COMMUNAUTÉ FRANÇAISE DE BELGIQUE

UNIVERSITÉ DE LIÈGE – GEMBLOUX AGRO-BIO TECH

ROLE DU GORILLE DES PLAINES DE L'OUEST (*GORILLA GORILLA GORILLA*) DANS LA RÉGÉNÉRATION DES FORETS DENSES HUMIDES ET INTERACTION AVEC L'EXPLOITATION SÉLECTIVE DE BOIS D'ŒUVRE

Barbara HAUREZ

Dissertation originale présentée en vue de l’obtention du grade de docteur en Sciences Agronomiques et Ingénierie Biologique

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Haurez Barbara (2015) Rôle du gorille des plaines de l'Ouest (*Gorilla gorilla gorilla*) dans la régénération des forêts denses humides et interaction avec l'exploitation sélective de bois d'oeuvre. Thèse de doctorat. Université de Liège – Gembloux Agro-Bio Tech, Belgique. 133 p. + annexe, 20 tabl., 24 fig.

Résumé

Selon l'IUCN, le gorille des plaines de l'Ouest (*Gorilla gorilla gorilla* Savage & Wyman) est une espèce en danger critique d'extinction. Or il jouerait un rôle important dans la dynamique des forêts tropicales. En effet, son régime hautement frugivore et son importante masse corporelle lui confèrerait un rôle majeur en tant que disperseur des graines de nombreuses espèces végétales. En outre, en installant ses sites de nidification au sein d'habitats forestiers à canopée ouverte, il déposerait la majorité des graines dans des environnements qui semblent favorables à leur germination et à la croissance des plantules. Cependant, en raison de l'expansion de l'exploitation forestière en Afrique Centrale, les services écologiques assurés par le gorille pourraient être menacés. L'objectif de cette thèse est de caractériser les impacts de l'exploitation forestière sur les populations de gorilles et le rôle de celles-ci dans la régénération forestière post-exploitation.

Les résultats montrent qu'une population viable de gorilles peut être maintenue en forêt exploitée de manière sélective (< 2 pieds ha^{-1}). En effet, bien que les gorilles aient tendance à fuir les forêts en cours d'exploitation, leur densité en forêt exploitée atteint sa valeur initiale, voire un niveau supérieur, endéans l'année suivant l'arrêt de l'exploitation. La sélection préférentielle des zones forestières à canopée ouverte pour la nidification a été confirmée, avant et après l'exploitation. Le dépôt des graines au sein d'habitats présentant des conditions lumineuses favorables est donc validé, bien que l'utilisation préférentielle des trouées d'abattage et des pistes forestières n'ait pas été observée au cours de la période de suivi (une année après l'exploitation).

Les graines de 59 espèces végétales ont été retrouvées dans des excréments de gorilles collectés pendant 20 mois. Un quart des ces espèces présentait un intérêt économique en raison de leur utilisation comme bois d'œuvre ou produits forestiers non-ligneux. Les unités fécales analysées contenaient entre une et six espèces différentes, et en moyenne 81,0 ± 107,8 graines intactes (0-566). Selon les espèces, les taux de germination ont varié de 0 à 100 %, avec une moyenne de 46 ± 36 %. Le gorille est le principal disperseur d'une espèce exploitée pour son bois d'œuvre, *Dacryodes normandii.* Durant la période de fructification, le gorille a consommé des fruits de cette espèce lors de 87,8 % des visites (durée moyenne de 85 ± 89 min.).

L'impact du passage dans le tractus digestif a été évalué pour deux espèces, *Santiria trimera* et *Chrysophyllum lacourtianum*. Ces espèces présentaient des taux de germination supérieurs après ingestion, en raison de la suppression de la pulpe et de la scarification de la graine. En outre, un effet positif de la matière fécale sur le développement des plantules a été observé pour trois espèces étudiées, *S. trimera*, *C. lacourtianum* et *Plagiostyles africana*. Enfin, le développement des plantules est favorisé dans les sites de nidification, sites de dépôt des graines les plus fréquents. Deux espèces étudiées, *S. trimera* et *D. normandii* ont montré une croissance de deux à dix fois plus rapide dans les sites de nidification qu'en forêt à canopée fermée. Le gorille est donc impliqué dans un processus de dispersion dirigée.

En conséquence, en l'absence de braconnage, les populations de gorille des plaines de l'Ouest semblent résilientes à l'exploitation sélective et jouent un rôle déterminant dans le processus de dispersion des graines, tant en termes quantitatifs que qualitatifs, dans les forêts exploitées.

Des pistes d'amélioration de la gestion des forêts exploitées qui hébergent des gorilles ont été proposées dans le but de favoriser leur préservation au sein des forêts concédées. En particulier, la généralisation des pratiques d'exploitation à faible impact est souhaitable.

Mots clés : *Gorilla gorilla gorilla*, exploitation forestière, dispersion des graines, comportement de nidification, conservation, aménagement forestier

Haurez Barbara (2015) Role of the western lowland gorilla (*Gorilla gorilla gorilla*) in the regeneration of tropical rainforests and interaction with selective timber exploitation. Ph.D Thesis. University of Liège – Gembloux Agro-Bio Tech, Belgium. 133 p. + appendix, 20 tabl., 24 fig.

Summary

According to the IUCN, the western lowland gorilla (*Gorilla gorilla gorilla* Savage & Wyman) is a critically endangered species. This species would play an important role in tropical forest dynamics. Indeed, its highly frugivorous diet and its large body mass would result in the implication of gorilla in the seed dispersal of many plant species. Moreover, by building its nest sites in open canopy forest, it would deposit the majority of seeds in habitats displaying potentially suitable light condition for their germination and for the subsequent seedling development. However, given the expansion of timber exploitation in Central Africa, ecological services dispensed by gorilla could be threatened.

The objective of this thesis is to characterize the impacts of timber exploitation on gorilla populations and the role of these populations in forest regeneration after logging.

The results demonstrate that a viable population of gorilla may be maintained in selectively logged forests (< 2 trees ha^{-1}). Indeed, although gorillas tend to flee areas during timber exploitation activities, their density in logged forest reaches its initial value, or even a higher level, within one year after the end of logging. The preferential selection of open canopy forest areas for nesting was verified, before and after logging. The deposition of seeds in habitats providing favorable light conditions is therefore confirmed, even though the preference for tree fall gaps and forest skid trails was not observed in the course of the monitoring period (one year after logging).

The seeds of 59 plant species were found in gorilla feces collected over a period of 20 months. A quarter of these species presented an economically value because of their use as timber or non-timber forest products. The analyzed fecal units contained between one and six different seed species, and on average 81.0 ± 107.8 intact seeds (0-566). Depending on the species considered, germination success varied from 0 to 100 %, with an average of 46 ± 36 %. The gorilla is the main disperser of a timber species, *Dacryodes normandii*. Over the fructification period, the gorilla consumed fruits of this species in 87.8 % of its visits (of an average length of 85 ± 89 min.).

The impact of gut passage was evaluated for two tree species, *Santiria trimera* and *Chrysophyllum lacourtianum*. These species displayed higher germination successes after gorilla ingestion because of both pulp suppression and seed coat scarification. In addition, a positive effect of fecal matrix on seedling development was observed for three studied species, *S. trimera*, *C. lacourtianum* and *Plagiostyles africana*. Finally, the development of seedlings is favored in nesting sites, the most frequent seed deposition sites. Two studied species, *S. trimera* and *Dacryodes normandii* displayed a growth between two and ten times faster in nest sites than in closed canopy forest. Therefore, gorilla is implicated in directed seed dispersal.

Consequently, when poaching is absent, western lowland gorilla populations seem to be resilient to selective logging and they play a critical role in the seed dispersal process, both quantitatively and qualitatively, in logged forests.

Some recommendations to improve the management of logged forest that host gorilla populations were proposed in order to favor their preservation within logging concessions. In particular, the generalization of reduced impact logging practices is advisable.

Key words: *Gorilla gorilla gorilla*, timber exploitation, seed dispersal, nesting behavior, conservation, forest management

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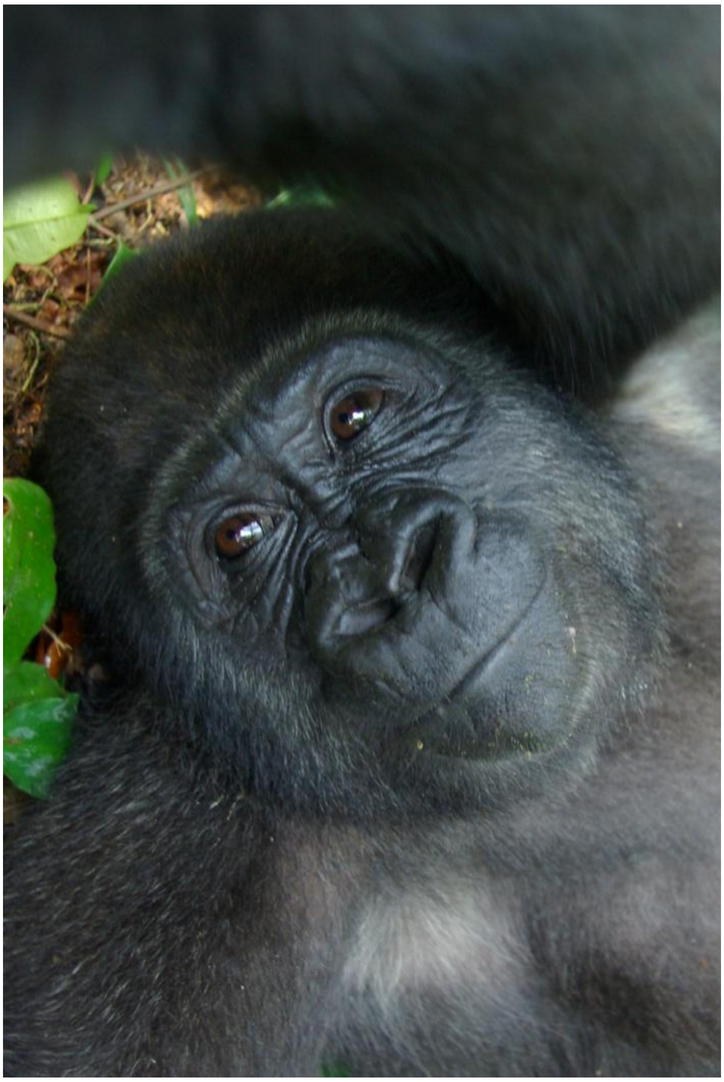
Liste des abbréviations

AAC	Assiette Annuelle de Coupe - Annual Allowable Cut
AIC	Akaike Information Criterion
CAR	Central African Republic
CEB-PWG	Compagnie Equatoriale des Bois Precious Woods Gabon
CFAD	Concession Forestière sous Aménagement Durable
CI	Confidence Interval
CIB	Congolaise Industrielle des Bois
CV	Coefficient de Variation - Coefficient of Variation
DF	Degree of Freedom
DPF	Detection Probability Function
EFI	Exploitation à Faible Impact
ESW	Effective Strip Width
FSC	Forest Stewardship Council
GDP	Gross Domestifc Product
GLM	Generalised Linear Model
GLMM	Generalised Linear Mixed Model
HCV	High Conservation Value
HCVF	High Conservation Value Forest
IUCN	International Union for the Conservation of Nature
MIST	Management Information System
NTFP	Non Timber Forest Product
ONG	Organisation Non Gouvernementale
PFNL	Produit Forestier Non-Ligneux
PSGE	Plan Stratégique Gabon Emergent
RIL	Reduced Impact Logging
SCNC	Standing Crop Nest Count
SD	Standard Deviation
SMART	Spatial Monitoring and Reporting Tool
THV	Terrestrial Herbaceous Vegetation
UICN	Union Nationale pour la Conservation de la Nature
WCS	Wildlife Conservation Society
WLG	Western Lowland Gorilla
ZSL	Zoological Society of London

PREMIÈRE PARTIE INTRODUCTION

CHAPITRE 1 INTRODUCTION GÉNÉRALE

Ce premier chapitre vise à introduire les concepts aurour desquels la recherche s'articule, ainsi que le contexte dans lequel elle s'insère. La pertinence, les objectifs de l'étude et la structure du présent document y sont aussi présentés.



Gorille des plaines de l'Ouest (*Gorilla gorilla gorilla* Savage & Wyman) © J. Laporte

1 LE RÔLE DE LA FAUNE DANS LE MAINTIEN DE LA DIVERSITÉ VÉGÉTALE DES FORÊTS TROPICALES

Les forêts tropicales constituent l'écosystème terrestre le plus diversifié (Meijaard & Sheil 2008; Mayaux *et al.* 2013; Diangha & Wiegleb 2014). A l'échelle locale, l'hypothèse de Janzen-Connell postule que la diversité végétale observée en forêts tropicales est liée à une variation spatiale de la probabilité de recrutement des plantules (Janzen 1970; Connell 1971; Schupp 1992; Whittaker *et al.* 2001). La distribution des graines est spatialement organisée autour du pied mère, la densité en graines étant la plus élevée directement sous la couronne et négativement corrélée avec la distance au pied mère. Ces graines, et par la suite les plantules qui en résultent, sont soumises à une pression de sélection densité-dépendante liée à deux facteurs : (1) la compétition intra-spécifique pour l'espace et les ressources, et (2) les agents pathogènes spécifiques, les prédateurs et les herbivores (Willson & Traveset n.d.; Janzen 1970; Connell 1971; Augspurger 1984; Schupp 1992). En conséquence, la mortalité des graines est plus importante à proximité d'adultes conspécifiques, et de manière générale aux zones présentant de fortes densités de graines, et la probabilité de survie des plants va augmenter avec la distance au pied producteur. La probabilité de recrutement des plants résulte de l'interaction entre la densité et la probabilité de survie des graines. Il est maximal à une distance donnée du plant mère, et décroit ensuite en raison de la raréfaction des graines (**Figure 1**). L'effet Janzen-Connell avantage les espèces végétales présentes à faible densité et limite l'expansion des espèces les plus abondantes, favorisant ainsi localement la diversité végétale.

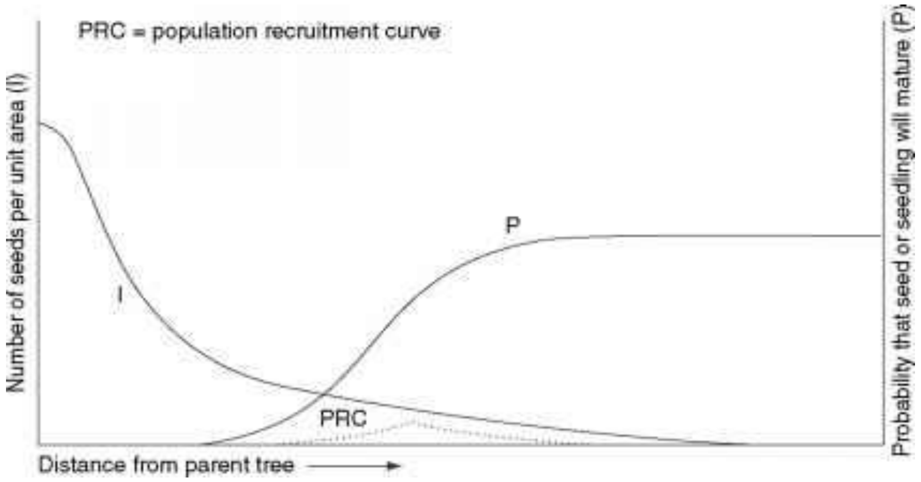


Figure 1 Représentation graphique du modèle de Janzen-Connell (Janzen 1970)**.** La densité de graines en un point décroit avec la distance au plant mère (*I*). Au contraire, la probabilité de survie des graines (et ultérieurement des plantules) augmente en fonction de la distance (*P*), en lien avec une pression réduite des prédateurs et pathogènes spécifiques. Le produit de ces courbes donne une courbe de recrutement (*PRC*) dont le sommet est localisé à une distance donnée du plant mère, où la probabilité de recrutement d'un nouvel individu adulte est maximale.

Bien que de nombreuses études ont démontré l'existence d'un effet Janzen-Connell (Harms et al. 2000; Wills et al. 2006; Swamy et al. 2011; Beaune et al. 2012c), il n'est pas généralisable car fortement spécifique (Hyatt *et al.* 2003). En particulier, l'effet isolé de la distance à un individu mature de la même espèce sur le recrutement des plantules semble faible (Hyatt *et al.* 2003; Poulsen *et al.* 2012). Malgré cela, le mouvement des graines au départ du plant parent, la dispersion des graines, est un mécanisme d'importance commune dans le cycle de développement de la plante et qui intervient dans la dynamique des populations végétales (Howe & Smallwood 1982).

La dispersion des graines est un des points clés de la théorie de Janzen-Connell et ses bénéfices sont nombreux. Le processus de dispersion des graines est donc déterminant pour le recrutement, la distribution et la dynamique des populations végétales (Nathan & Muller-Landau 2000). En effet, la distribution spatiale des graines par rapport à leur plant mère (*seed shadow*), et de manière générale par rapport aux autres graines et individus conspécifiques (*seed rain*), influence fortement la dynamique d'une espèce donnée (Willson & Traveset n.d.; Traveset et al. 2014). En premier lieu, leur dispersion permet aux graines d'échapper à la mortalité élevée observée à proximité du plant mère (effet Janzen-Connell) (*escape hypothesis*) (Janzen 1970; Howe & Smallwood 1982; Jansen & Zuidema 2001; Stoner & Henry 2008) mais aussi d'assurer un flux de gènes intra- et inter-populations (Willson & Traveset n.d.; Jordano et al. 2007; Stoner & Henry 2008). Elle possède donc une influence marquée sur la structuration génétique des populations végétales (Howe 1989). Les évènements de dispersion à longue distance, en particulier, jouent un rôle important dans la génétique des populations (Nathan & Muller-Landau 2000; Jordano *et al.* 2007; Nathan *et al.* 2008; Traveset *et al.* 2014). L'augmentation de la distance de dispersion mène également à un accroissement exponentiel de la surface à travers laquelle les graines sont distribuées (Jansen & Zuidema 2001), augmentant la probabilité d'atteindre un site non encore colonisé par l'espèce (*colonisation hypothesis*) (Howe & Smallwood 1982; Stoner & Henry 2008). Certains agents de dispersion, en particulier lorsqu'il s'agit d'organismes disperseurs, déposent fréquemment les graines au sein d'habitats présentant des conditions environnementales favorables à leur germination et au développement des plantules (*directed dispersal hypothesis*) (Howe & Smallwood 1982; Wenny & Levey 1998; Jansen & Zuidema 2001; Wenny 2001; Stoner & Henry 2008).

Pour favoriser la dispersion de leurs graines, les espèces végétales ont développé, au cours de l'évolution, différentes caractéristiques adaptées à leurs agents disperseurs propres (*dispersal syndrome*) (Howe & Smallwood 1982; Traveset *et al.* 2014). La dispersion peut être réalisée par la plante elle-même (via des processus de projection ou simplement par gravité) (autochorie) ou par des agents externes abiotiques - le vent (anémochorie) ou l'eau (hydrochorie)- ou biotiques - divers organismes disperseurs (zoochorie) (Howe & Smallwood 1982; Traveset *et al.* 2014). La distribution spatiale des individus matures d'une population végétale reflète leur mode de dispersion, les espèces zoochores présentant un degré d'agrégation nettement moindre que les espèces autochores et, dans une moindre mesure, que les espèces anémochores (Seidler & Plotkin 2006; Blake *et al.* 2009).

Les espèces animales constituent les acteurs majeurs de la dispersion des graines au sein des forêts tropicales (Forget *et al.* 2011). Entre 50 et 95 % des espèces tropicales produisent des fruits charnus adaptés à la consommation par des vertébrés, et donc à l'endozoochorie (dispersion via le système digestif d'un animal) (Howe & Smallwood 1982; Jansen & Zuidema 2001; Beaune et al. 2012b). En dehors des avantages en termes de distribution spatiale, l'endozoochorie affecte le destin des graines à travers différents mécanismes. Le passage des graines dans le tractus digestif peut impacter, négativement ou positivement, le destin des graines en supprimant l'effet inhibiteur de la pulpe (*deinihbition effect*) (Traveset 1998; Samuels & Levey 2005; Robertson *et al.* 2006; Traveset *et al.* 2007; Bradford & Westcott 2010), en altérant chimiquement ou mécaniquement les enveloppes séminales (*scarification effect*) (Traveset 1998; Traveset *et al.* 2007, 2012; Bradford & Westcott 2010) ou en prévenant les attaques de pathogènes et de prédateurs (Bradford & Westcott 2010; Fricke *et al.* 2013). La manipulation des graines dans la bouche résulte parfois en leur destruction suite à l'action des machoires et des dents, et donc à la prédation d'une certaine proportion des graines (Lambert & Garber 1998; Lambert & Chapman 2005). La matière fécale au sein de laquelle les graines sont déposées peut également jouer un rôle en favorisant la dispersion secondaire ou la prédation (Beaune *et al.* 2012a) ou en améliorant les performance des plantules (*fertilisation effect*) (Dinerstein

& Wemmer 1988; Traveset 1998; Jansen & Zuidema 2001; Traveset *et al.* 2001, 2007; Nchanji & Plumptre 2003). Enfin, le dépôt des graines en agrégats (mono-ou plurispécifiques) au sein des excréments engendre des phénomènes de compétition intra- et interspécifique pouvant influencer la germination des graines, mais aussi le développement ultérieur des plantules (Loiselle 1990; Murray 1998; Traveset 1998; Traveset *et al.* 2007).

L'efficacité du processus de dispersion (*seed dispersal effectiveness*), et donc la contribution à la régénération d'une espèce végétale donnée (Schupp 1993), dépend des facteurs quantitatifs (nombre de graines dispersées) et qualitatifs (probabilité qu'une graine se développera finalement en individu adulte, influencée par le traitement de la graine par l'agent disperseur et par le site de dépôt) caractérisant la dispersion (Schupp 1993; Schupp *et al.* 2010). La communauté animale dispersant les graines d'une espèce végétale va fortement influencer le destin de celle-ci, en présentant un patron de manipulations, traitements et dépositions variables et qui auront des effets différents sur la qualité du processus de dispersion et le recrutement des juvéniles (Lambert & Garber 1998; Traveset 1998; Chapman & Russo 2005; Jordano et al. 2007; Martínez et al. 2008; Nathan et al. 2008). La structure du paysage, en interaction avec les préférences des frugivores en termes d'habitats, entre également en compte dans ce processus (Jordano *et al.* 2007). La disparition d'une espèce de disperseur donnée aura donc des conséquences variables selon son identité (Lambert & Chapman 2005).

Les populations animales jouent un rôle prépondérant dans la dynamique des écosystèmes forestiers tropicaux (Estes et al. 2011; Petre et al. 2013; Malhi et al. 2014), mais aussi dans la régénération des milieux perturbés (Traveset *et al.* 2014). Les forêts tropicales sont actuellement soumises à de nombreuses modifications, la plupart anthropogènes, et la préservation des principaux disperseurs est menacée. En effet, la modification et la perte de l'habitat (Cordeiro & Howe 2001), la chasse et le braconnage (Fa & Brown 2009), et l'exploitation sélective (Kirika *et al.* 2008) altèrent les communautés animales des forêts tropicales. Ce déclin des populations animales engendre des perturbations au sein des mécanismes écologiques des écosystèmes forestiers tropicaux, notamment le processus de dispersion des graines, et peut avoir des conséquences économiques importantes à long terme (Hougner *et al.* 2006; Morris 2010; Markl *et al.* 2012).

2 L'IMPACT DE LA DÉFAUNATION SUR LA DISPERSION DES GRAINES

Le terme "défaunation" désigne le déclin, voire l'extinction, des espèces animales, principalement de grande taille, suite aux pressions anthropiques (Dirzo & Miranda 1990 cités par Galetti and Dirzo 2013; Kurten 2013). En Afrique Centrale, les causes majeures de ce phénomène sont l'exploitation non-viable des espèces animales (chasse, braconnage et commerce) et l'altération de l'habitat forestier (dégradation, fragmentation et destruction) (Galetti & Dirzo 2013).

Plusieurs études se sont penchées sur l'impact de la chasse en termes d'interactions faune-flore et les fonctions écologiques qu'elles représentent (Howe 2007; Kurten 2013; Boissier et al. 2014). En effet, la majorité, voire l'ensemble, des espèces impliquées dans le processus de dispersion des graines sont chassées pour leur viande (Beaune et al. 2012b). La défaunation engendre donc des perturbations profondes de l'écosystème forestier (Nasi et al. 2011; Malhi et al. 2014). L'impact des perturbations anthropiques est variable selon les espèces animales considérées. En particulier, les animaux de grande taille, qui présentent des taux d'accroissements démographiques et des densités faibles, sont plus fortement affectés (Bennett & Robinson 2000; Cardillo et al. 2005; Howe 2007; Peres & Palacios 2007; Fa & Brown 2009). Ils sont également plus sensibles à la perte et la dégradation de l'habitat car ils sont dépendants de domaines vitaux larges (Galetti & Dirzo 2013). Ils constituent des cibles préférentielles pour les chasseurs, car ils donnent lieu à des retours sur investissements plus élevés (Bennett & Robinson 2000; Jerozolimski & Peres 2003; Wright et al.

2007). A long terme, suite à l'exploitation sélective du gibier, seules les espèces les plus productives, généralement de petite taille, subsistent (Jerozolimski & Peres 2003; Fa & Brown 2009). Au vu de l'importance de la dispersion à longue distance (Nathan & Muller-Landau 2000), résultant généralement du fait des disperseurs de grande taille (Jansen & Zuidema 2001; Jordano *et al.* 2007; Nathan *et al.* 2008), sur les populations végétales, l'effet de la disparition de la grande faune se ferait ressentir à l'échelle paysagère (Nathan *et al.* 2008). Les impacts de la chasse semblent également varier selon le niveau trophique de l'espèce considérée (Bennett & Robinson 2000), les frugivores étant plus affectés que les autres groupes (Peres & Palacios 2007; Wright et al. 2007; Abernethy et al. 2013). Considérant les nombreuses caractéristiques qui influencent l'efficacité de la dispersion par un frugivore donné (Schupp 1993; Jordano *et al.* 2007; Stoner & Henry 2008; Schupp *et al.* 2010), il semble que la disparition d'un disperseur d'une espèce végétale engendre systématiquement une modification de son processus de dispersion. Les conséquences de cette altération sur la dynamique de population de l'espèce, et à plus large échelle sur la communauté végétale et animale, dépendent de la structure du réseau d'interactions interspécifiques (Donatti *et al.* 2011) et sont largement méconnues. En raison de la spécificité des interactions faune-flore, il apparaît peu probable que la disparition d'un disperseur puisse être compensée par une autre espèce animale qui remplirait les mêmes fonctions écologiques (Poulsen *et al.* 2002; Bueno *et al.* 2013; Kurten 2013) (mais voir aussi McConkey *et al.* (2014). En particulier, les services de dispersion réalisés par les grands mammifères, tels que les éléphants et les grands singes, sont difficilement remplaçables car il n'existe pas d'autres frugivores capables d'ingérer les graines de grande taille qu'ils dispersent (Kurten 2013).

De nombreuses études se sont intéressées à l'influence de la défaunation sur la composition végétale. La plupart d'entre-elles ont mis en évidence un développement privilégié des espèces végétales dispersées de manière abiotique, ou par les vertébrés de petite taille, au détriment des espèces dispersées par les animaux de grande taille (Chapman & Onderdonk 1998; Jansen & Zuidema 2001; Beckman & Muller-Landau 2007; Wright et al. 2007; Condit & Wright 2007; Howe 2007; Terborgh et al. 2008; Muller-Landau et al. 2008; Vanthomme et al. 2010; Markl et al. 2012; Effiom et al. 2013; Poulsen et al. 2013; Kurten 2013). De même, les espèces à petites graines semblent moins affectées par la disparition de certains frugivores (Chapman & Onderdonk 1998; Condit & Wright 2007; Wright et al. 2007; Markl et al. 2012), car la communauté de disperseurs qui interagissent avec elles est plus large et diversifiée (Beckman & Muller-Landau 2007; Babweteera & Brown 2008).

De manière générale, le nombre de graines non-dispersées, et donc retrouvées sous la canopée du plant mère, est plus élevé au sein de forêts dont la communauté animale a été décimée que dans des forêts intactes (Wang *et al.* 2007; Terborgh *et al.* 2008; Kirika *et al.* 2008; Brodie *et al.* 2009; Markl *et al.* 2012; Kurten 2013). Cela mène à une augmentation de l'effet Janzen-Connell (Terborgh *et al.* 2008) (**Figure 2**), une compétition accrue entre plantules (Muller-Landau 2007), un taux de recrutement réduit (Beaune 2015) et, en conséquence, une régénération moindre des espèces végétales concernées (Jansen & Zuidema 2001; Wright et al. 2007; Harrison et al. 2013; Caughlin et al. 2014). La quantité de graines dispersées à distance du plant producteur diminue, ainsi que le nombre de plantules (Wang et al. 2007; Wright et al. 2007; Blake et al. 2009; Brodie et al. 2009; Harrison et al. 2013; Kurten 2013). Une réduction du *seed shadow* est observée (Jordano *et al.* 2007; Effiom *et al.* 2013), en lien avec une raréfaction des évènements de dispersion à longue distance (Markl *et al.* 2012). En conséquence, la structure spatiale de la communauté végétale est altérée, notamment par une augmentation du degré d'agrégation des espèces endozoochores (Wang *et al.* 2007; Blake *et al.* 2009). Les flux de gènes entre populations et au sein des populations végétales sont également limités (Jordano *et al.* 2007), ce qui augmente le risque de réduction de la diversité par dérive génétique (Wang *et al.* 2007).

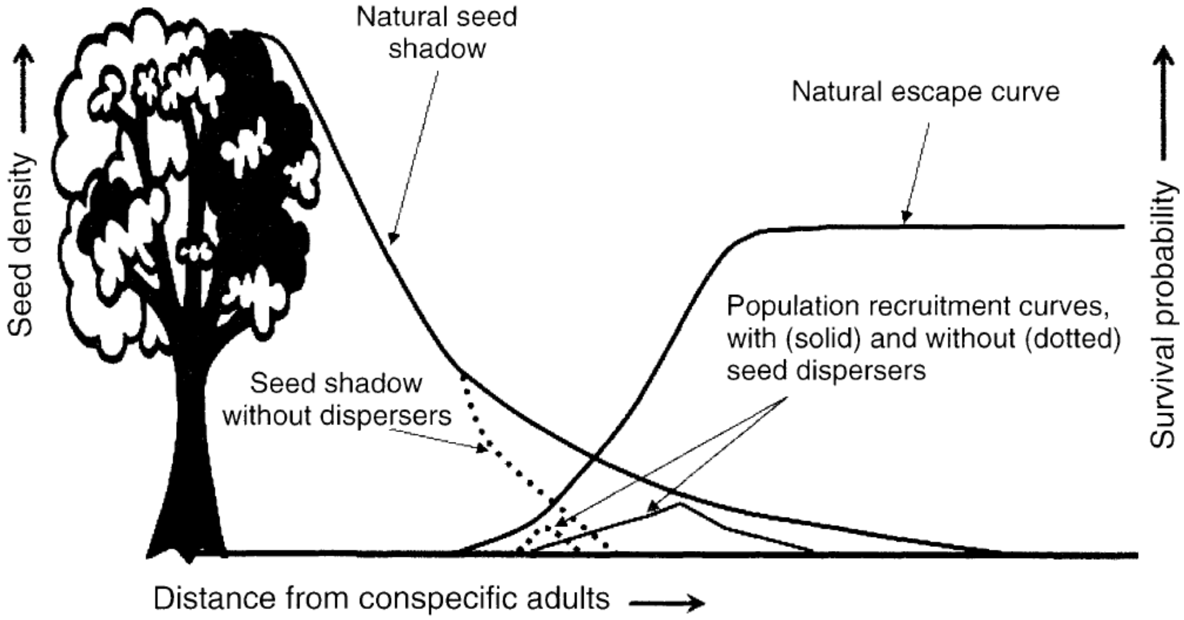


Figure 2 Représentation graphique du modèle de Janzen-Connell dans un contexte de défaunation (Terborgh *et al.* 2008)**.** En cas de déclin des disperseurs, la distance de dispersion des graines est réduite (troncation du *seed shadow*) La probabilité de recrutement des plantules est moindre, et son maximum se rapproche du plant mère (accroissement du degré d'agrégation).

Les impacts de la défaunation sur le recrutement et la survie des plantules varient d'une espèce à l'autre (Guariguata *et al.* 2000; Poulsen *et al.* 2013; Rosin 2014) (**Figure 3**) mais aussi en fonction de facteurs environnementaux (Kurten 2013). Cela s'explique notamment par une modification des taux de prédation et d'herbivorie variable selon les communautés étudiées. L'augmentation de la prédation des graines a été observée dans certains sites d'étude (Dirzo *et al.* 2007; Terborgh *et al.* 2008; Effiom *et al.* 2013) alors que dans d'autres sites, une diminution de la prédation des graines a été constatée (Beckman & Muller-Landau 2007; Holbrook & Loiselle 2009) ainsi qu'une réduction de la pression des herbivores (Poulsen *et al.* 2013). Les espèces héliophiles, à croissance rapide et faible densité de bois, plus compétitives, semblent avantagées (Poulsen *et al.* 2013). La diversité et la richesse spécifique des plantules et des juvéniles sont réduites au sein des forêts soumises au processus de défaunation (Howe 2007; Effiom et al. 2013; Harrison et al. 2013; Kurten 2013). A long terme, une homogénéisation de la communauté végétale et une diminution de sa diversité seraient à prévoir (Wang et al. 2007; Terborgh et al. 2008; Beaune et al. 2012b) ainsi qu'une réduction du stock de carbone (Poulsen *et al.* 2013).

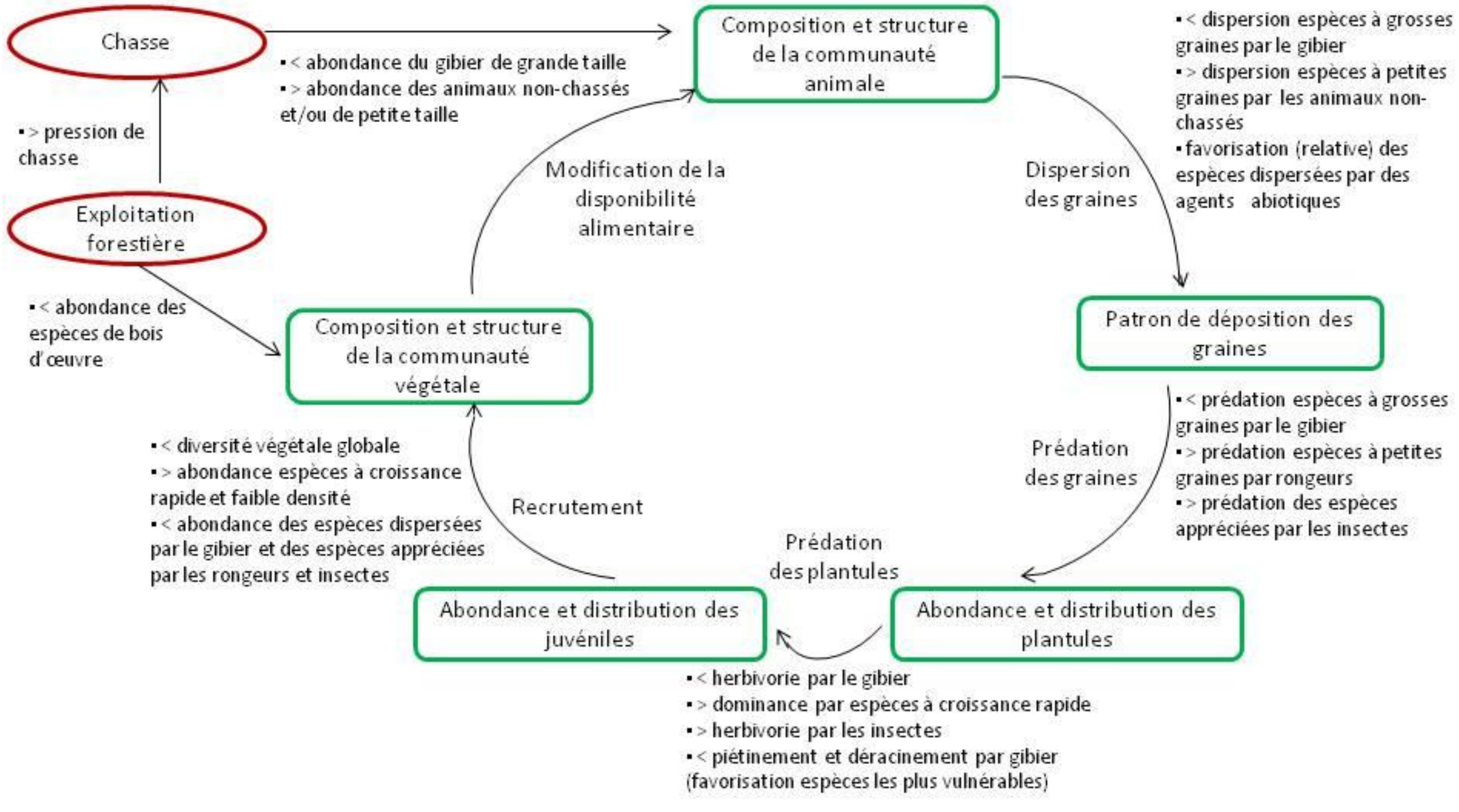


Figure 3 Schéma conceptuel présentant l'effet de la défaunation sur la régénération des essences forestières (adapté de Poulsen *et al.* 2013 et Rosin 2014)**.** < correspond à une diminution et > à une augmentation**.**

La modification des cortèges floristiques résultant de la défaunation peut avoir des conséquences économiques importantes. Pour les populations humaines forestières, qui dépendent encore fortement des produits forestiers pour leur alimentation quotidienne, la raréfaction du gibier pourrait se traduire par des carences en protéines ou micronutriments (Wilkie & Carpenter 1999; Nasi *et al.* 2011; Vinceti *et al.* 2013). En outre, de nombreuses espèces végétales endozoochores sont sources de produits forestiers non-ligneux (Meunier et al. 2015). Pour les sociétés d'exploitation forestières, la régénération des essences commerciales peut s'en trouver affectée. En effet plusieurs espèces de bois d'œuvre sont dispersées par les animaux (**Tableau 1**). La proportion des essences exploitées endozoochores va probablement augmenter simultanément à une valorisation croissante des essences dites secondaires (Jansen & Zuidema 2001; Rosin 2014). A moyen terme, les effets indirects d'une activité de chasse non-soutenable pourraient donc se faire ressentir sur le potentiel économique d'une forêt (Howe 2007).

Bien que difficilement généralisables (Nathan & Muller-Landau 2000; Lambert & Chapman 2005; Beckman & Muller-Landau 2007; Kurten 2013) et compliquées à évaluer (Robertson *et al.* 2006), les conséquences de la réduction des populations animales sur l'équilibre fonctionnel des forêts tropicales impacteront de manière déterminante la dynamique future de ces systèmes (Asquith et al. 1997; Howe 2007; Wright et al. 2007; Markl et al. 2012; Beaune et al. 2012b; Abernethy et al. 2013; Effiom et al. 2013; Galetti & Dirzo 2013). Les espèces végétales présentant des temps de génération longs, les effets de la diminution des disperseurs ne seront réellement appréciables que dans des dizaines d'années (Peres & Palacios 2007; Brodie *et al.* 2009). Des forêts qui semblent intactes peuvent en réalité avoir déjà perdu une grande partie de leur capacité de régénération (Redford 1992). Pour cette raison, les projets à long terme s'intéressant aux impacts de la défaunation sur les communautés végétales sont particulièrement nécessaires à la compréhension de ce phénomène.

Malgré l'importance reconnue de la communauté animale dans l'équilibre des écosystèmes forestiers tropicaux, le rôle des différentes espèces de disperseurs est encore peu documenté. Les primates, notamment, forment un groupe de frugivores abondamment représentés dans les forêts tropicales d'Afrique Centrale, et leur contribution en tant que disperseur est considérée comme incomparable (Poulsen *et al.* 2001; Lambert & Chapman 2005; Lambert 2011). Parmi eux, le gorille des plaines de l'Ouest (*Gorilla gorilla gorilla* Savage & Wyman, 1847) mérite une attention particulière (Petre *et al.* 2013).

