with the majority being buried at depths ≥10 cm (73.1%), at which depth the emergence of *Uapaca* seedlings seemed to be completely inhibited. Unless very few non-buried *Uapaca* seeds are escaping predation, it is likely that the influence of dung beetle activity in this case is negative. Our study demonstrates that this detrimental effect is less pronounced at sleeping sites than at secondary-forest sites, as 17.9% of buried seeds (20/112) were found at optimum depths (1–5 cm) compared to 1.2% (3/252) in old secondary forests, resulting in an estimated mean emergence probability for buried seeds of 12.8% at sleeping sites and 0.9% in old secondary forests. It seems therefore that seeds dispersed at sleeping sites that survive predation have a higher chance to produce established seedlings than seeds dispersed on trails in old secondary forests, thus leading to a higher effectiveness of *Uapaca* seed dispersal at sleeping sites. At the seedling stage this effectiveness might be further improved by the high irradiance levels characterizing sleeping sites as *Uapaca* species are (non-pioneer) light-demanding species (Hawthorne 1995). Furthermore, the possibility of previously-buried seeds being cycled closer to the soil surface by dung beetles during soil excavation (Santos-Heredia and Andresen 2014) may have a higher impact at sleeping sites as species composing the soil seed bank are mostly light-demanders and therefore will encounter adequate conditions for seed germination, and seedling establishment and growth (Daïnou et al. 2011).

6.6.3. Conclusion

Our study was unable to identify a habitat niche differentiation among the dung beetle community of the study site when considering gorilla sleeping sites (predominantly young secondary forest and light gaps) and old secondary forest. However, the different environmental conditions seemed to strongly influence dung beetle abundance which resulted in differing seed removal and burial patterns. In contrast to our predictions, these patterns do not support the widespread belief that seed burial by dung beetles improves the fate of seeds primarily dispersed by frugivores (but see Vulinec and Lambert 2009). As almost all documented seed burial data pertain to the Neotropics, where burial depths may be shallower and emergence probabilities higher (Andresen 2001, 2002, 2003; Andresen and Levey 2004; Culot et al. 2009, 2011; Estrada and Coates-Estrada 1991; Santos-Heredia et al. 2010), we therefore recommend addressing the paucity of data outside the

Neotropics in order to infer more generally the importance of dung beetles in the regeneration dynamics of tropical forests.

Appendix 1. List of dung beetle species and number of individuals caught in the gorilla-dung-baited pitfall traps placed in old secondary forest (OSF) and at western lowland gorilla sleeping sites (SS) in south-east Cameroon (March 2012). Dung-processing guild encompasses ball-rollers (B), dwellers (D), kleptoparasites (K) and tunnellers (T).

Tribe/Species	Guild	Body size (mm)	No. ind. (OSF)	No. ind. (SS)
Coprini				
complex *Catharsius gorilla* Thomson, 1858/*C. gorilloides* Felsche, 1907	T	24.5	31	63
Catharsius lycaon Kolbe, 1893	T	20.2	0	3
Copris camerunus Felsche, 1904	T	16.5	0	2
Copris truncatus Felsche, 1901	T	21.5	0	4
Heliocopris eryx Fabricius, 1801	T	39	0	2
Heliocopris helleri Felsche, 1903	T	35.3	2	4
Dichotomiini				
Pedaria morettoi Josso & Prévost, 2003	K	7.5	0	3
Pedaria oblonga Josso & Prévost, 2003	K	7	32	134
Pedaria spinithorax Paulian, Cambefort & Mauchamp, 1982	K	7.1	0	4
Oniticellini				
Clypeodrepanus strigatus Jansenss, 1953	T	4	0	1
Drepanoplatynus gilleti Boucomont, 1921	T	9	2	0
Eodrepanus morgani Barbero, Palestrini & Roggero, 1909	D	5	0	1
Liatongus sjoestedti Felsche, 1904	T	9.8	0	2

Oniticellus pseudoplanatus Balthasar, 1964	D	10.8	1	2
Onitini				
Lophodonitis carinatus Felsche, 1907	T	15	1	0
Onthophagini				
Caccobius cyclotis Cambefort, 1984	T	3.9	0	6
Caccobius elephantinus Balthasar, 1967	T	3.3	0	4
*Diastellopalpus conradti d'*Orbigny, 1902	T	24.5	0	1
Diastellopalpus laevibasis d'Orbigny, 1902	T	23.66	1	27
Diastellopalpus murrayi Harold, 1968	T	16.8	5	6
Diastellopalpus noctis Thomson, 1858	T	17	0	1
Milichus inaequalis inaequalis Boucomont, 1928	T	6	0	1
Milichus merzi Cambefort, 1983	T	7.8	15	16
Mimonthophagus apicehirtus d'Orbigny, 1915	T	10	1	1
Onthophagus barriorum Walter, 1991	T	5.2	1	1
Onthophagus cf. *biplagiatus* Thomson, 1858	T	5.5	0	2
Onthophagus cf. *umbratus* d'Orbigny, 1902	T	6.2	1	2
Onthophagus densipilis d'Orbigny 1902	T	8.5	7	8
Onthophagus fuscidorsis d'Orbigny, 1902	T	7	112	160
Onthophagus intricatus Moretto, 2010	T	4.8	8	3

Onthophagus justei Walter, 1989	T	4.1	32	25
Onthophagus pilipodex d'Orbigny, 1913	T	9	0	1
Onthophagus vesanus Balthasar, 1967	T	5.3	8	13
Pinacotarsus dohrni Harold, 1975	T	11	0	1
Proagoderus semiiris Thomson, 1858	T	12.7	4	9
Tomogonus crassus d'Orbigny, 1902	T	7.6	6	14
Sisyphini				
Neosisyphus angulicollis Felsche, 1909	B	6.6	13	8
Neosisyphus sp.	B	6.8	7	2
Sisyphus sp.1	B	4.3	17	21
Sisyphus sp.2	B	5	1	2

CHAPTER VII.

QUALITY OF SEED DEPOSITION

II. SEEDLING RECRUITMENT

7. Quality of seed deposition II: Seedling recruitment

Does the western lowland gorilla perform directed-dispersal services at sleeping sites? Insights from south-east Cameroon

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Petre C-A., Salah M., Tagg N., Beudels-Jamar R., Haurez B., Willie J. & Doucet J-L. (submitted to *Forest*)

ABSTRACT

One advantage of animal-mediated seed dispersal is a non-random deposition of seeds in sites particularly suitable for recruitment, a phenomenon known as directed-dispersal. At La Belgique research site, Cameroon, the western lowland gorilla establishes sleeping sites in areas with a predictably high light availability; and this is where half the daily faecal production occurs. This has been shown elsewhere to improve the post-dispersal fate of several species. To investigate if sleeping site environmental conditions improved the performances of seedlings that emerged from gorilla faeces, we focused on the most quantitatively-dispersed taxon, *Uapaca* spp. Our experimental design consisted of dividing each of 354 faeces encountered at 35 fresh sleeping sites between December 2010–March 2012 into two samples of equal mass; one half of each sample was marked at its original location and the other half was placed in a control site randomly chosen in the vicinity of the sleeping site. We monitored the growth and survival of any emergent seedlings until April 2014. Our results demonstrated that site selection for nesting is a highly important factor determining the seed dispersal effectiveness of *Uapaca* spp. by the western lowland gorilla as, overall, sleeping sites significantly improved the probability of producing 2-3 y old *Uapaca* recruits that, moreover, exhibited a significantly improved growth rate. In particular, swamp forests as nesting habitat provided the highest effectiveness. During the dry season, swamp forests are increasingly used as sleeping site habitat and this period corresponds to the peak in *Uapaca* spp. seed dispersal quantity (38.6% of the total seed load). On this basis, our study demonstrated a case of directed-dispersal of *Uapaca* spp. seeds in swamp forests by the western lowland gorilla.