Tableau 1 Espèces forestières d'Afrique Centrale productrices de bois d'œuvre dispersées par endozoochorie et leur principaux disperseurs

Famille	**Nom scientifique**	**Disperseurs**	**Type de fruit**	**Référence**
Anacardiaceae	*Antrocaryon klaineanum* Pierre	Gorille, autres primates, éléphant	Drupe charnue	White & Abernethy 1996
Burseraceae	*Dacryodes buettneri* (Engl.) H.J. Lam.	Autres primates, oiseaux	Drupe charnue	Williamson *et al.* 1990; Hecketsweiler 1992; Tutin & Fernandez 1993; White & Abernethy 1996; Rosin 2014
Burseraceae	*Dacryodes igaganga* Aubrév. & Pellegr.	Gorille, autres primates, éléphant, oiseaux	Drupe charnue	Hecketsweiler 1992
Burseraceae	*Dacryodes normandii* Aubrév. & Pellegr.	Gorille, autres primates, éléphant, oiseaux	Drupe charnue	Hecketsweiler 1992; White & Abernethy 1996; Fourrier 2013
Burseraceae	*Canarium schweinfurthii* Engl.	Gorille, autres primates, éléphant, oiseaux	Drupe charnue	Hecketsweiler 1992; White & Abernethy 1996; Petre *et al.* 2015b
Fabaceae	*Afzelia* spp.	Autres primates, éléphant, oiseaux	Gousse à graines arillées	Hecketsweiler 1992
Fabaceae	*Bobgunnia fistuloïdes* (Harms) J.H. Kirkbride & J.H. Wiersema	Autres primates, éléphant	Gousse	Hecketsweiler 1992; White & Abernethy 1996
Fabaceae	*Dialium pachyphyllum* Harms	Gorille, autres primates, éléphant, petits rongeurs	Gousse	Hecketsweiler 1992; Petre *et al.* 2015b
Fabaceae	*Erythrophleum ivorense* A.Chev. *et E. suaveolens* (Guill. & Perr.) Brenan	Gorille, autres primates	Gousse	Hecketsweiler 1992; Doran *et al.* 2002; Petre *et al.* 2015b
Fabaceae	*Gilbertiodendron dewevrei* (De Wild.) J.Léonard	Gorille	Gousse	Doran *et al.* 2002; Rosin 2014
Ebenaceae	*Diospyros crassiflora* Hiern	Autres primates, éléphant	Baie charnue	Hecketsweiler 1992
Moraceae	*Milicia excelsa* (Welw.) C.C.Berg	Oiseaux, chauve-souris, écureuils	Fruit composé charnu	Daïnou *et al.* 2012; Rosin 2014
Myristicaceae	*Pycnanthus angolensis* (Welw.) Warb.	Autres primates, oiseaux	Capsule à graine arillée	White & Abernethy 1996
Myristicaceae	*Staudtia gabonensis* Warb.	Autres primates, oiseaux, petits et gros rongeurs, écureuils	Capsule à graine arillée	Hecketsweiler 1992
Rubiaceae	*Nauclea diderrichii* Merr.	Gorille, autres primates, éléphant, ruminants, oiseaux, petits et gros rongeurs	Fruit composé charnu	Hecketsweiler 1992; Fourrier 2013; Rosin 2014; Petre *et al.* 2015b
Sapotaceae	*Autranella congolensis* (De Wild.) A.Chev.	Gorille, éléphants	Baie charnue	Hecketsweiler 1992; Doran *et al.* 2002; Rosin 2014
Sapotaceae	*Baillonella toxisperma* Pierre	Autres primates, éléphant, gros rongeurs	Baie charnue	Hecketsweiler 1992; White & Abernethy 1996; Rosin 2014
Sapotaceae	*Chrysophyllum africanum* A.DC.	Gorille, autres primates, éléphant	Baie charnue	Hecketsweiler 1992; White & Abernethy 1996; Fourrier 2013; Rosin 2014
Sapotaceae	*Chrysophyllum lacourtianum* De Wild.	Gorille, autres primates, éléphant, ruminants	Baie charnue	Hecketsweiler 1992; Petre *et al.* 2015b

3 PERTINENCE DE L'ÉTUDE, OBJECTIFS ET STRUCTURE DE LA THÈSE

Malgré que le gorille des plaines de l'Ouest soit reconnu comme un acteur important de la dynamique des forêts tropicales, son rôle en tant que disperseur est encore actuellement peu connu. Compte tenu de ses particularités écologiques, le gorille des plaines de l'Ouest pourrait jouer un rôle majeur dans la restauration des forêts exploitées. L'**Annexe 1** propose une synthèse des connaissances à ce sujet.

Etant donné qu'une part importante de l'aire de distribution des gorilles des plaines de l'Ouest est occupée par des concessions forestière (**Figure 4**), la préservation des gorilles ne peut se faire sans une meilleure connaissance de la manière dont l'exploitation forestière affecte cette espèce, et une définition plus claire des stratégies permettant de limiter ses impacts négatifs (Clark & Poulsen 2012).

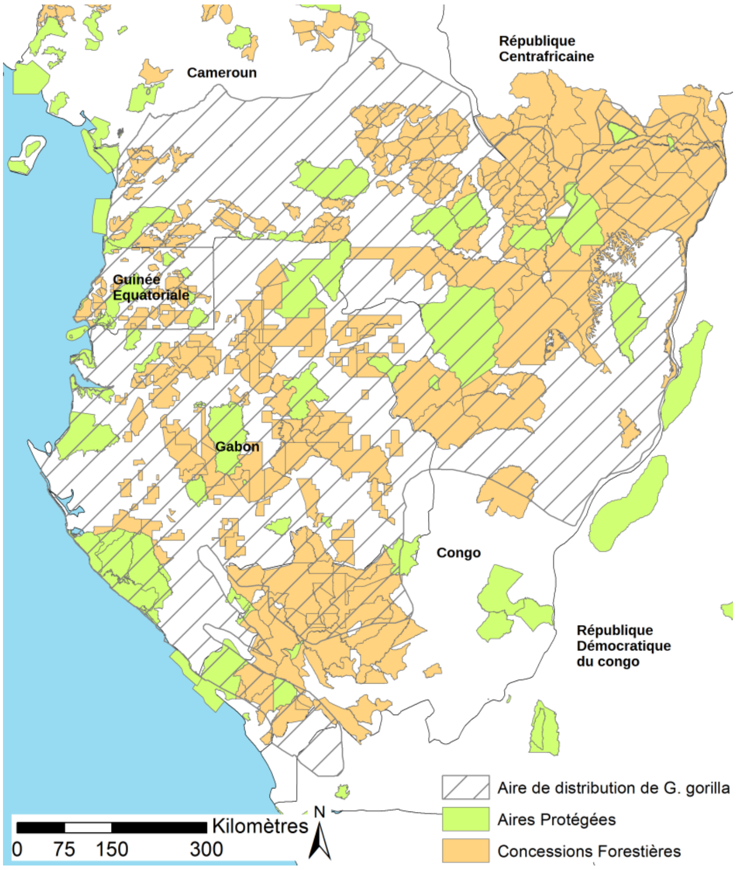


Figure 4 Aire de distribution du gorille (*Gorilla gorilla*) et localisation des concessions forestières et aires protégées en Afrique Centrale

L'objectif principal de cette thèse de doctorat est de décrire le rôle d'une espèce menacée, le gorille des plaines de l'Ouest, dans la régénération des forêts denses humides exploitées pour le bois d'oeuvre. Les impacts de l'exploitation sélective du bois d'oeuvre sur cette espèce sont également abordés. Spécifiquement, outre une caractérisation qualitative et quantitative des graines dispersées et de leur évolution au cours de l'année, la recherche s'attèle à décrire l'influence de ce primate sur la dynamique des forêts en cours d'exploitation. Une essence exploitée modèle a été sélectionnée pour cette caractérisation, l'Ossabel *Dacryodes normandii* Aubrév. & Pellegr. (Burseraceae). Les différentes questions de recherche qui sont abordées dans ce travail sont les suivantes :

1. *Quel est l'état actuel des connaissances relatives (1) au rôle du gorille en tant que disperseur des graines et (2) aux impacts de l'exploitation forestière et de la chasse sur le gorille et ses services de dispersion ?*

2. *Les concessions forestières constituent-elles des habitats favorables à la préservation des populations de gorilles, ainsi que de leurs services écologiques, en particulier la dispersion des graines ?*
3. *Quel est le potentiel quantitatif et qualitatif du gorille en tant que disperseur ?*
4. *Quelle est la contribution du gorille dans la dispersion d'une essence exploitée, l'Ossabel* Dacryodes normandii *?*

Des recommandations en termes de gestion forestière seront proposées à l'issue de ce travail.

La présente introduction constitue la **Première Partie** de cette thèse. Les concepts clés utilisés dans ce travail ont été développés dans le **Chapitre 1.** Le chapitre suivant (**Chapitre 2**) fait état des connaissances actuelles concernant les impacts de l'exploitation forestière et de l'activité de chasse qui y est souvent associée sur le gorille des plaines de l'Ouest, et les conséquences probable de son déclin sur la dynamique et la régénération forestière. Ce chapitre a été publié, sous forme de synthèse bibliographique, dans la revue *Biotechnology, Agronomy, Society and Environment* :

- HAUREZ B., PETRE C-A. & DOUCET J-L., 2013. Impacts of logging and hunting on western lowland gorilla (*Gorilla gorilla gorilla*) populations and consequences for forest regeneration. A review. *Biotechnology, Agronomy, Society and Environment*, **17**(2), 364-372.

Ensuite, **le Chapitre 3** décrit le site d'étude dans lequel la recherche a été entreprise.

La **Deuxième Partie** aborde l'évaluation des impacts de l'exploitation forestière sur les populations de gorilles. Elle est scindée en deux chapitres. Le **Chapitre 4** dresse un état des lieux de la population de gorille dans une zone exploitée 25 ans auparavant. Il permet d'obtenir une évaluation de l'impact de l'exploitation sur les populations de gorilles à long terme, en répondant à la question « une population viable de gorilles des plaines de l'Ouest peut-elle se développer au sein d'une forêt exploitée ? ». Ce chapitre est publié dans la revue *Biodiversity and Conservation* :

- HAUREZ B., PETRE C-A., VERMEULEN C., TAGG N. & DOUCET J-L., 2014. Western lowland gorilla density and nesting behavior in a Gabonese forest logged for 25 years: Implications for gorilla conservation. *Biodiversity and Conservation*, **23**(11), p. 2669-2687.

Le **Chapitre 5** présente une comparaison entre le premier inventaire, et deux inventaires ultérieurs réalisés 6 mois et 1 an après le passage du second cycle de l'exploitation. L'évolution directement après passage de l'exploitation de la densité en gorille, de l'utilisation de l'habitat pour la nidification et de la typologie des nids est abordée. Ce chapitre dresse une évaluation à court terme de l'impact des activités d'exploitation sur les gorilles. C'est un article accepté pour publication (avec modifications majeures) dans la revue *Forest Ecology and Management* :

- HAUREZ B., PETRE C-A., VERMEULEN C., TAGG N. & DOUCET J-L., *accepted*. Short term impact of selective logging on western lowland gorilla density. *Forest Ecology and Management.*

La **Troisième Partie** de ce document présente une caractérisation du potentiel du gorille en tant que disperseur via différents aspects. Le **Chapitre 6** consiste en une description qualitative (espèces dispersées, variation saisonnière et viabilité des graines) et quantitative des graines dispersées par les gorilles au sein du site d'étude. Pour certaines espèces végétales, une évaluation de l'effet du passage dans le tractus digestif et/ou de la présence de matière fécale sur le taux et la vitesse de germination est présentée. Ce chapitre est soumis à la revue *Biotropica* :

- HAUREZ B., TAGG N., PETRE C-A. & DOUCET J-L., *submited*. Assessment of the qualitative and quantitative effectiveness of western lowland gorilla (*Gorilla gorilla gorilla*) seed dispersal in Gabon. *Biotropica.*

Dans le **Chapitre 7**, la contribution du gorille dans la dispersion d'une espèce exploitable, l'Ossabel *Dacryodes normandii* est abordée. Les animaux disperseurs et prédateurs des graines du *D. normandii* ont été identifiés par le biais d'observations directes (*focal tree watches*) et indirectes (pièges photographiques), et leurs contributions respectives ont été évaluées sur base des résultats obtenus et de données disponibles dans la littérature. Il a été publié par *Journal of Tropical Ecology* :

- HAUREZ B., DAÏNOU K., TAGG N., PETRE C-A. & DOUCET J-L., 2015. The role of great apes in seed dispersal of the tropical forest tree species *Dacryodes normandii* (Burseraceae) in Gabon. *Journal of Tropical Ecology*, **31**(5), p. 395-402.

Ensuite, le **Chapitre 8** présente une évaluation de l'effet de la présence de matière fécale et de l'effet du site de dépôt (forêt à canopée fermée *vs.* site de nidification) sur la croissance et la survie des jeunes plantules pour plusieurs espèces [*Santiria trimera* (Oliv.) Aubrév. (Burseraceae), *Dacryodes normandii* Aubrév. and Pellegr. (Burseraceae), *Plagiostyles africana* Prain ex De Wild. (Euphorbiaceae) et *Chrysophyllum lacourtianum* De Wild. (Sapotaceae)]. Cet article est accepté pour publication dans la revue *Bois et Forêts des Tropiques* :

- HAUREZ B., PETRE C-A. & DOUCET J-L., sous-presse. Is western lowland gorilla a good gardener? Impact of deposition condition on seedling growth. *Bois et Forêt des Tropiques*, **324**(2), p. 38-49.

La **Quatrième Partie** correspond au **Chapitre 9** de ce document et consiste en une synthèse des résultats principaux obtenus tout au long de cette thèse. Il dresse les perspectives de recherche à approfondir ou développer.

CHAPITRE 2 LES IMPACTS DE L'EXPLOITATION FORESTIÈRE ET DE LA CHASSE SUR LES POPULATIONS DE GORILLE DES PLAINES DE L'OUEST (*GORILLA GORILLA GORILLA*) ET CONSÉQUENCES POUR LA RÉGÉNÉRATION FORESTIÈRE (SYNTHÈSE BIBLIOGRAPHIQUE)

L'importance des espèces animales dans la dynamique des écosystèmes forestiers tropicaux a été développée dans l'introduction générale. En outre, le processus de défaunation a été décrit, ainsi que ses liens avec les activités anthropiques. Le présent chapitre se focalise sur les impacts anthropiques sur le gorille des plaines de l'Ouest ainsi que sur les services écologiques qu'il dispense. Deux aspects sont plus particulièrement étudiés : (1) l'influence de l'exploitation sélective du bois d'oeuvre et (2) l'impact de la chasse et du braconnage. Enfin, le rôle du gorille en tant que disperseur est abordé.

Adapté de HAUREZ B., PETRE C-A. & DOUCET J-L., 2013. Impacts of logging and hunting on western lowland gorilla (*Gorilla gorilla gorilla*) populations and consequences for forest regeneration. A review. *Biotechnology, Agronomy, Society and Environment*, **17**(2), p. 364-372.

Abattage directionnel dans une concession forestière © J.-L. Doucet

Résumé

L'exploitation du bois d'œuvre se développe rapidement à travers les forêts du Bassin du Congo. Les surfaces dévolues à l'exploitation forestière ont rapidement augmenté au cours des décennies et couvrent aujourd'hui une part importante de l'aire de distribution du gorille des plaines de l'Ouest (Gorilla gorilla gorilla Savage & Wyman, 1847). Or, cette espèce en danger critique d'extinction (IUCN), pourrait jouer un rôle fondamental dans le maintien de la structure et de la composition des forêts tropicales humides. Cela serait lié à une dispersion efficace des graines due au caractère frugivore marqué de son régime alimentaire, aux temps de rétention élevés des aliments ingérés, aux longues distances quotidiennes parcourues, à une capacité volumique stomacale importante, et à son aptitude à avaler des graines de dimensions très variables. En outre, il tend à déposer la majeure partie des graines ingérées dans des micro-habitats potentiellement favorables au développement des plantules, dont les chablis artificiels (créés par l'abattage de bois d'œuvre). En conséquence, le gorille pourrait jouer un rôle fondamental dans les mécanismes de cicatrisation post-exploitation. Or, l'exploitation du bois d'œuvre possède deux principaux impacts antagonistes sur les populations de gorilles : (1) le développement de la végétation herbacée, constituant une ressource alimentaire de base et un matériau pour la construction des nids, au niveau des ouvertures forestières est bénéfique ; (2) l'augmentation de la chasse liée à l'ouverture des pistes pourrait s'avérer catastrophique. Au vu des impacts potentiels des concessions forestières sur la fonction écologique du gorille des plaines de l'Ouest, la mise en place de méthodes d'exploitation qui préservent les populations de gorille est primordiale pour une gestion durable de la forêt tropicale.

Mots clés : *Gorilla gorilla gorilla*, exploitation forestière, écosystème forestier, interaction écologique, Bassin du Congo

Abstract

Timber exploitation is rapidly expanding throughout the Congo Basin. Forest areas assigned to timber harvesting have sharply expanded over the decades and logging concessions now largely overlap with the range of western lowland gorilla (*Gorilla gorilla gorilla* Savage & Wyman, 1847). However this species, which is considered as critically endangered by IUCN, could play an essential role in maintaining the structure and composition of tropical rainforest notably through seed dispersal services. This is likely due to its frugivorous diet, high stomach capacity and ability to swallow seeds of variable sizes. Moreover gorillas have a long gut retention time of ingested food, travel long daily distances and deposit most ingested seeds in suitable habitats for plant development (such as logging gaps). Consequently, the preservation of the role of gorilla in forest regeneration is essential in the context of logged forest ecosystems. Timber harvesting has two major opposing impacts on gorilla populations: on the one hand, gorillas benefit from growth of herbaceous vegetation (e.g. Marantaceae and Zingiberaceae) following forest canopy opening, as such herbs provide both staple food and nest-building materials; on the other hand, gorilla populations suffer with the rise in hunting associated with logging activity, especially with road network installation. Considering the potential negative knock-on effects of logging concessions on the ecological function of western lowland gorilla, the implementation of timber harvesting methods that preserve gorilla populations is a considerable challenge for forest sustainability, as well as for gorilla's conservation.

Keywords: *Gorilla gorilla gorilla*, timber exploitation, forest ecosystem, ecological interactions, Congo Basin

1 INTRODUCTION

Ecological interactions between animal and plant species impact forest structure and composition (Beckman & Muller-Landau 2007; Howe 2007; Wang et al. 2007; Wright et al. 2007; Fa & Brown 2009). In particular, elephants and gorillas are recognized to have highly contributed to African forest expansion through seed dispersal (Rogers *et al.* 1998). Western lowland gorillas (*Gorilla gorilla gorilla* Savage & Wyman, 1847) are regarded as key dispersers because of their highly frugivorous diet and extended home range allowing long dispersal distances (Voysey *et al.* 1999; Tutin 2001; Stokes 2008). As a consequence, it is assumed that gorillas play an essential role in the maintenance of forest botanical structure and composition. Therefore, any reduction in gorilla densities, due to either anthropogenic or natural disturbances, could influence forest dynamics. Unfortunately western gorilla species is classified as critically endangered according to IUCN criteria (Walsh *et al.* 2008; Nelleman *et al.* 2010). Hunting is currently identified as the main threat faced by western lowland gorillas (Tutin 2001). Other threats include emerging disease epidemics (e.g., Ebola hemorrhagic fever), expanding human development, and habitat loss and fragmentation (Tutin 2001; Sanz *et al.* 2007; Mehlman 2008; Stokes 2008; Walsh *et al.* 2008). Their current population estimate is about 200,000 individuals throughout the forests of the Congo Basin (Nelleman *et al.* 2010). Consequences of gorilla decline on the forest ecosystem are relatively unknown but it is suspected that such population decreases may disrupt ecological relationships between plants and animals (Wright 2003).

Extractive industries, such as timber exploitation, provide important sources of income for the countries of the Congo Basin, as they contribute to the *Gross Domestic Product* (*GDP*) and are strongly involved in the development process of a country (Arnhem 2008; Clark *et al.* 2009). The extraction of timber trees changes the forest habitat through modification of vegetation structure and composition, and fragmentation of large forest areas (Clark *et al.* 2009). The construction of road networks related to the installation of extractive industries and the development of a country increases accessibility of the forest to hunters and therefore facilitates the bushmeat trade (Wilkie *et al.* 2000; Tutin 2001; Rieu & Binot 2006). The bushmeat requirements of rural and urban human populations are increasing as a result of two main drivers (Bennett *et al.* 2007). First, rural population densities are rising in line with human demographic growth and consequently, the number of people dependent on bushmeat for their protein intake is growing. Secondly, inhabitants of urban centers have access to rising incomes, simultaneously boosting the demand for bushmeat in cities. As a result, many large-bodied Central and West African wildlife species have already declined under the pressure of hunting and habitat loss (Bennett *et al.* 2007).

However, gorilla densities in properly managed logging concessions have been shown to equal or even exceed densities in reserves and national parks (Arnhem 2008; Stokes *et al.* 2010). In disturbed areas gorillas benefit from forest openings (logging gaps and old logging roads) for feeding and nesting, due to an abundance of herbaceous vegetation (Wright 2003; Matthews & Matthews 2004; Morgan & Sanz 2007; Walsh et al. 2008; van Kreveld & Roerhorst 2009; Clark et al. 2009; Stokes et al. 2010; Remis & Kpanou 2011).

Considering the importance of timber exploitation for the economy and development of Central African countries, logging is likely to further expand in the future with possible critical implications for wildlife (Rieu & Binot 2006; Walsh *et al.* 2008). Therefore a better understanding of the interactions between timber exploitation, gorilla populations and forest regeneration would be beneficial for continued synergy.

This paper aims to highlight the interactions between forest ecosystem, timber exploitation and western lowland gorillas. Biological characteristics of the gorilla linked with its ecological role and with the potential impacts of timber exploitation on its populations are explained. The resulting consequences on forest ecosystem resilience are then deduced. Based upon the analysis of the complex "forest ecosystem-timber exploitation-gorilla", the main perspectives for future research are presented.

To achieve these objectives, a bibliographic research has been undertaken on the database Scopus provided by Gembloux Agro-Bio Tech. The keywords "*Gorilla gorilla gorilla*", "logging", "Congo Basin", "seed dispersal" were used for the research. Master and PhD. thesis have been ignored, except the PhD. thesis of E. Arnhem because of the relevance of its subject. The 50 most relevant papers were selected and cited.

2 THE TIMBER EXPLOITATION INDUSTRY AND ITS IMPACTS ON FOREST PRIMATES

2.1 Timber industry in the Congo Basin

Industrial timber exploitation constitutes an essential economic activity for all countries of the Congo Basin [e.g., in Cameroon and in Gabon industrial logging accounts for 11% and 4% of the *GDP,* respectively (Arnhem 2008)]. It also greatly contributes to development, being a major source of employment.

Timber exploitation within this region is highly selective, focusing on a few economically valuable tree species. As a result, extraction rates are low, ranging from 0.5 to 3 stems ha^{-1} (Rieu & Binot 2006) and selective felling of valuable trees allows the forest to regenerate after timber extraction (Johns 1985). The implementation of *Reduced Impact Logging* (*RIL*) practices (e.g., narrower roads, planned skid-trail network, directional felling, closure of old logging roads, etc) by logging companies since the early 1990s has limited the damage to forest ecosystems caused by timber exploitation (Morgan & Sanz 2007; van Kreveld & Roerhorst 2009).

Furthermore, in the Congo Basin, a number of policies have been made in favor of sustainable forest management practices. Firstly, forestry legislation has been reviewed over the last two decades (Nasi *et al.* 2012) and more than half of the area subject to logging was being managed under approved sustainable management plan (Nasi *et al.* 2012). Secondly, the number of logging companies undergoing the process of certification is on the increase, reaching 5 million hectares (FSC 2012a). However, concessions with no management plan remain numerous, and such uncontrolled exploitation continues to negatively impact on the forest ecosystem (Nasi *et al.* 2012).

Considering the economic importance of timber and the probable expansion of extractive activities in line with development in tropical countries, the survival of many rainforest animal species depends on their ability to cope with logging activity (Johns 1985). For example, more than half the range of western African great apes falls within logging concessions (Morgan & Sanz 2007).

2.2 Effects of timber exploitation on primate communities

Logging activities affect animals because of daily human presence and noise disturbance from machinery and vehicles (van Kreveld & Roerhorst 2009); though these disturbances are relatively limited in time. There are four major factors resulting from timber exploitation that potentially impact on wildlife within and around logging concessions either singularly or in interaction with each other: (i) habitat alteration and fragmentation, linked to the road network, (ii) increase in human population density and (iii) increase in hunting (Nasi *et al.* 2012).

2.2.1 *Effects of habitat alteration and fragmentation.*

Primate community structure is strongly influenced by natural factors, such as habitat structure and plant species composition (Peres & Palacios 2007); consequently any change to vegetation caused by timber exploitation might indirectly impact upon primate populations. Logging activities can modify ecosystems by altering forest structure and composition, and leading to forest block fragmentation (Clark *et al.* 2009; Hardus *et al.* 2012). Particularly, the construction of roads required for timber harvesting induces local physical disturbances (e.g., changes in soil property and drainage patterns), erosion and fragmentation of landscape (Wilkie et al. 2000, 2007; Rieu & Binot 2006; Clark et al. 2009). Physical effects are also observed along roads, such as soil compaction and litter layer degradation (Malcolm *et al.* 2000). However, the intensity of these alterations varies with the type and, to a lesser extent, the age of the roads (Malcolm *et al.* 2000).

As well as fragmenting the forest, roads also act as barriers preventing the movement of certain species , such as strictly arboreal ones (Johns 1985; Laurance *et al.* 2006). Nonetheless, many species, including gorillas, are able to cross the roads (Laurance *et al.* 2006) and their fragmentation effect is consequently limited. Furthermore, the effect of roads on distribution and abundance of wildlife depends on the guild and species of animal (Nasi *et al.* 2012), but opposite effects have also been observed for a same species (Laurance et al. 2006; van Vliet & Nasi 2008; Clark et al. 2009; Remis & Kpanou 2011). Many animals also use roads for diurnal or nocturnal movements (Laurance *et al.* 2006); indeed, numerous tracks (e.g., elephant and forest buffalo dung, pangolin, duiker, chimpanzee and gorilla prints, etc.) are being observed on roads. Nevertheless, characteristics of roads, their location, dimensions and traffic levels (depending on the type of road) determine their effects on wildlife species (Nasi *et al.* 2012).

Canopy opening induced by road construction and other logging activities (i.e., skid trails and tree felling) leads to changes in local microclimate conditions (increase in insolation and temperature, and decrease in humidity) (Johns 1985) and a rapid colonization of the understory by herbaceous species is often observed (Malcolm *et al.* 2000; Matthews & Matthews 2004). Indeed, understory density is negatively correlated with canopy closure, and is significantly higher in logged than in unlogged forests (Malcolm *et al.* 2000). Wilkie *et al.* (1992) found that 6.8 % (ranging between 1.9 to 15.0 %) of the canopy cover in a timber concession in Congo was affected by selective tree felling and road construction. However, the evolution of logging methods and the development of *RIL* will potentially result in lowering these figures.

Selective logging may also lead to the destruction of trees that provide food for wildlife (Morgan & Sanz 2007), either through removal or damage caused by skid trails or tree felling. *Chrysophyllum lacourtianum* (De Wild., 1907), *Baillonella toxisperma* (Pierre, 1890) (Sapotaceae), *Dacryodes buettneri* [(Engl.) H.J.Lam, 1932] (Burseraceae) and *Nauclea diderrichii* [(De Wild. & T.Durand) Merr., 1915] (Rubiaceae) are examples of commercial tree species that feature in the diet of great apes, and whose exploitation may lead to alteration of food resource availability (Morgan & Sanz 2007). The felling of a tree is generally accompanied by the destruction of many vine and liana stems, the vegetative and reproductive parts of which are also consumed by various wildlife species, including primates (Johns 1985; Hardus *et al.* 2012). Consequently, primates may adapt their behavior either by reducing their movements in response to lower food intake, or by increasing ranging patterns in search of compensatory food resources (Johns 1985; Hardus *et al.* 2012). Intra- and inter-specific competition, as well as species breeding success, could also be affected by a change in food availability and quality (Johns 1985). Nevertheless, the high selectivity of timber exploitation in Central

Africa contributes to limiting the alteration of forest vegetation. In Gabon, the low tree harvest rate is associated with an interdiction to exploit certain species that are important to wildlife, such as Moabi (*B. toxisperma*) and Ozigo (*D. buettneri*). Thus, fruit availability in a forest may not be considerably altered by current logging practices (Arnhem 2008).

There are a number of factors influencing western lowland gorilla distribution in logged forest. Gorilla groups have been shown to flee active logging areas, but the disturbance caused by timber exploitation may be restricted to logging activities and a short period afterwards (from 7 weeks to 6 months) (Tutin 2001; Matthews & Matthews 2004; Arnhem 2008; van Kreveld & Roerhorst 2009; Clark *et al.* 2009). In some cases, gorilla distribution is not linked to (or weakly associated with) distance from main roads, or distance from human settlements (van Vliet & Nasi 2008; Stokes *et al.* 2010). In other cases, a strong positive correlation between gorilla abundance and distance from main roads has been shown (Clark *et al.* 2009). Another influencing factor is distance to unlogged forest acting as a refuge during the course of logging activities (Clark *et al.* 2009).

After exploitation activities gorilla densities return to their initial level and may even increase (Arnhem 2008; Clark et al. 2009; Remis & Kpanou 2011). This can be explained by the vegetation structure changes induced by logging (increase in understory density, notably from herbaceous species, following canopy opening) (Malcolm *et al.* 2000; Matthews & Matthews 2004). Under strict hunting regulation and anti-poaching control it seems that gorilla populations benefit from this growth of herbaceous vegetation (Wright 2003; Matthews & Matthews 2004; Morgan & Sanz 2007; Walsh et al. 2008; van Kreveld & Roerhorst 2009; Clark et al. 2009; Stokes et al. 2010; Remis & Kpanou 2011). Indeed gorillas consume *Terrestrial Herbaceous Vegetation* (*THV*) regularly and without any seasonality (Goldsmith 1999; Doran-Sheehy *et al.* 2004). Particularly, the pith of Marantaceae and Zingiberaceae offer an important year round source of protein (Oates 1996). Moreover gorillas commonly nest in open areas and plants of these two families are frequently used as nest construction materials (Tutin *et al.* 1995; Goldsmith 1999; Sanz *et al.* 2007; Stokes *et al.* 2010). Gorilla signs, such as nests and feeding remains, are generally common on old logging roads covered with *THV* (Wilkie et al. 2007; Arnhem 2008). As a consequence, the abundance of *THV* and other understory vegetation is a strong predictor of gorilla density (Oates 1996; Laurance *et al.* 2006).

Therefore, sustainably-managed timber exploitation would not be incompatible with gorilla conservation and the expansion of mechanized logging could be viewed as an opportunity for enhanced gorilla conservation, depending on poaching control, hunting regulation and frequency of ape-human contact (Morgan & Sanz 2007). On the contrary, densities of chimpanzees (*Pan troglodytes troglodytes* Blumenbach), which often live sympatrically with western lowland gorillas, have been shown to decrease during and after exploitation (Matthews & Matthews 2004). This can be explained by the strong territoriality of chimpanzees and by their dependence on primary and old secondary forests which renders them less adaptable to disturbance.

2.2.2 Effects of forest accessibility and human population growth.

The main negative effects of roads are due to the increase in forest accessibility: a road network created for timber exploitation provides easy and quick access for hunters and poachers into previously-inaccessible and remote parts of the forest (Tutin 2001; Laurance et al. 2006; Wilkie et al. 2007; van Vliet & Nasi 2008; Nasi et al. 2012).

Activity in a logging concession also means an increase in human population density at logging camps in the forest (Poulsen *et al.* 2009). This increase is partly explained by the numerous workers employed by timber companies, but also by the large number of people attracted by company infrastructure and facilities (Nasi *et al.* 2012). A concentration of people close to and within previously remote forest areas contributes to the degradation of forest habitat in terms of an increase in conversion of forest to agricultural lands (Wilkie *et al.* 2000).

More importantly, this greater concentration of people combined with easier access into the forest has two major consequences. Firstly it increases the likelihood of contacts between humans and wildlife (Morgan & Sanz 2007; van Kreveld & Roerhorst 2009) which might further increase disease distribution (Morgan & Sanz 2007; van Kreveld & Roerhorst 2009), therefore affecting patterns of pathogens and parasites (Johns 1985). This problem is particularly pertinent for great apes as they are phylogenetically close to humans and are susceptible to many of the same pathogens (notably Ebola hemorrhagic fever) (Tutin 2001). Secondly, it leads to an increase in hunting pressure (Rieu & Binot 2006; Wilkie et al. 2007; Clark et al. 2009; Poulsen et al. 2009), which is further facilitated by the use of logging vehicles for hunter and bushmeat transportation (Tutin 2001; Rieu & Binot 2006; Wilkie et al. 2007; Walsh et al. 2008). Road networks in previously remote forests and regular transport links to towns and cities in the region have resulted in an increased commercial bushmeat flow between logging concessions and urban areas (Rieu & Binot 2006), contributing to the switch from subsistence to commercial hunting (Poulsen *et al.* 2009). Hunters and poachers may also benefit from abandoned tarpaulins and settlements made during logging prospections that could be converted into hunting camps (Rieu & Binot 2006).

2.2.3 Effect of increase in hunting.

Because of easier access into the forest on logging roads, the increasing demand for bushmeat from urban markets and the evolution of modern hunting techniques (guns, wire snares, light, motorized transport, etc), logging concessions with no sustainable management plans or anti-poaching measures (e.g., strict accessibility controls) are subject to an increase in hunting and poaching pressure (Walsh et al. 2003; Rieu & Binot 2006; Wright et al. 2007; Fa & Brown 2009). As a result, a decline in mammal densities is generally observed (Wilkie *et al.* 2000; Walsh *et al.* 2003; Rieu & Binot 2006; Morgan & Sanz 2007; van Kreveld & Roerhorst 2009; Poulsen *et al.* 2009). Hunting pressure affects mammal distribution more than logging activities per se (van Vliet & Nasi 2008; Nasi *et al.* 2012).

The rise in demand for food resources caused by the large numbers of workers concentrated in logging camps and attracting immigrants results in the organization of commercial exchanges between logging camps and city markets, and in a further increase in localized hunting for consumption around these logging camps (Wilkie *et al.* 2000; Rieu & Binot 2006; Walsh *et al.* 2008; Poulsen *et al.* 2009; Nasi *et al.* 2012). Given the lower price and higher availability of bushmeat compared to farmed meat in rural areas, logging personnel can consume up to 2.5 times more bushmeat than urban workers (Rieu & Binot 2006). In addition to the provision of an important protein supply, bushmeat also provides a significant source of income, especially for men not employed by the logging company (Wilkie *et al.* 2000; Rieu & Binot 2006).

Assessing effects of hunting on fauna, and resulting impacts on plant communities, is difficult to achieve because most effects will only be detectable in the long term (Peres & Palacios 2007). The impact of hunting on a given animal population depends on the site, intensity of hunting pressure, preference of hunters and sensitivity of the species (Wright 2003; Remis & Kpanou 2011; Linder & Oates 2011).

Vulnerability to hunting notably depends on the degree of ecological specialization of the species, their anti-predator behavior and life history characteristics (Linder & Oates 2011). In many areas it seems that current levels of hunting are only sustainable for very prolific species, such as rodents and the blue duiker (Rieu & Binot 2006). Large-bodied species such as great apes are generally the most sensitive to hunting (Tutin 2001; Muller-Landau 2007; Peres & Palacios 2007; Wright et al. 2007; Bennett et al. 2007; Holbrook & Loiselle 2009; Fa & Brown 2009; Vanthomme et al. 2010), notably because they allow higher investment returns to poachers (Wright 2003; Linder & Oates 2011). Thus, large-bodied animals are usually the first to decline and disappear in hunted sites, and consequently, because of a selective pressure on wildlife populations, abundance of small-bodied non-hunted mammals tends to increase with hunting pressure (Peres & Palacios 2007). Specifically, hunting activities also affect the structure of primate communities and lead to a decrease in primate diversity (Linder & Oates 2011).

Gorillas are hunted throughout their range. Their meat is appreciated in certain regions (Cousins 1978), though in some countries western lowland gorilla is not a target species for bushmeat hunting but may be killed opportunistically (Tutin 2001; Walsh *et al.* 2003; Matthews & Matthews 2004; Mehlman 2008; Stokes *et al.* 2010). Furthermore, gorilla trophy hunting exists: gorilla skulls are considered a mark of prestige and the hand of a gorilla as a lucky charm (Cousins 1978). Gorillas are also killed in reprisal for plantation destruction (Cousins 1978; Tutin 2001) or as a reaction to the frightening charge displayed by silverbacks (Tutin 2001; Nelleman *et al.* 2010). Indeed, contrary to the charismatic reputation of gorillas in the northern hemisphere, African people generally experience fear, dislike and sometimes hate towards the gorilla (Cousins 1978; Tutin 2001). Mature members of a gorilla group may also be collaterally killed in the course of the capture of a gorilla infant destined for the pet market (Cousins 1978; Tutin 2001).

Western lowland gorillas are very sensitive even to low levels of hunting because of particular biological traits such as long life, low reproduction rate, late maturation and long inter-birth interval, high infant and juvenile mortality and complex social behavior (Oates 1996; Tutin 2001; Robbins *et al.* 2004; Rieu & Binot 2006; Morgan & Sanz 2007; Mehlman 2008; Stokes 2008; Walsh *et al.* 2008; Fa & Brown 2009; Linder & Oates 2011). Consequently, the major threat to the western lowland gorilla is probably hunting (Tutin 2001).

Wildlife is an essential actor in sustainable logging as it influences forest regeneration through a variety of processes, such as primary and secondary seed dispersal, pre- and post-dispersal seed predation and browsing on seedlings (Wright 2003; Rieu & Binot 2006). By altering the wildlife community, logging activity and the associated increase in hunting can disrupt these ecological interactions between animal and plant species (Beckman & Muller-Landau 2007; Howe 2007; Wang et al. 2007; Wright et al. 2007; Fa & Brown 2009).

3 WESTERN LOWLAND GORILLA SEED DISPERSAL AND EFFECTS OF TIMBER EXPLOITATION

3.1 Role of western lowland gorillas in seed dispersal

Wildlife species play a critical role in the balance of ecosystems by regulating the structure and productivity of plants (Bennett *et al.* 2007; Fa & Brown 2009). Western lowland gorillas in particular are essential actors in forest dynamics as they are important seed dispersers and play a role in maintaining forest structure (Tutin 2001; Stokes 2008).

G. g. gorilla is a highly frugivorous species. Fruit consumption is observed all year round and in large quantities: for example, Cipolletta (2004) found in Central African Republic that more than 90% of fecal samples contained fruit remains, including intact seeds. Due to their large body size, gorillas have the potential to disperse a high number of seeds. On average, a gorilla fecal unit contains 41 seeds (Poulsen *et al.* 2001). Poulsen *et al.* (2001) found that the gorilla population of the Dja Reserve [density of 1.7 gorillas per km²] in south-eastern Cameroon dispersed 464.7 (273.4–792.7) seeds per square kilometer per day (considering 41 seeds/fecal unit and 6.7 defecations/day). Considering all other primate species present in a greater overall density, western lowland gorillas accounted for more than a third of all dispersed seeds (Poulsen *et al.* 2001). Moreover most of the seeds dispersed by gorillas are viable after passage through the gut (Voysey *et al.* 1999; Poulsen *et al.* 2001); indeed, in a study comparing the gorilla with five primate species of the Dja Reserve [grey-cheeked mangabey (*Lophocebus albigena albigena* Gray), moustached monkey (*Cercopithecus cephus cephus* L.), white-nosed guenon (*Cercopithecus nictitans nictitans* L.), crowned guenon (*Cercopithecus mona pogonias* Bennet) and chimpanzee (*Pan troglodytes troglodytes* Blumenbach)], seeds passed through the gorilla gut displayed the highest germination rate (62 % of germination success) (Poulsen *et al.* 2001).One particularity of dispersal by gorillas is that dung, and consequently seeds, are mainly deposited at nest sites (Voysey *et al.* 1999), which means that seeds are directed to habitat types that are preferentially selected for nesting, i.e. open canopy areas (light gaps) with dense understory (Tutin *et al.* 1995; Goldsmith 1999; Voysey *et al.* 1999). These habitat types provide potential favorable environmental conditions for the germination of seeds, and the establishment and growth of seedlings (Rogers *et al.* 1998; Tutin 2001); conditions which are further enhanced by the flattening of vegetation caused when gorillas build their nests (Tutin 2001). Seedlings originating from seeds deposited by western lowland gorillas at nest sites show higher growth and survival rates than seedlings deposited under parent trees and conspecifics, or scatter-dispersed in intact forest or along trails (Rogers *et al.* 1998; Voysey *et al.* 1999). The *Daily Path Length* (*DPL*) of western lowland gorillas varies from 0.3 to 5.3 km, with an average of 2 to 2.5 km (Goldsmith 1999; Doran-Sheehy *et al.* 2004). The daily distance travelled is positively correlated with fruit consumption and hence is longer in wet than dry seasons (Goldsmith 1999; Cipolletta 2004; Doran-Sheehy *et al.* 2004). As a result of these extensive movement patterns and of high retention time, western lowland gorillas participate in long distance dispersal events (Poulsen *et al.* 2001), known to greatly impact the genetic diversity of plant populations by lowering the spatial genetic structure (Wang *et al.* 2007).

3.2 Effect of timber exploitation on seed dispersal and forest regeneration

As a result of species decline or disappearance through increased hunting or other modifications arising as a result of timber exploitation, compensatory changes may occur if another species also contributes to the ecological role of the species disturbed. But generally, potential compensatory species will be similar to the species in decline in terms of their ecological traits (such as diet, body size, reproduction traits, habitat), which is likely to make them similarly sensitive to such disturbances (Wright 2003; Fa & Brown 2009). Furthermore, in the case of seed dispersal, dispersal of the same plant by a compensatory species does not necessarily equate to playing the same role in its dispersion as the species in decline. For example, the compensatory species may remove fewer seeds, handle them in a different way, deposit them in a very different environment, or disperse them at reduced or increased distances, resulting in a completely altered dispersal pattern (Poulsen *et al.* 2001; Holbrook & Loiselle 2009).

Studies have demonstrated dispersal distances of animal-dispersed plant species to be lower in fragmented forests (Wright 2003) and in hunted forests (Condit & Wright 2007; Wang *et al.* 2007), and seed removal as being lower in hunted forests compared to undisturbed forests (Beckman & Muller-Landau 2007; Wang *et al*. 2007; Holbrook & Loiselle 2009; Vanthomme *et al.* 2010). The diversity of seeds dispersed by hunted species and the average size of the dispersed seeds are lower under high hunting pressure (Beckman & Muller-Landau 2007; Condit & Wright 2007; Howe 2007; Muller-Landau 2007; Fa & Brown 2009; Vanthomme *et al.* 2010). Large-seeded plant species would be more indirectly affected by hunting because hunters target large-bodied animals (Muller-Landau 2007; Peres & Palacios 2007; Wright *et al.* 2007; Bennett et al. 2007; Holbrook & Loiselle 2009; Fa & Brown 2009; Vanthomme *et al.* 2010), which are more likely to be able to swallow large seeds (Holbrook & Loiselle 2009). Consequently, the reduction in large-bodied animal populations caused by hunting is expected to particularly disrupt the dispersal process of large seeds (Vanthomme *et al.* 2010). The decline in large mammal densities may also lead to a rise in large-seeded species recruitment through a decrease in large seed predators (Beckman & Muller-Landau 2007; Condit & Wright 2007). In summary, hunting would alter large seed fate by reducing seed removal and dispersal, and increasing seed recruitment. Conversely, small-seeded species, non-game and abiotically-dispersed species are favored in abundance and richness (Howe 2007; Peres & Palacios 2007; Vanthomme *et al.* 2010).