7.1. Introduction

The location where seeds are dispersed is an important aspect in determining seed dispersal effectiveness (Schupp et al. 2010) as it influences the likelihood of an emergent seedling surviving and growing to adulthood (Nathan and Muller-Landau 2000). Among spatially-dependent mechanisms influencing plant fitness is the Janzen-Connell effect (Connell 1971; Janzen 1970), which confers an advantage to seeds dispersed beyond a certain distance from the parental source (Steinitz et al. 2011; Wills et al. 2006), understood to be a result of the reduction in host-enemy dynamics and intraspecific competition. Unlike the Janzen-Connell effect, other spatially-explicit mechanisms do not apply to all seeds dispersed away from the parental source, namely the phenomenon known as directed-dispersal (Howe and

Smallwood 1982). The term 'directed-dispersal' refers to the deposition of a high proportion of seeds in sites where the propagules have a predictably high probability of survival relative to at random sites, thus increasing plant fitness (Wenny 2001). Demonstration of cases of directed dispersal is rare, particularly for tropical vertebrate-dispersed plants, however it is likely to be more common than previously believed (Wenny 2001). It has been proposed that demonstrating that a disperser transports seeds to non-random sites which are well-suited for seedling establishment and growth constitutes convincing evidence of directed dispersal (Howe and Smallwood 1982). The western lowland gorilla constitutes a likely candidate for this phenomenon: in the Lopé National Park, Gabon, seedlings of four tree species appeared to exhibit improved performances at sleeping sites, where half of the daily faecal production occurred (Todd et al. 2008), compared to seedlings that emerged from faeces produced elsewhere (Rogers et al. 1998; Voysey et al. 1999b). The higher suitability of sleeping sites for seedling growth was further demonstrated experimentally at Bambidie, Gabon (Haurez et al. 2015). It appeared in both cases that the more open canopy of sleeping sites was one factor explaining this improvement of seedling performances. We demonstrated in a previous study that the western lowland gorilla population (*Gorilla gorilla gorilla*) at La Belgique research site, south-east Cameroon, establishes sleeping sites in areas with distinctive structural and compositional characteristics, with the degree of canopy openness being the most notable distinguishing factor (Petre et al. 2015a – see chapter 4). Therefore, it seems likely that the dispersal of seeds at sleeping sites by the western lowland gorilla at La Belgique also improves the fate of dispersed seeds and subsequent seedlings. This hypothesis was tested in the current study.

7.2. Methods

7.2.1. Study site

We conducted the study in the research site 'La Belgique' at the northern periphery of the Dja Biosphere Reserve, south-east Cameroon (013°07'–013°11'E, 03°23'–03°27'N). The research site comprises mixed lowland forest (600–700 m asl), in the transition zone between evergreen and semi-deciduous forests (Letouzey 1968). Climatic data recorded in the site between January 2010 and December 2012 correspond to an equatorial climate with a ten-month rainy season and a two-month dry season (December–January). Mean annual rainfall ranged between 1315–1831 mm and mean minimum and maximum daily temperatures were 19.8°C and 27.2°C, respectively. The site is dominated by secondary forest and comprises a dense network of watercourses and periodically inundated swamps (Willie et al. 2012).

7.2.2. Study species

We focused our study on the species of the genus *Uapaca* Baill. (Euphorbiaceae). Five species are present at La Belgique (*U. acuminata*, *U. guineensis*, *U. mole*, *U. pynaertii* and *U. vanhouttei*), the seeds of which being dispersed by the western lowland gorilla (Petre et al. 2015a – see chapter 4). As these species cannot be accurately distinguished macroscopically from seeds and from young seedlings, except *U. pynaertii* which presents much larger seeds and cotyledons, we worked at the taxon level. At La Belgique, this is the top quantitatively dispersed taxon, encompassing more than a third of the total seed load dispersed over a 3-y period (Petre et al. 2015a – see chapter 4). *Uapaca* seeds can be found potentially in every calendar month (Petre et al. submitted; see chapter 3 & 7). Working on this taxon therefore ensures a sufficient amount of data to test the impact of microsite selection on post-dispersal seed fate with naturally dispersed seeds.

7.2.3. Experimental design

From September 2009 to August 2012, we followed fresh western lowland gorilla trails in search of sleeping sites. Between December 2010 and March 2012, we located 35 sleeping sites, within 24h of their construction, and recorded habitat type (canopy gap, young secondary forest, old secondary forest, periodically inundated swamp forest; White 1986). We marked faecal samples for seedling establishment and growth monitoring. We divided each faecal sample of ≥200 g (N=354) into two parts of equal mass; we marked one at the exact location where we found the sample and displaced the other in the surrounding vegetation following a random compass bearing at a random distance ranging from 20 to 50 m. For each marked sample we recorded habitat type. At each sleeping site, we collected a minimum of three faeces for component seed numbering and species identification to represent the seed content patterns of all marked samples (Doran et al. 2002; see data analysis). We monitored marked faecal samples at increasing time intervals (ranging from 15 d to 6 mo) until April 2014. At each monitoring visit, we counted the number of seedlings in each marked sample, identified them individually (where possible) and measured the length of each seedling from the soil to the apex, to the nearest mm. In June–July 2012, we took hemispherical photos of the canopy with the lens of the camera positioned vertically 1m above each marked sample, and we analysed the images using the Gap Light Analyzer software (GLA 2.0) to obtain an estimate of canopy openness.

7.2.4. Data analysis

We performed all statistics in Statistica 10 with α level set at 0.05. Means are given with standard deviation (mean ± 1 SD). We tested the normality of the data matrix using a Kolmogorov-Smirnov test. For model construction, we evaluated the fit of the model with a Goodness-of-fit Chi-square test.

We assessed differences in the establishment and survival success (0,1) (dependent variable) using Generalised Linear Models with a binomial distribution and a logit-link function. We defined the establishment and survival success at the level of the faecal sample (i.e. any one sample with one or more established seedlings at the last monitoring session), given that the most likely best outcome of such clump-dispersal will be the recruitment of one single adult tree per faeces. We included *Site* (sleeping sites *vs*. control sites) and *Habitat* as fixed factors, and *Estimated number of seeds of Uapaca spp.* contained in the faecal sample, *Estimated number of seeds of all other co-dispersed species* in the faecal sample, *Percentage of canopy openness* and *Time since defecation* (time elapsed between the faeces production and the monitoring session) as covariates. We calculated the estimated number of seeds of *Uapaca* spp. and all other co-dispersed species within a faecal sample by multiplying the respective mean number of seeds contained per mass unit in the three faeces collected in each sleeping sites by the mass of the monitored sample.

We assessed differences in growth rate (dependent variable) between established *Uapaca* seedlings using ANCOVA models with a gamma distribution and an identity-link function, after having controlled that the relationship between seedling height and time was linear (Pearson correlation test: $R^2=0.36$; $p<0.001$). We used the height in centimetre to the nearest mm of the tallest seedling within any one sample at each monitoring session as the dependent variable. We included in the model *Site* and *Habitat* as fixed factors, and *Percentage of canopy openness* as the covariate. We tested the interaction between each of these four explanatory variables with *Time* (i.e. time elapsed between the faeces production and the monitoring session). A significant interaction results in a significant contribution of the explanatory variable to the observed differences in seedling height.

7.3. Results

At La Belgique, the western lowland gorilla used all four main habitat types for nest construction. In decreasing mean monthly use, these habitats were: young secondary forest (43.7%), canopy gap (34.9%), swamp forest (13.9%) and old secondary forest (7.5%). The mean canopy openness above faecal samples marked at the 35 sleeping sites was 13.4 ± 12.4% whereas it was 5.8 ± 6.0% above the samples marked in control sites. At the last monitoring session, 417 seedlings were found established in 106 faecal samples marked in 21 sites. Among these, *Uapaca* seedlings encompassed 55.7% of the cohort (N=219 seedlings).

7.3.1. Establishment success

Time since defecation was not a significant factor (Wald $chi^2=0.815$, df=1, p=0.366) suggesting that processes responsible for early-life seedling mortality already took most of their effect in each faecal sample and therefore differences in the length time seedlings were monitored did not introduced a bias in the results. Both categorical predictors were significant (*Site*: Wald chi^2=8.52, df=1, p=0.004; *Habitat*: Wald chi^2=24.4, df=3, p<0.001). Faeces marked at sleeping sites had a higher probability of having viable established seedlings (28.5% of faecal samples still held viable *Uapaca* seedlings at last monitoring session) than faeces marked in control sites (16.3%). Swamp forests provided the highest survival probability (51.3% of faecal samples still held viable *Uapaca* seedlings at last monitoring session), followed by canopy gaps (28.6%), young secondary forests (16.5%) and old secondary forests (14.3%). The *Estimated number of seeds of Uapaca spp.* contained in the faecal sample was significantly influencing positively the establishment and survival probability (Wald chi^2=13.1, df=1, p<0.001). Conversely, the *Estimated number of seeds of all other co-dispersed species* in the faecal sample was significantly influencing it negatively (Wald chi^2=12.4, df=1, p<0.001; parameter estimate=-0.131). No effect of *Percentage of canopy openness* was detected (Wald chi^2=0.722, df=1, p=0.396).

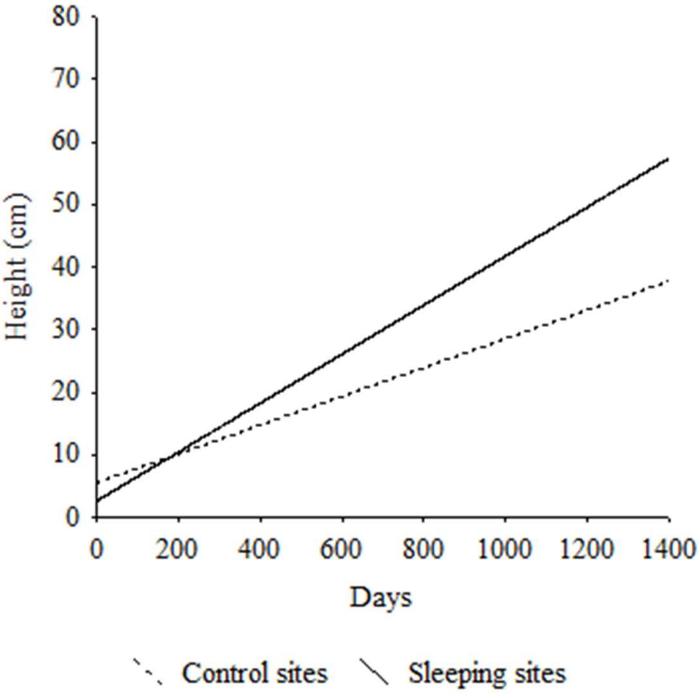

Figure 1. Mean growth rate of *Uapaca* spp. seedlings established in faeces of the western lowland gorilla at La Belgique research site, southeast Cameroon. Comparison between the slopes of the regression lines fitting a linear adjustment between the seedling height and time since defecation for seedlings established in faeces marked at sleeping sites (plain line; R^2=0.378; y=2.6+0.039x) and control sites (dashed line; R^2=0.371; y=5.54+0.023x).

7.3.2. Growth rate

There was a significant interaction between *Site* and *Time* (Wald $\chi^2=8.34$, df=1, p=0.004) and between *Percentage of canopy openness* and *Time* (Wald $\chi^2=287$, df=1, $p<0.001$), whereas the interaction between *Habitat* and *Time* was not significant (Wald $\chi^2=6.85$, df=3, p=0.077). Overall, *Uapaca* seedlings established in sleeping sites had a higher growth rate compared to those established in control sites (Figure 1), and the growth rate of *Uapaca* seedlings progressively became faster as the percentage of canopy openness was increasing (Figure 2).

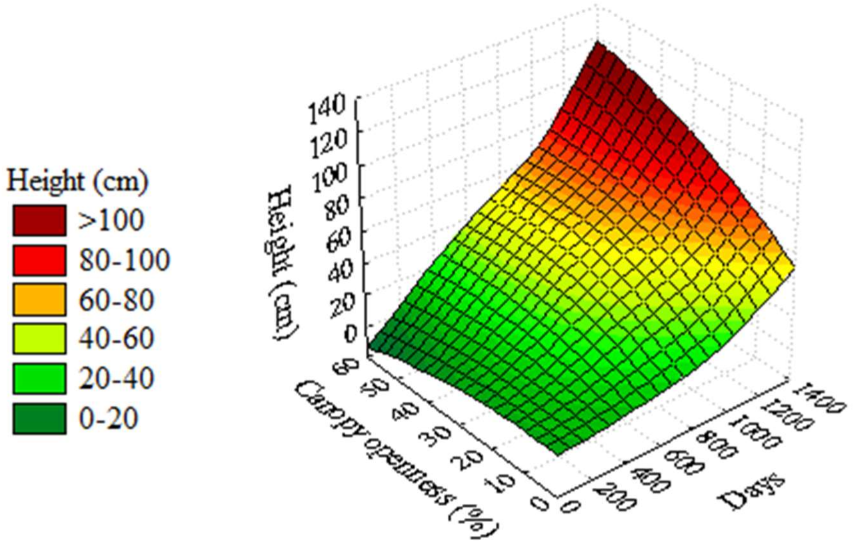

Figure 2. Effect of the percentage of canopy openness on the growth of *Uapaca* spp. seedlings established in faeces of the western lowland gorilla at La Belgique research site, southeast Cameroon, between December 2010 and March 2012.

7.4. Discussion

Among the determinants of the seed dispersal effectiveness of *Uapaca* spp. by the western lowland gorilla, site selection for nesting appears to be a predominant one. Seeds dispersed in sleeping sites exhibit an improved fate due to a globally higher suitability of environmental conditions for seedling establishment, survival and growth offered by the habitat type in general and the microsite within these habitats in particular in which nests are constructed.