The alterations in seed dispersal by western lowland gorillas in the context of timber exploitation have not as yet been investigated. Antagonistic effects of canopy opening and hunting on gorilla density and behavior may be very complex. Given the potential role of the western lowland gorilla in seed dispersal and maintenance of forest structure and composition (Rogers *et al.* 1998; Voysey *et al.* 1999; Stokes 2008), the importance of conducting a thorough scientific investigation into this topic is relevant and timely.

4 CONCLUSION AND PERSPECTIVES

Timber exploitation is an essential industry for the economy and development of the Congo Basin (Arnhem 2008; Clark *et al.* 2009). Logging provides work, income and infrastructure for rural people. However, timber exploitation might have important negative impacts on forest ecosystems, depending on management practices. Properly managed logging concessions could act as semi-protected corridors facilitating the movement of wildlife between national parks and reserves (Laurance *et al.* 2006; van Kreveld & Roerhorst 2009). Their extended areas could help to enable the persistence and genetic viability of species with large home ranges, such as the western lowland gorilla (Tutin 2001). As argued by Johns (1985): *"A large area of logged forest may support species that would be deleted from isolated refuges areas of primary forest"*. Furthermore, large private timber societies have disposal of regular financial means that are often lacking in conservation and research programs and could be partly invested for conservation (Nasi *et al.* 2012).

The evolution of western lowland gorilla abundance in forests subjected to logging depends on the effectiveness of the concession management plan. On the one hand, an increase in hunting within and around logging concessions might be deleterious for the western lowland gorilla given some of its biological traits (Oates 1996; Tutin 2001; Robbins *et al.* 2004; Rieu & Binot 2006; Morgan & Sanz 2007; Mehlman 2008; Stokes 2008; Walsh *et al.* 2008; Fa & Brown 2009; Linder & Oates 2011); whereas on the other hand, forest opening by timber exploitation (logging gaps, skid trails and logging roads) results in an increase in *THV* density, potentially attracting western lowland gorilla populations (Wright 2003; Matthews & Matthews 2004; Morgan & Sanz 2007; Walsh *et al*. 2008; van Kreveld & Roerhorst 2009; Clark *et al.* 2009; Stokes *et al.* 2010; Remis & Kpanou 2011).

Considering the large frequency of illegal hunting activities (hunters without any hunting license, hunting during closure time, with illegal capture or killing method, commercial hunting, etc.) (Rieu & Binot 2006), law enforcement to reduce hunting pressure in logging concessions is clearly important (Walsh *et al.* 2008). Nevertheless, despite the negative effects of bushmeat hunting on tropical ecosystems, it remains an important activity for local people; due to the easily accessible source of protein and growing source of income through the development of the commercial bushmeat trade (Wilkie *et al.* 2007; Poulsen *et al.* 2009). Actions to reduce hunting to sustainable levels must include the establishment of an alternative and reliable source of income and an affordable source of protein in order to avoid an uncontrolled expansion of hunting and bushmeat trading following the installation of a timber concession (Rieu & Binot 2006; Bennett *et al.* 2007; Poulsen *et al.* 2009; Nasi *et al.* 2012). Simple additional measures, such as the preferential hiring of local workers, could also limit the increase in hunting generated by the installation of a logging concession, as a result of engagement of local potential hunters (Morgan & Sanz 2007).

Despite the few studies investigating western lowland gorilla seed dispersal, the species is thought to play a fundamental function in seed dispersal of several plant species (Rogers *et al.* 1998; Voysey *et al.* 1999; Poulsen *et al.* 2001). Consequently, a decrease in gorilla density might deeply disrupt forest ecosystem stability. In order to assess the resulting disturbances future research should focus on: (i) assessment of the effect of passage through the gorilla gut on germination of seeds of dispersed species, including commercially valuable tree species, and a determination of the factors contributing to this effect (ii) determination of the influence of seed dispersal by gorillas on the genetic structure and diversity of the dispersed species, and an estimation of the spatial scale of this influence, (iii) comparison of seed dispersal by gorillas before, during and after logging activities, and (iv) impact of gorilla seed dispersal on forest after logging recovery. Moreover, the development of a precise and standardized method to estimate gorilla densities is critical to monitor the impact of logging and hunting on western lowland gorilla populations, and to compare densities over time or between sites.

CHAPITRE 3 PRÉSENTATION DU SITE D'ÉTUDE

Après avoir introduit les concepts abordés au cours de la recherche doctorale, et présenté l'état des connaissances relatives à la dispersion des graines par le gorille des plaines de l'Ouest et aux impacts de l'exploitation forestière dans les chapitres 1 et 2, le chapitre 3 définit les limites géographiques de la recherche et décrit brièvement les caractéristiques du site d'étude.

Route principale et forêt exploitée 4 années après le passage de l'exploitation au Gabon © J.-L. Doucet

Le Gabon est un pays d'Afrique Centrale qui s'étend entre 2°12' de latitude Nord et 3°55' de latitude Sud et entre les longitudes 8°20' et 14°40' (Doucet 2003). Traversé par l'Equateur, ce pays couvre une superficie de 267 667 km² (Reitsma 1988). Ses pays limitrophes sont la Guinée Equatoriale et le Cameroun au Nord, et la République du Congo à l'Est et au Sud, tandis que l'Océan Atlantique borde ses 750 km de côtes (Reitsma 1988).

Reconnu comme l'un des pays les moins densément peuplés d'Afrique centrale, le Gabon possède 1,67 millions d'habitants, soit une densité de population de 6,4 habitants par km² (Statistiques mondiales 2014). La répartition des habitants sur le territoire est très hétérogène, avec plus de la moitié de la population gabonaise concentrée dans les zones urbaines à proximité des villes principales (Libreville, Port-Gentil, Franceville) ou le long des voies de communication (Reitsma 1988; Doucet 2003; Nguimbi *et al.* 2006). La population urbaine en 2013 représentait 87,0% des habitants (Statistiques mondiales 2014). Cette faible densité humaine a permis au Gabon de conserver des massifs forestiers faiblement anthropisés, et notamment une faune relativement préservée. L'agriculture est peu développée et les besoins alimentaires sont majoritairement comblés par les importations, notamment au départ du Cameroun (Nguimbi *et al.* 2006). L'approvisionnement des ménages via les activités de chasse, pêche et cueillette est une habitude encore très répandue, particulièrement dans les villages localisés en périphérie de massifs forestiers. Une agriculture vivrière de subsistance est cependant pratiquée, avec la culture de manioc, taro, maïs, bananes à dessert et bananes plantains, etc. Cependant, la pression anthropique sur le milieu forestier se développe rapidement. En effet, l'économie au Gabon est orientée vers l'exploitation des ressources naturelles, et s'articule principalement autour de trois secteurs : le pétrole, l'exploitation forestière et les ressources minières (uranium, manganèse, or, etc.) (Doucet 2003; Nguimbi *et al.* 2006). Le Gabon a été une figure de proue de l'exploitation durable, avec de grandes sociétés forestières investies dans les processus d'aménagement avant même la ratification des cadres légaux. En 2001, un nouveau code forestier a été instauré, dans le but de mettre en place une gestion durable des forêts de production via l'établissement de plans d'aménagement, et de favoriser le développement économique du pays en soutenant les industries de transformation locale (Nguimbi *et al.* 2006; Makak & Mertens 2007). Aujourd'hui, la moitié des concessions gabonaises sont soumises à un plan d'aménagement et 17 % d'entre elles sont certifiées (de Wasseige *et al.* 2014).

Le site d'études est la concession forestière sous aménagement durable (CFAD) de *Precious Woods Gabon* (PWG). D'une superficie totale de 616 700 ha; elle est située dans le Sud-est du Gabon, entre 0°10' et 1°15' Sud et 12°30' et 14°05' Est (**Figure 5**). Le climat à Lastourville, située à 30 km de la base vie principale de la concession, se caractérise par l'alternance de quatre saisons, dont une seule peut être considérée comme réellement sèche (de juin à août) (**Figure 6**). L'altitude varie de 300 à 700 m, avec des pentes marquées par endroits, et le réseau hydrographique, composé de nombreux cours d'eau de moyenne et petite taille, est dense. La majeure partie de la CFAD est recouverte de forêt dense humide sempervirente. Une mosaïque de forêts-savanes, riche en jeunes peuplements d'Okoumés couvre environ 80 000 ha. La faune est relativement bien préservée et comporte des espèces rares et menacées comme le gorille des plaines de l'Ouest, le chimpanzé (*Pan troglodytes troglodytes* Blumenbach), l'éléphant de forêt (*Loxodonta cyclotis* Matschie), le buffle de forêt (*Syncerus cafer nanus* Sparrman) et le pangolin géant (*Smutsia gigantea* Illiger) (Demarquez & Jeanmart 2004).

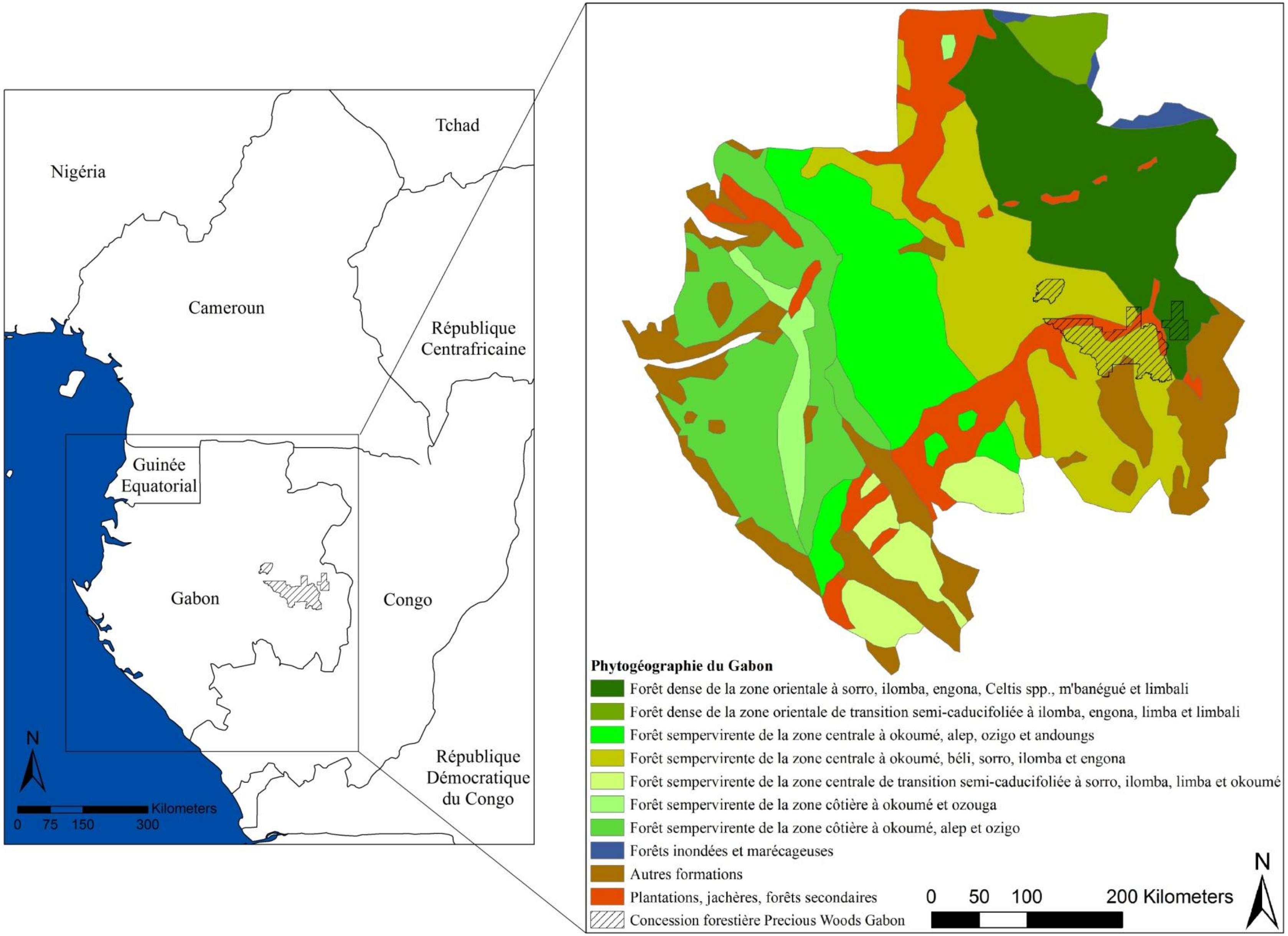


Figure 5 Localisation et phytogéographie du site d'étude (adapté de Caballe 1978)

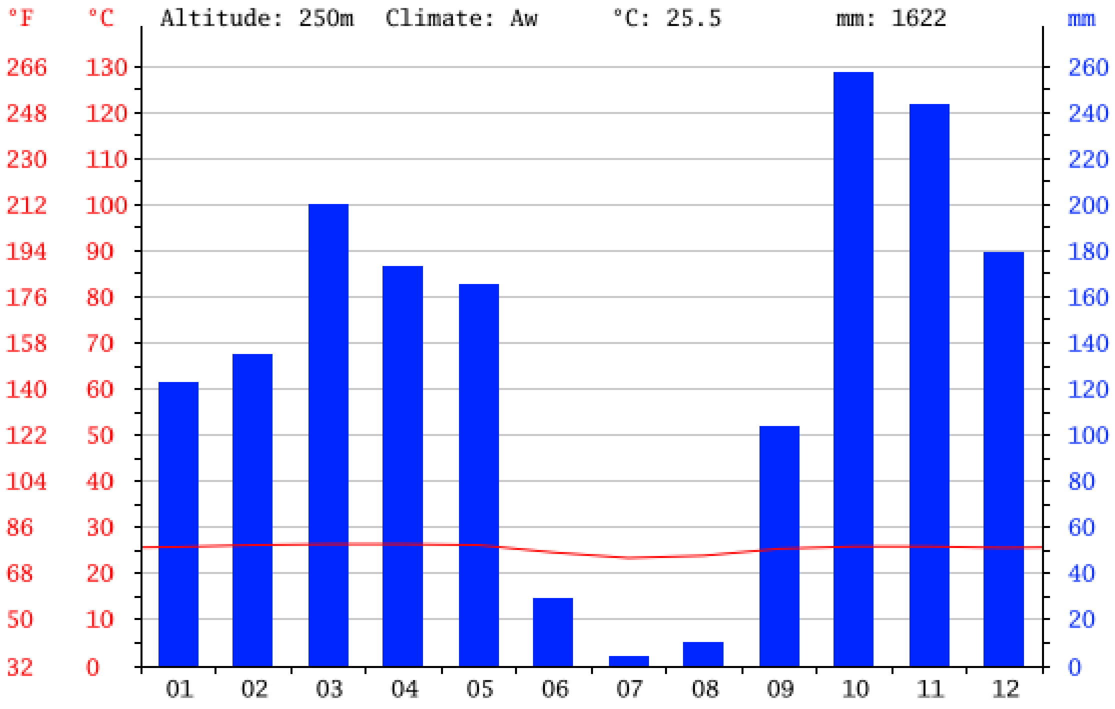


Figure 6 Diagramme ombrothermique de Lastourville (Climate Data, 2015)

DEUXIÈME PARTIE IMPACTS DE L'EXPLOITATION FORESTIÈRE SUR LES GORILLES DES PLAINES DE L'OUEST

CHAPITRE 4 DENSITÉ ET COMPORTEMENT NIDIFICATEUR DU GORILLE DES PLAINES DE L'OUEST DANS UNE FORÊT EXPLOITÉE

Les différentes caractéristiques du gorille présentées dans la section introductive de ce document suggèrent que le rôle de cette espèce dans la dynamique des forêts denses humides du Bassin du Congo pourrait être essentiel. Il a également été montré que l'exploitation forestière impacte négativement les populations de gorille, principalement en raison de l'activité de chasse. Cependant, il semble que l'abattage des arbres et la construction de pistes puissent mener à la création d'habitats favorables pour la nidification du gorille. L'exploitation du bois d'oeuvre serait donc compatible avec la préservation des populations de gorille, dans certaines conditions. Le chapitre suivant constitue une estimation de la densité en gorille et une caractérisation de leur comportement nidificateur au sein d'une forêt soumise à l'exploitation forestière sélective et pratiquée de manière durable.

Adapté de HAUREZ B., PETRE C-A., VERMEULEN C., TAGG N. & DOUCET J-L., 2014. Western lowland gorilla density and nesting behavior in a Gabonese forest logged for 25 years: Implications for gorilla conservation. *Biodiversity and Conservation*, **23**(11), p. 2669-2687.

Caractérisation des sites de nidifications de gorilles au Cameroun © B. Haurez

Résumé

Les forêts tropicales du Bassin du congo constituent des refuges de biodiversité, qui abritent encore un grand nombre d'espèces, notamment des vertébrés endémiques et/ou menacés d'extinction. Avec plusieurs autres espèces, le gorille des plaines de l'Ouest, espèce en danger critique d'extinction, contribue à la dynamique forestière via son rôle dans la dispersion des graines. Au regard de l'étendue croissante de l'exploitation du bois d'oeuvre au sein des écosystèmes forestiers tropicaux, la survie des populations de gorille dans les forêts exploitées pourrait s'avérer critique pour la conservation des écosystèmes forestiers. Nous avons estimé la densité en gorilles via un inventaire des sites de nidification dans une forêt du Sud-Est du Gabon exploitée depuis 25 ans. Le comportement nidificateur et l'utilisation de l'habitat ont été décrits et nous avons appliqués des modèles linéaires généralisés afin d'identifier les facteurs qui influencent l'utilisation diurne et nocturne de l'habitat par le gorille. La densité estimée en gorille sevrés, 1,5 gorilles km^{-2}, est comparable aux valeurs estimées au sein de certaines aires protégées et dans d'autres sites gérés de manière durable et situés dans leur aire de distribution. Le type d'habitat était le factor qui possède l'influence la plus marquée sur la distribution spatiale des sites de nidification. Nous avons observé une préférence pour la nidification en forêt de terre ferme à canopée ouverte, et dans les habitats ouverts en général, ce qui confirme les données issues d'études antérieures. L'utilisation diurne de l'habitat était fortement influencée par le type d'habitat et les activités humaines, et dans une moindre mesure par les routes (fonctionnelles et non-fonctionnelles) et les rivières. Nos résultats corroborent l'idée que les forêts exploitées constituent des habitats favorables pour les gorilles, à condition que la chasse et le braconnage soient contrôllés. Nous recommandons la collaboration entre les gestionnaires forestiers et les scientifiques pour améliorer le potentiel de conservation des forêts tropicales et optimiser les pratiques d'exploitation en lien avec la gestion de la faune.

Mots clés: *Gorilla gorilla gorilla*, comportement nidificateur, exploitation forestière, impact à long terme, Gabon, *standing crop nest count*

Abstract

The tropical forests of the Congo Basin constitute biodiversity refuges that still hold large numbers of species, including endemic and endangered vertebrates. Along with several key species, the critically endangered western lowland gorilla (WLG) potentially contributes to forest dynamics through seed dispersal. Considering the extensive influence of timber harvesting on tropical forest ecosystems, the survival of gorilla populations in logged forests might prove critical for forest ecosystem conservation. We estimated WLG density, through a nest count survey, in a forest in southeast Gabon that has been logged for 25 years. Nesting behavior and habitat use were described and we applied generalized linear models to identify the factors that influence gorilla day and night habitat use. The estimated density of weaned gorillas, 1.5 gorillas km^{-2}, is comparable with estimates from some protected areas and other sustainably managed sites within their range. Habitat type had the greatest influence on nest site distribution. We observed a preference for nesting in open *terra firma* forest, and open habitats in general, which supports the findings of previous studies. Habitat use during the day was strongly influenced by habitat type and human activities, and to a lesser degree by functional and non-functional roads, and rivers. Our results support the suggestion that logged forests are suitable habitats for WLG if hunting and poaching are controlled. We recommend collaborations between timber operators and scientists to improve the conservation potential of tropical forests and enhance the wildlife-management aspects of logging practices.

Keywords: *Gorilla gorilla gorilla*, nesting behavior, timber exploitation, long term impact, Gabon, standing crop nest count

1 INTRODUCTION

The Congo Basin is the second largest forested area in the world after the Amazonian forest (De Wasseige *et al.* 2009). It is a region of high biodiversity and a refuge for large endangered forest mammals (Dupuy 1998; Eba'a Atyi *et al.* 2010). However, activities that threaten forest animals and their habitats are expanding and increasing in pressure. Between 2000 and 2005, the mean annual deforestation and degradation net rates in the Congo Basin were 0.17% and 0.09% respectively (de Wasseige *et al*. 2012). Logging is one of the factors contributing to forest degradation but because it strongly contributes to the economy and development of Central African countries it will surely further expand (Rieu & Binot 2006; Walsh *et al*. 2008; Eba'a Atyi *et al*. 2010; de Wasseige *et al*. 2012). Thirty-five percent of Congo Basin forests were principally allocated for logging in 2010, while 26% were dedicated to conservation (de Wasseige *et al*. 2012; Nasi *et al.* 2012). The long-term survival of many forest animals may thus depend on their ability to persist in logged forests (Johns 1985).

Timber exploitation in the Congo Basin is evolving towards sustainable production and management: there are 14 million ha of managed forests, of which 6.6 million ha are certified for management under an independent label (respectively 8% and 4% of the Congo Basin forest) (de Wasseige *et al.* 2012; Nasi *et al.* 2012). In Gabon, managed production forests account for 29% of the forested area and forests certified for management comprise 14% (de Wasseige *et al*. 2012; Nasi *et al.* 2012). The certification standards notably include the implementation of forestry practices that promote the conservation of biodiversity, and the maintenance of ecosystem services and of high conservation value forests (HCVF) (Morgan *et al.* 2013).

More than 50% of the range of great apes in western Equatorial Africa lies in active logging concessions (Morgan & Sanz 2007). It is therefore essential to undertake great ape surveys outside the borders of protected areas to improve our knowledge of great ape population status and to assess responses to various types of human disturbance (Poulsen & Clark 2004).Together, Gabon and the Republic of Congo host about 80% of all western lowland gorillas (*Gorilla gorilla gorilla* Savage & Wyman) (Harcourt 1996). Despite low human population density in Gabon, and therefore low anthropogenic pressures, the country experienced a decline in its gorilla population of more than 50% between 1983 and 2000 (Walsh *et al.* 2003). This decline was mainly a result of commercial hunting, and its facilitation by the development of logging road networks and infrastructures, and the occurrence of several Ebola outbreaks in Gabon during the nineties (Huijbregts *et al.* 2003; Walsh *et al.* 2003). While Ebola outbreaks are unpredictable and cannot be human-controlled, this is not the case for the direct and indirect impacts of logging. Therefore, it is of paramount importance to understand the response of gorillas to logging-induced habitat modification in order to develop strategies which assure the preservation of WLG in Gabonese logging concessions. Assessing their status within certified logging concessions would help to control the effectiveness of 'ape friendly' practices.

We studied the long term impact of logging on WLG in a 617,000 ha certified concession in southeast Gabon that has been logged for 25 years. The following questions were addressed: (1) Is the average density of WLG in a sustainably managed logging concession comparable to densities observed in protected areas? (2) Do WLG preferentially use any particular habitat type(s) in a logged forest? (3) What are the factors explaining WLG day and night habitat use within the study site?

2 MATERIAL AND METHOD

2.1 Study site

The study site is a sustainably managed and certified (Forest Stewardship Council, FSC) logging concession of 617,000 ha, located in southeast Gabon (**Figure 7**). Allocated to a forest company since 1987, the site has undergone one complete felling cycle of 25 years. The management plan of the concession has been approved since 2000 and reduced impact logging (RIL) practices, such as controlled felling techniques and protection of future crop trees, have been applied since 2007 (Putz *et al.* 2008; Medjibe *et al.* 2013). The concession received its FSC label, given by Bureau Veritas, in 2008 (Medjibe *et al.* 2013). Before the implementation of the management plan, conventional logging was undertaken, harvesting the best quality trees of a few species without spatial or temporal planning (Demarquez & Jeanmart 2004). During the nineties, harvesting rates averaged 1 tree ha^{-1} (Demarquez & Jeanmart 2004). A second wave of timber harvesting was undertaken in 2013 (i.e., one year after our census) in a 13,410 ha annual allowable cut (AAC) (Bambidie AAC 2012, 0°44'–0°52' South, and 013°06'–13°17' East, accounting for 2.17% of the concession area).

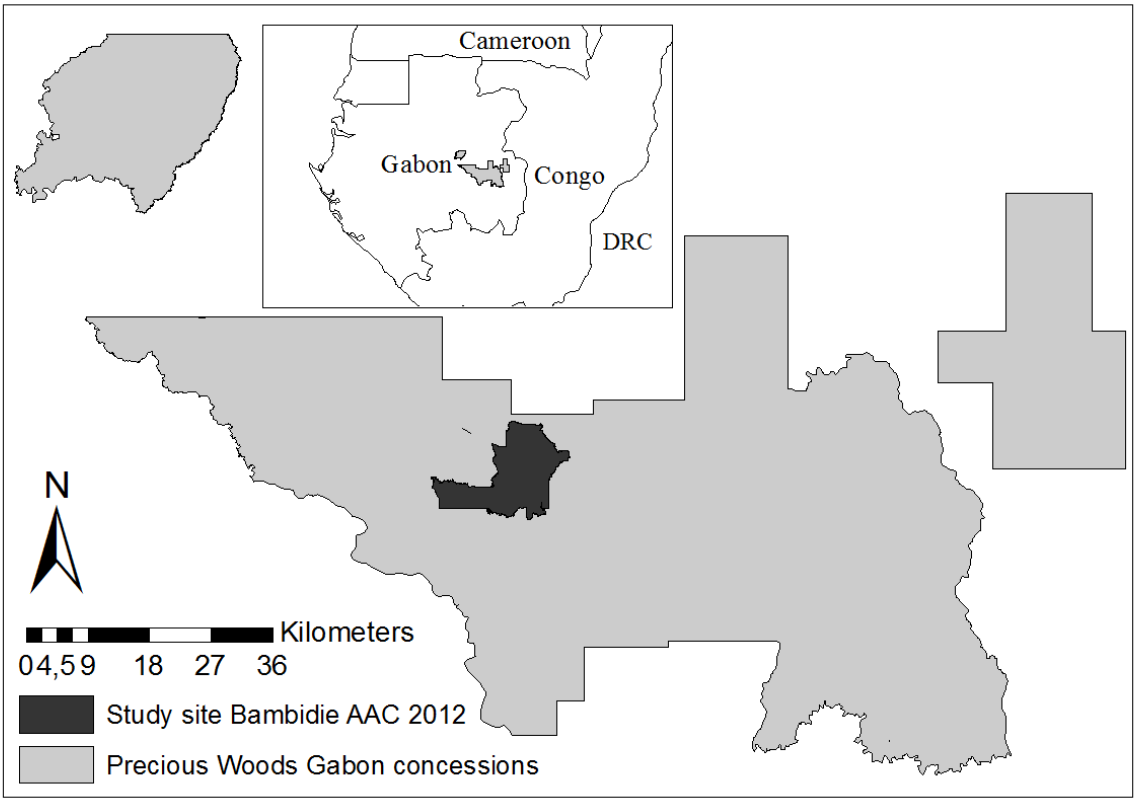


Figure 7 Geographical location of the study site

The site comprises a moist tropical evergreen forest characterized by the abundance of *Scyphocephalum ochocoa* Ward (Myristicaceae) and *Aucoumea klaineana* Pierre (Burseraceae) (Demarquez & Jeanmart 2004); a composition which lends for a categorization of old secondary forest (White 1986). The climate is equatorial, displaying two seasons with low precipitation (June–August and January–February) and two seasons with heavy precipitation (March–May and September–December). The total average annual rainfall is 1,700 mm and the average annual temperature is 26°C (Moupela *et al.* 2013). The highest temperatures are observed in February to April, while the lowest occur in July and August.

Yellow lateritic soils are dominant in the forests of this region (Martin *et al.* 1981).

2.2 Data collection

Data collection took place from January to June 2012. A two-week pilot census was undertaken in the month preceding the main census in order to estimate the sampling effort required to obtain a coefficient of variation (CV) of ≤20% on nest density estimates. This target CV was defined as a good balance between sufficient estimator precision and financial constraints (Varman & Sukumar 1995; Rainey *et al.* 2009). During the pilot census, twelve transects of 3000 m were walked leading to a total length of 36 km. Ten nest sites and 22 nests were detected from the transects. Following Buckland *et al.* (1993), these results indicated that if the pilot encounter rates of nests sites and nests were constant across all the study site, it would be necessary to walk 270 or 123 km of transect in order to not exceed the 20% CV threshold for nest sites and nests, respectively. Consequently, the figure of 270 km was taken as a minimum objective for total length of transects in the main study. Overall, 100 parallel line transects were subsequently walked by a team of two observers at an average speed of 1 km h^{-1}. Transects ranged from 1500 to 4100 m long, were placed 200 m apart (**Figure 8**) and were oriented North-South in order to be roughly perpendicular to the main rivers and consequently parallel to vegetation gradients (Stokes *et al.* 2010).

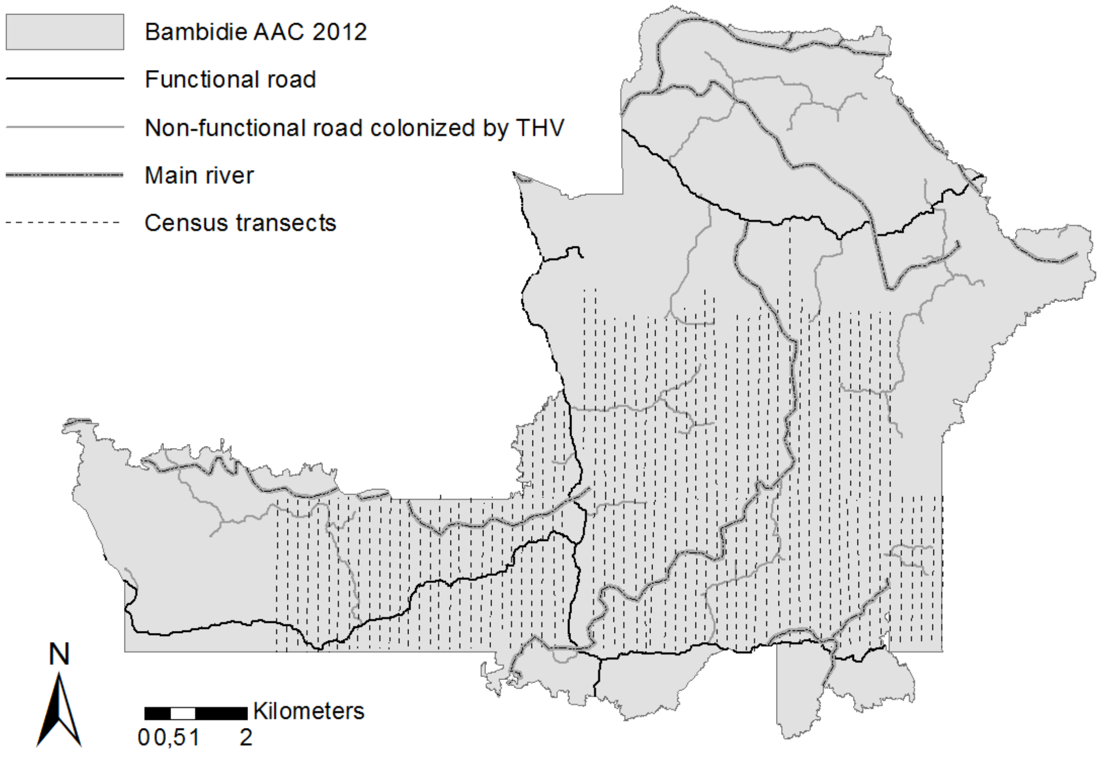


Figure 8 Bambidie AAC 2012 and transect placement

A total of 308 km of transects were walked once during the study period. A period of two weeks to two months separated transect opening and the passage of the census team. Records were made of gorilla signs (feces, prints, feeding remains, scent, vocalizations, and direct contacts), and visible gorilla nests and nest sites. Each time a nest was detected, the observers first walked a further 50 m to check for other visible nests (detected nests). Then, the observers left the transect to search in a 50 m radius around detected nests for nests that were not detectable from the transect (undetected nests). Additionally, all signs of hunting and human presence (thereafter referred to as 'human presence indices') observed along transects were recorded. The dominant habitat type and degree of canopy closure (presence (1) or absence (0) of canopy at three height classes, 2–10 m, 11–20 m and >20 m) were assessed every 50 m (Remis & Kpanou 2011). Habitat type classification followed the nomenclature presented in **Table 2**. For statistical reasons they were grouped into four main categories (**Table 2**). The representation of each habitat type in the study site was then estimated as the percentage of 50 m units of this habitat within the sample (Remis & Kpanou 2011).

Table 2 Vegetation type classification (adapted from Doucet, 2003)

Main type	Habitat types	Habitat description
Closed t*erra firma* forests	Periodically flooded forest	Forest located in sites that can be affected by floods. This habitat is characterized by the dominance of *Gilbertiodendron dewevrei* (De Wild.) J.Leonard (Caesalpiniaceae) and *Cleistanthus* spp. (Euphorbiaceae)
	Old secondary forests	Characterized by the dominance of long-life light-demanding species such as *A. klaineana*, *Lophira alata* Banks ex Gaertn.f. (Ochnaceae), *Piptadeniastrum africanum* (Hook.f.) Brenan, *Erythrophleum suaveolens* (Guill. & Perr.) Brenan.
	Forest with shallow soils	Habitat type developing on shallow soils, characterized by *Ganophyllum giganteum* (A.Chev.) Hauman (Sapindaceae), *Scaphopetalum blackii* Mast. (Sterculiaceae), *Warneckea* spp. (Melastomataceae), *Diospyros* spp. (Ebenaceae)
Open *terra firma* forests	Young secondary forest	Succession stage linked to the anthropogenic opening of the forest. The herbaceous stratum is highly present with numerous species of Marantaceae and Zingiberaceae. The Euphorbiaceae and the Rubiaceae are also abundant. Some characteristic species are *Musanga cecropioides* R. BR. & Tedlie (Moraceae), *Macaranga* spp. (Euphorbiaceae), *Barteria* spp. (Passifloraceae), *A. klaineana* (Burseraceae), *Nauclea diderrichii* (De Wild.) Merr. (Rubiaceae)
	Open vegetation type with Marantaceae and Zingiberaceae	Habitat type characterized by the dominance of Zingiberaceae (*Aframomum* spp.) and Marantaceae, an open canopy and the low representation (even most of the time, absence) of the tree component
	Old logging road	Old logging road, whose ground is either bare, or in the process of colonization by herbaceous and light-demanding vegetation
Flooded vegetation	Swamp forest	Forest established on waterlogged soils, or soils maintaining superficial groundwater in dry season. Presence of *Hallea* spp. (Rubiaceae) and Raphia spp. (Palmae)
	Pandanus spp. swamp	Swamp characterized by the abundance of *Pandanus* spp. (Pandanaceae)
	Flooded clearing	Open area within forest matrix, dominated by rushes (Cypericaceae). These clearings are regularly frequented by elephants and are commonly named *baïs* and *eyangas*
Bare soil or water	Logging road	Functional logging road, with completely bare soil.
	Hydrography	Any water feature (main river, streaming, lake, *etc.*)

A nest site was defined as a group of nests of the same age within 50 m of each other (Devos *et al.* 2008; Hicks *et al.* 2009; Stokes *et al.* 2010). Discriminating between signs of gorillas and the sympatric central chimpanzee (*Pan troglodytes troglodytes*, Blumenbach) is essential in any survey undertaken within sites where these two species are sympatric (Tutin *et al.* 1995; Kühl *et al.* 2009). Nest sites were attributed to gorillas when (1) at least one ground nest was present at the nest site or (2) one or more additional gorilla presence indices (feces or prints of the same age category, hair, fresh scent) were identified on the ground below the tree nests (Brugiere & Sakom 2001; Poulsen & Clark 2004; Morgan *et al.* 2006; Rainey *et al.* 2009; Hicks *et al.* 2009). Chimpanzee ground nesting occurs in central chimpanzees (Tagg *et al.* 2013), but has not been documented at this site and we did not observe chimpanzee signs on or close to any of the ground nests included in the study. Tree-nest-only nest sites with no gorilla signs were attributed to chimpanzees and were not included in our analysis. However, old gorilla nest sites may be mistakenly attributed to chimpanzees when only tree nests remain visible (Tutin *et al.* 1995); therefore, our calculated density value might be an underestimation.

Specific data recorded for each nest are presented in **Table 3.**

Table 3 Nest characterization data

Variable	Description	Reference
Detectability	Detectable (**1**) or undetectable (**0**) from transect	
Perpendicular distance to the transect	Distance from the center of the transect, to the center of the nest, m (precision: decimeter)	
Habitat type (see **Table 2** for details)	**Closed *terra firma* forest** **Open *terra firma* forest** **Flooded vegetation** **Bare soil or water**	Doucet (2003)
Nest type	**Zero**: bare ground **Minimum**: nest built with 1 or 2 herbaceous stems **Herbaceous**: nest built with at least 3 stems of herbaceous plants **Mixed**: nest built with herbaceous and ligneous vegetation **Ligneous**: nest built exclusively with ligneous vegetation **Tree nest**: nest built in a tree, with broken and bent branches (record of tree diameter and nest height)	Tutin *et al.* (1995)
Age category	**1 (fresh)**: vegetation still green and firm (1–2 days) **2 (recent)**: vegetation drying and changing color **3 (old)**: vegetation dead but nest still intact **4 (rotten)**: nest under disintegration process	Tutin *et al.* (1995)
Canopy opening	Presence (**1**) or absence (**0**) of canopy, measured at height classes: 2–10m, 11–20m, >20m	
Feces	Presence (**1**) or absence (**0**) of feces close to the nest	

Some additional nest sites were encountered during other activities in the forest, outside of the census transects (movements between census transects on the basal transect) or on transects that were walked a second time (to monitor nest decomposition, to search the forest for feces or to collect gorilla-food fruit species). These sites were characterized following the same process as for census sites and were integrated into the nesting behavior characterization but were excluded from the density estimation.

WLG density was estimated from nest and nest site counts along the transects using the standing crop nest count (SCNC) method. This method enables the surveying of a large area and achieves a higher level of precision in small areas when there are temporal and financial constraints (Hashimoto 1995; Blom *et al.* 2001; Laing *et al.* 2003; Kühl *et al.* 2009). Moreover, the SCNC method considers the abundance of apes over an extended period of time, resulting in an average estimation of density over a period of several months before and during the survey (Spehar *et al.* 2010). Following Buckland *et al.* (2001) the density of individual gorillas is obtained by dividing the density of nests by the nest production rate (1.0; Devos *et al.* 2008; Morgan and Sanz 2007; Tutin *et al.* 1995) and the average nest decay rate (78 days; Tutin *et al.* 1995). As an insufficient number of fresh nests were encountered during the study to calculate a site-specific nest decay rate, the value used was estimated from available data from a forest in Lopé Reserve, Gabon (located 250 km from and with very similar ecological conditions as our site) (Tutin *et al.* 1995; Doucet 2003). Indeed, recently, nest decay rates have been shown to be more similar across the forest zone than previously suspected (Maisels F., personal communication).

2.3 Data analysis

2.3.1 Distance sampling and gorilla density estimation.

Distance 6.0 release 2 software (Thomas *et al*. 2010) was used to calculate densities. Distance sampling is based on the determination of the probability of detection of an object as a function of its distance to the transect (Buckland *et al.* 2001). The detection probability function (DPF) allows a calculation of the effective strip width (ESW), which is used to estimate the sample area. The furthest 5% of observations from the transect were truncated before determination of the DPF to ensure a more robust analysis (Buckland *et al.* 2001). Model selection in Distance was based on the lowest values of Akaike information criterion (AIC) and the results of the Chi-square goodness of fit ($p > 0.05$) (Rainey *et al.* 2009; Clark *et al.* 2009; Stokes *et al.* 2010).

Distance sampling analyses were performed considering observations as: (1) individual detected nests and (2) nest sites (including detected and undetected nests), and the two analyses were compared. Individual nest analysis does not meet the assumption of independency of observations (Buckland *et al.* 2001; Hashimoto 1995; White and Edwards 2000) but avoids the issue of inaccurately estimating nest site size (Stokes *et al.* 2010). Moreover, it generally allows working on a larger sample size as more nests than nest sites are detected, thus improving the accuracy of the estimation. The decay rate is also a parameter that is determined at the level of individual nests (Stokes *et al.* 2010). With regards to the nest site analysis, the rapid disappearance of some nests, especially zero and minimum nest types, may have led to an underestimation of group size (Tutin *et al.* 1995). We controlled for the disappearance effect using a Student t-test to compare mean group sizes between fresh/recent (categories 1 and 2) and old/rotten (categories 3 and 4) nest sites.

The selected functions for the nest and nest site analyses were the Half-Normal function with a Cosine Adjustment Term and the Negative Exponential function, respectively. The Negative Exponential function, selected for the nest site density estimation, is sometimes criticized because of the absence of a ‘shoulder’ at the shortest distance from the transect line (Harris & Burnham 2001). The presence of a ‘shoulder’ is thought to better reflect reality, because the detectability of objects often decreases slightly close to the center line, then it drops off at some distance from the line. Here, perpendicular distance to the center of the nest site is calculated taking into account distance to nests detected from the transect and to nests that were not visible from the transect but detected when searching the forest (White & Edwards 2000). Consequently, the distribution of distances to nest site centers does not reflect this slight decrease in detectability.

2.3.2 Characterization of habitat use and nesting behavior

For each point of measure (every 50 m along transects and at each nest), a global value of canopy closure was obtained by summing the scores recorded at each of the three height classes. Subsequently, a canopy closure index (%) was calculated by dividing the sum by 3 (maximum canopy closure). A Student t-test was carried out to compare average canopy closure in the forest and above nests.

In order to differentiate habitat use during the day (foraging, resting and playing) and during the night (nesting behavior), gorilla presence indices for all signs excluding nest sites and for nest sites only were considered separately. Thereafter, the denomination ‘presence indices’ will refer to all indices excluding nest sites, and their analysis will reflect habitat use during the day. The ‘nesting behavior analysis’ will focus on nest sites and on the criteria leading to the selection of a site to spend the night. For both habitat use, potential habitat preferences were investigated with a Chi-square test comparing the observed distribution of gorilla signs among habitat types with their expected distribution based on habitat availability, and the determination of adjusted Wald-Bonferroni confidence intervals (CI) (Neu *et al*. 1974; Agresti & Coull 1998).