In dense forests, such as in the tropics, light availability is a limiting factor for recruitment (Whitmore 1996) and percentage of canopy openness is one of the main variables that differentiates sleeping sites from other sites in the forest (Petre et al. 2015a – see chapter 4). Despite this, the percentage of canopy openness was not a significant variable in the model explaining differences in establishment and survival success. In the present case of *Uapaca* spp., it is possible that the effect of the percentage of canopy openness on establishment and survival probabilities of the young recruit is only critical at the lowest values up to a certain threshold beyond which its effect becomes less important compared to other variables and translates mostly into an improved growth rate. Variables such as seed predation and herbivory are likely to contribute to the observed pattern of establishment and survival of *Uapaca* spp. seedlings across sites and habitats. In a previous study we showed that seed removal 48h post-dispersal was higher and seeds were buried deeper by dung beetles in old growth forests compared to at sleeping sites, which reduced the theoretical emergence probability of seedlings (Petre et al. 2015b – see chapter 6).

As observed with dung beetle activity, the specific environmental conditions at sleeping sites may also induce differences in patterns of seed predation and herbivory compared to other sites in the forest. These aspects must be considered in further research attempting to ascertain why sleeping sites improve the post-dispersal fate of seedlings. Indeed, it has been proposed that herbivory exerts the strongest impact on seedling recruitment, more than niche differentiation and density-dependent mortality (Clark et al. 2012).

All *Uapaca* species present at La Belgique, but *U. acuminata*, do well on hygromorphic soils as well as on terra firma (Breteler 2012), yet swamp forests provided the highest establishment and survival probabilities. This result can be partly explained by differences in the number of *Uapaca* seeds within faecal samples. The median estimated number of *Uapaca* seeds within monitored faecal samples was 2.8 for canopy gaps, 8.5 for old secondary forests, 9 for young secondary forests and 17.1 for swamp forests. Because the estimated number of *Uapaca* seeds was a highly determinant variable predicting the likelihood that a faecal sample will still exhibit viable *Uapaca* seedlings 2-3 y post-deposition; the higher proportion of faecal samples produced in swamp forests containing a large number of *Uapaca* seeds contributed to the higher suitability of this habitat type. A positive effect of the initial seed load on establishment and survival probabilities was also documented for several species dispersed by the western lowland gorilla in the Lopé National Park, Gabon (Voysey et al. 1999b), including one species of *Uapaca* (*U. guineensis*). This finding highlights the importance of seed limitation (i.e. the failure of seeds to arrive in saturating densities in all potential suitable sites) in determining recruitment limitation (Clark et al. 2013), and hence the role of the quantitative component in determining the seed dispersal effectiveness (Schupp et al. 2010). On this basis, it appears that the suitability of canopy gaps for the establishment and survival of *Uapaca* spp. is largely underestimated as despite having received the smallest proportion of faecal samples with a sufficient *Uapaca* seed content, this habitat ranked second in the observed establishment and survival probabilities. Furthermore, it appears that our experimental design of dividing the faeces into two samples of equal mass, consequently reducing the initial number of seeds, had introduced a bias in the general picture of the seed dispersal effectiveness of *Uapaca* spp. by the western lowland gorilla.

Uapaca spp. trees can potentially bear ripe fruit every calendar month of the year (Petre et al. submitted; see chapter 3 & 7), due to very irregular within- and between-year fructification timing amongst conspecifics (Fourrier 2013), and because of staggered fructification of species (either centred around July–August or the dry season of December–January; Petre et al. submitted; see chapter 3). Despite its extended availability and resulting seed dispersal throughout the year, a peak in consumption and dispersal by gorillas occurs around the dry season, from November/December to February/March, where it may be the only species dispersed by this species. During these months, more sleeping sites are constructed in swamp forests by the western lowland gorilla (Figure 3). Swamp forests harbour a dense carpet of herbaceous vegetation (Willie et al. 2012), favoured as nesting material (Willie et al. 2014), which becomes accessible when the swamp forests are dry. As a result, a higher proportion of dispersed *Uapaca* spp. seeds are located in swamp forests during dry months, which appeared to significantly improve the establishment success of emergent seedlings. This concordance between seed dispersal quantity and seed deposition site quality is particularly high during the month of January where 50% of sleeping sites were found in this habitat and 38.6% of the total amount of *Uapaca* spp. seeds are dispersed. According to the definition of directed-dispersal as being a non-random dispersal of a large proportion of seeds in sites particularly well-suited for seedling establishment, survival and growth (Howe and Smallwood 1982), our study demonstrated that for this specific time of the year, the western lowland gorilla performs directed-dispersal of *Uapaca* spp. towards swamp forests.

CHAPTER VIII.

DISCUSSION

8. Discussion

8.1. Summary of main findings

In the third chapter, addressing the first research question, I demonstrated that the frugivorous diet of the western lowland gorilla at La Belgique research site is diverse with as many as 20 taxa providing important fruit resources based on the quantity and duration of consumption. I further demonstrated the existence of two taxa comprising fallback fruit resources, namely *Klainedoxa* spp. and *Uapaca* spp. Among these two taxa, the fruits of *Uapaca* spp. are likely to play a greater role in the fitness of the gorilla study population as they occur at a much higher abundance and consequently provide a more reliable fruit resource in times of scarcity of other important fruits. Trees of *Uapaca* therefore represent a good candidate for being involved in a mutualistic relationships with the western lowland gorilla at La Belgique research site, as long as the fruit handling behaviour results in most seeds being swallowed intact.

In the fourth chapter, I showed that the western lowland gorilla disperses a minimum of 58 different taxa as well as numerous additional unknown morphotypes, and estimated an average of 289 seeds dispersed per day per individual. Despite this great diversity of seeds dispersed, there exist large variations in the amount of seed dispersed among those taxa, where *Uapaca* seeds dominate the seed load with a relative quantity of 36.5%; thus reinforcing the hypothesis there may be a case of plant-gorilla mutualism. Through a compositional and structural characterization of gorilla sleeping sites and random sites in the forest, I showed that sleeping sites constitute an optimal habitat for the regeneration of light-demanding species (i.e., canopy gaps and young secondary forests); consequently, seedlings emerging at sleeping sites will experience a predictably higher light availability, which may lead to improved development. As half the daily faecal production of gorillas may take place at sleeping sites, I hypothesized that the western lowland gorilla may perform directed dispersal for some taxa. Overall, the regular dispersal of seeds into regenerating forest patches suggests that the western lowland gorilla is likely to be a key agent in the process of forest gap-phase dynamics by bringing seeds of long living and light-demanding species.

In this fourth chapter, I also demonstrated that passage through the western lowland gorilla gut conserves the viability of most seeds, as they were excreted whole with no physical damage in most cases (0.9% only of *Uapaca* spp. seeds are found broken in faeces). In addition, when compared to seeds extracted manually from ripe fruits, gorilla-dispersed seeds generally exhibited a germination success unchanged (case of Uapaca spp.) or enhanced. This was further confirmed in the fifth chapter where I investigated the impact of gut passage on seed germination performances, while controlling for genetics, seed age, period of seed production within the fructification season of individual trees, and gut retention time. Even in the case of tree species for which no apparent effect of gut passage on seed germination success was evident when compared to manually-extracted seeds (as in the fourth chapter), there may still be a benefit from gut passage, by way of removal of the fruit skin and pulp, which may otherwise inhibit germination or prolong germination latency. I found an effect of gut retention time on germination probability for only one species out of five tested species, *Myrianthus arboreus*, for which the correlation was positive. As half the seed load ingested by gorillas during any given feeding session is excreted (mostly undamaged) after 44h (i.e. the median retention time), and given the long daily travel distances of gorillas (documented in the literature as an average of 2 km), frequent dispersal distances of viable seeds measurable at the kilometre scale would be likely. From our study it is hypothesized that the western lowland gorilla performs effective long-distance dispersal and hence is likely to be very important for the spatial dynamics of its dispersed species and serves to favour gene flow between populations.