In order to identify the factors that influence the spatial distribution of gorilla presence indices and of nest sites in the study site, a generalized linear model (GLM) was adjusted separately to gorilla presence indices (‘day use’) and to nest sites (‘night use’), with a binomial response and a logit link function. The response variables were presence (1) or absence (0) of a gorilla presence indice or a gorilla nest site, and the sampling units considered are the 50 m transect segments. The factors hypothesized to explain the probability of finding gorilla presence indices, or nest sites, in a segment are integrated into the GLM (**Table 4**). The model was selected from the maximal model and by taking into account all factors and interactions of the first order and suppressing non-significant interactions and factors, step by step (backward stepwise selection). The interactions of orders higher than one were not considered because of their complex interpretation from a biological point of view. Factors or interactions with coefficients lower than $1\text{x}10^{-4}$, representing a very low actual influence on the response, were also discarded from the model. This selection method was used in order to find a compromise between the accuracy and simplicity of the model.

Table 4 Factors tested in the day and night habitat use analysis

Factor type	Factor characterizing the 50 m segment
Biotic factor	Habitat type
	Distance to river
Anthropogenic factor	Distance to functional road
	Distance to non-functional road colonized by herbaceous vegetation
	Number of human presence indices

All statistical analyses were computed in Minitab 15 (Minitab statistical software, 2007) and R software version 2.15.1 (R Development Core Team 2015).

3 RESULTS

3.1 Distance sampling and gorilla density estimation

With a survey effort of 308 km, 82 nest sites were encountered, totaling 470 nests, of which 270 were detected from the transects. Although we used nests to estimate WLG density, we encountered a gorilla group on four occasions during the course of the survey (visual contact). The nest and nest site encounter rates were 0.88 and 0.27 per km walked, respectively. The mean nest site size, excluding the 5% furthest observations and used to convert nest site density to nest density in the nest site analysis was 5.52 nests. The results of the two Distance sampling analyses are provided in **Table 5**.

Table 5 Results of Distance sampling analyses

Density estimate analysis	Detection probability function	Density nests km^{-2}	95% CI (nests km^{-2})	%CV	Density weaned gorillas km^{-2}
Nests	Half-Normal with Cosine Adjustment Term	116.7	83.4–163.5	17.2	1.50
Nest sites	Negative Exponential	106.1	68.3–164.7	22.6	1.36

The ESW values obtained were 3.69 and 4.27 m for the nest and nest site analyses, respectively. Based on these values, the resulting proportion of area sampled of the census were 0.85 and 0.98%, respectively. The objective of obtaining a maximum CV of 20% was achieved for the nest analysis (17.2%) and almost achieved for the nest site analysis (22.6%).

Group sizes were not significantly different between fresh/recent and old/rotten sites [DF = 87, t = −1.54, p = 0.127]. Thus, using the entire dataset to estimate nest site size will not result in an underestimated mean because of the disappearance of some nests. Mean nest site size was 5.8 nests/nest site [range 1–29, SD = 5.31 nests]. The average nest group size, excluding solitary nests, was 7.3 nests/nest site [range 2–29, SD = 5.25 nests].

Considering the large overlap between the two density CIs, we can conclude that, in our case, there is no significant difference between the estimation of density based on individual nests and the estimation of density based on nest sites. Therefore, density estimates based on individual nests will be chosen as the reference value for the present study since its precision is greater, and individual nest-based estimates are considered of higher value (Grossmann *et al.* 2008; Kühl *et al.* 2009; Stokes *et al.* 2010).

3.2 Nest building

Over the whole study period 89 nest sites, containing 515 nests, were encountered and characterized during both census survey and other activities in the forest.

The observed proportions of different nest types are presented in **Figure 9**.

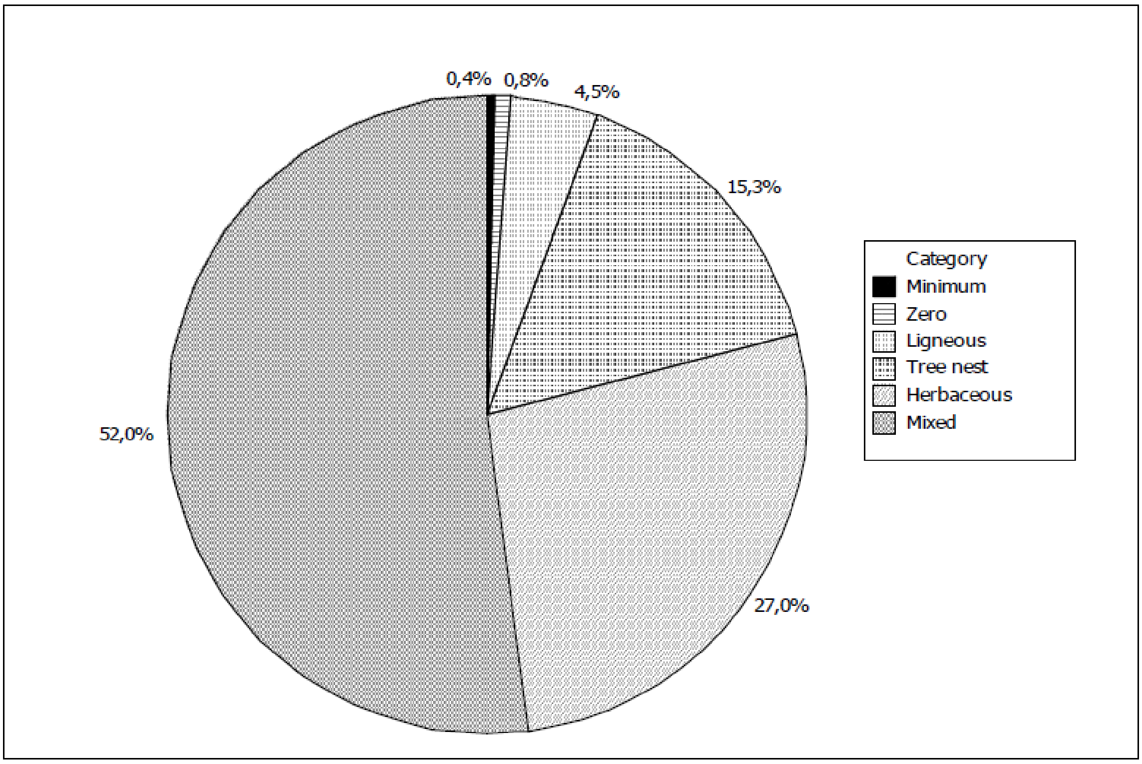


Figure 9 Proportion of gorilla nest types (n = 515)

The majority of nests were built using both herbaceous and ligneous materials (52.0%). Nests built using herbaceous plants (minimum, mixed and herbaceous nests) accounted for 79.4%.

3.3 Habitat use

Day use and night use of the different habitat types, and habitat availability within the study site are shown in **Table 6**. Chi-square goodness of fit analysis revealed no significant difference between availability and day use of habitat type [DF = 3, $\chi^2 = 4.546$, p = 0.208]. Considering night use (nesting behavior), more gorilla nest sites than expected were found in open *terra firma* forest and fewer nest sites than expected were found in closed *terra firma* forest [DF = 3, $\chi^2 = 302.369$, $p < 0.001$].

Table 6 Comparison of habitat availability and habitat use

Main habitat type	Habitat availability (%)	Day habitat use Presence indices excluding nest sites (%) [CI]	Night habitat use Nest sites (%) [CI]
Closed *terra firma* forest	78.7	80.6 [76.7–84.1]	**11.1 [4.3–23.5]**
Open *terra firma* forest	14.7	13.8 [10.9–17.4]	**82.7 [69.4–91.4]**
Flooded vegetation type	5.2	5.0 [3.3–7.5]	6.2 [1.2–17.4]
Bare soil or water	1.4	0.6 [0.1–1.9]	0 [0–8.7]

Adjusted Wald Bonferroni CI were calculated following Agresti & Coull (1998) and Neu *et al.* (1974). Values of habitat use that are significantly different from habitat availability are given in bold

The preference for nesting in open habitats was highlighted by a Student t-test comparing the mean canopy closure index above nests (25.1%) and above systematic points along census transects (61.0%) [DF = 6073, t = 31.58, $p < 0.001$].

Overall encounter rates of gorilla and human presence indices were 1.96 km^{-1} and 0.05 km^{-1}, respectively. The models obtained to explain habitat use during the day (assessed through gorilla presence indices) and habitat use during the night (based on nest site distribution) are detailed in **Table 7**. The distribution of gorilla presence indices and the distribution of nest sites are influenced by different factors. Day use model includes human presence, distance to river, distance to functional road and distance to non-functional road. The night use of habitat is mainly influenced by habitat type, and marginally by distance to river. No interaction was proved significant.

Table 7 GLM of the probability of presence of gorilla indices and probability of presence of nest sites

Response	R²	Factor	Coefficient	% of explained deviance	Sign. (Chi-square)
Indices	0.009	Intercept	-2.925		***
		Human presence indices	-12.30	0.10	*
		Distance to river (m)	2.857x10^{-4}	0.3	***
		Distance to functional road (m)	1.410x10^{-4}	0.09	**.**
		Distance to non-functional road (m)	3.894x10^{-4}	0.39	***
Nests	0.22	Intercept (Habitat type-Closed *terra firma* forest)	-6.529	20.75	***
		Habitat type-Open *terra firma* forest	3.424		
		Habitat type-Flooded vegetation	2.101		
		Habitat type-Bare soil or water	-11.41		
		Distance to river (m)	4.388x10^{-4}	0.08	*

Presence indices model: Residual Deviance: 4003, Null Deviance: 4039, AIC: 4013; Nest sites model: Residual Deviance: 648.4, Null Deviance: 825.3, AIC: 658.4. [**.** p=0.05; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$]

4 DISCUSSION

4.1 Gorilla density in a sustainably managed logged forest

Gorilla density in Bambidie AAC 2012 (1.5 weaned gorillas km^{-2}) falls within the range of documented WLG densities at other sites, although much lower and higher figures are also reported (**Table 8**). It is remarkably similar to estimates obtained from other sustainably managed forests, such as the average density observed in CIB (Congo) (Clark *et al.* 2009) and that in Dzanga Ndoki National Park (CAR) (Bloms *et al.* 2001).

Table 8 Estimated western lowland gorilla densities within Central Africa

Study site	Nest density (nests km^{-2})	Gorilla density (gorillas km^{-2})	CV (%)	Reference
Sustainably managed logging concessions				
Bambidie AAC 2012 Wildlife management (FSC) Gabon	116.7 [83.4–163.5]	1.50	17.2	This study
Pokola (CIB) Wildlife management (FSC) Congo	373.6 [207.4–672.8]	4.08 [2.27–7.36]	28.9	Stokes *et al.* (2010)
Kabo (CIB) Wildlife management (FSC) Congo	197.6 [93.5–417.4]	2.16 [1.02–4.56]	36.1	Stokes *et al.* (2010)
Loundougou (CIB) Wildlife management (FSC) Congo	71.2 [31.3–161.9]	0.78 [0.34–1.77]	40.7	Stokes *et al.* (2010)
CIB (average) Wildlife management (FSC), logged forest Congo		1.57 [1.36–2.71]	11.0	Clark *et al.* (2009)
CIB (average) Wildlife management (FSC), unlogged forest Congo		1.92 [1.27–1.94]	17.6	Clark *et al.* (2009)
Average		**2.0**		
Protected areas				
Lopé Reserve Gabon		0.3–1.0		White (1994)
Petit Loango Gabon	23.86	0.21		Furuichi *et al.* (1997)
Dja Reserve Cameroon	162.8 [85.7-309.2]	2.08 [1.09-3.95]	32.4	Latour (2010)
Lokoué, Odzala National Park Congo		3.22 [1.61–6.44]	34.7	Devos *et al.* (2008)
Goualougo Triangle, Nouabalé Ndoki National Park Congo		2.63 [1.42–4.90]	31.6	Devos *et al.* 2008
Nouabalé-Ndoki National Park Congo	93.2 [53.9–161.3]	1.02 [0.59–1.77]	26.8	Stokes *et al.* 2010
Lac Télé Community Reserve DRC		2.91 [1.6–5.6]		Poulsen & Clark (2004)
Dzanga Ndoki National Park Central African Republic		1.6 [1.1–2.3]		Blom *et al.* (2001)
Average		**1.95**		
Conventional logging concessions and non-protected areas				
Mokabi Congo	14.1 [4.8–41.3]	0.15 [0.05–0.45]	53.5	Stokes *et al.* (2010)
La Belgique Cameroon		0.15 [0.04–0.59]		Tagg & Willie (2013)
Campo Cameroon		0.2		Matthews & Matthews (2004)
Ngotto forest CAR		0.4 [0.23–0.69]		Brugiere & Sakom (2001)
Average		**0.225**		

WLG densities in logging concessions with management plans, including wildlife management strategies, are high and sometimes among the highest ever recorded (Clark *et al.* 2009; Stokes *et al.* 2010). These high densities might be linked to the enhanced growth of understory cover, and particularly herbaceous vegetation (e.g., *Aframomum* sp. (Zingiberaceae), *Megaphrinium* sp. and *Sarcophrinium* sp. (Marantaceae)) (Wright 2003; Matthews & Matthews 2004; Laurance et al. 2006; Morgan & Sanz 2007; van Kreveld & Roerhorst 2009; Clark et al. 2009; Stokes et al. 2010; Remis & Kpanou 2011) that provides gorillas with staple food and nest building material (Tutin *et al.* 1995; Oates 1996; Goldsmith 1999; Doran-Sheehy *et al.* 2004; Sanz *et al.* 2007; Stokes *et al.* 2010; Willie *et al.* 2014). This hypothesis is supported by the high number of nests built using terrestrial herbaceous vegetation (THV), highlighting the importance of THV as a nest building material. Growth of THV is enhanced in open canopy environments, such as felling gaps, skid trails and logging roads (Malcolm & Ray 2000; Matthews & Matthews 2004). Indeed, THV density is often linked to canopy openness and light availability (Malcolm & Ray 2000; Willie *et al.* 2012). Our results suggest that WLG prefer to nest in open areas within the forest. These data are consistent with the findings of other studies (Tutin *et al.* 1995; Goldsmith 1999; Sanz *et al.* 2007; Devos *et al.* 2008; Stokes *et al.* 2010; Willie *et al.* 2012).

This study underlines the potential complementary role in wildlife protection of logging concessions in addition to protected areas. In the context of forest certification and HCVF maintenance, our results suggest that sustainably managed selective logging may be a potential scheme for gorilla population conservation. WLG could be seen as a model species as it is critically endangered, is considered a keystone species and has a role in forest regeneration (Rogers *et al.* 1998; Voysey *et al.* 1999; Petre *et al.* 2013). Logged forests may act as semi-protected buffer zones or forest corridors connecting conservation areas, and may thereby contribute to the conservation estate of WLG (Clark *et al.* 2009). Landscape management in a mosaic structure of multi-use areas is thought to be efficient (Johns 1985; Nasi *et al.* 2012). Thus, protected areas adjacent or close to logging concessions may act as refuges during logging, mitigating the negative impacts of timber harvesting and associated activities on wildlife (van Kreveld & Roerhorst 2009; Clark *et al.* 2009). This multi-use scenario would enable the persistence of species that are highly affected by logging activities and related disturbances, as well as those whose extensive forest range requirements are sometimes not met solely by protected areas.

However, although WLG may persist and even thrive in sustainably managed logged forest, this will not necessarily be the case if hunting is not controlled (Haurez *et al.* 2013). In logging concessions with no established wildlife management strategies, hunting intensity often rises uncontrollably and gorilla densities can rapidly decline (Morgan & Sanz 2007; van Kreveld & Roerhorst 2009; Stokes *et al.* 2010). Indeed, in forests harvested for timber, indirect effects of logging, in particular an increase in hunting, can impact upon gorilla populations more than direct effects of logging, such as habitat alteration and fragmentation (van Vliet & Nasi 2008; van Kreveld & Roerhorst 2009).

In this study, we only considered the impacts of logging on WLG. Consequently, our results could not be extended to other species. The impacts of logging on mammals have been addressed by several studies (Nasi *et al.*, 2012 and reference therein). Mammal abundance has shown various responses to logging-induced disturbance, depending on animal guild and species but also on local conditions. However, the global trend is consistent with that observed for gorillas in our study: species distribution in logging concessions seems to be more influenced by road networks and hunting pressure than by logging activities *per se* (Nasi *et al.* 2012). On the contrary, however, the sympatric chimpanzee has been shown to be seriously disturbed by logging during and after exploitation (Matthews *et al.*, 2004). In contrast to WLG, chimpanzees exhibit strong territoriality and rely on old forests for foraging and nesting (Matthews & Matthews 2004; Arnhem 2008). As a result they may be less adaptable to disturbance and population displacement. Furthermore, while most studies have focused on the impact of logging on mammals (Matthews & Matthews 2004; Laurance *et al.* 2006; Arnhem 2008; van Vliet & Nasi 2008; Clark *et al.* 2009; Stokes *et al.* 2010), other groups (birds, insects, reptiles, amphibians, etc) should also be included in order to produce a broad assessment of the impacts of logging on wildlife.

4.2 Nesting behavior and habitat use

As expected, both the Chi-square test and the GLM analysis differentiate habitat use during the day and during the night. For the model explaining habitat use during the night, the negative values of the coefficients related to the habitat types infer that the probability of presence of a gorilla nest site in a given habitat type is lower than 50 %. This is not surprising, as nest sites occur at a relatively low density overall and are relatively rare.

The day use model includes four factors. During the day, habitat type (following our classification) does not influence gorillas'movement and gorillas use the different habitat types in proportion to their availability. A low encounter rate of human indices was observed in Bambidie AAC 2012 (0.05 km^{-1}). This value is similar to that observed in a permanent research site in Cameroon (0.03 km^{-1}) (Tagg *et al.* 2013). In comparison, the encounter rate of human signs in the Dja Reserve (Cameroon) was 2.6 km^{-1} in 2009 (Latour 2010). The low value recorded in our study might reflect the efficiency of hunting management and sensitization programs undertaken by the logging society at the study site. Yet, even with such a low hunting pressure, the distribution of human indices negatively impacts upon WLG movement during the day. This could reflect an avoidance by gorillas of regularly used hunting zones and trails (Tagg & Willie 2013). However, given the rarity of human presence indices, their inclusion in the model could be driven by fortuitous match with the response and should therefore be considered with caution. The probability of finding gorilla presence indices also slightly increases with increasing distance from roads (functional and non-functional) and distance to rivers. Roads constitute potential paths used by people for access into the forest. However, there was no significant interaction between human indices and distance to roads in the GLM. Also, WLG groups are frequently observed crossing functional roads in our study site as well as in other sustainably managed concessions (Haurez B. personal observation, Laurance *et al.* 2006). As shown by previous studies, the influence of functional logging roads on WLG behavior is complex to assess and likely depends on many additional and interacting factors, such as hunting pressure. Results from other logging concessions are inconsistent: in Mandji concession (southwest Gabon), a mosaic of forests both unlogged and logged numerous times, there was no relationship between gorilla signs and distance to roads, and gorillas were regularly observed close to villages (van Vliet & Nasi 2008). In contrast, in four logging concessions in northern Republic of Congo, distance to roads had a strong influence on WLG presence (Clark *et al.* 2009). The contrasting effects of distance to roads, human presence and hunting on gorilla abundance may in part depend upon whether or not gorilla meat is consumed, or whether or not sensitization activities are underway at the site. Finally, the weak influence of roads on gorilla presence indices in our study, as well as observed road crossing by WLG, might be explained by the relative proximity of road networks to any given point in the study site. Indeed, the most remote forest segments surveyed were situated only 4 and 2.3 km from functional and non-functional roads, respectively. Extending such a census to areas situated 10 to 20 km from roads may provide a fuller picture. Testing the influence of roads at different spatial scales would allow to identify the optimal scale of influence (Serckx 2014). At last, non-functional roads colonized by THV may have antagonistic effects on WLG: these forest paths may be used by hunters, but abundant THV provides gorillas with staple food and nest building material. As we did not quantify the density of THV, these antagonistic effects might be confounded in our analysis.

The low value of the coefficient of determination R^2 for this model (0.009) indicates that other factors not included in our study may also influence WLG habitat use during the day. The distribution of food trees, and food sources in general (notably density of THV), is an important variable known to drive ape foraging (Goldsmith 1999; Willie *et al.* 2012), but was not directly considered in this study. In the context of the conservation of WLG in a logging concession, it would be useful to identify key food sources at the study site in order to develop a management plan which includes the preservation of these resources. In Gabon, forest legislation already includes the protection of four species which constitute important food resources for wildlife: *Baillonella toxisperma* (Pierre, 1890), *Tieghemella africana* (Pierre, 1890) (Sapotaceae), *Dacryodes buettneri* ((Engl.) H.J.Lam, 1932) (Burseraceae) and *Irvingia gabonensis* ((Lanen.) Baill, 1886) (Irvingiaceae). Extraction of these species is forbidden and timber operators are required to develop measures to prevent damage during logging activities.

Effects of seasonality were not investigated in this study, as the study took place predominantly in the rainy season. The cryptic characteristic of presence indices could also lead to loss of precision, as some signs might be missed (e.g. feces or prints). A long-term research study, based on nest-to-nest follows, could be undertaken in order to obtain more precise data on seasonal habitat use.

The GLM describing night habitat use only comprises two factors. Despite its simplicity, the coefficient of determination of this model is relatively high (0.22), affirming its suitability. 'Habitat type' remains the most important factor explaining the spatial distribution of nest sites, with a higher probability of nest site presence in open *terra firma* forests. In addition, the probability of a nest site being present increases slightly with distance from rivers. This is unlikely to be due to human accessibility of the forest by means of the river as canoes are not used for people transport at the study site (Haurez B. personal observation). Instead, as the census was carried out during the rainy season, it is possible that the influence of rivers could be explained by the avoidance of flooded areas. However, the low value of the coefficient may suggest a complex relationship between habitat use during the night and rivers. WLG may, for example, avoid nesting close to rivers until a critical distance (i.e., where flooded zones end), but not be influenced by the river beyond this point.

5 CONCLUSION

Our high density estimate of WLG in an AAC logged 25 years previously supports the hypothesis that logged forests may constitute suitable habitats for gorillas, if hunting is controlled. Indeed, WLG preferentially nested in open *terra firma* forest, a habitat type which naturally occurs but which is also created by logging activities. While our estimation of WLG density was obtained at a limited scale (one AAC), it supports the results of larger scale landscape studies which have suggested a potential role of logging concessions in the enhancement of WLG conservation (Clark *et al.* 2009; Stokes *et al.* 2010). While gorillas move evenly among habitat types during the day, the influence of human presence on their movements infers an importance of this indirect impact of logging on wildlife. Consequently, the implementation of hunting control strategies in any timber society is of crucial importance, as well as the enforcement of wildlife legislation all across the Congo Basin. In logged forests, the implementation of monitoring programs would allow stakeholders to verify the stability of human activity levels in the forest, assess the effectiveness of wildlife management activities, and ensure the conservation of WLG populations post-timber harvesting. Ape-friendly practices already implemented in some logging concessions (Morgan & Sanz 2007; Arnhem 2008; Clark *et al.* 2009) must be generalized.

Although selective timber exploitation may negatively impact upon wildlife populations (Haurez *et al.* 2013), it remains one of the most economically-viable use of tropical forests that simultaneously preserves the forest ecosystem, and is therefore preferable to forest conversion for cash-crop plantations (Johns 1985). However, what may be the case for gorillas cannot be generalized to all rainforest wildlife: while sustainable logging might be compatible with WLG preservation, timber harvesting may be deleterious to other species, notably central chimpanzees (Matthews & Matthews 2004). Besides, the potential preservation of some wildlife species within logging concessions should not be a pretext for replacing protected areas by logged forest. The preservation of relatively pristine areas remains crucial considering the expansion of anthropogenic disturbance, our limited knowledge of the functioning of such an ecosystem and the negative impacts that might result from its loss.

In light of the inevitable expansion of logging concessions throughout the forests of the Congo Basin, collaborative efforts between forest managers of timber societies, conservationists, ecologists and scientists are critical to the maintenance of wild great ape populations (Morgan & Sanz 2007; Stokes *et al.* 2010; Poulsen & Clark 2012; Nasi *et al.* 2012).

CHAPITRE 5 IMPACT À COURT TERME DE L'EXPLOITATION FORESTIÈRE SUR LES POPULATIONS DE GORILLES DES PLAINES DE L'OUEST

Le chapitre précédant a montré que des populations de gorilles des plaines de l'Ouest peuvent exister au sein d'Assiettes Annuelles de Coupe en forêt exploitée durablement, et ce à des densités comparables à celles observées au sein d'aires protégées. Dans le but de préciser l'effet de l'exploitation du bois d'oeuvre sur les gorilles, le chapitre 5 présente une comparaison entre les résultats d'un inventaire réalisé dans une Assiette Annuelle de Coupe 25 ans après la première rotation, et les résultats de deux inventaires réalisés dans la même AAC six mois et un an après le second cycle d'exploitation. Il constitue donc une évaluation de l'impact à court terme de l'exploitation sur une population de gorilles.

Adapté de HAUREZ B., PETRE C-A., VERMEULEN C., TAGG N. & DOUCET J-L., ACCEPTED. Short term impact of selective logging on western lowland gorilla density. *Forest Ecology and Management.*

Estimation de l'ouverture de la canopée à l'aide d'un clinomètre au Gabon © J-L. Doucet

Résumé

L'exploitation forestière sélective concerne une large proportion des forêts tropicales. Au sein de ces écosystèmes, la communauté des frugivores est impliquée dans de nombreux processus écologiques, nottamment la dispersion des graines. Cependant, les impacts de l'exploitation sur la faune sauvage et sur le processus de dispersion des graines ne sont pas clairement compris. Considérant sa tendance à installer ses nids dans des trouées, le gorille des plaines de l'Ouest est supposé assurer une dispersion "dirigée" pour une grande variété d'espèces végétales. Les forêts de production préservées du braconnage semblent abriter des densités élevées de gorilles, mais le suivi des populations de gorille au sein de forêts soumises à l'exploitation est peu documenté. Cette étude évalue l'évolution de la densité en gorille et du comportement nidificateur après l'exploitation forestière, au sein d'une forêt concédée du Sud-Est du Gabon. Des inventaires des sites de nidification ont été réalisés le long de transects linéaires, avant et après le second cycle d'exploitation. La densité en gorille chute de 1,5 à 1,0 gorille km^{-2} quatre à six mois après l'exploitation, pour ensuite augmenter à nouveau et atteindre la valeur de 2,6 gorilles km^{-2}1à à 12 mois après l'exploitation. Une préférence persistante pour la nidification en forêt de terre ferme à canopée ouverte a été observée au cours des trois inventaires. Cette étude démontre la résilience des gorilles des plaines de l'Ouest à l'exploitation sélective du bois d'oeuvre, et tend à monter qu'ils offrent une contribution continue à la dispersion dirigée des graines. Ainsi, le rôle des gorilles des plaines de l'Ouest dans la régénération des forêts exploitées semble fondamental. La préservation de cette espèce devrait donc faire l'objet d'une attention particulière pour les gestionnaires forestiers.

Mots clés: *Gorilla gorilla gorilla*, exploitation sélective, Gabon, comportement nidificateur, transects linéaires

Abstract

Selective timber production is implemented over a large proportion of the world's tropical forests. Within these forest ecosystems, the frugivore community contributes important ecological services through animal-mediated seed dispersal. However, there is no clear understanding of the impacts of logging on wildlife or of the extent to which seed dispersal is preserved in logged forests. Given its tendency for nesting in light gaps, the western lowland gorilla is likely to provide directed-dispersal services to a wide range of tree species. Production forests preserved from poaching have been reported to harbor high densities of gorillas, but the monitoring of gorilla populations subjected to logging is poorly documented. This study investigated gorilla density and nesting behavior after timber exploitation in a logging concession in southeast Gabon. Nest count censuses were performed on line transects, before and after the second felling cycle. Gorilla density dropped from 1.5 to 1.0 weaned gorilla km^{-2} four to six months after logging, then rose to 2.6 gorillas km^{-2} 10-12 months after logging. A consistent preference for nesting in open canopy *terra firma* forest was observed during all censuses. This study demonstrates the resilience of the western lowland gorilla to selective timber harvesting, and argues that they offer a continued contribution to directed-dispersal services. Therefore, the role of gorilla in logged forest recovery is thought to be important. The preservation of this species should receive particular consideration by forest managers.

Key words: *Gorilla gorilla gorilla*, selective logging, Gabon, nesting behaviour, linear transects

1 INTRODUCTION

Selective logging is an important economic activity in tropical forests (Mayaux et al. 2013). Today, more than 20 % of the world's tropical forests have already been selectively logged (Blaser et al. 2011), and at least a quarter of the remaining undisturbed forests are designated for multiple use, including timber production (FAO 2010). Although forest cover is little affected by timber harvesting, logging contributes to tropical forest degradation because it opens new roads in remote areas and therefore increases human pressure on forest ecosystems (Mayaux et al. 2013; de Wasseige et al. 2014). Therefore, timber extraction is identified as one of the major threats facing tropical forest ecosystems. The impacts of logging activities on wildlife have been studied throughout the tropics (Knop et al. 2004; Cowlishaw et al. 2009; Bicknell & Peres 2010; Hardus et al. 2012), but generalization of these impacts is not straightforward. Indeed, in addition to their high specificity, the impacts of logging on animal species are highly dependent on harvesting rates, logging practices and time since logging (Laufer et al. 2013; Struebig et al. 2013; Burivalova et al. 2014). Moreover, the effects of logging have often been studied by comparing logged and unlogged zones, without taking into account the initial differences in animal communities between the sites.

The role of vertebrates in forest ecosystem dynamics is well known, especially in the tropics where 50-95 % of plant species produce fruits adapted to endozoochory (Howe & Smallwood 1982). The persistence of seed dispersers is particularly important in the context of logged forests, in order to ensure forest regeneration (Rosin 2014; Bicknell et al. 2015). Among seed dispersers, the western lowland gorilla (*Gorilla gorilla gorilla*, hereafter referred to as the WLG) is likely to play an important role because it provides directed dispersal services to various plant species (Tutin et al. 1991; Rogers et al. 1998; Voysey et al. 1999; Haurez et al. 2015), some of which provide valuable timber and non-timber forest products (NTFPs). Therefore, the maintenance of viable WLG populations within logged forests is thought to contribute to the sustainability of timber exploitation. Given the opening of the canopy generated by timber harvesting, logging concessions are expected to be suitable habitats for gorillas (Arnhem 2008; Haurez et al. 2014). If felling gaps, skid trails and old logging roads are preferentially selected by the WLG for nesting as shown by Arnhem (2008) in Cameroon, its dispersal services would be directed to the more disturbed zones of the forest, therefore securing its role in forest recovery. Moreover, as more than 50 % of the distribution area of African great apes is located within logging concessions (Morgan & Sanz 2007), their persistence depends on their ability to cope in the face of timber exploitation. To our knowledge, only one rigorous before-and-after study of WLG populations subjected to logging activities has been undertaken (Arnhem 2008), but seed dispersal was not considered. At this site, WLG were less abundant during and up to 1 year after the end of logging activities, and their abundance increased over the initial level more than 1 year after logging (Arnhem 2008). Such studies should be repeated in other forests before generalizing from the results (Morgan & Sanz 2007).

This study is the follow-up of an initial evaluation of WLG population, undertaken 25 years after the first felling cycle and aimed at assessing long term impacts of logging on WLG (Haurez et al. 2014). The objective of the present research was to assess the short-term impact of timber exploitation on WLG density and nesting behavior. Specifically, considering Arnhem (2008), the following hypotheses were tested: (1) that WLG density will be reduced one to six months after timber harvesting but will recover its initial level within one year; (2) that the preference of the WLG to nest in open *terra firma* forest is consistent and persists after logging; and (3) that the zones impacted by logging activities that display open canopy and associated dense terrestrial herbaceous vegetation are included in the preferred nesting habitat.

2 METHODS

2.1 Study site

Precious Woods Gabon is a sustainably-managed and certified (Forest Stewardship Council) logging concession located in southeast Gabon. This 617,000 ha moist evergreen forest presents high densities of botanical species characteristic of old secondary forest (White 1986), such as *Scyphocephalium ochocoa* Warb. (Myristicaceae) and *Aucoumea klaineana* Pierre (Burseraceae) (Demarquez & Jeanmart 2004). The site has been the subject of a logging management plan since 2000, and reduced impact logging (RIL) techniques have been implemented since 2007 (Demarquez & Jeanmart 2004; Medjibe et al. 2013). In particular, hunting pressure is regulated through law enforcement, road control and closure, frozen meat supply to company workers and the spatial and temporal organization of hunting activities (Demarquez & Jeanmart 2004). The mean logging intensity in 2013 was 1.01 trees ha^{-1}, accounting for 8.34 m³ ha^{-1} (Precious Woods Gabon 2014). The total average annual rainfall is 1,700 mm, mainly distributed through two rainy seasons (March-May and September-December) (Moupela et al. 2013). A dry season (monthly precipitation <100 mm) is observed from June to August. The average annual temperature is 26°C, with minimum values occurring in July and August (Moupela et al. 2013) and the highest temperatures being observed from February to April. The first felling cycle occurred in the Annual Allowable Cut (AAC) of Bambidie (13,410 ha, 0°44' - 0°52' South and 013°06' - 013°17' East), accounting for 2.17 % of the concession (13,410 ha), in the early 1990s. The second felling cycle in the same AAC took place from July to November 2013.

2.2 Data collection

The first census (Census 1) of this study took place from January to July 2012, with the objective to assess the long term impacts of logging on the western lowland gorilla. WLG density in the AAC of Bambidie was estimated at 1.5 weaned gorilla km^{-2} 25 years after the first felling cycle (Haurez *et al.* 2014). Nesting behavior was characterized by a preferential selection of open canopy *terra firma* forest for nest building (Haurez *et al*. 2014), confirming that observed at other study sites (Tutin *et al*. 1995; Willie et al. 2012; Petre *et al*. 2015b). Detailed information regarding the sampling scheme, nest count, habitat description and availability assessment, and the nest site characterization, is provided in Haurez *et al*. (2014).

In order to determine the short term impacts of timber harvesting activities and to assess the viability of the gorilla population in the site, two additional censuses were undertaken. They took place in March 2014 (Census 2) and from September to November 2014 (Census 3), four to six months and 9 to 11 months after the second felling cycle, respectively. The logging intensity in the AAC of Bambidie was 1.01 tree ha^{-1} (8.30 m³ ha^{-1}) (Precious Woods Gabon 2014). The same methodology (density estimation, habitat availability assessment and nesting behavior characterization) was followed as in Census 1 (Haurez *et al*. 2014), but sampling effort varied as a result of logistical constraints. During Censuses 1, 2 and 3, 308 km, 76 km and 106 km were monitored, respectively **Figure 10**.

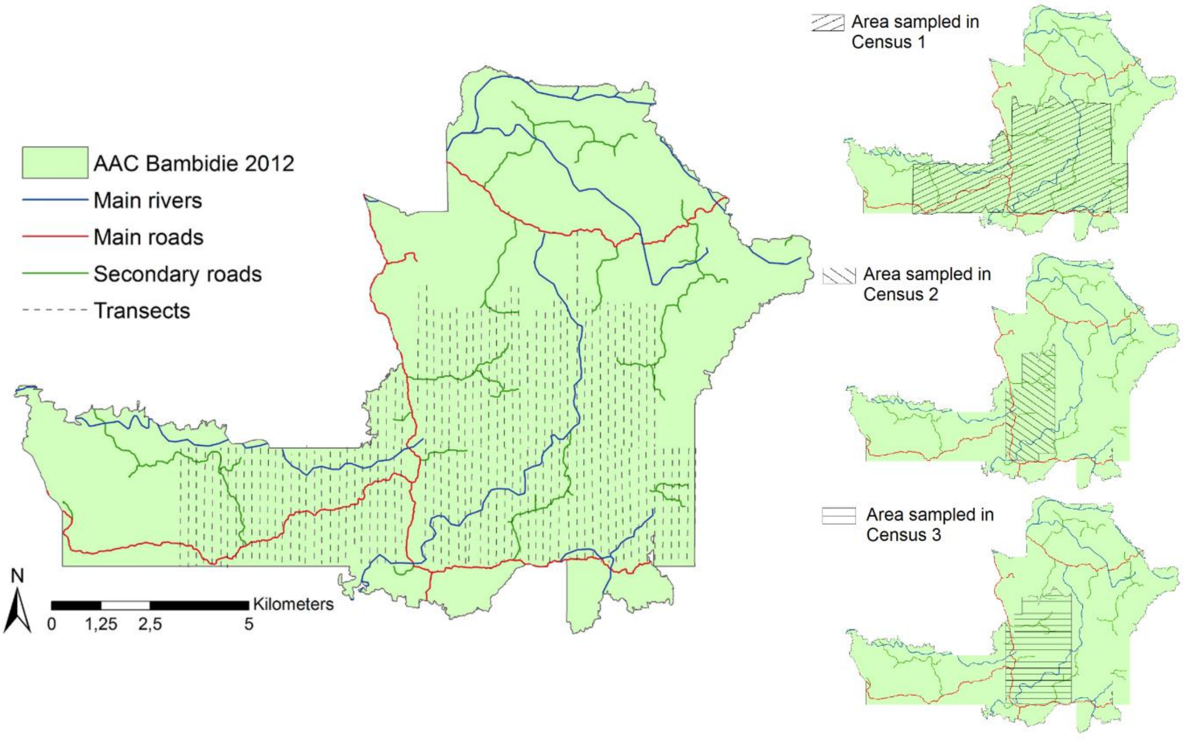


Figure 10 Bambidie AAC, transects placement and area sampled for the three censuses

WLG density was estimated from detected nest counts and their respective distances from the transect line, using the standing crop nest count (SCNC) method (Hashimoto 1995; Kühl *et a*l. 2009; Spehar *et al.* 2010). The estimated density of nests was then converted to the number of weaned individual gorillas by dividing it by nest production (1.0 nest day^{-1}) and decay rates (Tutin *et al*. 1995; Buckland *et al.* 2001; Morgan & Sanz 2007; Devos *et al*. 2008). As an insufficient number of fresh nests were encountered at the study site to calculate a site-specific nest decay rate, a specific value was estimated for each census from available data from the Lopé Reserve (located 250 km from our site, and presenting very similar ecological conditions) (Tutin *et al.* 1995; Doucet 2003). As mean gorilla nest decay rate varies depending on nest type , census-specific decay rates were weighed according to the frequency distribution of nest type observed during the census:

$$Mean\ nest\ decay\ rate = \frac{\sum_i Nest\ decay\ rate_i \times Number\ of\ nests_i}{Total\ number\ of\ nests}$$ (Equation 1)

where $Mean\ nest\ decay\ rate$ = generalized averaged nest decay rate for the census considered, $Nest\ decay\ rate_i$= average nest decay rate for the *i* type of nest, $Number\ of\ nests_i$ = number of nests of the type *i* detected during the census considered and $Total\ number\ of\ nests$ = total number of nests detected during the census considered.

In order to assess the evolution of hunting pressure in relation to logging activities, all signs of hunting and human presence (thereafter referred to as 'human presence indices') observed along transects were recorded during each census.

2.3 Data analysis and census comparison

2.3.1 Distance sampling and gorilla density estimation.

All density estimations were calculated using Distance Sampling software version 6.02 (Thomas *et al.* 2010). In order to enhance the robustness of the estimation, the furthest 5 % of observations from the transect were truncated before the analysis (Buckland *et al*. 2001). Model function and adjustment term selection was realized by taking into account the lowest Akaike Information Criterion (AIC) and the results of the Chi-square goodness of fit (p-value > 0.05) (Rainey *et al.*, 2009; Clark *et al.* 2009; Stokes *et al*. 2010). As the sampling effort was variable between censuses, separate Distance Sampling analyses took into account all transects walked for each census (complete analysis), and only the transects (76 km of Census 2) that were common to all censuses (restricted analysis). For Censuses 1 and 3, the results of the complete and restricted analyses were compared using Equation 1. In the case of no significant differences, the complete analysis was retained for the overall comparison, as its precision is higher (lower coefficient of variation, CV). Subsequently, the evolution of WLG density over time was assessed through the comparison of the results of the three censuses. Pairwise comparisons were realized with a d-test, considering the normally distributed variable *d* (Bailey 1959):

$d = \frac{|\widehat{Y_1} - \widehat{Y_2}|}{\sqrt{(var(\widehat{Y_1}) + var(\widehat{Y_2}))}}$ (Equation 2)

where $\widehat{Y_1}$ = WLG density estimated for Census 1 in Distance; $var(\widehat{Y_1})$ = variance of the estimation of $\widehat{Y_1}$; $\widehat{Y_2}$ = WLG density estimated for Census 2 in Distance; $var(\widehat{Y_2})$ = variance of the estimation of $\widehat{Y_2}$. The variance of Distance analysis is estimated by:

$\sigma^2 = (cv * mean)^2$ (Equation 3)

Density comparisons were realised between Census 1 and Census 2, between Census 2 and Census 3 and finally between Census 1 and Census 3.

We compared hunting pressure between censuses with generalized linear models (GLM) adjusted to encounter rates of human presence indices, with a Poisson distribution and a log link function. A Chi-square test was used to assess the significance of the fixed factor "Census".

2.3.2 Characterisation of habitat use and nesting behavior.

Comparisons of habitat type availability, habitat use for nesting (assessed with a Neu's test comparing habitat availability and the distribution of nest sites among habitat types), and frequency of construction of different nest types among censuses were made using Chi-square tests of independence, and the determination of adjusted Wald-Bonferroni confidence intervals (CI) (Neu et al. 1974; Agresti & Coull 1998). Grouping patterns between censuses, deduced from the number of nests at nest sites, were compared pairwise with an ANOVA test after the verification of application conditions. All statistical analyses were computed in R software version 3.2.1 (R Development Core Team 2015). For all statistical tests, the Type I error (α) threshold was fixed at 0.05.

3 RESULTS

3.1 Evolution of gorilla density with time after timber harvesting

The comparisons between complete and restricted sampling analyses for the Censuses 1 and 3 showed no significant differences between the estimated nest densities (**Table 9**). Therefore, for these censuses, the complete sampling analyses were kept as references.