In the sixth and seventh chapter I showed how the environmental conditions of sleeping sites may impact upon post-dispersal seed and subsequent seedling fate, using the top quantitatively dispersed taxon, *Uapaca* spp., as a case study. At first, dung beetle activity at sleeping sites appeared less detrimental for *Uapaca* seedling emergence compared to the situation in old secondary forest sites (where a large proportion of seeds are dispersed on feeding trails). I then demonstrated that sleeping sites constituted a habitat type of higher suitability for the survival, establishment and growth of *Uapaca* seedlings than other sites in the forest. The model suggested that the observed improvement in survival and establishment success could not be attributed directly to the canopy openness of sleeping sites, and instead I proposed that additional variables not investigated in the present study, such as herbivory, may account for this difference. Nonetheless, the openness of the canopy at sleeping sites translated into an improved growth of *Uapaca* seedlings. I observed a positive influence of the seed deposition habitat type, whereby seedlings of *Uapaca* spp. dispersed in swamp forests have a higher probability of surviving beyond establishment. Although gorilla sleeping sites are generally established on *terra firma*, swamp forests are increasingly used during the driest months of the year, a period which also coincides with the peak in *Uapaca* spp. seed dispersal by the western lowland gorilla. For this period of the year, it appears that the western lowland gorilla performs directed dispersal, and hence is likely to be a particularly important agent in the plant fitness of these species. This last chapter therefore succeeded to provide a case study for the theory proposed in the third chapter by demonstrating a case of plant–animal mutualism whereby the genus *Uapaca* and the western lowland gorilla contribute towards the fitness of each other.

8.2. Species diversity of gorilla-seed dispersal

Over the course of the study, I identified the seeds of 58 taxa in western lowland gorilla faeces. I consider the two seed dispersal sydromes that have been described based on the fruit characteristics of species dispersed by the vertebrate community of Makokou, Gabon: seeds of succulent, brightly-coloured, small-sized fruits which are dispersed mostly by birds and monkeys (‘bird-monkey syndrome’), and seeds of large, dull-coloured, dry fibrous fruits which are mostly dispersed by ungulates and rodents (‘ruminant-rodent-elephant syndrome’) (Gautier-Hion et al. 1985). Within the bird-monkey syndrome, a similar partitioning of dispersed species characteristics, distinguishing between the seed dispersal activity of cercopithecines and hornbills, was documented in the Dja Biosphere Reserve, Cameroon (Clark and Poulsen 2001; Poulsen et al. 2002). These studies unanimously suggest that the dispersal service of each syndrome and groups within the syndromes cannot be (fully) compensated by the other. In these studies in Gabon and Cameroon, data on the role of great apes were missing from the analyses, despite their presence in the study sites. It would be interesting to consider how and if the western lowland gorilla fits in with regards to these two proposed syndrome categories, as fruits of the 58 taxa whose seeds were identified in faeces in the present study possess the characteristics of both syndromes. In the Dja Biosphere Reserve, another study suggested that the degree of overlap in species diversity of seed dispersal was small between gorillas and cercopithecines, with cercopithecines dispersing 15-25% of gorilla-dispersed species and gorillas dispersing 5-15% of cercopithecine-dispersed species only (Poulsen et al. 2001). Large-bodied animals, such as the western lowland gorilla, often have a more generalist diet than do smaller animals, incorporating a wider variety of species (Blake et al. 2009). The morphology of the gastrointestinal tract of gorillas is characteristic of a frugivorous-folivorous diet (Chivers and Hladik 1980), enabling the processing of food items with high fibre content and low digestibility (Calvert 1985; Doran-Sheehy et al. 2009; Rothman et al. 2006); consequently increasing the diversity of fruits on which they are able to feed. Furthermore, as opposed to large-bodied rodents and ungulates, the western lowland gorilla is able to harvest fruits directly from the canopy (Iwata and Ando 2007; Remis 1999; Tutin et al. 1995), which potentially reduces any vertical partitioning that may exist with other seed disperser groups (e.g. birds).

With a mean body weight of 90 and 180 kg for adult females and males, respectively (Caldecott and Miles 2005), the western lowland gorilla is the largest arboreal seed disperser in the forests of the Congo Basin. As a result of its large gape width, the western lowland gorilla ingests seeds of most species that it consumes (91.1% at Nouabalé-Ndoki National Park; Nishihara 1995). The seed dimension threshold above which the western lowland gorilla tends to spit out instead of swallow seeds is 40–50 mm and 7–9 cm^3 (J. Head, unpubl. data; Nishihara 1995; Tutin and Fernandez 1993). The western lowland gorilla at La Belgique was found to disperse seeds of up to 53 mm long (*Anonidium mannii*) and 9 cm^3 in volume (*Trichoscypha oddonii*). Forest elephants are the only other frugivore capable of dispersing seeds larger than this through endozoochory, with seeds up to 90 mm long found in their faeces (*Balatines wilsonniana*; Chapman et al. 1992). In comparison, some cercopithecines tend to spit out seeds longer than 4 mm (Kaplin and Moermond 1998; Lambert 1999), and chimpanzees have been reported to not swallow seeds of volume exceeding 4.2 cm^3 (Tutin and Fernandez 1994). Forget et al. (2007) state that birds and arboreal mammals of both the Neotropics and Paleotropics do not swallow seeds longer than 40 mm, and Feer (1995) recorded the upper limit for duikers at 30 mm. However, it should be noted that some bats are able to transport large-seeded fruits away from the parental source and some rodents may scatter-disperse seeds measuring up to 80 mm in length (Forget et al. 2007), though only over short distances.

8.3. Seed dispersal effectiveness

8.3.1. Seed dispersal quantity

The large body-size of the western lowland gorilla governs the amount of food intake required to sustain daily energy expenditures, and hence influences the quantity of seeds ingested and dispersed. When a group of western lowland gorillas feeds in a tree, a large proportion of the available fruit crop is removed (Voysey et al. 1999a) – thus contributing to the reproductive processes of the tree. Furthermore, previous results of seed addition experiments generally reveal a positive influence on the density of established seedlings (Clark et al. 2007), thus inferring a further advantage of such large-scale fruit crop removal. My results demonstrated that the number of seeds contained in a faecal sample increases the likelihood that a seedling will become established and survive its first 2-3 years. Hence, the feeding, grouping and nesting behaviour of the western lowland gorilla, whereby large quantities of fruits are consumed and seeds deposited in faeces in a clumped pattern at group sleeping sites, may have a positive effect on the overall probability that a new adult tree will colonize the site and is therefore likely to enhance its seed dispersal effectiveness.