Table 9 Results and comparisons of the analyses for the restricted and complete censuses

Census	Period	Complete sampling effort (km)	Complete analysis nest density estimation (nest/km²) (CI)	Restricted analysis nest density estimation (nest/km²) (CI)	Comparison restricted and complete analyses
Census 1	January-July 2012	308	116.7 (83.4-163.5)	150.0 (82.9-274.3)	d = 0.69, DF > 30, p = 0.49
Census 2	March 2014	76	64.9 (32.6-129.5)	64.9 (32.6-129.5)	NA
Census 3	September-November 2014	106	176.3 (113.5-274.1)	178.7 (106.5-299.7)	d = 0.040, DF > 30, p = 0.97

The densities estimated were 1.5, 1.0 and 2.6 weaned WLG km^{-2} for Censuses 1 to 3, respectively. Pairwise comparisons between the successive censuses resulted in a non-significant difference between Censuses 1 and 2 (d = 1.71, DF > 30, p = 0.087), but a significant increase in estimated WLG density between Censuses 2 and 3 (d = 2.48, DF > 30, p = 0.013) (**Table 10**). Estimated values for Censuses 1 and 3 were not significantly different (d = 1.36, DF > 30, p = 0.17).

Table 10 Results and comparisons of the analyses for the consecutive complete censuses. Bold values display significant differences

Census	Nest decay rate (days)	WLG density (WLG/km²)	CV (%)	WLG density comparisons
Census 1	78	1.5	17.2	Censuses 1 and 2: d = 1.71, DF > 30, p = 0.087
Census 2	63.5	1.0	34.9	**Censuses 2 and 3: d = 2.48, DF > 30, p = 0.013**
Census 3	67.3	2.6	22.0	Censuses 1 and 3: d = 1.36, DF > 30, p = 0.17

The observed human signs encounter rates did not significantly differ between censuses (Census 1 = 0.068 signs km^{-1}, Census 2 = 0.079 and Census 3 = 0.094; mean encounter rate = 0.076 signs km^{-1}) (χ^2 = 0.65, DF = 3, p = 0.72).

3.2 Evolution of nesting behaviour and grouping pattern

The availability of habitat type differed between censuses (**Table 11**). Particularly, there was an increase in occurrence of forest impacted by logging (from 1.1 to 26.2 %) between Censuses 1 and 2, with a decrease in open- and closed-canopy *terra firma* forests (from 14.5 to 5.7 %, and from 78.4 to 48.3 %). Census 3 was very similar to Census 2. Habitat use for nesting was similar in the three censuses, with a marked global preference for nesting in open-canopy *terra firma* forest (mean habitat availability = 9.2 %, mean habitat use = 64.6 %) and a general avoidance of closed-canopy *terra firma* forest (mean habitat availability = 64.4 %, mean habitat use = 13.6 %) (**Table 12**). Therefore, the preferential selection of open *terra firma* forest for nesting is consistent over time, and does not appear to be significantly influenced by timber harvesting activities. In Census 3, a weak preference for nesting in flooded vegetation is also observed.

Table 11 Estimated habitat type availability for the three censuses. Comparison of estimated habitat type availability between censuses are made with Chi-square tests and adjusted Wald-Bonferroni confidence intervals (CI) (Neu et al. 1974; Agresti & Coull 1998). Comparison between Censuses 1 and 2: $\chi^2 = 2095.56$, DF = 5, $p < 0.001$; Comparison between Censuses 2 and 3: $\chi^2 = 21.05$, DF = 5, $p < 0.001$; Comparison between Censuses 1 and 3: $\chi^2 = 2358.74$, DF = 5, $p < 0.001$

Vegetation type	Census 1 (%)	Census 2 (%) (CI)	Census 3 (%) (CI)	Comparison Censuses 1 and 2	Comparison Censuses 2 and 3	Comparison Censuses 1 and 3
Hydrography (rivers and streams)	0.5	1.1 0.5-2.1)	1.0 (0.5-2.7)	Similar	Similar	Similar
Closed canopy *terra firma* forest	78.4	48.3 (45-51.7)	49.7 (46.8-56.6)	Decrease	Similar	Decrease
Open canopy *terra firma* forest	14.5	5.7 (4.3-7.5)	5.5 (4.3-8.8)	Decrease	Similar	Decrease
Flooded vegetation type	5.1	7.1 (5.6-9.1)	4.1 (3.1-7.1)	Increase	Similar	Similar
Forest impacted by logging	1.1	26.2 (23.4-29.3)	25.5 (23.1-31.7)	Increase	Similar	Increase
Undetermined	0.5	11.5 (9.5-13.8)	14.2 (12.3-19.1)	Increase	Increase	Increase

Table 12 Comparison of habitat availability and habitat use for nesting for the three censuses. Comparison of habitat type availability and habitat use for nesting are made with Chi-square tests and adjusted Wald-Bonferroni confidence intervals (CI) (Neu et al. 1974; Agresti & Coull 1998). Census 1: $\chi^2 = 273.69$, DF = 3, $p < 0.001$; Census 2: $\chi^2 = 70.37$, DF = 3, $p < 0.001$; Census 3: $\chi^2 = 172.32$, DF = 3, $p < 0.001$

	Census 1			Census 2			Census 3		
Vegetation Type	Habitat availability (%)	Habitat use for nesting (%) (CI)	Habitat use	Habitat availability (%)	Habitat use for nesting (%) (CI)	Habitat use	Habitat availability (%)	Habitat use for nesting (%) (CI)	Habitat use
Closed canopy *terra firma* forest	79.2	9.8 (3.4-21.8)	Avoidance	55.3	17.6 (0.0-53.0)	Avoidance	58.6	13.3 (3.6-32.0)	Avoidance
Open canopy *terra firma* forest	14.6	79.3 (65.6-88.8)	Preference	6.5	58.8 (26.4-86.5)	Preference	6.5	55.6 (36.4-73.4)	Preference
Flooded vegetation type	5.1	7.3 (1.9-18.7)		8.2	11.8 (0.0-47.1)		4.8	17.8 (6.4-37.0)	Preference
Forest impacted by logging	1.1	3.7 (0.0-13.9)		30.0	11.8 (0.0-47.1)		30.1	13.3 (3.6-32.0)	

The frequency distribution of nest types is independent of logging period (**Table 13**). The dominant nest type across all three censuses is the mixed type (combination of herbaceous and ligneous material) (mean proportion of mixed nests = 49.1 %). Herbaceous plants constitute the most important nest building material; they are present in 77.3 % of nests on average (Census 1 = 78.3 %, Census 2 = 78.3 %, Census 3 = 75.3 %). However, nest site size significantly differed between the three censuses (**Figure 11**), temporarily increasing from 5.7 to 9.3 nests per nest site four to six months after the end of logging activities (F = 4.98, DF = 96, $p < 0.05$), but dropping again, from 9.3 to 5.6 nests per nest site, 10-12 months after logging (F = 4.85, DF = 42, $p < 0.05$). Nest site size at Census 3 is not significantly different from the initial value observed at Census 1 (F = 0.0064, DF = 109, $p = 0.94$).

Table 13 Comparison of the frequency distribution of nest types between the three censuses. Comparison of the frequency distribution of nest types between censuses are made with Chi-square tests and adjusted Wald-Bonferroni confidence intervals (CI) (Neu et al. 1974; Agresti & Coull 1998). Comparison between Censuses 1 and 2: $\chi^2 = 7.12$, DF = 4, $p = 0.13$; Comparison between Censuses 2 and 3: $\chi^2 = 3.84$, DF = 4, $p = 0.43$; Comparison between Censuses 1 and 3: $\chi^2 = 7.48$, DF = 4, $p = 0.11$

Nest types	Census 1 (%)	Census 2 (%) (CI)	Census 3 (%) (CI)	Comparison Censuses 1 and2	Comparison Censuses 2 and 3	Comparison Censuses 1 and 3
Tree	16.0	13.0 (7.4-21.7)	15.7 (10.6-22.6)	Similar	Similar	Similar
Herbaceous	25.5	32.3 (23.5-42.5)	25.9 (19.4-33.6)	Similar	Similar	Similar
Ligneous	4.9	8.7 (4.2-16.5)	9.0 (5.2-14.9)	Similar	Similar	Increase
Minimum + Zero	1.1	0.6 (0.0-5.8)	0.0 (0.0-3.1)	Similar	Similar	Similar
Mixed	52.6	45.3 (35.4-55.6)	49.4 (41.4-57.5)	Similar	Similar	Similar

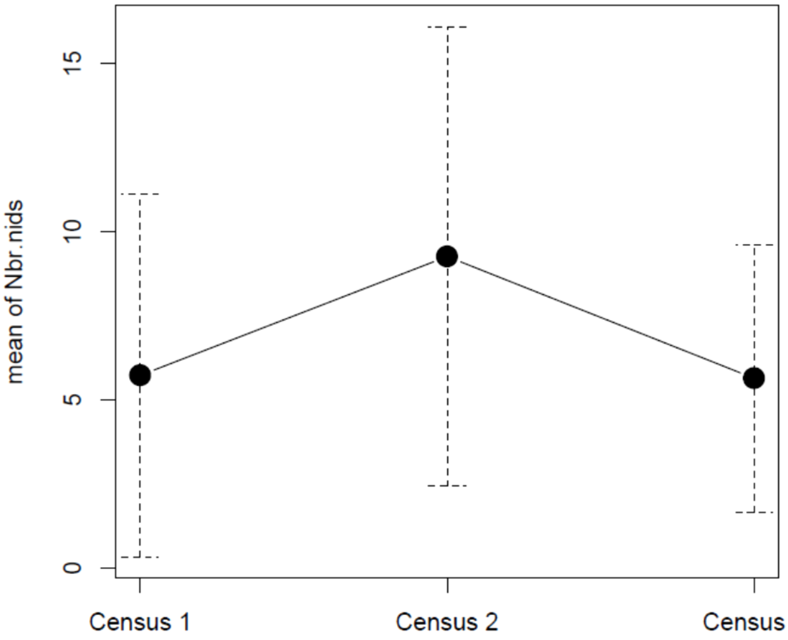


Figure 11 Observed nest site size for the three censuses. Mean nest site size ± SD [range]: Census 1: 5.7±5.4 [1-29], Census 2: 9.3±6.8 [1-23], Census 3: 5.6±3.8 [1-19]. Comparison between Censuses 1 and 2: F = 4.98, DF = 96, $p < 0.05$; Comparison between Censuses 2 and 3: F = 4.85, DF = 42, $p < 0.05$; Comparison between Censuses 1 and 3: F = 0.0064, DF = 109, $p = 0.94$

4 DISCUSSION

The evolution of WLG density over time after the second felling cycle was characterized by a non-significant drop in WLG density immediately following (4-6 months) timber harvesting. Subsequently, the density rose again to exceed the initial value (1 year after timber felling); however, the difference to the initial estimated density was not significant. This evolution of gorilla density is similar to that observed by Arnhem (2008). As the third census was undertaken during a different season than the previous two censuses, the observed variation in local gorilla abundance might be biased by seasonal differences in habitat use. Despite their frequent use in great apes studies, nest count censuses lead to some biases (Bradley *et al*. 2008). However, the observation that there was no significant difference in density one year after timber harvesting (between Censuses 1 and 3) might indicate that gorillas are relatively resilient to logging, as proposed by previous studies (Arnhem 2008; Clark *et al*. 2009; Stokes *et al.* 2010). Indeed the gorilla density estimated for Census 3 (2.6 gorilla km^{-2}) is similar to that observed in protected areas, such as in the Dja Reserve in Cameroon (2.1 gorilla km^{-2}) (Latour 2010), in the Nouabalé-Ndoki National Park in Congo (2.6 gorilla km^{-2}) (Devos et al. 2008) or in the Lac Télé Community Reserve in Democratic Republic of Congo (2.9 gorilla km^{-2}) (Poulsen & Clark 2004). Chimpanzees, on the contrary, seem to be more sensitive to disturbances (Morgan *et al*. 2013).

Although habitat availability was impacted by logging (mostly due to the conversion of open- and closed-canopy *terra firma* forest to forest impacted by logging), the nesting behavior of the WLG, in particular its preference for nesting in open canopy *terra firma* forest, remained consistent over the study period. This is important with regards to the role of gorillas as seed dispersers. Due to their preference for nesting in open canopy areas (Tutin *et al*. 1995; Stokes *et al.* 2010; Willie *et al.* 2012; Haurez *et al.* 2014), and their high rate of defecation at nest sites (Todd *et al*. 2008), gorillas deposit the majority of dispersed seeds in habitat types which offer favorable light conditions for seed germination and seedling development (Tutin *et al*. 1991; Rogers *et al*. 1998; Voysey *et al*. 1999; Haurez *et al*. 2015). Our study suggests that this directed-dispersal service provided by gorillas is not lost in the face of selective logging activities with low extraction rates.

Several studies have highlighted the potential benefits for the WLG of canopy and forest opening by logging, as a result of the increase in terrestrial herbaceous vegetation in these open habitats (Wright 2003; Matthews & Matthews 2004; Laurance *et al*. 2006; Morgan & Sanz 2007; van Kreveld & Roerhorst 2009; Clark *et al*. 2009; Stokes *et al.* 2010; Remis & Kpanou 2011). The present study revealed no preference for nesting in forest zones impacted by logging (i.e. logging roads, skid trails and felling gaps), although nest sites have been observed in this habitat type (**Table 12**) and the frequent use of terrestrial herbaceous vegetation as nesting material was confirmed (**Table 13**). The absence of a selection towards forest opened by logging activities could be explained by the time-span of the study, which was too short to encompass the development of terrestrial herbaceous vegetation following canopy opening. Indeed, at the time of the third census, very few of the zones impacted by logging had yet been colonized by Marantaceae and Zingiberaceae (B. Haurez, pers. observ.). Therefore, a longer monitoring could help to determine the time-span over which logging increases terrestrial herbaceous vegetation availability and benefits gorillas. Such data might prove useful to set recommendations for gorilla monitoring in the FSC framework.

Nest types are consistent throughout the study, with a majority of nests featuring herbaceous vegetation among their building material. This observation confirms the importance of herbaceous vegetation, and particularly plants belonging to the Marantaceae and Zingiberaceae families, in the nesting process (Tutin *et al*. 1995; Willie *et al*. 2014; Haurez *et al*. 2014).

Nest site sizes observed during Censuses 1 (5.7±5.4 nests per nest site) and 3 (5.6±3.8 nests per nest site) are consistent with values recorded at other sites (Fay *et al*. 1989; Brugiere & Sakom 2001), although much lower values have also been reported (Matthews & Matthews 2004). Average nest site size during the second census is relatively high (9.3±6.7 nests per nest site). Some very large nest sites (more than 15 nests) were observed in the AAC Bambidie during all three censuses. Nest site size peaked four to six months after logging operations, and then subsequently returned its initial level within one year. This could be explained as adaptations to altered food resource availability, distribution, or disturbance by logging activities leading to a shift in grouping patterns (Remis 1997; Cipolletta 2004). As human signs encounter rates did not significantly change between the censuses, an influence of human activity on gorilla grouping patterns seems unlikely. However, these results have to be interpreted with caution as the number of nests observed and recorded at a nest site does not always reflect group size (Tutin *et a*l. 1995; Bradley *et al*. 2008; Arandjelovic *et al*. 2010).

5 CONCLUSION

Considering the results of our study, the following observations can be made: (1) WLG density was not significantly affected in the short term (6 months to 1 year) after timber exploitation, therefore gorilla populations appear to be resilient to the direct impacts of this anthropogenic disturbance; (2) the WLG displayed a marked preference for nesting in open *terra firma* forests consistent before and after logging activity, therefore their directed-dispersal services are likely to persist in selectively logged forest; and (3) that forest sites modified by logging and presenting an open canopy (felling gaps, skid trails and logging roads) were not preferentially selected for nesting.

There is growing evidence of the resilience of gorilla populations to selective timber harvesting and associated logging activities from different regions across the Congo Basin (this study, Arnhem 2008, Clark *et al*. 2009, Stokes *et al.* 2010). Considering the proportion of Central African forests managed as logging concessions, the persistence of gorilla populations in logged forests should be viewed as an opportunity to expand an effective conservation of this threatened species into this land-use type (Clark *et al.* 2009). Given their careful management, logging concessions might serve as semi-protected areas, buffer zones and corridors for gorillas, mitigating the negative effects of human disturbance in other land-use types. However, the increase in hunting pressure often associated with logging could jeopardize the preservation of gorilla populations within concessions, emphasizing the critical need for timber exploitation companies to work in close collaboration with conservation managers for the protection of WLG from poaching and uncontrolled hunting.

The maintenance of gorilla populations, and hence a continuation of their dispersal services, in logged forests could offer benefits in terms of forest recovery following timber harvesting. The present study was unable to support the hypothesis that gorillas preferentially select logged habitats for nesting, though long term monitoring is necessary to confirm this observation. Moreover, the relation between extraction rates and impact of logging on gorilla populations should be investigated more thoroughly.

To further investigate the impact of timber extraction on gorilla seed dispersal services, and therefore the role of gorillas in logged forest recovery, a comparative characterization of seed dispersal effectiveness in logged and unlogged forests would be necessary.

TROISIÈME PARTIE CARACTÉRISATION DU POTENTIEL QUALITATIF ET QUANTITATIF DU GORILLE DES PLAINES DE L'OUEST EN TANT QUE DISPERSEUR

CHAPITRE 6 DESCRIPTION QUALITATIVE ET QUANTITATIVE DES GRAINES DISPERSÉES

Dans la deuxième partie de cette thèse de doctorat, nous avons vérifié si les forêts soumises à une exploitation forestière sélective, et gérées de manière durable, constituaient des habitats favorables pour les populations de gorilles des plaines de l'Ouest. Nos résultats montrent que la densité en gorilles au sein d'une Assiette Annuelle de Coupe est comparable aux valeurs observées dans certaines aires protégées, et ce autant 25 ans après la première rotation qu'un an après le second cycle d'exploitation. La troisième partie de ce traval s'intéresse au rôle du gorille dans la régénération des forêts exploitées. Dans le premier chapitre de cette section, les composantes qualitative (espèces dispersées, viabilité des graines et impact du passage dans le tractus digestif) et quantitative (nombre de graines dispersées et fréquence de dispersion des espèces) de la dispersion des graines par le gorille sont caractérisées.

Adapté de : HAUREZ B., TAGG N., PETRE C-A. & DOUCET J-L., *SUBMITTED*. Assessment of the qualitative and quantitative effectiveness of western lowland gorilla (Gorilla gorilla gorilla) seed dispersal in Gabon. *Biotropica.*

Analyse des excréments de gorilles © B. Haurez

Résumé

La dispersion des graines par les animaux est prépondérante au sein des forêts tropicales. En plus des avantages liés au déplacement des graines au départ de leur pied producteur, l'endozoochorie peut être bénéfique pour les graines via la suppression de la pulpe, la scarification des téguments, l'inhibition de certains pathogènes et la présence de matière fécale. Dans cette étude, nous avons investigué la dispersion des graines par le gorille des plaines de l'Ouest (*Gorilla gorilla gorilla*) au Sud-est du Gabon, au travers d'analyses d'excréments et de tests de germination. Des excréments frais de gorille ont été collectés et nettoyés dans le but d'identifier et de dénombrer les graines dispersées par le gorille. La viabilité des graines après passage dans le tractus digestif a été estimée par des test de germination dans une pépinière au sein du site d'étude. Pour évaluer l'impact du passage dans le tractus digestif sur le taux et le délai de germination, des tests comparatifs ont été installés impliquant quatre traitements: (1) graines ingérées débarrassées de leur matière fécale, (2) graines ingérées avec de la matière fécale, (3) graines issues de fruits entourées de pulpe et (4) graines issues de fruits débarrassées de la pulpe. L'analyse de 180 excréments a résulté en l'identification de 59 espèces. Des test de germination ont été réalisés pour 55 espèces et le taux de germination moyen atteint 46 % (0-100 %). L'impact du passage dans le tractus digestif a été évalué pour deux espèces, *Santiria trimera* et *Chrysophyllum lacourtianum*, qui montrent des taux de germination supérieurs après ingestion. Les résultats de cette étude montrent que le gorille disperse efficacement les graines de nombreuses espèces, dont la plupart produisent du bois d'œuvre ou des produits forestiers non-ligneux, ou sont caractéristiques des forêts gabonaises. En conséquence, nous recommandons la prise en compte du rôle du gorille dans la dynamique forestière dans les futurs projets de conservation.

Mots clés: dispersion des graines, *Gorilla gorilla gorilla*, dynamique forestière, Afrique Centrale, passage dans le tractus digestif, effet de déinhibition, effet de scarification

Abstract

Animal-mediated seed dispersal is preponderant in tropical forests. In addition to the spatial advantages of transporting seeds away from their parent source, endozoochory can provide benefits to seeds through pulp removal, seed coat scarification, pathogen inhibition and fecal matrix presence. In this study, we investigated seed dispersal by the western lowland gorilla (*Gorilla gorilla gorilla*) in Southeast Gabon, through fecal analyses and germination trials. Fresh gorilla feces were collected and washed in order to identify and count the seeds dispersed by gorillas. Seed viability after gut passage was estimated with germination trials in a nursery at the study site. To assess the impact of gut passage on germination success and delay, comparative trials were run with four treatments: (1) gut passed seeds cleaned of feces, (2) gut passed seeds within a fecal matrix, (3) seeds from fresh fruits surrounded by pulp, and (4) seeds from fresh fruits cleaned from pulp. The analysis of 180 fecal units resulted in the identification of 59 species. Germination trials were realized for 55 species and the average germination success reached 46 percent (0-100 %). The impact of gut passage was investigated for two species, *Santiria trimera* and *Chrysophyllum lacourtianum*, that both displayed higher success after ingestion. The results of this study show that gorillas effectively disperse seeds of numerous plant species, many of which provide timber or non-timber forest products or are typical of Gabonese forests. Therefore, we recommend the consideration of the role of gorillas in forest dynamics in future forest conservation projects.

Key words: seed dispersal, *Gorilla gorilla gorilla*, forest dynamics, Central Africa, gut passage effect, deinhibition effect, scarification effect

1 INTRODUCTION

In tropical forests, between 50 and 95 percent of plant species rely on animals for the dispersal of their seeds (Howe & Smallwood 1982; Beaune *et al*. 2012b). This mechanism is recognized as critical for ecosystem maintenance, as it sets the template for tree recruitment and the dynamics of plant populations. Seed dispersal benefits plants through several spatially-related processes (*i.e.* those proposed by the escape, colonization and directed dispersal hypotheses), as defined by Howe & Smallwood (1982). Animal-mediated seed dispersal provides further advantages. Passage through the frugivore gut may influence seed fate because of the removal of the fruit pulp; the pulp contains secondary compounds that can inhibit germination or act as a physical barrier to gas and water exchanges between the embryo and its environment, and its removal can have a deinhibition effect (Traveset 1998; Robertson *et al.* 2006; Traveset *et al*. 2007), and prevent the attraction of seed pathogens (Fricke *et al.* 2013). Mechanical and chemical abrasion of the seed coat can enhance seed germination potential (known as the scarification effect) (Traveset 1998; Traveset *et al*. 2007). The inherent deposition of seeds in the fecal matrix may also be beneficial because feces provide minerals and moisture for the seed (Traveset *et al.* 2001, 2007). On the other hand, the presence of the fecal matrix may lead to the development of pathogens or predators, and it may contain chemical inhibitors which prevent germination (Traveset 1998; Traveset *et al.* 2007; Beaune *et al*. 2012a). Unfortunately, studies focusing on the impact of endozoochory often rely on incomplete experimental designs, which are unable to disentangle possible deinhibition and scarification effects (Samuels & Levey 2005).

Among Central African frugivores, the western lowland gorilla (*Gorilla gorilla gorilla* Savage & Wyman, thereafter referred to as the WLG) is considered to be an efficient disperser because of its highly frugivorous diet, its large body mass and its pattern of seed deposition (Todd *et al.* 2008), i.e. seeds are directed to open canopy sites particularly suitable for seed germination and seedling growth (Rogers *et al.* 1998; Voysey *et al.* 1999; Petre *et al*. 2013; Haurez *et al.* 2015). However, dispersal effectiveness is also influenced by seed germination probability after gut passage, and the quantitative component of dispersal (Schupp 1993). Those factors have been poorly documented in the case of the WLG, leading to a lack of precision regarding its seed dispersal function.

The main objective of this study was to assess the quantitative and qualitative seed dispersal effectiveness of the WLG in a logging concession in Southeast Gabon. The following specific questions were addressed: (1) what are the plant species dispersed by gorillas at the study site and what are their respective abundances in gorilla feces? (2) What is the specific viability of seeds dispersed by gorillas? (3) What is the impact of gut passage on seed germination success and germination delay? Specifically, we wanted to identify the processes influencing germination in gorilla-dispersed seeds, and assess the existence of deinhibition or scarification. We hypothesized (1) that seed germination success after gut passage is higher because of scarification and deinhibition, (2) that these effects also reduce germination delay, and (3) that the presence of a fecal matrix affects seeds by increasing the germination delay.

2 METHODOLOGY

2.1 Study site

This study was carried out in a sustainably-managed and certified (Forest Stewardship Council) logging concession in Southeast Gabon (0°30'-1°00' S, 12°30'-14°00' E) from February 2011 to November 2014. The study area covers 617,000 ha and the vegetation mostly comprises moist tropical evergreen forest dominated by *Scyphocephalium ochocoa* Ward (Myristicaceae) and *Aucoumea klaineana* Pierre (Burseraceae) (White 1986; Demarquez & Jeanmart 2004) (**Figure 12**). It is an old secondary forest as characterized by White (1986). The climate is equatorial with an average annual rainfall of 1700 mm mainly distributed through two rainy seasons (March-May and September-December) (Moupela *et al.* 2013). A dry season, with monthly precipitation lower than 100 mm, is observed from June to August. The average annual temperature is 26°C, with the highest temperatures being recorded in February to April, and the lowest in July and August (Moupela *et al.* 2013).

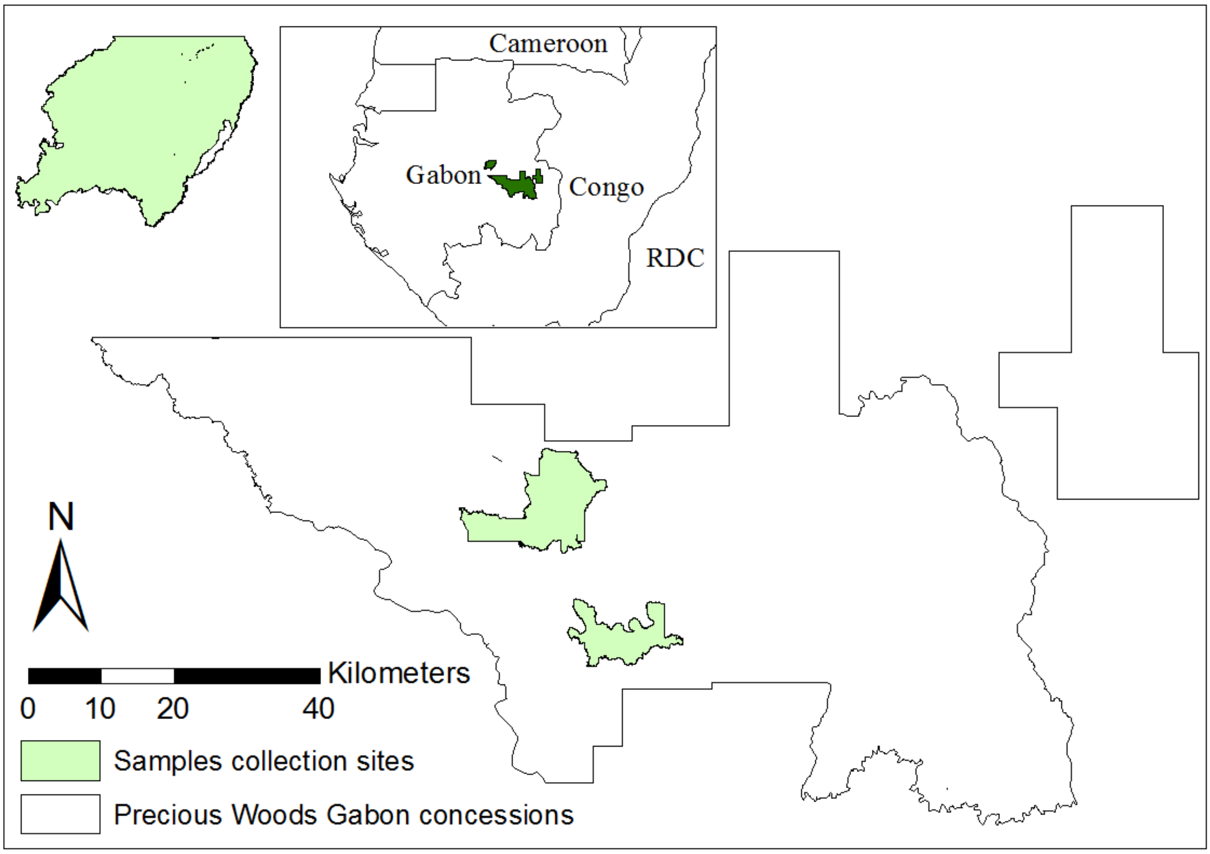


Figure 12 ***Precious Woods Gabon*** **logging concessions and location of the sample collection sites**

2.2 Fecal collection and analysis

Fecal collection was undertaken over 20 complete months throughout the study period (February-April 2011, January-July and November-December 2012, June-August 2013, December 2013-April 2014 and September-November 2014), mainly at sleeping sites at the time of nest count censuses along linear transects. The fecal sample was complemented with opportunistic encounters of feces during other research activities. For the fecal analysis, we only considered fresh and recent fecal samples that had not been disturbed by dung beetles or other agents. Overall, 180 fecal units were collected, with a monthly mean of 15±13.1 (range 0-36). All fecal samples were washed and sieved on the collection day. Seeds were identified to species level when possible by experts in Central African forest botany (Doucet J-L. and Boubady A.) and using the "Flore du Gabon" (Aubréville 1961, 1962, 1968; Koechlin 1964; Le Thomas 1969; Fouilloy & Halle 1973; Leroy *et a*l. 1984; Villiers 1989), and counted when ≥ 5 mm. For seeds ≤ 5 mm, only presence/absence data were recorded. For each fecal unit, observed species and their respective number of seeds were recorded. We investigated their use as timber and important non-timber forest products (Meunier *et al.* 2015).

2.3 Viability of dispersed seeds and impact of gut passage on seed germination

The seeds used in the germination trials came from the analyzed fecal units and were supplemented by seeds from some fresh or recent feces that had been lightly disturbed by external agents before their collection. A visual inspection was made to determine the proportion of damaged seeds. For each species, one to five seeds were conserved for the constitution of a seminotheque. The remaining intact seeds were sowed in a nursery at the study site. They were placed individually in plastic bags filled with soil collected from within the forest. Germination success was monitored in order to assess the viability of gut passed seeds and was defined as the visible emergence of a seedling stem above the soil surface (Nchanji & Plumptre 2003). Because of logistical constraints, monitoring periods varied between species and averaged eight months (1-15 months). Therefore, our viability estimates are conservative.

For two species, *Chrysophyllum lacourtianum* De Wild. (Sapotaceae) and *Santiria trimera* (Oliv.) Aubrév. (Burseraceae), the availability of fresh fruits allowed us to install comparative trials including four treatments: (T1) gut passed seeds cleaned of feces; (T2) gut passed seeds with fecal matrix, (T3) seeds from fresh fruits surrounded by pulp and (T4) seeds from fresh fruits cleaned of pulp. The seeds used in each germination trial belonged to the same 'seed lot' (defined as seeds of the same species, collected from the same fecal sample or the same tree and sown at the same time) in order to limit genetic or physiological effects. For these species, we recorded germination success (1 = germination, 0 = absence of germination) and germination delay (days before germination) for each sown seed. At the end of the monitoring periods (9 months for *S. trimera* and 15 months for *C. lacourtianum*), non-germinated seed viability was assessed through seed section.

2.4 Data analysis

As the impact of gut passage on seed germination has been observed to be species-specific (Traveset 1998; Petre *et al.* 2015b), we analyzed each species separately. Following Samuels & Levey (2005), the existence of a deinhibition effect was assessed by testing the difference in germination between seeds from fresh fruits surrounded by pulp (T3) and seeds from fresh fruit cleaned of pulp (T4). A scarification effect was indicated by a difference in germination between seeds from fresh fruit cleaned from pulp (T4) and gut passed seeds cleaned of fecal matrix (T1).

All statistical analyses were performed in R (R Development Core Team 2015). To compare germination successes between treatments, we used generalized linear mixed models (glmm) and general linear models (glm) with the package "lem4" and the functions "glmr" and "glm". As we considered the germination event as the response variable (germination = 1, no germination = 0), the distribution was defined as binomial with a logit link function. The significance of a given factor was tested by comparing models with and without this factor with the function "anova" and χ^2 tests. Models were selected considering their Akaike Information Criterion (AIC) values (the best model displaying the lowest AIC).

Average germination delays (defined as the number of days between seed sowing and seedling emergence) were estimated for each treatment in each lot. We compared these average germination delays with ANOVA (function "aov") after verification of the application conditions.

For both analyses, the statistical models included treatment as a fixed factor and seed lot as a random factor. When the factor treatment was significant, the mean germination success and delays between the different treatments were compared using a Tukey's test (function "glht" from the package "multcomp").

3 RESULTS

3.1 Plant species dispersed and viability of dispersed seeds

Considering the 180 fecal units analyzed in this study, 59 different species were observed to be dispersed by the WLG (**Table 14)**. Nineteen taxa were identified to species level, and 16 to genus. The 24 remaining species were distinguished but not identified (41 percent of species). Most (16 species) were found only once in the fecal samples, and many were represented by only one seed (8 species). Indeed, the relative frequency of species in the fecal samples (i.e. the proportion of fecal units containing the species) and the representation of species (i.e. the ratio of the total number of the seeds of a species divided by the total number of seeds found throughout the study) varied greatly among species. The most frequent taxa (frequency > 10 percent) were *Santiria trimera*, *Aframomum* sp., *Chrysophyllum lacourtianum*, *Landolphia* spp., *Dialium pachyphyllum* and *Dacryodes klaineana*, and the most represented taxa (representation > 5 percent) were *Santiria trimera*, *Dialium* spp., *Dialium* sp1, *Aframomum* sp. and *Dialium pachyphyllum* (**Table 14**). The number of species per fecal unit (monthly weighed mean = 2.4±1.1 species, range = 0-6) and the number of seeds per fecal unit (monthly weighed mean = 58.0±31.8 seeds, range = 0-566) were highly variable between fecal samples.

Table 14 List of species dispersed by western lowland gorilla in *Precious Woods Gabon* concession, Southeast Gabon. The **relative frequency** is the proportion of fecal units containing the species and the **representation** is the ratio of the total number of the seeds of a species divided by the total number of seeds found throughout the study.

Family	Species	Uses	Relative frequency (%)	Total no of intact seeds	No. of damaged seeds	Representation (%)
	Absence of seeds		5.0	NA	NA	NA
Anacardiaceae	*Antrocaryon klaineanum* Pierre	NTFP (fruits), timber	2.2	45	0	0.3
	Pseudospondias microcarpa (A.Rich.) Engl.	NTFP (fruits)	4.4	43	1	0.3
	Trichoscypha abut Engl. & Brehmer	NTFP (fruits)	0.6	1	0	<0.1
Annonaceae	*Greenwayodendron suaveolens* (Engl. & Diels) Verdc.		0.6	31	0	0.2
	Hexalobus crispiflorus Rich		1.1	14	0	0.1
Apocynaceae	*Landolphia* spp.		12.8	562	2	4.0
	Landolphia sp1		2.2	23	1	0.2
	Landolphia sp2		9.4	550	13	4.0
	Landolphia sp3		3.9	54	0	0.4
	Landolphia sp4		0.6	47	1	0.3
	Landolphia sp5		2.2	56	2	0.4
Burseraceae	*Canarium schweinfurthii* Engl.	Timber, NTFP (fruits, medecine)	2	14	0	0.1
	Dacryodes klaineana (Pierre) H.J. Lam.	NTFP (fruits)	10.6	356	1	2.6
	Dacryodes normandii Aubrév. & Pellegr.	Timber, NTFP (fruits)	5.0	170	0	1.2

	Santiria trimera (Oliv.) Aubrév.	NTFP (fruits, medicine)	32.2	3392	4	24.4
Ebenaceae	*Diospyros* sp.		3.9	25	0	0.2
Euphorbiaceae	*Plagiostyles africana* (Müll.Arg.) Prain		7.2	572	0	4.1
	Uapaca gabonensis Pierre		1.1	11	2	0.1
	Uapaca sp.		8.3	69	0	0.5
Fabaceae	*Dialium pachyphyllum* Harms	Timber	11.1	850	0	6.1
	Dialium sp1		9.4	1764	0	12.7
	Dialium sp3		5.0	77	4	0.6
	Dialium sp4		3.9	81	1	0.6
	Dialium spp.		8.9	2967	3	21.3
	Parkia gaboensis A. Chev.		3.3	171	1	1.2
Marantaceae	*Megaphrinium* sp1		3.9	89	0	0.6
	Megaphrinium sp2	NTFP (leaves)	6.1	79	0	0.6
	Indeterminate 11		0.6	2	0	<0.1
Moraceae	*Musanga cecropioides* R.Br. ex Tedlie	NTFP (medicine)	1.1	NA	NA	NA
	Myrianthus arboreus P. Beauv.	NTFP (fruits)	1.1	4	0	<0.1
Sapindaceae	cf *Eriocoelum* sp.		3.3	29	0	0.2
Sapotaceae	*Chrysophyllum lacourtianum* De Wild.	Timber, NTFP (fruits)	14.4	429	0	3.1
	Indeterminate 23		3.9	13	0	0.1
Tiliaceae	*Grewia coriacea* Mast.		3.3	23	0	0.2
	Grewia brieyi De Wild.		0.6	5	0	<0.1
	Grewia sp.		0.6	33	0	0.2
Ulmaceae	*Celtis tesmannii* Rendle	Timber	8.3	235	3	1.7
Zingiberaceae	*Aframomum* sp.	NTFP (fruits)	20.6	853	0	6.1
Indeterminate	Indeterminate 1		0.6	3	0	<0.1
	Indeterminate 2		0.6	1	0	<0.1
	Indeterminate 3		6.7	94	2	0.7
	Indeterminate 4		2.2	3	1	<0.1
	Indeterminate 5		0.6	1	0	<0.1
	Indeterminate 6		0.6	1	0	<0.1
	Indeterminate 7 cf *Diospyros* sp.		1.1	3	1	<0.1
	Indeterminate 8		0.6	2	0	<0.1
	Indeterminate 9 cf *Cissus dinklagei* Gilg & M.Brandt		0.6	5	0	<0.1
	Indeterminate 10		0.6	1	0	<0.1
	Indeterminate 12		1.1	33	0	0.2
	Indeterminate 13		0.6	8	0	0.1
	Indeterminate 14		0.6	1	0	<0.1
	Indeterminate 15		0.6	1	0	<0.1

	Indeterminate 16 cf *Irvingia* sp.	1.1	2	0	<0.1
	Indeterminate 17	0.6	1	0	<0.1
	Indeterminate 18	0.6	1	0	<0.1
	Indeterminate 19	0.6	NA	NA	NA
	Indeterminate 20	2.2	10	0	0.1
	Indeterminate 21	0.6	2	0	<0.1
	Indeterminate 22	0.6	19	0	0.1
	Total general		**13931**	**44**	

Germination trials were undertaken for 55 species (**Table 15**) to assess seed viability after gut passage. The number of seeds sown depended on seed availability. The mean observed germination success was 46 percent and ranged from 0 percent to 100 percent.

Table 15 List of species dispersed by western lowland gorilla in *Precious Woods Gabon* concession tested for seed viability after gut passage, Southeast Gabon.

Family	Species	No. sown seeds	No. germinated seeds	Germination success (%)
Anacardiaceae	*Antrocaryon klaineanum*	37	32	86%
	Pseudospondias microcarpa	35	30	86%
	Sorindeia sp.	117	76	65%
	Trichoscypha abut	18	18	100%
Annonaceae	*Hexalobus crispiflorus*	30	8	27%
	Polyalthia suaveolens	28	13	46%
Apocynaceae	*Landolphia* sp.	1	0	0%
	Landolphia sp1	28	18	64%
	Landolphia sp2	28	16	57%
	Landolphia sp3	18	15	83%
	Landolphia sp4	10	10	100%
Burseraceae	*Canarium schweinfurthii*	12	8	67%
	Dacryodes klaineana	253	221	87%
	Dacryodes normandii	53	36	68%
	Santiria trimera	583	462	79%
Ebenaceae	*Diospyros* sp.	113	22	19%
	Diospyros sp2	40	22	55%
	Diospyros sp3	3	1	33%
Euphorbiaceae	*Plagiostyles africana*	161	112	70%
	Uapaca guineensis	11	1	9%
	Uapaca sp.	61	36	59%
Fabaceae	*Dialium* sp.	4	0	0%

	Dialium sp1	228	73	32%
	Dialium sp2	414	24	6%
	Dialium sp3	46	9	20%
	Dialium sp4	63	5	8%
	Parkia bicolor	70	64	91%
Marantaceae	*Megaphrinium* sp1	10	2	20%
	Megaphrinium sp2	55	27	49%
	Megaphrinium sp3	6	4	67%
Moraceae	*Musanga cecropioides*	20	11	55%
	Myrianthus arboreus	3	1	33%
Sapindaceae	cf *Eriooelum* sp.	20	19	95%
Sapotaceae	*Chrysophyllum lacourtianum*	228	179	79%
	Sapotaceae	33	13	39%
Tiliaceae	*Grewia coriacea*	422	2	0%
	Grewia pinatifida	4	4	100%
Ulmaceae	*Celtis tesmannii*	51	37	73%
Zingiberaceae	*Aframomum* sp.	140	39	28%
Indeterminate	Indeterminate 9 cf *Cissus dincklagei*	5	2	40%
	Indeterminate 24	85	0	0%
	Indeterminate 4	1	0	0%
	Indeterminate 5	1	0	0%
	Indeterminate 22	16	0	0%
	Indeterminate 7 cf *Diospyros* sp.	1	0	0%
	Indeterminate 3	52	0	0%
	Indeterminate 8	1	1	100%
	Indeterminate 25	5	0	0%
	Indeterminate 12	28	11	39%
	Indeterminate 13	4	0	0%
	Indeterminate 14	1	0	0%
	Indeterminate 26	1	1	100%
	Indeterminate 15	1	0	0%
	Indeterminate 16 cf *Irvingia* sp.	2	0	0%
	Indeterminate 17	1	0	0%
	Total general	**3708**	**1698**	**46%**

3.2 Impact of gut passage on seed germination

The results of the germination trials assessing the impact of gut passage on seed germination are displayed in **Table 16**. At the end of the monitoring periods, all non-germinated seeds were dead. Regarding the germination success of *Santiria trimera*, the fixed factor treatment ($\chi^2 = 121.4$, df = 3, $P < 0.001$) and the random factor seed lot ($\chi^2 = 6.6$, df = 1, $P < 0.001$) were both significant, as well as their interaction ($\chi^2 = 32.7$, df = 9, $P < 0.001$). Therefore, there was a significant effect of the treatment on *S. trimera* germination success, which varied with seed lot. On average, the gut passed seeds without fecal matrix displayed a germination success of 57 percent, which was higher than the germination successes observed with the other treatments (gut passed seeds with fecal matrix: 37 percent, fresh fruit seeds with pulp: 4 percent, fresh fruit cleaned seeds: 8 percent). Considering germination delays, there were no significant differences between treatments (F = 0.28, df = 3, P = 0.838) and the mean germination delay was 18±6 d.

Table 16 Results of the comparative germination trials of species dispersed by the western lowland gorilla in *Precious Woods Gabon* concession tested for seed viability after gut passage, Southeast Gabon. The column "Tukey's test" displays the significant differences between treatments

Species	Treatment (no. of seeds tested)	Mean germination success (SD) (%)	Tukey's test	Mean germination delay ± SD (days)	Tukey's test	% of seeds attacked by fungi
Santiria trimera	Gut passed (n = 98)	57 (50)	a	18±6	a	0
	Gut passed with fecal matrix (n = 60)	37 (49)	b	17±3	a	0
	Fresh fruit with pulp (n = 124)	4 (20)	b	20±9	a	0
	Fresh fruit without pulp (n = 133)	8 (26)	b	19±7	a	0
	Total	**22 (42)**		**18±6**		**0**
Chrysophyllum lacourtianum	Gut passed (n = 177)	80 (40)	c	40±9	b	1
	Gut passed with fecal matrix (n = 40)	85 (36)	c	50±6	c	0
	Fresh fruit with pulp (n = 40)	0	NA	NA	NA	0
	Fresh fruit without pulp (n = 178)	23 (42)	d	48±10	c	29
	Total	**50 (50)**		**43**±10		**12**

As no seeds from fresh fruit of *Chrysophyllum lacourtianum* surrounded by pulp germinated, this modality was discarded from the analysis. The best model for *C. lacourtianum* germination success included only the factor treatment (χ^2 = 141.8, df = 2, P < 0.001). Seeds passed in the gorilla gut showed higher germination success (gut passed seeds without fecal matrix: 80 percent, gut passed seeds with fecal matrix: 85 percent) than seeds from fresh fruits cleaned of pulp (23 %). Twenty-nine percent of the seeds of this later treatment (n = 52) were attacked by a fungi (**Figure 13**). This fungi was also observed on only two (1 %) gut passed seeds without fecal matrix. The germination delays for this species were significantly influenced by seed treatment (F = 6.4, df = 2, P = 0.0090). Gut passed seeds without fecal matrix displayed shorter mean germination delays (40 d) than gut passed seeds with fecal matrix (50 d) and cleaned seeds from fruits (48 d). Gut passed seeds with fecal matrix and seeds cleaned of pulp did not differ in terms of their germination delay.

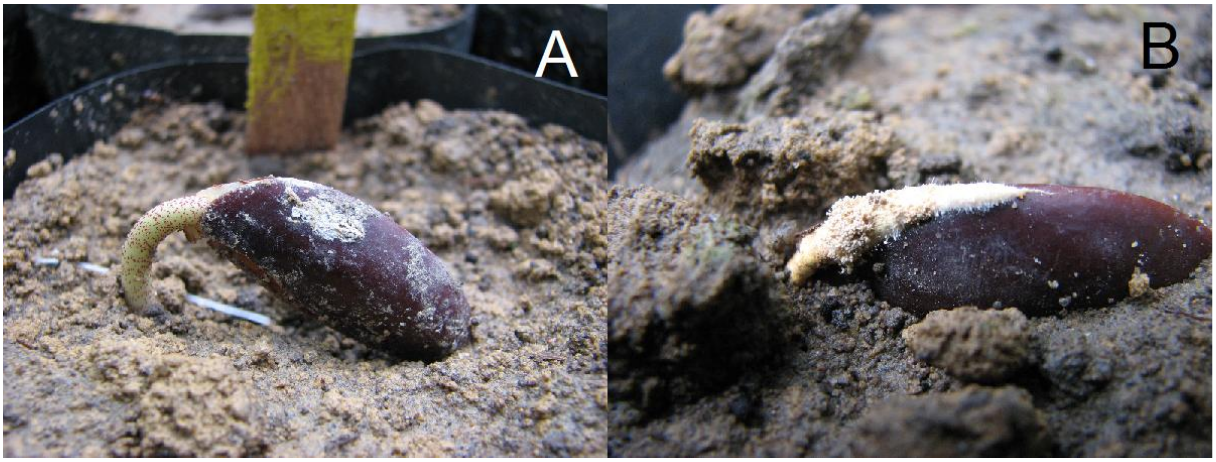


Figure 13 Seeds of *Chrysophyllum lacourtianum* (A) intact germinated seed, (B) seed attacked by a fungal pathogen

4 DISCUSSION

During the course of this study, 59 species were identified as being dispersed by the western lowland gorilla (WLG). Even with our relatively short study period, this number falls within the range of species dispersed by gorillas at other study sites (Poulsen *et al*. 2001; Head *et al*. 2011; Petre *et al.* 2015b). The majority of these species (51 %) were weakly represented, with fewer than three occurrences in fecal units or/and fewer than 10 seeds found in the feces in total (**Table 14**). These low occurrences of species in feces and the low number of seeds collected in fecal units partly explain the high number of undetermined species, as it was not always possible to grow seedlings to facilitate identification.

In general, the total number of seeds found for a given species did not reflect the frequency of presence of this taxa in gorilla feces, except for *Santiria trimera* which is the most frequently- and most abundantly-dispersed species. For all species, the number of damaged seeds found in gorilla feces is very low. Although our study would benefit from a larger sample of fecal units analyzed per month and a more temporally-even sampling effort, the results provided here are consistent with the pattern described by Petre *et al.* (2015a) in Cameroon. The evaluation of the WLG seed load provided suggests a predominance of a few taxa (the species *Santiria trimera* and the genus *Dialium* collectively accounted for nearly 60 percent of all dispersed species). This dominance of a few species in the seed load could partially reflect the importance of certain fruit species in the gorilla diet and diet preferences, but it may also reflect plant species abundances and seasonal fruit availability *(Petre et al.* 2015b). Indeed, the most frequent and most abundant species found in gorilla feces in the present study, *S. trimera*, also displays the highest density at the study site (30.2 trees/ha, dbh>10cm) (Doucet 2003), and *Aframomum* sp., the second most frequent species, is a herbaceous species highly abundant in open-canopy and disturbed forests in Gabon (White *et al.* 1995). Moreover, the third most frequent species, *Chrysophyllum lacourtianum*, has been observed to display two fruiting periods at the study site (June-July in the South and November in the North of the study site) (**Figure 14**).

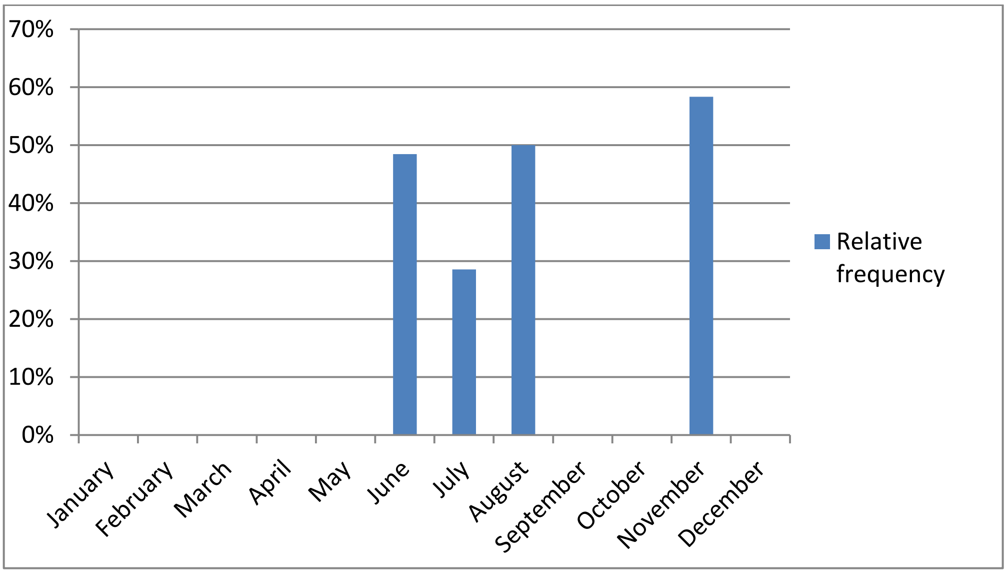


Figure 14 Seasonal variation in relative frequency of *Chrysophyllum lacourtianum* seeds in gorilla feces

The 59 species observed to be dispersed by gorillas at the study site belonged to at least 21 genera and 14 families. On the 35 identified taxa dispersed by the WLG, more than one-third (37 %) provide valuable timber and/or non-timber forest products. The WLG is also involved in the seed dispersal of several plant species typical of the Gabonese forest: S*antiria trimera, Plagiotyles africana, Dacryodes klaineana, D. normandii, Polyalthia suaveolens* and *Grewia coriacea* (Doucet 2003).

The comparative germination trials highlighted a positive effect of gut passage on germination success for *Santiria trimera* and *Chrysophyllum lacourtianum*. In both tested species, the existence of a scarification effect was observed, but a deinhibition effect was only present for *C. lacourtianum* seeds. For this species, almost 30 percent of the seeds from fresh fruit cleaned of pulp displayed signs of a fungal infection. This fungi was observed for only 1 percent of gut passed seeds without fecal matrix. The majority (98 %) of the infected seeds did not germinated. Therefore, gut passage is suggested to inhibit the development of this fungi. Indeed, the pulp that remains attached to undispersed seeds is more likely to be targeted by predators and pathogens, and consequently, the seed destroyed by their actions (Lambert & Chapman 2005; Fricke *et al*. 2013). Additional experiments could allow to identify the fungal agent responsible for seed contamination and compare the fungal load between gut passed and control seeds (Fricke *et al.* 2013).

It is likely that primates select preferentially healthy fruits with viable seeds, while fruits gathered for the germination trials may have been less fit than those selected for consumption by primates and therefore less likely to germinate (Idani 1986; Poulsen *et al*. 2001). The selection of high quality fruit, potentially linked with more viable seeds, deserves more attention.

Germination delay was shortened for *C. lacourtianum* after gut passage, but the presence of a fecal matrix slowed germination to a level comparable to that of seeds not subjected to gut passage. However, no effect of seed treatment on germination delay was observed for *S. trimera*. Complementary studies are needed to shed the light on the impact of early germination on seedling growth and recruitment probability.

A recent study examining gorilla gut passage effect on seed germination suggested that phylogenetic relatedness was not an important factor in explaining the response of a seed to gut passage (Petre *et al.* 2015a). The authors proposed to test for a differential effect of fruit skin and fruit pulp as components of the deinhibition effect. Pulp composition could also highly influence the exchange of gas and the osmotic environment of the seed (Traveset 1998; Yagihashi *et al.* 2000), therefore impacting the fate of the embryo. We recommend integrating treatments that independently consider the effects of fruit skin, fruit pulp and pulp juice, and to undertake chemical analysis of fruit skin and pulp to identify the factors that can explain the existence, or absence, of deinhibition. Chemical analysis may also shed light on the mechanisms linked with the presence and effects of fecal matrix, i.e. the presence of secondary compounds that delay germination.

5 CONCLUSION

In this study, we have shown that seed passage in western lowland gorilla gut positively influences seed germination of some species, and that both scarification and deinhibition effects may be involved in germination enhancement. The presence of fruit pulp and fecal matrix lengthen or does not affect germination delay. Seeds dispersed by gorilla are not damaged and their viability averages 50 %.

The western lowland gorilla is implicated in the seed dispersal of many species, which are typical of Gabonese forests (e.g. *Santiria trimera* and *Plagiostyles africana*) (Doucet 2003), present restricted geographical distribution (e.g. *Dacryodes normandii* and *Cola lizae* N. Hallé) (Tutin *et al.* 1991; Doucet 2003), are harvested for timber (e.g. *Dacryodes normandii*, *Dialium pachyphyllum*, *Chrysophyllum* spp.) or provide NTFPs to local populations (e.g. *Santiria trimera*, *Dacryodes klaineana*, *Pseudospondias microcarpa*, *Trichoscypha* spp.). Therefore, gorilla provides seed dispersal services that are both ecologically and economically important. We recommend the consideration of its role in tropical forest dynamic in future conservation projects.

CHAPITRE 7 CONTRIBUTION DU GORILLE DES PLAINES DE L'OUEST DANS LA DISPERSION D'UNE ESPÈCE EXPLOITÉE, L'OSSABEL (*DACRYODES NORMANDII* BURSERACEAE)

Le chapitre 6 démontre que le gorille des plaines de l'Ouest réalise une dispersion de qualité pour un grand nombre d'espèces végétales, dont la plupart présente un intérêt économique ou alimentaire pour les populations locales. Les graines dispersées par le gorille présentent des taux de germination variables, mais relativement élevés. En outre, le passage dans la tractus digestif semble avoir un impact positif sur la germination des graines. Dans le but de préciser l'importance économique des services de dispersion dispensés par le gorille, le chapitre suivant décrit la contribution du gorille dans la dispersion d'une essence exploitée pour son bois d'oeuvre, avec pour modèle le *Dacryodes normandii*.

Adapté de HAUREZ B., DAÏNOU K., TAGG N., PETRE C-A. & DOUCET J-L., 2015. The role of great apes in seed dispersal of the tropical forest tree species *Dacryodes normandii* (Burseraceae) in Gabon. *Journal of Tropical Ecology*, **31**(5), p. 395-402.

Canopée d'un *Dacryodes normandii* en fructification © J-L. DOUCET

Résumé

L'identification des disperseurs et prédateurs des graines est essentiel pour comprendre les effets des perturbations anthopiques, et du processus de défaunation qui y est associé, sur la dynamique des forêts tropicales d'Afrique Centrale. Dans cette étude, les animaux impliqués dans la dispersion et la prédation des graines du *Dacryodes normandii* (Burseraceae), une essense forestière dispersée par endozoochorie, endémique des forêts gabonaises, onté été identifiés dans un site du Sud-Est du Gabon en utilisant deux méthodes complémentaires : les observations directes et le suivi de tas de fruits à l'aide de pièges photographiques. L'effort d'échantillonnage total (172h d'observations directes et 796 jours de piégeage photographique) ont mené à l'identification de six espèces de disperseurs et de huit espèces de prédateurs des graines de *D. normandii*. Avec des fréquences élevées (88% et 57% de leurs visites, respectivement) and des longues durées de visite (85 et 23 minutes, respectivement), le gorille des plaines de l'Ouest et le chimpanzé commun ont été identifiés comme les principaux disperseurs de cette espèce. Les graines ingérées par le gorille présentent des taux de germination élevés (68%). Les rongeurs ont été identifiés comme prédateurs des graines de *D. normandii*, mais ils sont potentiellement impliqués dans le processus de dispersion secondaire par *scatter-hoarding*. Les résultats de cette étude soulignent l'importance des grands singes dans la dispersion de cette espèce arborée.

Mots clés: Afrique, frugivore, *Gorilla gorilla gorilla*, forêt exploitée, *Pan troglodytes troglodytes*, primates, dispersion des graines, prédation des graines, forêt tropicale humide

Abstract

The identification of seed dispersers and predators is essential to understand the effect of anthropogenic disturbances, and the associated defaunation process, on tropical forest dynamics in Central Africa. In this study, the animals involved in seed predation and dispersal of *Dacryodes normandii* (Burseraceae), an endozoochorously dispersed tree species endemic to Gabonese forests, were identified in a site in south-east Gabon using two complementary methods: direct observation and camera-trap monitoring of fruit piles. The combined sampling effort (172 h of direct observations and 796 d of camera trapping) led to the identification of six disperser and eight predator species of *D. normandii* seeds. With high frequency of consumption (88% and 57% of their visits, respectively) and long visit duration (83 and 23 min, respectively), the western lowland gorilla and central chimpanzee were identified as the main dispersers of this species. Seeds passed through the gorilla gut exhibited high germination success (68%). Rodents were identified as predators of *D. normandii* seeds, potentially displaying rare secondary dispersal through scatter-hoarding. The results of this study highlight the importance of great apes in the seed dispersal of this tree species.

Keywords: Africa, frugivory, *Gorilla gorilla gorilla*, logged forest, *Pan troglodytes troglodytes*, primates, seed dispersal, seed predation, tropical rain forest

1 INTRODUCTION

Animal-dispersed plant species interact with a cohort of frugivores, whose roles regarding population dynamics depend on their specific characteristics. The number of seeds dispersed by an animal species is linked to the importance of fruits in its diet, as well as its food preferences (Schupp 1993). Both factors influence the frequency of consumption of a given plant species, and ultimately seed dispersal quantity (Schupp 1993). Seed processing in the mouth and gut might alter seed germination potential, and therefore hamper the dispersal services provided by a given frugivore (Schupp 1993). The action of granivorous species as predators, or scatter-hoarding dispersers, might also influence seed fate (Schupp 1993). As the disperser's characteristics influence seed dispersal effectiveness, fruit features determine which animals consume a plant species (Gautier-Hion *et al.* 1985) and therefore its community of dispersers. It is important to study the role of mammals in the regeneration processes of animal-dispersed plant species in order to assess the impacts of the phenomenon of ‘defaunation’ (Galetti & Dirzo 2013; Kurten 2013). Large mammals are thought to be effective dispersers, but are also disproportionately affected by anthropogenic pressure (Wright 2003; Linder & Oates 2011). Central African great apes (western gorilla, *Gorilla gorilla*; chimpanzee, *Pan troglodytes* Blumenbach; and bonobo, *Pan paniscus* Schwartz) are a good example of such species. Great apes are important dispersers because of their highly frugivorous diet, large body mass and extended home range (Voysey *et al*. 1999; Poulsen *et al*. 2001; Beaune *et al.* 2013).

This study took place in a logged forest in Gabon. Among the dominant plant families found in Gabonese forests, species of the family Burseraceae are characterised by a high level of endemism (Aubréville 1962; Doucet 2003). Those belonging to the genera *Dacryodes, Canarium* and *Santiria,* which provide important timber and/or non-timber forest products (Aubréville 1962, Doucet 2003), are zoochorous and are consumed by the endangered great apes (Williamson *et al.* 1990; Tutin *et al.* 1991; Tutin & Fernandez 1993). But the main seed dispersers of these plant species are not known; neither is their exact influence on plant fitness.

The objective of this work was to describe the respective roles of vertebrates involved in the seed dispersal and predation of a poorly-known zoochorous tree species endemic to Gabon, *Dacryodes normandii* Aubrév. & Pellegr. (Burseraceae), and to assess their importance in the dispersal process. We tested the following three hypotheses. (1) Considering that *D. normandii* fruit can be categorised in the bird-monkey syndrome (Gautier-Hion *et al.* 1985), large birds and monkeys will be dispersers of its seeds. However, we expect large mammals to provide important dispersal services to this species. In particular, great apes will be the main dispersers of this species in terms of the quantity of dispersed seeds and the high quality of seed treatment in their mouth and gut. (2) Large rodents will be mainly involved in seed predation (Hecketsweiler 1992), but considering their scatter-hoarding behaviour, they will occasionally disperse *D. normandii* seeds.

2 METHODOLOGY

2.1 Study site

This study was carried out in a sustainably managed and certified (Forest Stewardship Council) logging concession in south-east Gabon (0°30'-1°00' S, 12°30'-14°00' E) from December 2013 to March 2014. The study area covers 617,000 ha and the vegetation mostly comprises moist tropical evergreen forest. It is an old secondary forest as characterised by White (1986), dominated by *Scyphocephalium ochocoa* Ward (Myristicaceae) and *Aucoumea klaineana* Pierre (Burseraceae) (White 1986; Demarquez & Jeanmart 2004). In similar forests in central Gabon, it has been shown that about 60% of tree species are dispersed through endozoochory (Doucet 2003). Western lowland gorilla (*Gorilla gorilla gorilla* Savage & Wyman) and central chimpanzee (*Pan troglodytes troglodytes* Blumenbach) coexist sympatrically within the study site. The climate is equatorial with an average annual rainfall of 1700 mm (Moupela *et al.* 2013), with two seasons of heavy precipitations (March-May and September-December) and two seasons of lower precipitations. The average annual temperature is 26°C (Moupela *et al.* 2013), with the highest temperatures being recorded from February to April, and the lowest in July and August.

2.2 Study species

Dacryodes normandii is a medium to large canopy tree, endemic to the evergreen forests of Gabon (Doucet 2003). It provides timber and non-timber forest products (Aubréville 1962). It has intermediate light requirements, as it tolerates shade at seedling stage but becomes light-demanding when mature (Doucet 2003). *Dacryodes normandii* is dioecious and female trees produce obovoid drupes of 3.5 cm in length, black/purple in colour, with a thin exocarp and a sweet-sugary, juicy and soft pulp (Aubréville 1962). Fruiting is observed for trees from 13 cm dbh (Doucet 2003). Fruit production is defined as supra-annual, occurring at intervals longer than 1 y (Fourrier 2013). Flowering takes place from September to November and fruits are produced from October to February (Aubréville 1962; Hecketsweiler 1992; Doucet 2003; Fourrier 2013). Fruits are available for 1.6 mo on average (Fourrier 2013). Within the study site and during the study period, unripe fruits were observed in December, and ripened from January to February (B. Haurez, pers. obs.). The average density of *Dacryodes normandii* in the study site is 54.8 stems km^{-2} (for dbh >20 cm) (Demarquez & Jeanmart 2004).

2.3 Identification and contribution of vertebrate seed dispersers

2.3.1 Direct observations

In December 2013, six mature trees of *Dacryodes normandii* with the main part of the crown visible from the ground (hereafter referred to as focal trees), were visited and examined for signs of fruiting (mainly unripe fruits in the canopy and on the ground). In order to ensure independence of observations, focal trees were located at least 1 km apart (Babweteera & Brown 2008). Observations were made with binoculars between 06h30 and 17h30 in periods of availability of both unripe and ripe fruits (from mid-December to end of February). Observers were hidden in a position providing the best visibility of the focal tree canopy. For all vertebrate visits to focal trees the following information was recorded: animal species; feeding behaviour when eating fruits and/or seeds (Chapman & Chapman 1996; Kitamura *et al.* 2006); time and duration of visits; and number of animals observed (Kitamura *et al.* 2006). Sampling effort was defined as the number of observation hours.

2.3.2 Camera trapping

Camera traps (GameSpy Moultrie M-80XT, approximate detection range 13.5 ± 1.5 m) were installed beneath 10 mature fruiting trees, located at least 1 km from each other (Babweteera & Brown 2008). A pile of fresh *Dacryodes normandii* fruits was placed in front of the camera to attract frugivores (adapted from (Kitamura *et al.* 2006; Babweteera & Brown 2008; Seufert *et al*. 2009; Moupela *et al*. 2013). Cameras were monitored weekly from December 2013 to March 2014. They were automatically activated any time a movement occurred within the range of the detector. An independent visit was defined as (1) consecutive records of individuals of different species, (2) non-consecutive records of individuals of the same species, and (3) consecutive records of individuals of the same species taken more than 30 min apart (O'Brien *et al.* 2003). For all independent visits, the following data were recorded: animal species, feeding behaviour when applicable, time and duration of visits, and the number of animals detected (Chapman & Chapman 1996; Kitamura *et al.* 2006). Sampling effort was defined as the number of trap days, i.e. the number of active cameras multiplied by the number of operating days (24 h).

2.3.3 Role of great apes and rodents

To determine the fate of fruits and seeds of *Dacryodes normandii* potentially removed by terrestrial rodents, rodent burrows were sought in the vicinity of four of the focal trees. Twenty-one burrows were found and excavated and seeds were counted and identified to the most precise taxonomic level. Their status was recorded ('intact' when the seed was undamaged, and 'predated' when the seed was broken or rotten and the embryo eaten).

Fresh gorilla faeces collected at nest sites were inspected to investigate the presence of *Dacryodes normandii* seeds during the fruiting period (January–February) in 2012 and 2014. A total of 49 faecal units were analysed. Seed viability after gut passage was assessed through germination trials under the same conditions in both years in a nursery at the study site (n = 53 gut passed seeds). A control treatment, involving seeds extracted from *Dacryodes normandii* fresh fruits and cleaned from pulp (n = 64 control seeds), was also realised. Seeds were sown individually in soil collected from the study site. The nursery was watered on a daily basis. Germination trials involving seeds collected in chimpanzee faeces were not performed because of the complexity of identifying chimpanzee faeces with certainty.

2.4 Data analysis

All photographed or directly observed mammal species were identified following Kingdon (1997) and birds using Serle & Morel (1993). On pictures where only parts of the animals' bodies were visible, they were identified to the most precise taxonomic level possible or classified as 'undetermined'. Additionally, to avoid incorrect identifications, all red duiker species (*Cephalophus callipygus* Peters, *C. dorsalis* Gray, *C. nigrifrons* Gray, *C. leucogaster* Gray, *C. ogilbyi* Waterhouse) were collectively classified as *Cephalophus* spp.

The duration of visits involving consumption was calculated as the time difference between arrival and departure of the animal directly observed, or the time between the first and last photographs of the visit. As the relative amount of fruit consumed, a component of dispersal effectiveness, is influenced by the frequency of visits and their duration (Schupp 1993), an index of fruit consumption, I_{FC} was computed as follows (adapted from Moupela *et al.* 2013):

$I_{FC} = (N_{obs.cons} / N_{obs.}) D$ (1)

with $N_{obs.cons}$ = number of observations of a given species involving consumption of fruits, N_{obs} = total number of observations of this species, and D = mean length of visit involving consumption of fruits. The ecological functions of different animal species were determined using the information provided by pictures and fruit remnants, as well as from existing literature. Animals were classified into four categories (adapted from Gautier-Hion *et al.* 1985 and Moupela *et al.* 2013): (1) predator: those that destroy the seeds; (2) disperser: those that consume fruits while leaving seeds intact and removing them from the vicinity of the parent trees; and (3) neutral: those that show no interest in *D. normandii* fruits. All species displaying null I_{FC} were considered neutral.

The effect of passage in gorilla gut on seed germination was evaluated through the comparison of germination success of gut-passed seeds with that of control seeds, with a Chi² test.

3 RESULTS

3.1 Identification and contribution of seed dispersers

In 172 h of direct observations, three species of *Dacryodes normandii* disperser were identified: one arboreal primate, the putty-nosed monkey (*Cercopithecus nictitans nictitans*), and two large birds, the white-crested hornbill (*Tropicranus albocristatus*) and the great blue turaco (*Corythaeola cristata*) (**Table 17**).

In a total of 796 camera-trap days, 572 vertebrate detection events occurred (97.2% involving mammals, 1.7% birds and 1.1% undetermined). Twenty-six species or groups of species were identified from camera-trap pictures, accounting for 71.3% of detection events. The remaining 28.7% involved undetermined animals, mostly Muridae (24.0%). Three of the identified species acted predominantly as seed dispersers: two great apes, the western lowland gorilla and the central chimpanzee, and the African forest elephant (*Loxodonta cyclotis,* Proboscidea) (**Table 17**). Both great ape species frequently consumed *D. normandii* fruits and their consumption events were relatively long, resulting in the highest I_{FC} observed (74 and 13 respectively). Elephants less frequently consumed *D. normandii* fruits and their visits were much shorter (I_{FC} of 0.13).

The remaining species (n = 8) observed to interact with *D. normandii* fruits were likely to act mainly as predators. They were involved less frequently in consumption events and their visits were consistently shorter than 10 min (I_{FC} = 0.86–0.0073) (**Table 17**).

No *D. normandii* seeds were found in the 21 prospected rodent burrows (mean depth ± SD = 36 ± 10 cm, range = 20-70 cm). Two destroyed seeds of another species of Burseraceae (*Santiria trimera* (Oliv.) Aubrév.) were found (**Table 18**). These results support the evidence that terrestrial rodents are mainly predators of *D. normandii* and that dispersal events through scatter-hoarding are likely to be rare.

Table 17 Animal species involved in consumption events during direct and indirect observations of *Dacryodes normandii* trees in a Gabonese logging concession from December 2013 to March 2014, ordered by I_{FC}. $N_{obs.cons}$ = number of observations of a given species involving consumption of fruits, N_{obs} = total number of observations of this species and D = mean length of visit involving consumption of fruits, $I_{FC} = (N_{obs.cons} / N_{obs.}) D$

Species	Common name	N_{obs}	$N_{obs.cons}$	D (min)	I_{FC}	Role
Gorilla gorilla gorilla Savage & Wyman	Western lowland gorilla	8	7	85	74	Disperser
Pan troglodytes troglodytes Blumenbach	Central chimpanzee	7	4	23	13	Disperser
Cercopithecus nictitans nictitans L.	Putty-nosed monkey	2	2	5	5.0	Disperser
Tropicranus albocristatus Cassin	White-crested hornbill	1	1	3	3.0	Disperser
Funisciurus pyrropus Cuvier	Fire-footed rope squirrel	7	1	6	0.86	Predator, disperser (occasional through scatter-hoarding or dropping during transport)
Corythaeola cristata Vieill.	Great blue turaco	3	2	1	0.67	Disperser
Cephalophus silvicultor Afzelius	Yellow-backed duiker	28	3	3	0.32	Predator
Artherurus africanus Gray	Brush-tailed porcupine	33	2	5	0.30	Predator, disperser (occasional through scatter-hoarding or dropping during transport)
Epixerus ebii Temminck	Ebian palm squirrel	25	3	2	0.24	Predator, disperser (occasional through scatter-hoarding or dropping during transport)
Loxodonta cyclotis Matschie	African forest elephant	39	5	1	0.13	Disperser
Cricetomys emini Wroughton	Giant pouched rat	35	2	1	0.057	Predator, disperser (occasional through scatter-hoarding or dropping during transport)
Cephalophus spp.	Red duikers	101	5	1	0.050	Predator
Funisciurus isabella Gray	Lady Burton's rope squirrel	65	1	1	0.015	Predator, disperser (occasional through scatter-hoarding or dropping during transport)
Undetermined Muridae	Murid	137	1	1	0.0073	Predator, disperser (occasional through scatter-hoarding or dropping during transport)

Table 18 Results of excavation of rodent burrows in the search for Dacryodes normandii seeds in a Gabonese logging concession

Seed species	Family	Occurrence	Total number of seeds
Antrocaryon klaineanum Pierre	Anacardiaceae	1	1
Canarium schweinfurthii Engl.	Burseraceae	2	2
Dacryodes buettneri (Engl.) H.J. Lam.	Burseraceae	2	10
Diogoa zenkeri (Engl.) Exell & Mendonça	Olacaceae	2	3
Elaeis guineensis Jacq.	Arecaceae	1	1
Olacaceae spp.	Olacaceae	12	119
Panda oleosa Pierre	Pandaceae	1	30
Pseudospondias microcarpa (A.Rich.) Engl.	Anacardiaceae	1	15
Santiria trimera (Oliv.) Aubrév.	Burseraceae	2	2
Undetermined	Undetermined	1	11
Empty burrows		15	
Total		**40**	**194**

We observed that 18% of fresh gorilla faeces analysed (n = 49) contained *D. normandii* seeds (number of seeds = 170, mean number of seeds per faecal sample ± SD = 18.9 ± 14.4, range = 0–49), which exhibited a germination success of 68% (n = 53 seeds sown). The germination success displayed by seeds passed through the gorilla gut was not significantly different from that of seeds extracted from fresh fruits (n = 164 seeds sown, mean germination success = 73%) (df = 1, $\chi^2 = 0.74$, P = 0.39).

4 DISCUSSION

Owing to direct and indirect observations, the present study identified six disperser species of *Dacryodes normandii*, among which primates were the most important. In particular, supported by I_{FC} high values, great apes are likely to be the main dispersers of this species. Rodents, squirrels and duikers are mainly predators of *D. normandii* seeds.

4.1 Importance of great apes in seed dispersal of *Dacryodes normandii*

Among primate species, the western lowland gorilla is considered a very effective seed disperser (Tutin *et al.* 1991; Haurez *et al.* 2013; Petre *et al.* 2013) and an essential actor in forest dynamics and maintenance of forest structure (Tutin 2001). Seeds dispersed by gorillas are generally viable (Voysey *et al.* 1999; Poulsen *et al.* 2001; Petre *et al.* 2015b). The high germination success displayed by seeds of *D. normandii* collected in gorilla faeces (68%), which does not differ from that of unpassed seeds, attests to their preservation during gut passage. In other sites, consumption of *D. normandii* fruits has already been reported . Since gorillas exhibit (1) a high frequency of visiting fruiting *D. normandii* trees, (2) long visit durations in cases of consumption, and (3) the consumption of a large number of fruits at each visit, they may provide reliable dispersal services for this tree species. Furthermore, more than 50% of gorilla dung is deposited at nest sites (Todd *et al.* 2008) and gorillas preferentially select open habitats for nesting (Tutin *et al.* 1995; Willie *et al.* 2012; Haurez *et al.* 2014; Petre *et al.* 2015b), which offer suitable conditions for seed germination and seedling growth (Tutin *et al.* 1991; Rogers *et al.* 1998; Voysey *et al.* 1999). *D. normandii* has intermediate light requirements (Doucet 2003), therefore suggesting that its seeds and seedlings may benefit from the light conditions characteristic of gorilla nest sites (Tutin *et al.* 1991; Rogers *et al.* 1998; Voysey *et al.* 1999). As a consequence, gorilla may provide directed dispersal for *D. normandii* (Howe & Smallwood 1982), as has been observed for other plant species with different degrees of shade tolerance (from high tolerance to shade intolerance) (Voysey *et al.* 1999; Petre *et al.* 2015b). However, the fate of gorilla-deposited seeds of *D. normandii* is still largely unknown. A study encompassing all stages from faecal deposition to sapling recruitment may help to reliably assess the likely importance of gorillas in the regeneration of *D. normandii*.

The chimpanzee is considered a high-quality disperser (Gross-Camp & Kaplin 2011), displaying seed swallowing, spitting and wadging behaviours, depending on the plant species (Lambert 1999; Chapman & Russo 2005; Gross-camp & Kaplin 2005). Chimpanzees generally disperse viable seeds (Wrangham *et al.* 1994), although their impact on germination potential depends on the taxon considered (Gross-camp & Kaplin 2005). *Dacryodes normandii* pulp is a valuable food resource for the chimpanzee in Gabon, and its seeds are commonly observed in chimpanzee faeces (Tutin & Fernandez 1993). However, data on the disperser effectiveness of chimpanzee for this species are lacking.

4.2 Other dispersers and predators of *Dacryodes normandii*

Medium- and small-sized primates, for example *Cercopithecus* spp. (Gautier-Hion *et al.* 1985; Lambert 1999), are important dispersers (Poulsen *et al.* 2001; Chapman & Russo 2005), dispersing seeds through defecation and spitting (Chapman & Russo 2005). The present study highlights a role in *D. normandii* seed dispersal for the putty-nosed monkey (*C. n. nictitans*). This species is known to consume the fruit pulp of five species of Burseraceae that share fruit characteristics with *D. normandii* (Gautier-Hion *et al.* 1980; Poulsen *et al.* 2001, 2002), and *Santiria trimera* seeds exhibit enhanced germination after dispersal by this monkey (Poulsen *et al.* 2001).

The role of the African forest elephant in seed dispersal is well documented (Blake *et al.* 2009; Campos-Arceiz & Blake 2011). The elephant consumes *D. normandii* fruits, without destroying their seeds, as evidenced by the presence of whole seeds in dung (Feer 1995a; Fourrier 2013), and can therefore be considered as a disperser of this species (Gautier-Hion *et al.* 1985). However, considering their low I_{FC} (0.13) and the fact that, based on camera-trap observations, they appear to only consume *D. normandii* opportunistically while moving, their role is likely to be of lesser importance.

Dacryodes normandii belongs to one of the three most important families for specialised avian frugivores (Snow 1981). The present study has suggested a dispersal role for the white-crested hornbill (*Tropicranus albocristatus*) and the great blue turaco (*Corythaeola cristata*), even though the overall number of observations of birds feeding on *D. normandii* was surprisingly low. Turacos and hornbills are endozoochorous dispersers, as passage through their gizzards does not destroy seeds (Gautier-Hion *et al.* 1985).

Three squirrels (*Funisciurus pyrropus, F. isabella* and *Epixerus ebii*), two species of terrestrial rodents (*Atherurus africanus* and *Cricetomys emini*) and one undetermined Muridae were observed to handle *D. normandii* fruits. All these taxa are predominantly seed predators (Emmons 1980; Gautier-Hion et al. 1985; Beaune et al. 2012b), but may contribute to short-distance dispersal through food hoarding and seed dropping during transport to and from the cache (Emmons 1980; Gautier-Hion *et al.* 1985;

Moupela *et al.* 2013). However, as no seed of *D. normandii* was found in the prospected burrows, these dispersal events are thought to be rare.

Fallen fruits are an important food resource for duikers (Seufert *et al.* 2009). *Cephalophus* spp. have been shown to act both as seed dispersers (mostly for species with medium-sized fruit and hard stones) and predators (for those with less resistant seeds) (Gautier-Hion *et al.* 1985; Beaune *et al.* 2013b). The red duikers spit out hard seeds (e.g. *Antrocaryon klaineanum*) during rumination (Gautier-Hion *et al.* 1985), but the seed size and the weak coat resistance of *D. normandii* suggests a vulnerability to crushing and destruction during mastication (as with *Santira trimera*, Gautier-Hion *et al.* 1985; Feer 1995b).

5 CONCLUSIONS AND PERSPECTIVES

This study identified six taxa as dispersers of *Dacryodes normandii* seeds and eight as seed predators, out of 14 vertebrate taxa observed consuming the fruits. As some frugivores may fulfil multiple roles, complementary and specific studies (faecal analysis and germination experiments, seed displacement monitoring, identification and germination trials of seeds in rodents' burrows, rumen and stomach content characterisation, etc.) are required to contribute to a fuller understanding of the extent of seed predation and dispersal of *D. normandii*.

The main dispersers identified in this study are great apes: the western lowland gorilla (*Gorilla gorilla gorilla*) and, to a lesser extent, the central chimpanzee (*Pan troglodytes troglodytes*). African great apes are known to disperse the seeds of many species some of which provide timber and non-timber forest products (this study, Williamson *et al.* 1990; Tutin & Fernandez 1993; Doucet 2003; Fourrier 2013; Petre *et al.* 2015b) or are endemic to the Gabonese forests (this study, Tutin *et al.* 1991). In particular, the western lowland gorilla is thought to provide incomparable dispersal services because of seed dispersal directed to open-canopy habitats (Rogers *et al.* 1998; Voysey *et al.* 1999; Petre *et al.* 2013).

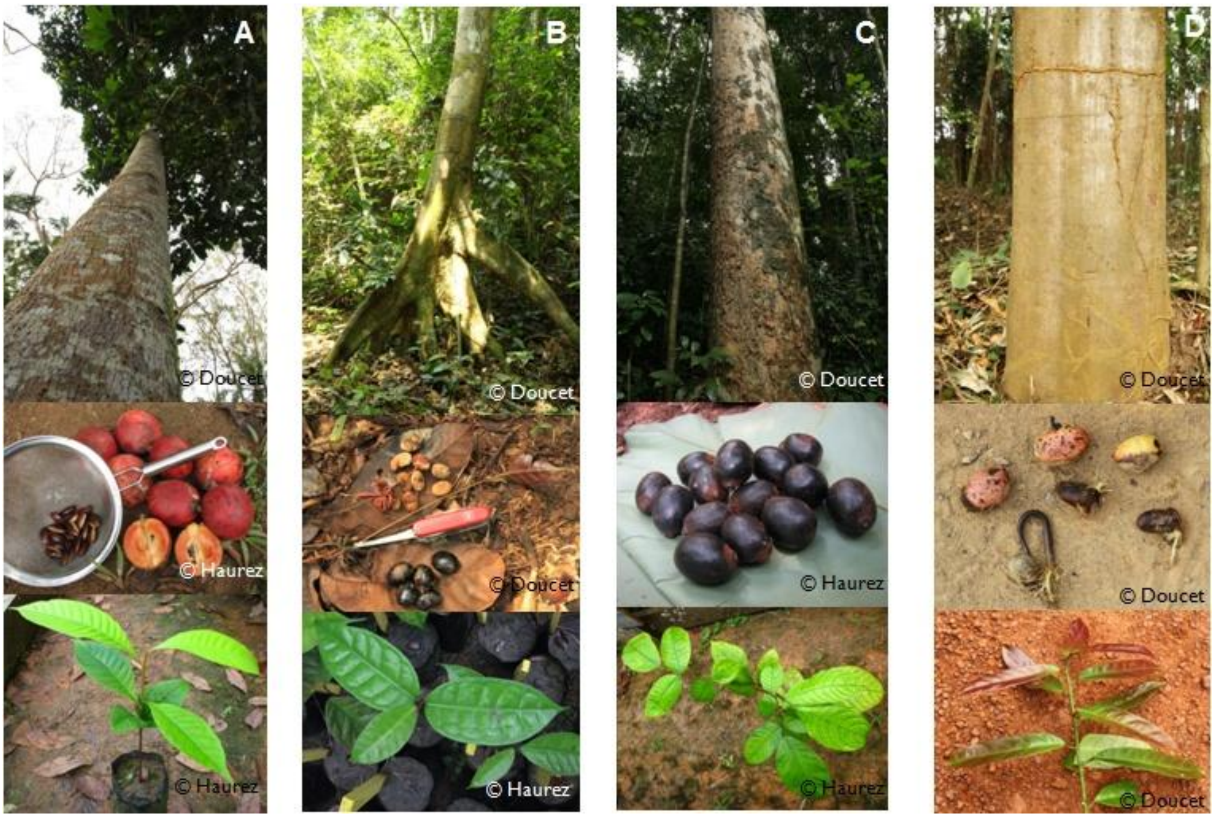
Gorillas and chimpanzees are endangered; threatened by habitat loss and modification, epidemic diseases (such as Ebola hemorrhagic fever), commercial hunting (for bushmeat, the pet market and trophies) and persecution as a result of human-wildlife conflicts (Walsh *et al.* 2008). The depletion of great apes would result in changes in seed dispersal and seedling recruitment which would in turn impact upon forest ecosystem dynamics and regeneration (Wright *et al.* 2000; Effiom *et al.* 2013; Petre *et al.* 2013).