8.3.2. Seed dispersal quality

The western lowland gorilla at La Belgique and other sites across its range commonly sleeps in ground nests, thus implying that sleeping sites must offer sufficient ground surface devoid of woody material, where nests can be constructed, and a sufficiently open canopy to enable the growth of herbaceous vegetation which is commonly used as a nesting material. This further implies that when the western lowland gorilla defecates at sleeping sites, it exposes passed seeds to this vertical space which is conducive to plant growth: where a new tree can root and its crown develop. The situation is different for most arboreal frugivores that nest or perch in trees, as deposited seeds will encounter some degree of vertical space occupancy (i.e. at the very least, the vertical space will be occupied by the tree used for nesting or perching). The recruitment success of seeds dispersed in the immediate understorey is mostly determined by chance (Brokaw and Busing 2000), as established seedlings require some degree of canopy opening, for example, the falling of a nearby adult tree; an event which is unpredictable in space and time. Seedlings able to survive long periods of slow growth in the understorey will therefore have an advantage over short-lived species (Montgomery and Chazdon 2002), as they are more likely to eventually encounter the required conditions. For instance, in a Panamanian forest, it has been shown that 1-cm diameter stems of slow-growing species can be as old as 80 y (Hubbell 1998). For seeds dispersed at gorilla sleeping sites, where the required vertical space is immediately and reliably present, this random constraint is removed.

Dispersal limitation is defined as the failure of a seed to arrive in a suitable site, thus enabling the less-competitive species to recruit by forfeit (Hubbell et al. 1999), and is therefore considered to be the main reason for the high tree diversity of tropical forests. As a result, dispersal at sleeping sites is likely to be particularly important for species that are not able to survive in the shade of adult trees (but not exclusively). Gorilla-assisted dispersal into open-canopied sites will therefore increase the per capita success of dispersed seeds, compared to those non-dispersed and those deposited directly under the crown of the parental tree or a sleeping/perching tree within the forest. In a long-term study conducted in Barro Colorado Island, Panama (Hubbell et al. 1999), it was shown that seedling recruitment success in gaps was not significantly different between pioneers, non-pioneer light-demanders and shade-bearers; this was attributed to dispersal limitation. Dispersal at gorilla sleeping sites is therefore likely to reduce the degree of dispersal limitation of species not able to survive in shaded environments.

In addition to the above-cited advantages for tree population dynamics, dispersal directed to western lowland gorilla sleeping sites may also contribute to the hyperdiversity of tree communities. As demonstrated in chapter 3 (*Seed dispersal quantity*), the structural and compositional characteristics of the vegetation present at western lowland gorilla sleeping sites reveal that such sites represent patches of regenerating forest (i.e. tree fall gaps and young secondary forests). Hence, gorilla dispersal activity, serving to enrich the seed rain in these patches with species absent from the vicinity, will increase the diversity of the seedling template from which adult tree recruitment will eventually occur and subsequently contribute to the overall diversity of the forest through active contribution to gap-phase dynamics by bringing long-lived light-demanding species absent from the soil seed bank.

For some species, seed dispersal at sleeping sites directed to less preferred habitats may also be highly effective. This was well illustrated in chapter 7, where seedlings of *Uapaca* exhibited a higher establishment and survival success in swamp forests. Whereas the aforementioned effectiveness of seed dispersal at sleeping sites when established in canopy gaps is inferred based on the concordance of environmental condition attributes of seed deposition sites and seedling physiological requirements, a niche-based increase of seed dispersal effectiveness of *Uapaca* when directed to swamp forests was empirically demonstrated. This present case of “directed-dispersal” results from an increase in the dispersal of *Uapaca* seeds during the season when swamp forests, which represent the most suitable habitat for the recruitment of *Uapaca* juveniles, are increasingly used for nesting. This emphasizes the subtile character of such process, and suggests that other such cases may exist, but rendered more cryptic due to a lower dispersal quantity component.

In summary, the large body-size of the western lowland gorilla, its social cohesiveness and the environmental condition of the microsites selected for nesting, constitute important traits determining the quantity and quality of its potential seed dispersal service. Overall, the non-random deposition of seeds in open-canopied forest patches may promote directed-dispersal of most species and contributes to forest-gap dynamics, while species such as *Uapaca* that establish preferentially on hygromorphic soil would highly benefit from gorilla seed dispersal at sleeping sites during particular months of the year. These combined characteristics make the singularity of the seed dispersal activity of the western lowland gorilla and promote it to the rank of effective seed disperser.

8.4. Long distance dispersal

Body mass is an important factor in determining the amount of time that ingesta remains in the digestive tract of single-stomached animals (Demment and Van Soest 1985); however, the proportion and quantity of dietary items low in digestibility (i.e., structural plant parts) in the diet are the main determinants of retention time (Clauss et al. 2008), with a higher proportion resulting in longer retention times. With a lack of gastrointestinal specialisation, the efficient digestion of low quality dietary items is achieved through extended exposure to allo-enzymes in the digestive tract (Clauss et al. 2008). Thus, for species of similar body mass, the higher the proportion of structural plant parts in the diet, the longer the gut retention time; whereas for species consuming the same proportion of structural plant parts, the higher the food intake, the longer the gut retention time. This explains, for instance, why more folivorous primate species have a much longer retention time than more frugivorous primate species of similar body mass (Lambert 2002), and why highly frugivorous chimpanzees have a similar or shorter gut retention time (mean retention time of 31.5h; range: 14–86h; Lambert 2002) than do considerably lighter primate species (i.e. with a 6- to 50-fold lower body mass; Clauss et al. 2008). The western lowland gorilla is the largest of all primate species, and structural plant parts comprise a large proportion of its diet at least in some periods of the year (Doran-Sheehy et al. 2009); as a result, its gut retention time (mean = 50.6h; range:) is among the longest of all primates that consume fruit (Clauss et al. 2008). Indeed, the western lowland gorilla gut retention time even exceeds that of sympatric elephants (mean gut retention time: 20.2–39.5h; maximum: 114h; Campos-Arceiz and Blake 2011 and references therein). The relevance to seed dispersal is clear: as seeds are retained in the gorilla gut for such long periods of time, the potential for deposition far away from the parental tree is increased.

In a review of long-distance dispersal, Cain et al. (2000) consider any dispersal events exceeding 100 m to be considered long distance. For instance, arboreal monkeys, considered as a highly effective seed disperser group (Lambert 2011), disperse seeds mainly through cheek-pouching, followed by seed-spitting; behaviours which lead to fruit pulp removal from the seeds (Lambert 1999) and result in most seeds being dispersed only at short distances (i.e. <100 m; Clark et al. 2005; Fourrier 2013). In a case study of seed dispersal of *Strychnos mitis* by the redtail monkey (*Cercopithecus ascanius*) in Uganda, 88% of seeds processed were spat out and, of these, 83% were ejected within 10 m from the feeding tree (and 56% within 1 m) (Lambert 2001). The same pattern of short dispersal distances has been observed in the Dja Biosphere Reserve, Cameroon, where 98–99% of wind-dispersed seeds, 95–97% of bird-dispersed seeds and 77–92% of monkey-dispersed seeds were transported no further than 60 m away from the parental source (Clark et al. 2005). Western lowland gorillas exhibit long daily path lengths (average of 2 km; Remis 1997), and, combined with their long gut retention times, suggests that ingested seeds are likely to be transported >100 m from their parental source, with the possible exception of those ingested during late in the day and close to sleeping sites.

The aforementioned 100-m dispersal distance threshold also reflects the typical scale of spatial clustering commonly found among tropical plant populations (Fourrier 2013; Seidler and Plotkin 2006). Therefore, successful dispersal at greater distances will contribute to gene flow between conspecific clusters and to the colonization of new sites and the eventual founding of new cluster. In the Lopé National Park, it is hypothesised that the observed aggregative pattern of occurrence of clusters of *Cola lizae* trees is a result of successful directed-dispersal events by western lowland gorillas at sleeping sites, while the occurrence of individuals within clusters results from distance-restricted and scatter-dispersal by birds and monkeys through seed spitting (Fourrier 2013). Consequently, it is likely that the western lowland gorilla contributes to some degree to the metapopulation dynamics of all species that it disperses.

Other large-bodied frugivores are also expected to perform long-distance dispersal events regularly. Forest elephants have a much larger home range than any other mammal frugivore (Blake et al. 2009). At Ndoki Forest, Congo, a mean annual home range size of 1213 km² has been measured, with maximum distances covered in 24h, 48h and 72h of 24 km, 37 km and 57 km, respectively (Blake et al. 2009). With a gut retention time averaging 20–40h (but sometimes as long as 140h) (Campos-Arceiz and Blake 2011), forest elephants of Ndoki Forest are expected to disperse seeds over (extremely) long distances on a daily basis. Chimpanzees, with a mean gut retention time of 31.5h (Lambert 2002) and a mean daily path length of 1.7 km, are also expected to regularly perform long-distance dispersal events. However, these two species are faced with many of the same conservation concerns as the western lowland gorilla (Blanc 2008; Oates et al. 2008; Walsh et al. 2008), such as intense anthropogenic disturbance, and hence are likely to be absent or reduced to extremely low densities from forests from which the western lowland gorilla has been extirpated. Among remnant frugivores of such defaunated forests, candidates for long-distance dispersal performance would be hornbills, large-bodied duikers and red river hogs (Forget et al. 2007). Seed processing in the gut of the latter two taxa, however, tends to result in considerable seed damage (Beaune et al. 2012b; Feer 1995). Hornbills are large birds able to disperse seeds up to 40 mm long (Forget et al. 2007) and as far as 7 km away from the parental source (Holbrook and Smith 2000). However, hornbill fruit choice differs from that of primates (Clark et al. 2001; Gautier-Hion et al. 1985; Poulsen et al. 2002), suggesting that there would be no compensation for many species. Therefore, defaunation of large-bodied mammals from forests poses a threat to the metapopulation dynamics (including recruitment, gene flow, colonization, range expansion; Cain et al. 2000; Nathan and Muller-Landau 2000) of animal-dispersed species due to a lack of long-distance dispersal events.

8.5. *Uapaca*–western lowland gorilla mutualism

All along this thesis, the contribution to the regeneration of *Uapaca* trees by the western lowland gorilla has been highlighted; while in the first chapter the unique dietary function fulfilled by the fruits of *Uapaca* for the western lowland gorilla has been demonstrated. At La Belgique, there exist therefore a case of plant-animal mutualism whereby both organisms contribute to each other fitness, in ways probably unsurpassed by other organisms of the same kind. But, as opposed to the plant-gorilla mutualism documented at La Lopé National Park (Gabon), involving the endemic tree *Cola lizae*, this interaction is not exclusive as the seeds of *Uapaca* are dispersed by a variety of other frugivores (Poulsen et al. 2001; Voysey et al. 1999a).

The range at which a *Uapaca*–gorilla mutualism may occur is probably restricted to the zone where *Uapaca* swamp forests are well represented such as around the Dja Biosphere Reserve whose soil is particularly hygromorph (Peh 2009) and hence favour the recruitment of *Uapaca* trees that consequently occur in high densities (Fig. 1). In this region, there could be implications for the conservation of the western lowland gorilla from this case of mutualism. First, the density of *Uapaca* spp. can be used to assess the suitability of a site and identify priority conservation areas (e.g., High Conservation Value forest areas of logging concessions). Secondly, in the specific case of context of logging, efforts can be done to reduce secondary impact of extractive activities on *Uapaca* populations. This particular type of forests with abundant populations of *Uapaca* occupies 14.2% of the Cameroonian range of the western lowland gorilla, and within this forest type, 61.4% of the area is allocated to logging companies (Fig. 1). Therefore, the measures proposed would concern large populations of western lowland gorillas.

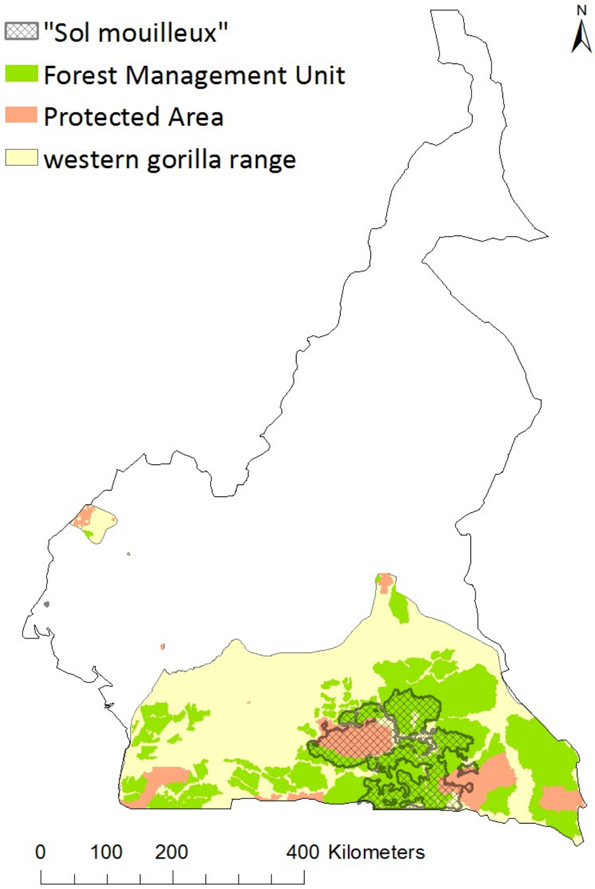

Figure 1. Map of Cameroon showing the area covered by the type of forest referred to as “forêts sur sol mouilleux avec vallées à *Uapaca paludosa*” by Letouzey (1968) in relation to the range of western lowland gorilla and with the area occupied by Forest Management Units for logging and Protected Areas.

8.6. Research limitations and recommendations

The main limitation of the present study is its medium-term length. To accurately assess seed dispersal effectiveness and confirm the proposed directed dispersal it would be necessary to track the full path of the tree species from seed to adult; which could span decades in the case of long-lived tree species. Genetic analyses cannot be used to overcome this problem, as can be the case for the Janzen-Connell hypothesis, for example, as this would only serve to identify the parental source of a plant but could not be used to identify the vector at the origin of its dispersal from the parental source.