Therefore, this study encourages the implementation of great ape conservation strategies as critical to ensuring the preservation of tropical forest ecosystems. The maintenance of great ape dispersal services may also participate in the sustainable management of timber and non-timber forest product species.

CHAPITRE 8 EFFET DES CONDITIONS DE DÉPÔT DES GRAINES DISPERSÉES PAR LE GORILLE SUR LE DESTIN DES PLANTULES

Dans les chapitres précédents, nous avons montré que le gorille des plaines de l'Ouest dispense des services de dispersion de qualité pour de nombreuses espèces, et qu'il est notamment impliqué, parfois en tant que principal disperseur, dans la dispersion d'essences de bois d'oeuvre. Le Chapitre 8 s'intéresse à l'effet des conditions de dépôt des graines sur le devenir des plantules. Plus particulièrement, nous allons évaluer l'impact du dépôt dans de la matière fécale et l'impact du dépôt au sein de sites de nidification à canopée ouverte sur la croissance et la survie des plantules.

Adapté de Haurez B., Brostaux Y., Petre C-A. & Doucet J-L., In Press. Is the western lowland gorilla a good gardener? Evidence for directed dispersal in Southeast Gabon. *Bois et Forêt des Tropiques*, **324**(2), p. 38-49.



Fûts, fruits et/ou graines et plantules de quatres espèces dispersées par le gorille des plaines de l'Ouest. (A) *Chrysophyllum lacourtianum*, (B) *Santiria trimera*, (C) *Dacryodes normandii* et (D) *Plagiostyles africana.* © B. Haurez & J.-L. Doucet

Résumé

Dans les forêts tropicales d'Afrique Centrale, le gorille des plaines de l'Ouest dépose la plupart des graines qu'il disperse dans des nids installés en forêt à canopée ouverte, propices à la croissance de plantules, laquelle est susceptible d'être renforcée par l'effet fertilisant des matières fécales entourant les graines. Cet effet fertilisant n'avait jamais été testé. Notre étude visait ainsi à déterminer si le dépôt de graines par les gorilles (i) dans une matrice fécale et (ii) dans leurs nids présente un avantage pour le développement des plantules (taux de croissance et de foliation) et pour leur survie (% de plantules survivantes). Pour évaluer l'effet de la matrice fécale, des graines de *Santiria trimera* (Burseracée), *Chrysophyllum lacourtianum* (Sapotacée) et *Plagiostyles africana* (Euphorbiacée) recueillies dans des déjections de gorilles ont été semées en pépinière avec et sans matrice fécale. Des plantules de *Santiria trimera* et *Dacryodes normandii* (Burseracées) ont été installées dans des nids et en forêt de terre ferme à couvert fermé afin d'évaluer l'impact du site dépôt des graines sur le développement et la survie des plantules. Nos observations montrent une influence positive de la matrice fécale sur le développement des plantules des essences étudiées, mais aucun effet sur leur survie. Concernant les sites de dépôt, les taux de croissance observés étaient de deux à dix fois plus élevés dans les nids qu'en forêt à couvert fermé. Le développement accru des plantules est corrélé positivement avec l'ouverture du couvert forestier. Des études *in situ* de la germination et de la croissance et la survie des plantules sont nécessaires pour mieux caractériser le destin des graines dispersées par les gorilles. Cependant, nos résultats tendent à prouver que les gorilles jouent un rôle de dispersion dirigée important en déposant les graines en forêt à couvert ouvert.

Mots-clés: *Gorilla gorilla gorilla*, effet fertilisant, dispersion dirigée, comportement de nidification, dispersion des graines, croissance des plantules, survie des plantules, Gabon

Abstract

Within Central African tropical forests, the western lowland gorilla deposits the majority of its dispersed seeds in nest sites presenting high light conditions, that can favour seedling growth. Moreover, the faecal matrix surrounding the seeds can act as a fertilizer and further enhance seedling development. This fertilisation effect had not been tested yet. This research aimed to determine if seed deposition by gorillas (i) in faecal matrix and (ii) at nest sites is advantageous for seedling development (growth rate and foliation rate) and survival (% of surviving seedlings). To assess the effect of faecal matrix, seeds of *Santiria trimera* (Burseraceae), *Chrysophyllum lacourtianum* (Sapotaceae) and *Plagiostyles africana* (Euphorbiaceae) collected from gorilla faeces were sown in a nursery with and without faecal matrix. Seedlings of *Santiria trimera* and *Dacryodes normandii* (Burseraceae) were installed at nest sites and at closed canopy *terra firma* forest sites to evaluate the impact of seed deposition on seedling development and survival. Faecal matrix was observed to positively influences seedling development on a specific basis, but showed no effect on survival. Regarding seed deposition sites, the observed development rates were two to ten times higher at nest sites than at closed-canopy forest. This enhanced seedling development was positively correlated to canopy openness. *In situ* studies of seed germination, and seedling growth and survival are needed to characterise more precisely the fate of gorilla-dispersed seeds. However, our results offer evidence that gorillas provide important directed dispersal services by depositing seeds most frequently in open canopy sites.

Key words: *Gorilla gorilla gorilla*, fertilisation effect, directed dispersal, nesting behaviour, seed dispersal, seedling growth, seedling survival

1 INTRODUCTION

The majority of tropical plant species (50–95 %) possess fleshy fruits adapted to vertebrate consumption, and hence animal-mediated seed dispersal (Howe and Smallwood, 1982). The general advantages of endozoochory are escape from distance- and density-dependent mortality under the mother tree (Janzen-Connell effect) (Janzen, 1970; Connell, 1971), colonisation of new habitats and sites, and gene flow among and between populations (Howe and Smallwood, 1982; Howe, 1989, Jansen and Zuidema, 2001; Stoner and Henry, 2008). In addition, endozoochory may lead to directed dispersal in cases when the disperser deposits most seeds in favourable sites (Howe and Smallwood, 1982; Jansen and Zuidema, 2001). Passage through the digestive tract and deposition in faecal manure may also enhance seed dispersal effectiveness (Dinerstein and Wemmer, 1988; Jansen and Zuidema, 2001; Traveset *et al.,* 2001, 2007). The spatial distribution pattern of dispersed seeds depends on disperser physiology (gut passage time) and behaviour (daily path length, habitat use, nesting behaviour, etc.) (Stoner and Henry, 2008; Bueno *et al.,* 2013). Because of these species-specific factors, functional redundancy between two frugivore species is limited (Bueno *et al.,* 2013 but see Mcconkey *et al.,* 2014). As a result of anthropogenic disturbances, many forest-living animal populations, especially large mammals that provide important dispersal services, are threatened by decline, or even local extinction (Wright, 2003; Andriantsaralaza *et al.,* 2013). Understanding the role of these vertebrates in plant regeneration is important to reveal the potential effects of 'defaunation' (Galetti and Dirzo, 2013; Kurten, 2013). Such knowledge is particularly relevant when high value tree species, either used for timber or non-timber products by rural populations, are dispersed by threatened mammals (Daïnou *et al.,* 2012; Rosin, 2014).

Among Central African frugivores, the critically endangered western lowland gorilla (*Gorilla gorilla gorilla* Savage and Wyman) is considered a key disperser (Petre *et al.,* 2013). This species disperses seeds in a spatially and temporally bimodal pattern with more than 50% of seeds deposited at nest sites (Todd *et al.,* 2008), which are preferentially installed in open habitats (Tutin *et al.,* 1991; Rogers *et al.,* 1998; Voysey *et al.,* 1999; Petre *et al.,* 2015a). Seedling growth is enhanced in tree fall gaps, even for shade tolerant species (Howe *et al.,* 1985; Popma and Bongers, 1988 and references therein; Schupp *et al.,* 1989), and a beneficial effect of deposition at gorilla nest sites was observed for three tree species at Lopé, Gabon (Tutin *et al.,* 1991; Rogers *et al.,* 1998; Voysey *et al.,* 1999). As logged forest is one habitat type preferentially selected by gorillas for nesting (Arnhem, 2008), their dispersal services are thought to be critical in the context of logged forests. However, the fate of seedlings remains poorly studied. Some studies showed that seed predation pressure by rodents was higher at tree fall gaps (Schupp, 1988a), while other demonstrated that seedling survival was higher because of a lower pathogen pressure (Schupp *et al.,* 1989). A study in Cameroon demonstrated that seed deposition at gorilla nest sites benefits dispersed seeds as a result of a lower mean burial depth by the dung beetle community, compared to what was observed in closed canopy forest areas (Petre *et al.,* 2015b). These potential advantages brought by seed deposition at nest sites require further investigation and to our knowledge, no study has yet been undertaken to assess the fertilisation effect of the gorilla faecal matrix on seedling growth.

This study assessed the impact of being deposited in a faecal matrix, and at nest site locations, on seedling growth and seedling survival. Specifically, the following hypotheses were tested: (1) the presence of a faecal matrix surrounding the seeds enhances seedling growth and survival; (2) seedling growth is faster and seedling survival is higher at nest sites than at closed canopy *terra firma* forest sites; (3) seedling survival is lower under a conspecific tree (Janzen-Connell effect) (Janzen, 1970; Connell, 1971); (4) enhanced seedling development in open canopy nest sites results from higher light availability.

2 METHODS

2.1 Study site

Precious Woods Gabon is a 617,000 ha sustainably managed and certified logging concession located in Southeast Gabon. The total average annual rainfall is 1,700 mm, mainly distributed through two rainy seasons (March-May and September-December) (Moupela *et al.,* 2013). A dry season (monthly precipitation <100 mm) is observed from June to August. The average annual temperature is 26°C, with minimum values recorded in July and August (Moupela *et al.,* 2013). The highest temperatures are observed in February to April. The concession comprises a lowland evergreen forest dominated by Burseraceae and Fabaceae. The study was carried out in an area of 13,410 ha (Bambidie AAC 2012, 0°44'–0°52' South, and 013°06'–13°17' East) where gorilla density was estimated at 1.5 weaned gorilla/km² (Haurez *et al.,* 2014). Nesting behaviour at this site was characterised by a preferential selection of open canopy *terra firma* forest for nest building (Haurez *et al.,* 2014).

2.2 Study species

Four tree species typical of the study area were selected: *Santiria trimera* (Oliv.) Aubrév. (Burseraceae), *Plagiostyles africana* Prain ex De Wild. (Euphorbiaceae), *Dacryodes normandii* Aubrév. and Pellegr. (Burseraceae) and *Chrysophyllum lacourtianum* De Wild. (Sapotaceae) (Doucet, 2003). Their average densities in the logging concession were previously estimated to be 30.2, 7.6, 1.6 and 0.20 trees ha^{-1} (dbh > 10 cm), respectively (the density given for *C. lacourtianum* was estimated based on the density of *Chrysophyllum* spp.) (Doucet, 2003; Medjibe *et al.,* 2013). All are evergreen, shade-bearer (*C. lacourtianum, S. trimera* and *D. normandii*) or non-pioneer light-demanding species (*P. africana*) (Doucet, 2003; Petre *et al.,* 2015a). Two (*C. lacourtianum* and *D. normandii*) are timber species, and the fruits of three (*C. lacourtianum, S. trimera* and *D. normandii*) are valuable non-timber forest products (NTFPs) (Aubréville, 1962; Lemmens, 2007; Brink, 2008). The four tree species are also used by local populations for various medicinal and cultural purposes (Aubréville, 1962; Lemmens, 2007; Brink, 2008; Schmalzer and Lemmens, 2008). Gorillas consume fruits of these species in abundance whenever they are available and their seeds are not destroyed by passage through the gorilla gut (Fourrier, 2013; B. Haurez pers. obs.; C.-A. Petre, pers. obs.) (**Figure 15**). The use of the different species, as well as the number of repetitions, for our experiments was based on the availability of seeds and faecal matrix, or seedlings at the time of the trials.

Figure 15 Seeds of Santiria trimera deposited in a faecal unit at a western lowland gorilla nest site in Southeast Gabon

2.3 Fertilisation effect of faecal matrix on seedling growth and survival

The fertilisation effect of the presence of a faecal matrix was assessed through seedling growth trials in a nursery for three of the species: *C. lacourtianum*, *P. africana* and *S. trimera* (**Figure 16**).

Figure 16 Seedlings of Chrysophyllum lacourtianum growing in a nursery in Southeast Gabon

Seeds extracted from gorilla faeces (**Figure 17**) were sown following three treatments: (1) cleaned seeds directly sown in the soil, (2) cleaned seeds placed in a ovoid ball of faecal material (approximately 5x3x2 cm). A control treatment was realised for *C. lacourtianum* and *S. trimera*, with seeds extracted from fruits. Because all seeds found under *P. africana* trees were already germinated, the control treatment was not implemented for this species. Each seed was sown singly in a plastic bag filled with soil collected from the study site. In order to limit the effect of variability of gorilla diet composition on the faecal matrix treatment (as a result of differences in food chemical composition), all faeces to be used in a trial were mixed together before forming the faecal ball. Seed germination was monitored daily. Growth rate (cm day^{-1}), foliation rate (number of leaves day^{-1}) and proportion of surviving individuals (%) were calculated (Popma and Bongers, 1988; Loiselle, 1990) after 12 months. Depending on seed availability, five trials were realised for *C. lacourtianum* and *S. trimera*, and only one for *P. africana* (**Table 19**). Every trial involved seeds coming from the same faeces or the same tree (control treatment) sown on the same day.

Figure 17 Collection of a fresh gorilla faecal unit on a logging road in Southeast Gabon © J-L. Doucet

Table 19 Description of the fertilisation effect trials

Trial	Treatment	No. seeds sown	No. seeds germinated	No. surviving seedlings
Chrysophyllum lacourtianum				
CL1	Seed from faeces	6	5	5
	Seed from faeces in faecal matrix	6	6	6
	Control	6	0	NA
CL2	Seed from faeces	1	1	1
	Seed from faeces in faecal matrix	1	1	0
	Control	1	0	NA
CL3	Seed from faeces	7	6	6
	Seed from faeces in faecal matrix	7	7	6
	Control	7	0	NA
CL4	Seed from faeces	14	14	14
	Seed from faeces in faecal matrix	14	12	11
	Control	14	7	6
CL5	Seed from faeces	12	11	10
	Seed from faeces in faecal matrix	12	12	12
	Control	12	0	NA
Plagiostyles africana				
PA1	Seed from faeces	50	37	33
	Seed from faeces in faecal matrix	50	34	30
Santiria trimera				
ST1	Seed from faeces	6	4	4
	Seed from faeces in faecal matrix	6	6	6
	Control	6	0	NA
ST2	Seed from faeces	4	4	4
	Seed from faeces in faecal matrix	4	4	4
	Control	4	1	NA
ST3	Seed from faeces	8	0	NA
	Seed from faeces in faecal matrix	8	0	NA
	Control	8	0	NA
ST4	Seed from faeces	8	8	7
	Seed from faeces in faecal matrix	8	5	4
	Control	8	0	NA
ST5	Seed from faeces	3	1	0
	Seed from faeces in faecal matrix	3	1	1
	Control	3	1	0

2.4 Effect of deposition site on seedling growth and survival

In order to test the effect of deposition site on seedling growth and survival, nursery-raised seedlings of *S. trimera* (11 months old) and *D. normandii* seedlings (1 month old) were planted in 1 m² plot, 30 cm apart (1) at nest sites in open canopy *terra firma* forest, and (2) in closed canopy *terra firma* forest. For *D. normandii*, a third treatment comprised seedlings installed (3) in closed canopy *terra firma* forest under a mature fruiting conspecific. This treatment was undertaken to test for the influence of the proximity to a conspecific on predator and pathogen pressure (Janzen-Connell effect) (Janzen, 1970; Connell, 1971). The surrounding vegetation was kept intact in each plot. For *S. trimera*, two repetitions were performed for each treatment, and for *D. normandii*, four repetitions were performed for treatment 2 and three for treatments 1 and 3. Fifteen seedlings and five seedlings were installed in each plot for *S. trimera* and *D. normandii*, respectively. All the seedlings of a given species were installed the same day. Seedling growth (growth rate and foliation rate) and survival (% of surviving seedlings) were assessed for *S. trimera* and *D. normandii* after 18 and 9 months, respectively.

2.5 Effect of light availability on seedling growth and survival

Canopy openness was measured at each seedling plot using hemisphere pictures taken with a 4.5 mm Sigma circular fisheye lens on a Canon EOS D50 camera. Two repetitions of pictures were taken at the centre of the plots between 6.00 and 7.30 am, at 1 m height, with the lens placed vertically on a tripod and the camera oriented North. Shutter speed and aperture were set as to maximize the contrast between the canopy and the sky. Canopy openness was estimated with Gap Light Analyzer 2.0 using a standard image to define the hemisphere circle. A mean measure of canopy openness (%) was calculated for each plot by averaging the values obtained for the two repetitions. The resulting mean canopy openness value was used as a proxy for light availability at the site.

2.6 Data analysis

Generalized Linear (Mixed) Models or General Linear (Mixed) Models were adjusted to evaluate the effect of (1) faecal matrix and (2) type of site on seedling growth (growth rate and foliation rate) and seedling survival rate (**Figure 18**). Trial repetitions and plots, respectively, were used as a random factor to take into account potential uncontrolled variability of the response in the initial models, but were discarded when non significant. Depending on the adjusted models, the significance of a factor was assessed by comparing the models with and without the factor with a Chi-square test or an F-test. In order to test the influence of light availability, estimated by canopy openness, on seedling growth rate, foliation rate and proportion of surviving seedlings, Linear Regression Models and Generalized Linear Models were performed.

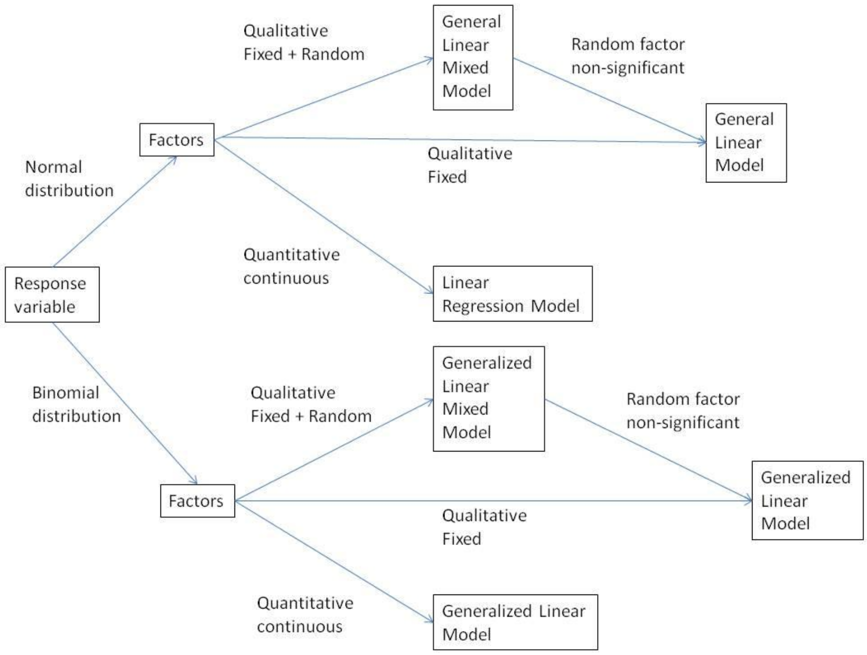


Figure 18 Schematic representation of statistical tests. Comparision of models to assess the significance of a factor were performed with Chi-square tests (mixed models) or F-tests (fixed models).

All statistical analyses were performed in R 3.1.3 (R Core Team, 2012) using the package lme4 and the function ‘glmer’ for Generalized Linear Mixed Models, ‘lmer’ for General Linear Mixed Models, ‘glm’ for Generalized Linear Models and ‘lm’ for Generalized Linear Models.

3 RESULTS

3.1 Fertilisation effect of faecal matrix on seedling growth and survival

These results are displayed in **Figure 19**. In the case of *S. trimera*, only two seeds under the control treatment germinated, and both seedlings died. Therefore, the control treatment was conserved in the analysis only for *C. lacourtianum.* Seedlings of *S. trimera* and *C. lacourtianum* showed no increase in growth rate (*S. trimera*: df = 1, $\chi^2 = 0.65$, p = 0.42, and *C. lacourtianum*: df = 2, $\chi^2 = 0.59$, p = 0.75) but a light increase in foliation rate (*S. trimera*: df = 1, $\chi^2 = 3.91$, p = 0.048, and *C. lacourtianum*: df = 2, $\chi^2 = 6.46$, p = 0.040) in relation to the presence of a faecal matrix. A positive effect of presence of a faecal matrix on seedling growth (df = 2 and 61, F = 426, $p < 0.001$) and foliation rate (df = 1 and 69, F = 14.60, $p < 0.001$) was observed for *P. africana*. The presence of a faecal matrix did not affect survival of the tested species (*S. trimera*: df = 1, $\chi^2 = 0.31$, p = 0.578, *C. lacourtianum*: df = 2, $\chi^2 = 1.37$, p = 0.50, *P. africana*: df = 1, $\chi^2 = 0.016$, p = 0.90).

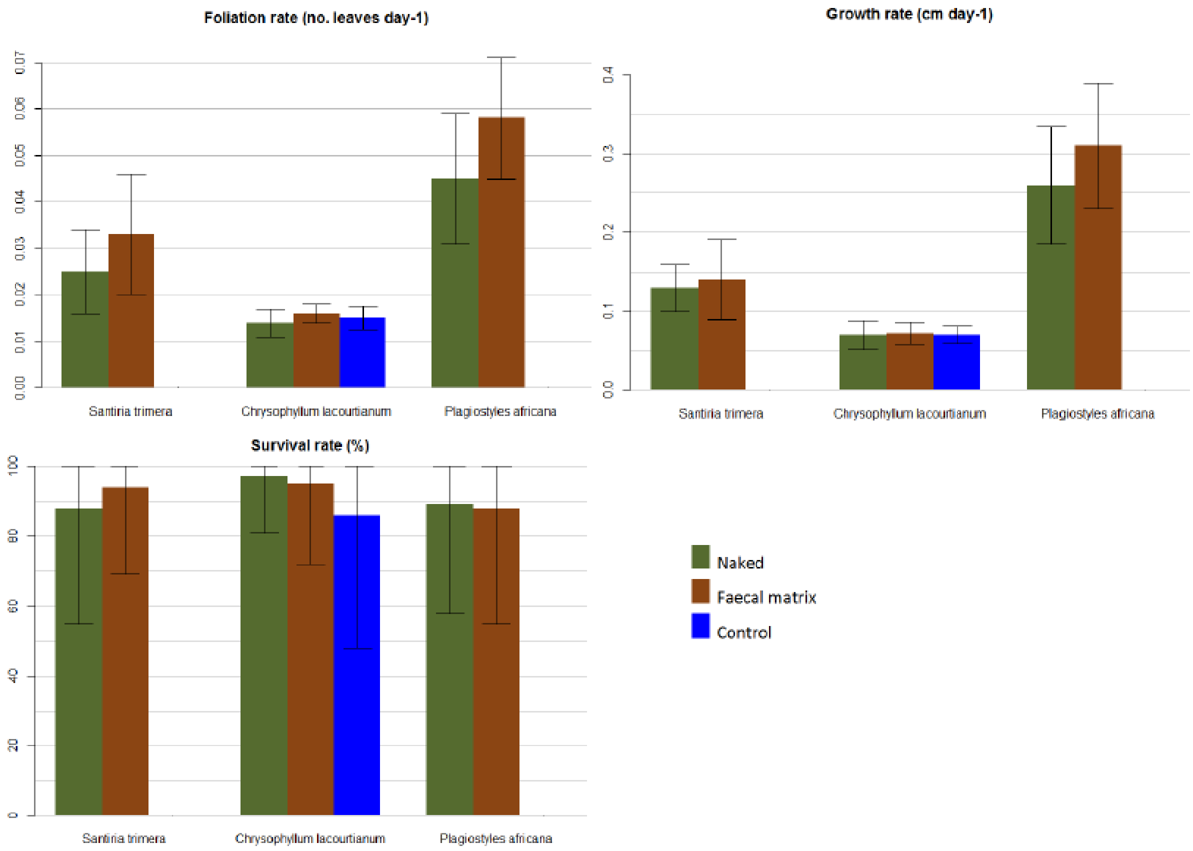


Figure 19 Observed seedling growth rate, foliation rate and survival for three tree species dispersed by western lowland gorillas with (Faecal matrix) and without (Naked) the presence of a faecal matrix surrounding the seeds

3.2 Effect of deposition site on seedling growth and survival

Table 20 presents a synthesis of the parameters recorded in the experimental plots. The results related to deposition sites are presented in **Figure 20**. For both species, the growth rate (*S. trimera*: df = 1, χ^2 = 9.77, p = 0.0018, and *D. normandii*: df = 2, χ^2 = 14.7, p < 0.001) and foliation rate (*S. trimera*: df = 1, χ^2 = 5.27, p = 0.027, and *D. normandii*: df = 2, χ^2 = 18.4, p < 0.001) were significantly related to deposition site. Growth rate and foliation rate of *S. trimera* seedlings were 10 and two times higher at nest sites than in closed canopy *terra firma* forest, respectively. For *D. normandii*, seedlings deposited in nest sites presented growth rates about five times faster than in closed canopy forest (both away from and under a conspecific). Foliation rate was approximately 10 times higher at nest sites than in closed canopy forest away from a conspecific. The foliation rate under a conspecific was negative, which could indicate a higher herbivore or pathogen pressure.

Table 20 Parameters recorded at the different deposition site plots

Site	Mean canopy openness (%)	Mean growth rate (cm day^{-1})	Mean foliation rate (no. leaves day^{-1})	Survival (%)
Santiria trimera				
Nest site 1	7.5	0.1068	0.0289	100
Nest site 2	1.8	0.0031	0.0065	82.4
Forest 1	2.9	0.0037	0.0072	80
Forest 2	2.7	0.0034	0.0077	93.8
Dacryodes normandii				
Nest site 1	6.3	0.0286	0.0076	80
Nest site 2	11.2	0.0758	0.0170	80
Nest site 3	6.9	0.0556	0.0129	100
Forest 1	3.6	0.0121	0.0030	100
Forest 2	3.6	0.0146	0.0015	100
Forest 3	4.6	0.0092	0.0008	100
Forest 4	2.9	0.0031	0.0008	100
Conspecific 1	3.6	0.0058	-0.0023	100
Conspecific 2	3.6	0.0062	-0.0015	100
Conspecific 3	1.8	0.0202	0.0028	80

Survival of *S. trimera* seedlings was not significantly related to deposition site (df = 1, $\chi^2 = 0.0024$, p = 0.96). However, a marginal influence was detected for *D. normandii* (df = 2, $\chi^2 = 5.71$, p = 0.057), with a lower survival rate at nest sites, and to a lesser extent under a conspecific.

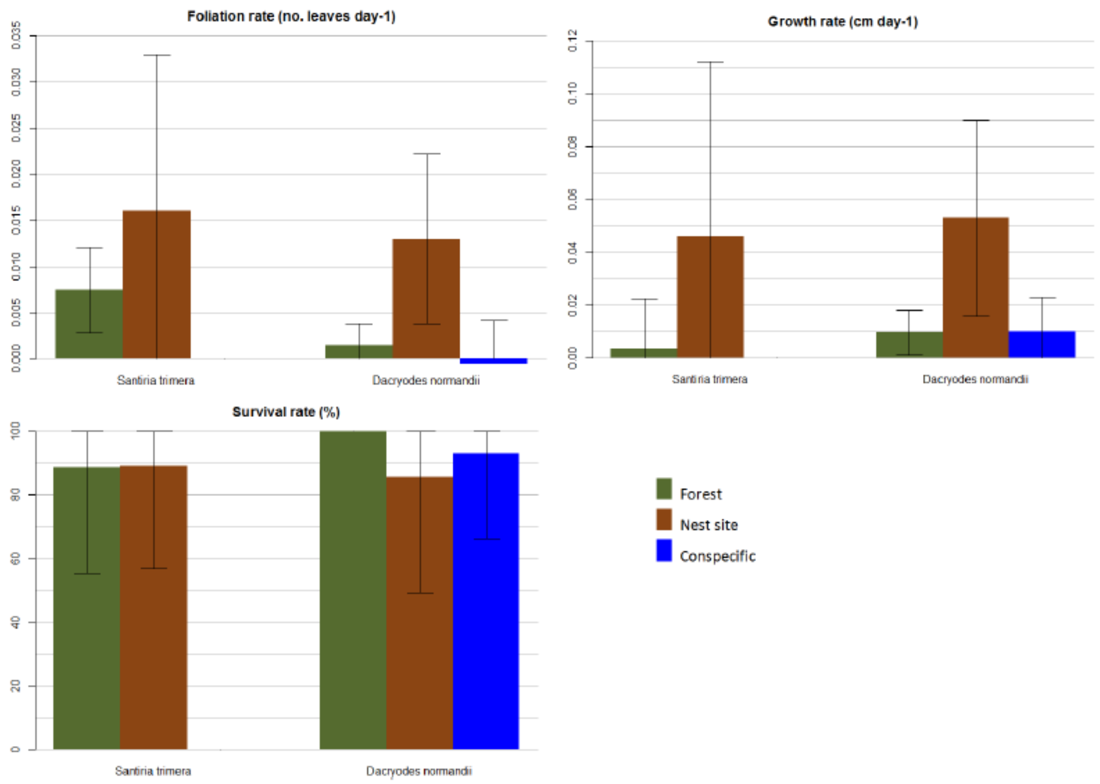


Figure 20 Observed seedling growth rate, foliation rate and survival for two tree species dispersed by western lowland gorillas deposited at three different types of site (closed canopy forest (Forest), nest site (Nest site) and closed canopy forest under a conspecific (Conspecific))

3.3 Effect of light availability on seedling growth and survival

Seedling growth (*S. trimera*: df = 1 and 46, F = 75.2, p < 0.001, and *D. normandii*: df = 1 and 45, F = 44.4, p < 0.001) and foliation rate (*S. trimera*: df = 1 and 45, F = 39.4, p < 0.001, and *D. normandii*: df = 1 and 45, F = 37.2, p < 0.001) were positively correlated to canopy openness for both tested species (**Figure 21** and **Figure 22**). In light of these results, and those obtained when addressing the effect of type of site, it appears that the potential positive effect of deposition at nest sites on seedling growth (**Figure 23**) was linked to the light availability at nest sites. However, in the case of *D. normandii*, the addition of the factor "Type of site" explained the variability in foliation rate better than the factor "Canopy openness" alone (df = 3, F = 11.83, p = 0.0080); but this was not the case for *S. trimera* (df = 1, χ^2 = 3.5386, p = 0.060). For both species, survival rate was not significantly correlated to canopy openness (*S. trimera*: df = 1 and 51, F = 1.75, p = 0.192, and *D. normandii*: df = 1 and 48, F = 1.12, p = 0.295).

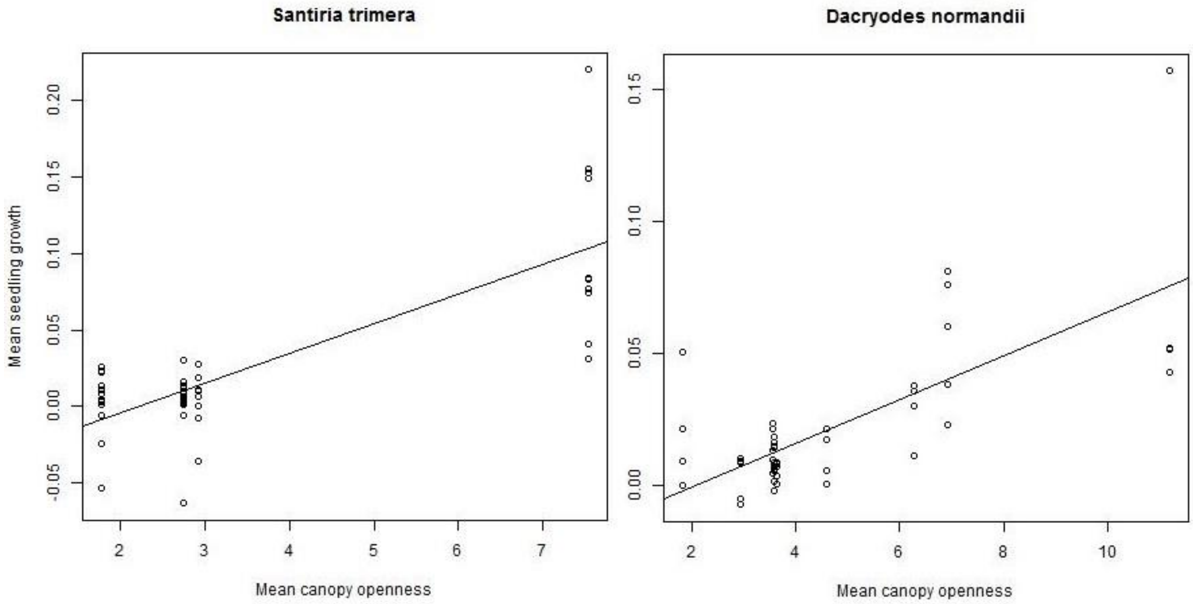


Figure 21 Graphic representation of the linear model regression of seedling growth in function of canopy openness for the species *Santiria trimera* (y=-0.042560+0.019351x, p<0.001) and *Dacryodes normandii* (y=-0.016789+0.008237x, p<0.001)

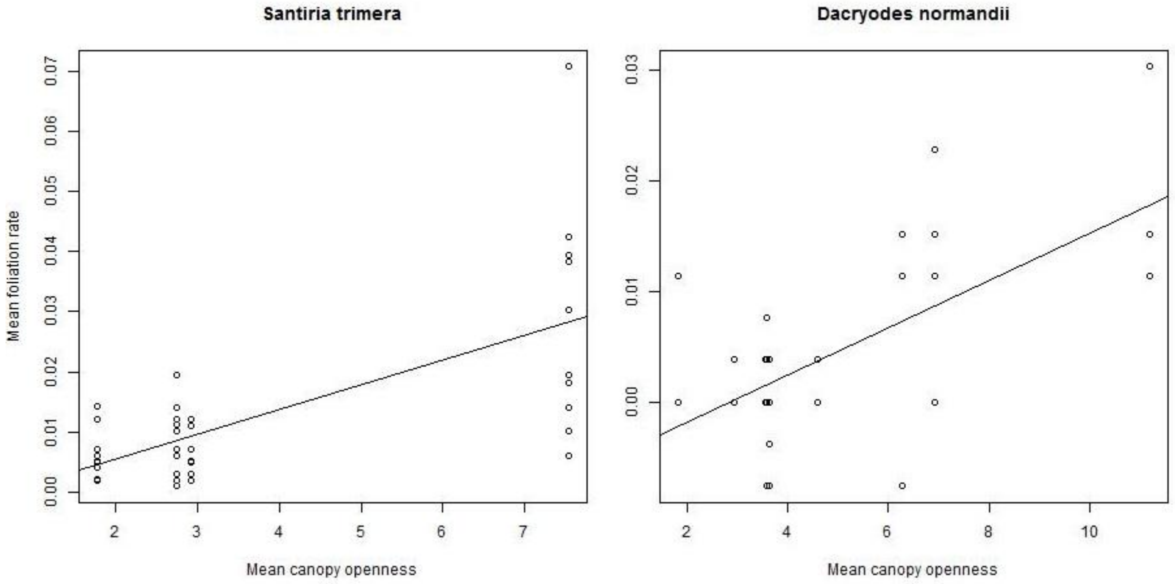


Figure 22 Graphic representation of the linear model regression of seedling foliation rate in function of canopy openness for the species *Santiria trimera* (y=-0.0026593+ 0.0041168x, p<0.001) and *Dacryodes normandii* (y=-0.0060362+ 0.0021258x, p<0.001)

Figure 23 Comparison of *Santiria trimera* seedlings installed in (A) closed canopy terra firma forest and (B) western lowland gorilla nest site, after 18 months in southeast Gabon

4 DISCUSSION

We observed the existence of a positive effect of faecal matrix on seedling growth and foliation rates for *Plagiostyles africana*, but only a weak effect on foliation rate for *Santiria trimera* and *Chrysophyllum lacourtianum*. Gorilla fertilisation effect is therefore species-specific, as demonstrated for other vertebrates (Dinerstein and Wemmer, 1988; Traveset *et al.,* 2001, 2007). Nevertheless, although some differences were not significant, observed mean growth rates and foliation rates for seedlings of all tested species growing within a faecal matrix were higher than that of seeds directly sown in soil. Moreover, the positive effect of manure depends on its composition, with the faecal matrix of frugivores also consuming animal material being more beneficial than that of dispersers which feed on vegetation only (Traveset *et al.,* 2001). Antagonistic effects have also been observed, as frugivore manure might contain chemical compounds that negatively affect seed germination and seedling survival (Traveset *et al.,* 2001, 2007). Such effects were not observed in our study.

Our results highlight a positive effect of deposition at nest sites on seedling growth and foliation rates for both tested species, *Santiria trimera* and *Dacryodes normandii*, particularly in relation to the open canopy conditions of nest sites. Seedlings growing from seeds deposited at open canopy nest sites by gorillas benefit from the higher light availability. Seeds deposited at nest sites installed in closed canopy *terra firma* forest would not experience such an advantage (although a supplementary effect of deposition site on foliation rate and seedling survival is observed for *Dacryodes normandii* that might be linked to pathogens and/or herbivore pressure). We therefore provide evidence for the ‘directed dispersal hypothesis’ as put forward in Howe and Smallwood (1982). Our study further demonstrates the role of gorillas in directed dispersal of seeds, by depositing seeds most frequently in open canopy sites. The role of gorillas in forest regeneration is therefore highly likely to be essential, particularly as gorillas disperse seeds of many large forest tree species (Fourrier, 2013; Petre *et al.,* 2015a). Open canopy forests, and their associated higher light availability, have also been observed to be advantageous to seedlings of species described as adapted to shade (Howe *et al.,* 1985; Popma and Bongers, 1988 and references therein; Schupp *et al.,* 1989), suggesting subtle effects of light availability on seedling growth (Hatshorn, 1978 cited by Howe *et al.,* 1985). A beneficial effect of both the presence of dung as manure and high light availability on seedling growth was observed for seedlings of *Trewia nudiflora* L. (Euphorbiaceae) when dispersed by *Rhinoceros unicornis* L. (Dinerstein and Wemmer, 1988). It is possible that the interaction between faecal matrix and high light conditions would bring further benefits to seedlings originating from seeds dispersed by gorillas. The implementation of *in situ* seedling development experiments could shed light on such potential interactions.

Dacryodes normandii showed no clear effect of proximity to a mature conspecific on seedlings survival. The Janzen-Connell (Janzen, 1970; Connell, 1971) effect was observed to be highly specific in tropical species (Howe, 1989; Chapman and Russo, 2005). Moreover, this effect might be influenced by the density of adult trees of the considered species within the site, with a satiation of predators occurring at high densities and hampering a distance-dependent mortality (Schupp, 1988b). The marginal effect of proximity to a conspecific observed for *Dacryodes normandii* could indicate a ‘clump-syndrome’ (Howe, 1989; Chapman and Russo, 2005). This is often the case for species dispersed by large frugivores and therefore adapted to aggregated deposition in faecal clumps (Lambert and Chapman, 2005). Considering the high density and fruit characteristics of *Santiria trimera*, as well as its tendency to root-graft (Howe, 1989; Doucet, 2003; B. Haurez, pers. obs.), it seems reasonable to suppose that this species also exhibits ‘clump-syndrome’. This ‘clump-syndrome’ analysis is supported by the observation of many persistent seedlings of *D. normandii* and *S. trimera,* with no apparent damage, developing from faecal units (B. Haurez, pers. obs.) (**Figure 24**). However, in order to better understand the fate of seeds dispersed by western lowland gorillas, the implications of clumped deposition should also be addressed. Indeed, intra- and interspecific competition for nutrients and light will affect the growth and survival of seedlings dispersed by large vertebrates in this way (Dinerstein and Wemmer, 1988; Loiselle, 1990).

Figure 24 Cluster of seedlings of Santiria trimera (Burseraceae) developing in a western lowland gorilla faecal unit, Southeast Gabon

The absence of distance and/or density-dependent mortality might also be due to the fact that the experiments were performed with seedlings and not with non-germinated seeds. Therefore, seed predation by rodents was not assessed in this study. Indeed, the fate of dispersed seeds is influenced by secondary dispersal and post-dispersal seed predation by rodents and dung beetles (Lambert and Chapman, 2005). The study of seed germination, seedling growth and survival in non-disturbed faecal units deposited at nest sites and in the forest along trails would help to characterise more precisely the fate of gorilla-dispersed seeds.

5 CONCLUSION

These results confirm our hypothesis that seedling development is enhanced at gorilla nest sites because of favourable light conditions. Although faecal matrix was observed to enhance seedling development in some cases, its effect seems to be species-specific. We did not detect the existence of a strong Janzen-Connel effect affecting seedlings survival under a conspecific for our tested species.

In this study, we highlighted the impact of gorilla seed dispersal on seedling growth and survival of four tree species, characteristic of the forest of Central Gabon and economically valuable. A number of additional species, which are exploited for their timber and non-timber forest products, also rely on gorillas for seed dispersal (eg. *Pseudospondias microcarpa* and *Trichoscypha* spp. (Anacardiaceae), *Nauclea didderrichi* (Euphorbiaceae), *Dialium* spp. (Fabaceae), *Myrianthus arboreus* (Moraceae)) (Fourrier, 2013; Petre *et al.,* 2015a). Therefore, the dispersal services performed by gorillas within the forest ecosystem are both environmentally and economically essential. They are particularly important in the context of logged forest and sustainable forest management.