The diet of any animal is influenced by the combination of species available at any time, with some being preferred over others, and their respective fruit availability. During the study period, changes in species association in gorilla faecal units were found to be frequent, with some species being dispersed during only one fruiting season and in very high quantities (e.g. *Dialium pachyphyllum* and *Celtis tessmannii*). As some species exhibit a supra-annual fructification pattern (i.e. when the time between two consecutive periods of fructification exceeds 1year), it is probable that fructification of some species did not occur within the timeframe of the study though they may constitute important dietary items for the western lowland gorilla and thus be dispersed in large quantity when present. This is highlighted by the case of *Celtis tessmannii*: data of fruiting phenology were collected on 10 individuals in five consecutive fruiting seasons (2009–2013), including the whole study period, and ripe fruit was observed in only one month (August 2010; all 34 faecal samples contained *C. tessmannii* seeds with an average of 47 seeds per 100 g of faecal material). If we had started the study a year later (September 2010), we would not have observed the important contribution by the western lowland gorilla to the seed dispersal of *C. tessmannii*. Similarly, *Erythrophleum suaveolens* was dispersed during one season within the study period but ignored during the other two, despite the fact that fruits were available, and had our study period not encompassed the former season we would have concluded that the western lowland gorilla does not contribute to the dispersal of this species. These examples highlight the relevance of the length of the study period, and demonstrate the importance of analysing faecal samples over as many years as possible to increase the chances of observing species that are rare, but are nonetheless dispersed by the western lowland gorilla.

We advocate the need to re-run seed passage experiments with captive gorillas while maintaining a higher level of control over the diet (e.g., fiber content) and testing for differences in gut retention time according to seed characteristics and gorilla age and sex. This would permit an adequate comparison of gut retention time patterns between seeds of different species, and offer explanations for the high variability in gut retention time between seeds of the same species ingested during the same feeding session by a group of western lowland gorillas (as observed in the present study). Such information could contribute to the construction of a mechanistic model of seed shadow or dispersal kernel and in the measurement of dispersal distances. A comprehensive knowledge of gorillas' movement on a daily basis over the course of different seasons would also be required for the construction of this model (Corrêa Côrtes and Uriarte 2012). These data could only be obtained with habituated groups of western lowland gorillas. Alternatively molecular markers can be used to accurately measure dispersal distances and describe how the western lowland gorilla contributes to metapopulation dynamics.

Concerning the effect of gut passage on germination performances, it would be interesting to re-run the trials with other species in order to obtain a fuller understanding of the respective influences of scarification and deinhibition. We suspect that the deinhibition effect can be driven in some cases by the physical properties of the fruit skin and we propose adding a fourth seed treatment that could verify this, consisting of seeds surrounded by the fruit mesocarp only ('deskinned' fruit). We also propose testing for changes in seed coat structure (thickness, permeability, mechanical resistance, etc) as a result of passage through the gut, in order to understand the underlying mechanism of the seed scarification effect. Finally, concerning the effect of retention time on germination success, we recommend vastly increasing the sample size for each test species in order to obtain a sufficient number of seeds of shortest and longest retention times). If the scarification effect is a result of modifications to the seed coat structure caused by gastroinstestinal fluids, it seems logical for the degree of changes in germination performances to be determined by the time spent in the vertebrate gut (as the longer the exposure time to gastroinstestinal fluids, the higher the modification to the seed coat structure is likely to be). If this argument were to hold true, any species exhibiting a scarification effect would reveal differing responses (i.e. the magnitude of the change in germination performances) to gut retention time.

I advocate an investigation into the effect of faeces aggregation on seed burial by dung beetles. Faeces aggregation has been shown in some sites with some primate species to increase the proportion of seeds removed, probably because the higher volume of faeces increases the intensity of the signal, which attracts more secondary dispersers. However, the western lowland gorilla produces a considerably large volume of faecal matter per faecal unit and gorilla social units can comprise a dozen or more individuals; therefore, we suspect there would be a dilution effect resulting instead in a reduction in the proportion of seeds removed. Neotropical species of dung beetles exhibit a restricted response area estimated to be less than 50-m radius. As such, the number of dung beetles that can be attracted to an area will be limited by the number present within the response area, even if the intensity of the signal is increased, as is likely with the large faecal volumes produced by a group of western lowland gorillas. On the other hand, dung beetles will experience a reduction in competition for resource acquisition and conversely have more time to process the resource, thus potentially resulting in more seeds being buried and at greater depth.

In order to test the hypothesized higher effectiveness of seed dispersal at sleeping sites for species other than *Uapaca*, a much higher monthly sample size of sleeping sites and faecal samples would have been required. Most tree species bear ripe fruits for short periods of time and some are not dispersed in high quantity enough to provide a sample size of established seedlings statistically large enough. An experimental design using manually reconstituted faeces containing a known number of seeds in a fixed amount of faecal material might be used to overcome this issue, though it would have to deal ideally beforehand or more carefully during the interpretation of the results with several potential bias factors (e.g., changes in attractiveness to dung beetles and rodents with faeces age).

I recommend an assessment of the role of seed predation and herbivory at sleeping sites and other forest areas in modifying seed dispersal effectiveness. It is possible that the high concentration of faeces at western lowland gorilla sleeping sites may play a role in the attraction of rodents, and that the subsequent high concentration of emerging seedlings may influence pathogen transmission and herbivore attraction.

Furthermore, the effect of drought stress experienced by established seedlings during the driest months also requires investigation. It has been shown in a moist tropical forest in Ghana that this stress is reduced for seedlings established in forest gaps compared to those established in the shade of canopy trees, because of a reduced depletion of soil water due to lower densities of roots and transpiring leaves (Veenendaal et al. 1996). These aspects should be experimentally investigated in order to maintain a higher level of control over all potential explanatory variables, and to strive to shed light on the underlying mechanisms of directed dispersal at sleeping sites.

8.7. Conclusion

The western lowland gorilla is an emblematic species of Central African forests facing conservation concerns like many other large-bodied tropical species. Being the largest arboreal frugivore in Central Africa, it is suggested that the western lowland gorilla occupies a central position in the seed dispersal network. Hence, its disappearance from forests could result in a cascade of disruptive effects eventually impacting upon more plant species than those with which it directly interacts. Indeed, the western lowland gorilla constitutes a perfect umbrella taxon not only for resident animal populations but for the whole forest ecosystem.

This research serves to further demonstrate the potential importance of the seed dispersal services of this great ape by highlighting singularly inherent characteristics that are not likely to be fully compensated by other frugivores. The number of seeds dispersed per individual gorilla per day is probably among the highest of all sympatric frugivores, as might be the diversity of species dispersed, and it has been demonstrated elsewhere that even the much higher densities of smaller frugivores (i.e. cercopithecines) would not allow quantitatively the compensation of the seed dispersal service provided by the western lowland gorilla (Poulsen et al. 2001). Hence, the disappearance of the western lowland gorilla would result in a significant reduction of the animal-mediated seed rain at the population and community level. This consequence of the potential disappearance of the western lowland gorilla from any area would be exacerbated for the largest-seeded species, as the only other frugivores able to disperse effectively such seeds through endozoochory (i.e., chimpanzees and elephants) are also highly sensitive to local extinction. In addition, regardless of seed size, there are further benefits of the site selection and the clumping pattern of the large quantities of seeds deposited by gorilla groups in sleeping sites, where seedling recruitment probability might be enhanced, that may not be mirrored by other frugivore species. As a consequence, the extirpation of this frugivore from a given area is likely to disrupt ecological processes that will inevitably impact upon the whole structure and composition of the forest in the long-term. Ensuring viable populations of western lowland gorilla through law enforcement, forest and wildlife management plans, alternative and sustainable rural livelihood activities are crucial issues.

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