Although *in situ* experiments investigating the fate of seedlings emerging from seeds in undisturbed gorilla faeces are required, this study has served to underline the importance of the western lowland gorilla as a seed disperser. Given the growing evidence for its directed dispersal of a wide range of important plant species in tropical forests, the ensured conservation of gorillas is likely to be critical to the maintenance of Central African rainforests and their economic viability.

QUATRIÈME PARTIE CONCLUSIONS

"Par gestion durable des ressources forestières, on entend une gestion qui maintient notamment leur diversité biologique, leur productivité, leur faculté de régénération, leur vitalité et leur capacité à satisfaire de manière pérenne, les fonctions économique, écologique et sociale pertinentes, sans causer de préjudices à d'autres écosystèmes."

Article 17 de la Loi N°016/2001, portant code forestier en République gabonaise

CHAPITRE 9 CONCLUSION GÉNÉRALE ET PERSPECTIVES

Ce chapitre synthétise les principales observations réalisées au cours de cette thèse. Des implications sylvicoles visant à améliorer le caractère durable de l'exploitation forestière, et son potentiel en terme de conservation des espèces animales, sont développées. En outre, plusieurs perspectives de recherche sont proposées dans le but d'approfondir les connaissances relatives au rôle du gorille dans la dynamique des forêts du Bassin du Congo.

Gorille des plaines de l'Ouest © J-Y De Vleeschouwer

Dans ce travail, nous nous sommes intéressés à la place du gorille, en tant que disperseur des graines, dans la dynamique des forêts denses humides tropicales exploitées, au Gabon. Dans un premier temps, nous allons reprendre de façon très synthétique les principaux résultats en regard des questions de recherche.

Quel est l'état actuel des connaissances relatives (1) au rôle du gorille en tant que disperseur des graines et (2) aux impacts de l'exploitation forestière et de la chasse sur le gorille et ses services de dispersion?

Pour cette question de recherche, se référer au Chapitre 2 et à l'Annexe 1.

Les concessions forestières constituent-elles des habitats favorables à la préservation des populations de gorilles, ainsi que de leurs services écologiques, en particulier la dispersion des graines?

1. Les forêts exploitées sous aménagement durable et gérées de manière responsable (gestion intégrant en particulier la mise en place d'une stratégie de gestion et de contrôle de la chasse) peuvent, au même titre que les aires protégées, abriter des populations viables de gorilles des plaines de l'Ouest à long terme ;
2. A court terme, l'exploitation forestière sélective à faible taux de prélêvement (1-2 pieds / ha en moyenne) ne semble pas avoir d'impact négatif sur la densité en gorille des plaines de l'Ouest au sein d'une Assiette Annuelle de Coupe ;
3. Les gorilles des plaines de l'Ouest installent leurs sites de nidification préférentiellement au sein de forêts de terre ferme à canopée ouverte, et ce même en forêt perturbée par une exploitation sélective (1-2 pieds / ha en moyenne).

Quel est le potentiel quantitatif et qualitatif du gorille en tant que disperseur?

1. Les espèces dispersées par le gorille sont diverses, et leurs graines sont généralement viables après passage dans le tractus digestif. Le gorille est impliqué dans la dispersion de plusieurs espèces exploitées pour la production de bois d'œuvre, ou fournissant des produits forestiers non-ligneux aux populations locales. Les graines sont dispersées de manière agrégée, avec un nombre variable de graines par unité fécale ;
2. Pour les espèces testées, le passage des graines dans le tractus digestif du gorille a un effet positif sur la germination des graines (suppression de la pulpe et scarification des téguments) ;
3. L'influence de la matière fécale, dans laquelle les graines dispersées par les gorilles sont déposées, sur la germination des graines, et la croissance et la survie des plants est variable selon l'espèce végétale considérée. Les excréments de gorilles exercent un effet fertilisant sur le développement des plantules de certaines espèces ;
4. Le gorille des plaines de l'Ouest est impliqué dans un processus de "*directed dispersal*" car il dépose la majorité des graines dispersées dans ses sites de nidification, préférentiellement installés au sein de forêt de terre ferme à canopée ouverte et qui présentent des conditions favorables au développement des plantules. La croissance des plants est positivement corrélée à l'ouverture de la canopée du site où ils sont installés.

Quelle est la contribution du gorille dans la dispersion d'une essence exploitée, le Dacryodes normandii*?*

1. Le gorille des plaines de l'Ouest est le principal agent de dispersion du *Dacryodes normandii* (Burseraceae), essence endémique gabonaise exploitée pour son bois et dont les fruits sont importants pour les populations humaines et animales ;
2. La viabilité des graines de *Dacryodes normandii* n'est pas altérée par le passage dans le tractus digestif du gorille ;
3. Les plantules de *Dacryodes normandii* bénéficient de la forte disponibilité en lumière observée au niveau de certains sites de nidification. Elles présentent une croissance cinq fois plus rapide que les plantules déposées en forêt à canopée fermée, et un taux de foliaison dix fois plus élevé.

De par son action comme disperseur d'espèces végétales caractéristiques du milieu forestier et d'importance économique, la préservation du gorille dans les forêts soumises à des pressions anthropiques peut influencer massivement la conservation future de ces écosystèmes (Chapman & Russo 2005).

1 RÔLE DU GORILLE DANS LA DYNAMIQUE FORESTIÈRE

En regard des résultats synthétisés ci-dessus, différentes perspectives de recherche peuvent permettre de préciser le rôle du gorille dans la dynamique forestière.

Dans ce travail, nous n'avons pas observé une sélection préférentielle des trouées d'abattage et des pistes forestières pour la nidification du gorille, peut-être en raison d'un délai trop court (chapitre II.2). Cependant, l'utilisation fréquente de ces sites pour la nidification a été rapportée dans une concession forestière au Cameroun (Arnhem 2008). En conséquence, nous recommandons une étude approfondie du comportement nidificateur du gorille en forêt exploitée, visant particulièrement **l'identification précise des critères qui influencent la nidification dans les trouées d'abattage et les pistes forestières**. Ainsi, les gestionnaires forestiers pourraient tenir compte de ces critères dans les pratiques d'exploitation, dans le but d'augmenter l'utilisation des zones impactées comme sites de nidification. De cette manière, le rôle des gorilles dans la régénération des forêts exploitées pourrait être maximisé.

Afin de caractériser de manière précise et complète les fonctions remplies par le gorille dans la dynamique forestière, la collaboration et l'échange d'informations entre primatologues qui étudient la dispersion des graines par les gorilles des plaines de l'Ouest doit être encouragée. Nous proposons le **développement d'une base de données en réseau reprenant les données relatives à la dispersion des graines par les gorilles**, en suivant l'exemple du portail A.P.E.S. (http://apesportal.eva.mpg.de/). Les différents aspects à aborder sont l'établissement d'une liste (exhaustive) des espèces dispersées par les gorilles, la détermination de la viabilité des graines dispersées et de l'impact du passage dans le tractus digestif et l'évaluation de l'impact du dépôt dans les sites de nidification. Afin d'inciter les exploitants forestiers à s'investir dans la préservation des gorilles, il pourrait s'avérer utile d'évaluer la valeur économique des services de dispersion dispensés par cette espèce (voir Hougner *et al.* 2006). Dans un second temps, la base de données pourrait être étendue à d'autres espèces animales qui remplissent le rôle de disperseurs au sein des forêt tropicales d'Afrique Centrale.

Différentes technologies en cours de développement comportent un fort potentiel d'application à la recherche en forêts tropicales humides. Nous recommandons **leur utilisation pour la gestion des**

populations de gorilles dans les concessions forestières. Bien que présentant encore un coût relativement élevé, les **méthodes génétiques** peuvent s'appliquer à de nombreux domaines tels l'étude du régime alimentaire (Quéméré *et al.* 2013), du comportement de nidification (Bradley *et al.* 2008), de la représentation au niveau des tableaux de chasse (Eaton *et al.* 2010), de la dispersion des graines et particulièrement de l'estimation des distances de dispersion (Godoy & Jordano 2001; Grivet *et al.* 2005; Hardesty *et al.* 2006; Jordano *et al.* 2007; Robledo-Arnuncio & García 2007; Smouse *et al.* 2012) et des dynamiques de populations des espèces végétales en lien avec la dispersion (Daïnou *et al.* 2010; Duminil *et al.* 2010). Les techniques de biologie moléculaire s'avèrent particulièrement utiles dans le cadre des inventaires et des suivis des populations de gorilles (Bradley *et al.* 2008; Arandjelovic *et al.* 2010). La combinaison des techniques usuelles d'estimation indirectes de la densité avec des méthodes génétiques permet de s'affranchir des biais rencontrés via le comptage des nids (Bradley *et al.* 2008; Arandjelovic *et al.* 2010). L'évolution rapide de ces méthodes contribue à les rendre financièrement abordables dans le cadre de projets de recherche.

L'utilisation des **pièges photographiques** peut aussi apporter des précisions dans de nombreux domaines (l'estimation de l'abondance ou de la densité, l'utilisation de l'habitat, la dispersion des graines, etc.) (chapitre III.3, Kitamura *et al.* 2006; Head *et al.* 2012, 2013; Moupela *et al.* 2013; Trolliet *et al.* 2014). Bien que le coût financier initial puisse être relativement important, les pièges photographiques permettent d'obtenir des informations pertinentes sans demander un investissement majeur en terme de temps et de personnel (par rapport à la réalisation de comptage de nids par inventaires pédestres). Les observations directes présentent de grands avantages, mais le processus d'habituation est extrêmement chronophage, éthiquement contesté et non applicable pour tous les contextes car il comporte des risques importants pour les populations de gorilles dans les zones où cette espèce est chassée. Les observations indirectes à l'aide de pièges photographiques peuvent, en partie, palier ces problèmes.

Enfin, les **drones** sont actuellement utilisés pour l'inventaire et le suivi de populations animales en Afrique de l'Ouest. Bien que la visibilité en forêts tropicales humides rende complexe l'application de ces méthodes en Afrique Centrale, les drones ont été utilisés récemment dans le cadre d'un inventaire des chimpanzés par comptage des nids (van Andel *et al.* 2015). En fonction de l'évolution technique des drones et étant donné la sélection préférentielle d'habitats ouverts pour la nidification, la méthode décrite pourrait être appliquée aux inventaires de gorilles, ou du moins faciliter leur suivi et la gestion de certains habitats importants au sein des concessions forestières, notamment les clairières humides (*bais*) (Linchant J. et Lisein J., communications personnelles). Les drones pourraient ainsi être utilisés pour identifier les zones d'habitat potentiellement favorable pour les gorilles, au sein desquelles seraient mis en place des inventaires pédestres ultérieurs. Les drones présentent aussi un potentiel dans le cadre de la lutte anti-braconnage et du suivi des activités de chasse.

2 EXPLOITATION FORESTIÈRE ET IMPACT SUR LES POPULATIONS DE GORILLES

En considérant les résultats de cette thèse, mais aussi ceux d'études récentes menées dans différentes régions, plusieurs recommandations concernant la gestion des populations de gorilles au sein de forêts exploitées peuvent être proposées.

Sur base des résultats des inventaires des populations de gorille (chapitre II.1 et chapitre II.2), il apparaît que l'exploitation forestière est une activité qui permet la conservation de populations viables de gorilles des plaines de l'Ouest. Cependant, il est important de souligner les conditions au sein desquelles cette observation a été réalisée. La société *CEB-Precious Woods Gabon* est soucieuse d'une exploitation à faible impact (EFI). Elle est certifiée par le *Forest Stewardship Council* (*FSC*) et, dans ce cadre, elle met en place des pratiques qui se veulent durables et peu délétères pour l'écosystème forestier. Bien que la proportion et l'étendue des surfaces concédées certifiées soit en augmentation, les sociétés productrices de bois tropicaux pratiquant l'exploitation dite "conventionnelle" sont encore majoritaires (actuellement, 38 % des surfaces concédées en Afrique Centrale sont aménagées, et 17 % certifiées) (Picard *et al.* 2012; de Wasseige *et al.* 2014). De ce fait, il convient de rester critique quand au rôle possible des concessions forestières dans la préservation des gorilles des plaines de l'Ouest. Celui-ci est totalement dépendant des pratiques d'exploitation, et en particulier de l'application de stratégies de gestion de l'activité de chasse.

Afin de limiter les impacts négatifs de l'exploitation, diverses dispositions légales ont été instaurées par les pays du Bassin du Congo. En outre, la mise en place de schémas de certification, le plus connu étant *FSC*, a aussi participé à l'amélioration de la gestion forestière tant au niveau environnemental, qu'économique et social (Diangha & Wiegleb 2014). Concernant la faune, l'accent législatif est mis sur la réglementation de l'activité de chasse, avec peu de recommandations concrètes en termes de gestion faunique au sein des concessions forestières (*Receuil des textes législatifs et Réglementaires en matière des eaux et forêts* 2011; Maréchal *et al.* 2012). Les processus d'aménagement forestier et de certification impliquent la mise en place de différentes mesures telles que l'évaluation et le suivi des populations animales (avec parfois des espèces cibles), l'estimation des impacts de l'exploitation sur la faune, la mise en protection de zones importantes pour les communautés animales, des pratiques de lutte anti-braconnage, etc. (Maréchal *et al.* 2012). En général, les méthodes de collecte des données et d'analyses ne sont pas définies ou varient selon les pays, ce qui limite les possibilités de comparaison entre les différentes sociétés (Maréchal *et al.* 2012). Dans le but de permettre une meilleure capitalisation des données d'inventaires et de suivi, que ce soit au sein de concessions forestières ou dans des aires protégées, nous recommandons une **harmonisation des méthodes d'évaluation et de monitoring de la faune en Afrique Centrale**. Les différentes pratiques constituant cette méthodologie commune, applicable à tout le Bassin congolais, pourraient être définies lors d'un atelier placé sous l'égide de la COMIFAC, réunissant les acteurs de la conservation (ONG de conservation locales et internationales, gestionnaires forestiers et gestionnaires d'aires protégées, experts scientifiques de la faune d'Afrique Centrale, représentants gouvernementaux et organismes de certification). A terme, l'intégration de cette méthodologie dans les exigences des organismes de certification, voire dans les législations nationales règlementant l'aménagement forestier, devrait être l'aboutissement de cette démarche.

Notre évaluation de l'impact à court terme de l'exploitation forestière sur les populations de gorille a montré que la densité de gorille a tendance à baisser (bien que non significativement) suite aux activités d'exploitation, pour ensuite retourner à son niveau initial environ une année après leur arrêt (chapitre II.2). Le cadre temporel utilisé dans notre étude était cependant trop court que pour tenir compte de l'effet de la colonisation des trouées d'exploitation et des pistes forestières par les herbacées. En outre, les inventaires entrepris dans le cadre de cette étude présentent le désavantage d'être très localisés. Ils sont relativement précis, mais n'apportent des informations que sur une zone restreinte de la concession forestière (2,17 % de la surface concédée). Nous suggérons l'adoption d'inventaires des populations de gorilles basés sur deux méthodologies complémentaires:

- Un **inventaire pédestre, le long de transects linéaires distribués de manière systématique, à l'échelle de la concession**, idéalement réalisé avant le début de l'exploitation forestière, à taux d'échantillonnage faible (voir Clark *et al.* 2009; Stokes *et al.* 2010). Cet inventaire global aurait pour but d'identifier les zones où des populations de gorilles sont présentes, et de localiser les habitats où elles sont abondantes. Une carte de la distribution spatiale de l'abondance des populations de gorille au sein de la concession en découlerait. Dans la mesure du possible, la collecte des données relatives aux gorilles pourrait être intégrée à un inventaire faunistique global, et se dérouler lors de l'inventaire d'aménagement (généralement à un taux voisin de 1 % et le long de layons espacés de 2 km) ;

- Pour les zones où les gorilles sont présents, des **inventaires organisés sur base quinquennale permettant un suivi des populations à long terme**. Pour ceux-ci , nous recommandons un taux d'échantillonnage de 1%, qui permettrait d'obtenir une valeur de densité de précision acceptable (coefficient de variation avoisinant les 20% pour un taux de rencontre des nids de 0,88 nid par kilomètre parcouru, voir chapitre 2 de cette thèse).

Une **meilleure planification des assiettes annuelles de coupe (AAC) et de leur succession spatiale et temporelle** est souhaitable. En effet, nous avons observé que les gorilles ont tendance à éviter les zones soumises aux activités d'exploitation. Bien que le gorille des plaines de l'Ouest ne soit pas une espèce territoriale, il convient d'éviter d'engendrer des mouvements trop importants des groupes pour éviter des perturbations de leur structure sociale. Dans la mesure du possible (en l'absence de contraintes topographiques majeures), nous suggérons d'intégrer aux autres contraintes, la carte de répartition spatiale des gorilles pour définir les limites des AAC. Dans la mesure du possible, une AAC ne devrait pas être centrée sur une zone de forte abondance en gorilles, ni totalement cloisonnée par des limites naturelles ou artificielles susceptibles d'entraver ou d'altérer les mouvements des gorilles, tels que les rivières et les routes permanentes. Compte tenu du caractère territorial des chimpanzés, la planification des assiettes annuelles de coupe devrait également tenir compte de cette espèce.

L'importance croissance du *FSC* au sein des concessions d'Afrique Centrale participe probablement à l'expansion de l'EFI et à une amélioration de la durabilité de l'exploitation de bois d'œuvre (Karsenty *et al.* 2008). Pour renforcer cette tendance, les gouvernements des pays du Bassin du Congo devraient **légiférer les pratiques d'EFI** afin d'assurer leur adoption par les sociétés forestières toutes nationalités confondues. En particulier, nous recommandons la protection des espèces végétales importantes pour les populations de gorilles, telles que le *Chrysophyllum lacourtianum,* dont les individus en fructification sont massivement visités par les gorilles mais aussi les chimpanzés et les éléphants (B. Haurez, observation personelle), une planification routière qui réduit au minimum la construction de pistes dans les zones à fortes densités de gorilles, la fermeture efficace et effective des routes par des barrières gardées ou fixes et la réouverture des anciennes routes plutôt que l'installation de nouvelles pistes. Le coût de la mise en place de pratiques moins néfastes pour le milieu forestier est difficilement estimable; il présente une variation géographique importante, mais dépend aussi de l'échelle spatiale et temporelle considérée et de l'unité de mesure (coût par m³ de bois produit, coût par unité de surface ou de temps) (Medjibe & Putz 2012). Afin que le coût de ces stratégies ne soit pas un facteur limitant pour leur application, un système de prime, similaire au programme REDD +, pourrait être mis en place afin de **récompenser les bénéfices en terme d'écosystème** (Medjibe & Putz 2012).

Certains aspects de l'écologie des populations de gorille n'ont pas été abordés. Il serait particulièrement intéressant **d'étendre l'étude de l'impact de l'exploitation sur l'écologie alimentaire** (régime alimentaire et budget d'activités). En effet, une altération de la distribution et de la disponibilité en ressources alimentaires étant un effet potentiel direct de l'exploitation (Morgan & Sanz 2007), des données concernant les capacités d'adaptation des gorilles seraient précieuses. La plasticité alimentaire et comportementale est un trait qui favorise la survie des espèces animales au sein de forêts dégradées (Milich *et al.* 2014). Les gorilles de montagne ont déjà montré qu'ils adaptent le temps consacré à l'alimentation en fonction de la qualité de leur environnement (Watts 1988), et le régime du gorille des plaines de l'Ouest est influencé par la composition botanique de son habitat (Rogers *et al.* 2004). L'accroissement de la disponibilité en espèces herbacées suite à l'exploitation pourrait, pour le gorille des plaines de l'Ouest, compenser une éventuelle diminution des ressources fruitières liée à l'exploitation et la dégradation de pieds producteurs. Dans ce cas, le rôle du gorille dans la dispersion des espèces ligneuses pourrait être altéré. Il convient donc de réaliser un suivi de l'évolution des espèces dispersées par les gorilles, et de l'abondance de leurs graines dans les excréments, au sein d'une forêt soumise à l'exploitation. En outre, la modification du régime alimentaire peut également entrainer l'altération du budget d'activités (Masi *et al*. 2009) et d'autres fonctions biologiques, notamment la reproduction, tel qu'observé chez d'autres primates (Johns 1985). Une méta-analyse comparant les services de dispersion des graines par le gorille au sein de sites à végétation contrastée pourrait également apporter des précisions à ce niveau.

2.1 Chasse

Afin d'assurer une réelle durabilité de l'exploitation des forêts tropicales pour la production de bois d'œuvre, et le maintien des nombreux services écosystémiques qu'elles génèrent, les sociétés forestières doivent garantir la préservation des processus intervenant dans la dynamique des forêts (Rosin 2014). Au vu de l'importance de la dispersion des graines par les grands mammifères au sein des forêts d'Afrique Centrale (chapitre III.3 de ce travail, Beaune *et al.* 2013b), cette durabilité ne pourra être atteinte sans une conservation efficace des populations animales au sein des concessions forestières, et notamment la mise en place de stratégies fonctionnelles de lutte contre la chasse abusive et le braconnage (Rosin 2014). Il a été démontré que l'exploitation à faible impact, soumise à un plan d'aménagement qui intègre notamment la gestion de la faune, est conciliable avec la préservation des populations de gorilles (cette étude; Clark *et al*. 2009; Stokes *et al.* 2010), à condition que la pression de chasse soit limitée à un faible niveau. Au sein de notre site d'étude, bien que cette pression soit relativement faible, elle exerce une influence marquée sur l'utilisation de l'habitat par les gorilles (voir chapitre II.1). Nous insistons donc sur **l'importance d'une gestion efficace de la chasse dans les forêts concédées**. En outre, la chasse reste, avec les maladies épidémiques sur lesquelles nous avons peu d'emprise, la menace principale qui pèse sur les populations de gorilles (Walsh *et al.* 2003). De manière générale, le problème de la chasse tient une place prépondérante au sein de la problématique de la conservation de la faune en forêt d'Afrique Centrale (Galetti & Dirzo 2013).

Nous recommandons une **planification spatiale des activités de lutte anti-braconnage** (LAB) sur base de cartes de répartition de la pression de chasse régulièrement mises à jour, et des cartes de répartition des espèces rares et menacées, en particulier du gorille. Afin de faciliter cette planification, nous proposons aux gestionnaires forestiers de mettre un place un système de *reporting* permanent des activités de braconnage. Pour toute activité de chasse illégale ou de braconnage observée, les informations suivantes seraient encodées dans une base de données gérées par le responsable faune et chasse : date et heure de l'évènement, type d'activité, description sommaire, coordonnées géographiques, nom de la personne ayant rapporté l'information. L'ensemble des ouvriers et cadres qui se déplacent en forêt, mais aussi les éventuelles équipes scientifiques travaillant au sein de la concession, seraient en charge d'alimenter ce système. La base de données serait complétée par les informations collectées dans le cadre des patrouilles anti-braconnage internes et celles organisées par le Ministère des Eaux et Forêts. Les observations directes en indirectes de gorilles (en particulier les sites de nidification), voire des autres espèces rares et menacées, pourraient également être intégrées dans ce système. Dans cette optique, les outils tels que le logiciel *Spatial Management and*

Reporting Tool (*SMART*, anciennement *Management Information System* (*MIST*)), mis en place dans certains parcs nationaux (Makombo & Schmitt 2003; http://www.smartconservationsoftware.org) peut être utilisé au sein des concessions forestières, comme c'est déjà le cas au Gabon et au Cameroun (Abernethy K. et Arnhem E., communications personnelles).

Afin de tenir compte de l'importance de la chasse en terme de sécurité alimentaire et d'activité génératrice de revenus mais aussi d'un point de vue culturel (Auzel & Wilkie 2000; Wilkie *et al.* 2007; Bennett *et al.* 2007; Abernethy *et al.* 2013), tout en intégrant la préservation des espèces animales menacées, le renforcement de l'interdiction de chasser les espèces menacées, combinée à une gestion raisonnée des prélèvements des espèces résilientes pourraient rencontrer simultanément les objectifs de conservation des ressources naturelles et de développement des populations rurales (Nasi *et al.* 2011). Le modèle de gestion de la faune puits-source (aire chassée et aire refuge) fonctionne bien lorsque la densité humaine est relativement faible, ce qui est le cas dans les zones rurales et forestières du Gabon, et lorsque la zone mise en protection est effectivement préservée des activités humaines (voir Remis & Jost Robinson 2012). Dans des zones à fortes densités, le renforcement des lois et le développement d'alternatives à la viande de brousse et au revenu de sa commercialisation sont essentiels pour limiter la pression de chasse (FitzGibbon *et al.* 2000). La **mise en place d'activités alternatives à la chasse** devrait être une priorité pour les exploitants forestiers, et pour la recherche en forêt tropicale (Abernethy *et al.* 2013). L'établissement de collaborations (ou le renforcement des collaboration existantes ; voir Clark & Poulsen 2012) entre chercheurs, acteurs de la conservation et sociétés forestières pourrait servir de base de travail. En effet, grâce à leur connaissances relatives aux espèces animales, les chasseurs constituent souvent de très bons pisteurs et assistants pour la collecte de données en forêt (Clark & Poulsen 2012). Leur implication dans des projets de recherche et de conservation met l'accent sur la valeur économique des espèces animales, via leur préservation plutôt que leur commerce. Cela assurerait un accès à des revenus alternatifs à ceux du commerce de viande de brousse.

Concernant les sources alternatives de protéines, le problème est particulièrement complexe. Dans les pays du Bassin du Congo, jusqu'à 90 % des apports protéiques sont encore issus de la viande de brousse (Fa *et al*. 2015) et celle-ci constitue un élément important pour la santé humaine (Fa *et al.* 2015). Les tentatives de développement de l'élevage se sont souvent avérées viables uniquement lorsque la viande de brousse était déjà devenue inaccessible (en zone urbaine ou périurbaine, et lorsque les forêts sont déjà dépeuplées) (Houben *et al.* 2004; Rieu & Binot 2006). En effet, la plupart des peuples d'Afrique Centrale sont peu enclins à s'investir dans cette activité, surtout lorsque son coût est supérieur et son efficience (retour sur investissement temporel) est moindre que celle de la chasse (Fimbel *et al.* 2000). L'efficacité des alternatives à la viande de brousse dépend aussi des facteurs qui influencent sa consommation (Foerster *et al.* 2012). Dans certaines communautés rurales, la consommation de viande de brousse est considérée comme un besoin, et sera facilement abandonnée lorsque le niveau de vie augmente. Au contraire, la viande de brousse est parfois considérée comme un produit de luxe dont la consommation ira croissante avec les revenus du ménage (Nasi *et al.* 2011; Foerster *et al.* 2012). En outre, l'importance culturelle de la chasse et les préférences gustatives des communautés africaines ne doivent pas être négligées. L'intégration des populations locales dans l'élaboration de tout plan de gestion de la faune est primordiale et nécessite des études socio-et ethnologiques (Fimbel *et al.* 2000; Bennett *et al.* 2007; Jost Robinson *et al.* 2011; Maréchal *et al.* 2012; Jost Robinson & Remis 2014), notamment pour la conception d'alternatives alimentaires aux produits de la chasse (Wicander & Coad 2015). Il est notamment recommandé de développer les pratiques existentes à l'aide de technologies modernes plutôt que d'introduire de nouvelles actvités, qui nécessitent une appropriation par les populations locales (Wicander & Coad

2015). Au sein des concessions forestières, il est du devoir des exploitants d'assurer un approvisionement constant et suffisant en viande et en poisson d'élevage, et ce à prix concurrentiel par rapport à la viande de brousse, pour les ouvriers.

2.2 Potentiels des concession forestières en termes de conservation et de recherche

Malgré que l'exploitation forestière engendre des modifications au sein de l'écosystème forestier, elle constitue une activité qui remplit à la fois un objectif de viabilité économique, et peut aussi satisfaire certaines des exigences de conservation de l'écosystème forestier (Johns 1985; Putz *et al.* 2001, 2012; Meijaard & Sheil 2008; Clark *et al.* 2009; Berry *et al.* 2010; Edwards *et al.* 2014; Bruggeman *et al.* 2015). En termes de biodiversité, l'exploitation forestière sélective et à faible impact constitue le mode d'exploitation de la forêt le moins délétère (Putz *et al.* 2001; Gibson *et al.* 2011; Edwards *et al.* 2014). En outre, une concession forestière étant généralement allouée pour une période de 20 à 40 ans (Karsenty *et al.* 2008; Putz *et al.* 2012), l'application des stratégies de gestion et de conservation de la faune est assurée à relativement long terme par rapport à des projets de recherche et de conservation dont la durée de vie est parfois inhérente à la bonne volonté des bailleurs. Or, le nombre d'années durant lesquelles un effort de conservation a été appliqué influence positivement la persistance de populations de grands singes (Tranquilli *et al.* 2012). De plus, les concessions couvrent généralement de grandes surfaces, qui présentent également un avantage pour le maintien d'espèces inféodées au milieu forestier, en particulier à large domaine vital, et des services qu'elles fournissent (dispersion des graines, pollinisation, prédation,..) (Edwards *et al.* 2014). En conséquence, bien que les forêts préservées des activités anthropiques soient irremplaçables (Johns 1985; Meijaard & Sheil 2008; Clark *et al.* 2009; Gibson *et al.* 2011; Edwards *et al.* 2014), la protection des forêts exploitées ne doit pas être négligée et leur conversion évitée autant que possible (Putz *et al.* 2001; Meijaard & Sheil 2008; Berry *et al.* 2010; Gibson *et al.* 2011; Edwards *et al.* 2014). Le caractère bénéfique potentiel des concessions forestières sur la conservation des populations de gorilles ne doit en aucun cas mener à une augmentation des pressions anthropiques sur les forêts préservées, ni à une diminution de la valeur des écosystèmes forestiers protégés. Au contraire, la gestion des forêts concédées doit se faire en intégration dans une stratégie de conservation à l'échelle paysagère, au service des aires protégées, et les impacts négatifs de l'exploitation doivent être minimisés.

Etant donné les caractéristiques présentées par les concessions forestières - surface étendue, présence à long terme, viabilité économique, présence d'infrastructures et de facilités logistiques - et qui font souvent défaut aux projets de recherche et d'écotourisme (Johns 1985; Meijaard & Sheil 2008; Tranquilli *et al.* 2012; Edwards *et al.* 2014), il semble particulièrement pertinent d'encourager le développement de modèles de gestion intégrée des forêts exploitées (Meijaard & Sheil 2008; Abernethy *et al.* 2013; Edwards *et al.* 2014). En particulier, la **collaboration entre sociétés forestières, ONG de conservation et organismes de recherche** permet la réalisation de projets scientifiques à long terme, et la mise au point et l'expérimentation de pratiques d'exploitation et de gestion plus durable pour la faune et la flore (Frumhoff 1995; Clark & Poulsen 2012; Morgan *et al.* 2013; Diangha & Wiegleb 2014). Les avantages financiers de tels projets sont mutuellement bénéfiques : les coûts logistiques sont réduits pour les chercheurs, tandis que les exploitants peuvent profiter de programme de suivi à moindre frais. Des données précieuses relatives aux populations animales et aux activités anthropiques sont facilement récoltées lors d'activités de recherche. La présence à long terme d'équipes scientifiques, ou/et d'exploitants forestiers, constitue une présence active en forêt, qui peut avoir un effet bénéfique sur les populations de primates (Refisch & Koné 2001; Meijaard & Sheil 2008; Campbell *et al*. 2011; N'Goran *et al*. 2012; Edwards *et al*. 2014; Tranquilli *et al.* 2014; Tagg *et al.* 2015), notamment en limitant les activités des chasseurs et braconniers dans la zone. En conséquence, la pression de chasse au sein de forêts allouées à l'extraction des ressources est parfois moindre que dans les zones voisines en dehors des limites des concessions (Laurance *et al.* 2006). Il a d'ailleurs été observé que les concessions industrielles peuvent jouer le rôle de zones refuges pour la faune sauvage (Vanthomme *et al.* 2013). Un suivi régulier des populations animales permet aussi de détecter plus rapidement l'émergence d'une épidémie (Genton *et al.* 2012). Ce mode de gestion multidisciplinaire (exploitation forestière-recherche scientifique - conservation de la biodiversité) engendrerait aussi une création d'emplois alternatifs pour les chasseurs professionnels (voir section *Chasse*) (Clark & Poulsen 2012; Jost Robinson & Remis 2014). Des projets tels que celui mené au Congo (République du Congo) par la ZSL et le WCS (Clark & Poulsen 2012) sont à encourager.

La mise en place de stratégies de monitoring des populations animales et des impacts de l'exploitation forestière sur leurs densités et comportements à long terme permet aussi de détecter des modifications différées de l'écosystème, telle que des dettes d'extinction et des changements au fil des générations. De même, un suivi continu assurant un feedback de l'efficacité des stratégies d'exploitation permettrait d'adapter celles-ci régulièrement (Frumhoff 1995; Morgan *et al.* 2013). Nous insistons donc sur **l'importance de développer des projets de collaboration à long terme**.

2.3 Gestion spatiale du territoire

La préservation de surface étendues de forêt est un critère crucial pour la conservation des gorilles car, en permettant une dynamique méta-populationnelle, elle limite les effets d'évènements tels que les épidémies et favorise les migrations d'individus (Genton *et al.* 2012; Edwards *et al.* 2014). Adjacentes à des aires destinées à la conservation, les concessions jouent le rôle de zones tampons, en les préservant des activités anthropiques illégales et de la dégradation (Morgan *et al.* 2013). De ce fait, à l'échelle paysagère, les massifs forestiers peuvent être gérés pour rencontrer simultanément des objectifs de production, de conservation, et de recherche tout en étant économiquement viables (Putz *et al.* 2001; Bennett *et al.* 2007; Abernethy *et al.* 2013; Bruggeman *et al.* 2015).

La préservation des zones forestières, dégradées ou non, pourrait être facilitée par une réorganisation nationale du territoire, qui concentrerait les activités agricoles dans les régions déjà fortement perturbées, en y favorisant des pratiques durables (Vanthomme *et al.* 2013). De même, cette réorganisation devrait établir une planification raisonnée du réseau routier qui permettrait de limiter l'ouverture de nouvelles routes (et la création d'accès au milieu forestier), tout en maximisant l'efficience des axes routiers existants. Dans le cadre de son Plan Stratégique Gabon Emergent (PSGE), le gouvernement gabonais prévoit d'améliorer les connaissances en terme de préservation des ressources naturelles et d'assurer la gestion durable des écosystèmes forestiers (notamment via une meilleure gestion de la faune et une lutte efficace contre le braconnage) (République Gabonaise 2012). Une planification plus cohérente de l'aménagement du territoire est notamment visée (République Gabonaise 2012). La démarche du gouvernement gabonais constitue une opportunité pour l'évolution vers une exploitation plus durable des massifs forestiers. Il est primordial que la faune, et les ressources forestières en général, soit effectivement prise en compte dans la mise en place du "nouveau modèle de développement" recherché par le Gabon, et que les objectifs définis par le PSGE se traduisent par des actions concrètes.

Le **modèle de gestion spatiale parc-réserve, mis en place au niveau d'aires protégées, pourrait être adapté aux concessions forestières**. Dans ce cas, une portion de la concession serait préservée des activités d'exploitation et autres activités humaines (Johns 1985). Cette aire servirait de refuge aux gorilles, et aux populations animales en général, mais permettrait aussi de réapprovisionner en gibier les zones soumises à la chasse (Frumhoff 1995; Fimbel *et al.* 2000; Clark *et al.* 2009; Jost Robinson *et al.* 2011). L'identification et la gestion de zones à haute valeur de conservation (ou *High Conservation Value, HVC*) de type 1 (*HCV1*[1]) dans le cadre de la certification *FSC* rencontre parfaitement cette stratégie, à condition que l'exploitant forestier exerce un suivi et un contrôle efficace de la zone (Morgan *et al.* 2013). Dans cette optique, les zones de fortes densités de grands singes, ou de concentration des ressources alimentaires et/ou habitat de nidification, devraient être définies *HVC* et gérées en conséquence (Morgan *et al.* 2013). La carte de la distribution spatiale de l'abondance des populations de gorille au sein de la concession servirait de base de travail pour l'identification des sites *HVC* et des séries de conservation[2] suivant la méthodologie proposée par Anthonissen (2014). La mise en place d'une gestion spatiale en mosaïque, présentant des zones non exploitées de petite taille reparties au sein d'une matrice étendue de forêt soumise à l'exploitation, permet de limiter les impacts négatifs sur le milieu forestier (Arnhem 2008; Abernethy *et al.* 2013; Edwards *et al.* 2014). En conséquence, nous recommandons aux exploitants forestiers de **sélectionner plusieurs zones de forêts *HVC1* et séries de conservation et de veiller à leur bonne répartition spatiale au sein de leurs concessions**. Dans le but d'y assurer une présence régulière, nous proposons **d'intégrer préférentiellement les zones *HVC1* dans les programmes de recherche** et d'y organiser des contrôles anti-braconnage sur base mensuelle. En outre, certaines zones revêtent une importance particulière pour les gorilles (et la faune en général), de manière saisonnière (par exemple des sites présentant de fortes densités d'essences clés pour l'alimentation, durant leur fructification). Leur répartition géographique et temporelle doit être définie, et l'absence de perturbations doit être assurée durant les périodes de forte fréquentation faunique. Une surveillance anti-braconnage doit aussi être organisée à ces périodes, sans pour autant troubler les populations animales.

2.4 Vers une autre approche des concessions forestières

En regard des caractéristiques des concessions forestières certifiées, nous suggérons **leur intégration au sein du réseaux des aires protégées telles que définies par *l'International Union for Conservation of Nature* (*IUCN*)**[3]. Dans son état actuel, la classification des aires protégées ne présente pas de catégorie au sein de laquelle les concessions forestières pourraient être inclues, bien que la catégorie VI, reprenant les aires protégées avec utilisation durable des ressources naturelles[4] leur corresponde relativement bien.

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[1] **HVC1** : Zones forestières abritant des concentrations de biodiversité importantes aux échelons mondial, régional ou national (par exemple l'endémisme, les espèces menacées, les zones refuges) (FSC 2012b)

[2] La **série de conservation** est constituée des zones à l'intérieure de l'UGF, qui sont reconnues pour leur grande richesse en biodiversité. Il s'agit entre autres des régions dans lesquelles on retrouve les espèces fauniques ou floristiques endémiques et/ou une grande concentration de la faune sauvage (FSC 2012b)

[3] Une **aire protégée** est un espace géographique clairement défini, reconnu, dédié et géré, par des moyens légaux ou autres, afin de favoriser la conservation à long-terme de la nature et des services écosystémiques et des valeurs culturelles qui y sont liés. (IUCN, 2008)

[4] Les **aires protégées de la catégorie VI** préservent des écosystèmes et des habitats, ainsi que les valeurs culturelles et les systèmes de gestion des ressources naturelles traditionnelles qui y sont associés. Elles sont généralement vastes, et la plus grande partie de leur superficie présente des conditions naturelles ; une certaine proportion est soumise à une gestion durable des ressources naturelles ; et une utilisation modérée des ressources naturelles, non industrielle et compatible avec la conservation de la nature, y est considérée comme l'un des objectifs principaux de l'aire.

Plusieurs pistes proposant une autre approche des concessions forestières certifiées en termes de conservation de la biodiversité et des écosytèmes forestiers sont à explorer :

- une modification de la définition de la catégorie VI afin de pouvoir y inclure les concessions soumises à l'exploitation sélective du bois d'oeuvre, à faible taux d'extraction et selon des pratiques durables (concessions soumises à une gestion durable labelisées par un système de certification internationallement reconnu) ;
- l'intégration de certaines zones des concessions forestières, par exemple les forêt *HVC*, dans le réseau des aires protégées de catégorie VI ;
- la définition d'une septième catégorie d'aires protégées adaptées aux concessions forestières gérées durablement. Cette catégorie reprendrait les vastes zones forestières semi-naturelles (soumises à une exploitation des ressources à faible impact), en particulier celles qui sont adjacentes à (zones tampons) ou qui connectent (corridors) d'autres aires protégées de catégories Ia[5], Ib[6] et II[7].

Quelle que soit l'approche privilégiée, une attention particulière doit être apportée aux bénéfices mutuels pour le secteur de la conservation, d'une part, et pour les concessions forestières, d'autre part. Il ne s'agit pas de remplacer les aires protégées "classiques" par des forêts exploitées, mais bien d'étendre les surfaces forestières gérées durablement et d'assurer leur préservation par des pratiques de gestions multiples et complémentaires. De même, étant donné que le choix de la certification est, pour les entreprises forestières, dominé par les bénéfices financiers, il convient de s'assurer que celui-ci reste une opportunité économique. Cela pourrait être permis grâce à un système de mécanismes incitatifs (réduction des taxes pour les concessions certifiées, payement pour services environnementaux, etc.). Bien que l'établissement de tels mécanismes s'avère complexe, leur mise en place pourrait être nécessaire à l'existence future de la certification.

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[5] Les **aires protégées de la catégorie Ia** sont des aires protégées mises en réserve pour protéger la biodiversité et aussi, éventuellement, des caractéristiques géologiques/géomorphologiques, où les visites, l’utilisation et les impacts humains sont strictement contrôlés et limités pour garantir la protection des valeurs de conservation. Ces aires protégées peuvent servir d’aires de référence indispensables pour la recherche scientifique et la surveillance continue.

[6] Les **aires protégées de la catégorie Ib** sont généralement de vastes aires intactes ou légèrement modifiées, qui ont conservé leur caractère et leur influence naturels, sans habitations humaines permanentes ou significatives, qui sont protégées et gérées aux fins de préserver leur état naturel.

[7] Les **aires protégées de la catégorie II** sont de vastes aires naturelles ou quasi naturelles mises en réserve pour protéger des processus écologiques de grande échelle, ainsi que les espèces et les caractéristiques des écosystèmes de la région, qui fournissent aussi une base pour des opportunités de visites de nature spirituelle, scientifique, éducative et récréative, dans le respect de l’environnement et de la culture des communautés locales.

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ANNEXES

Annexe 1 PETRE C-A., TAGG N., HAUREZ B., BEUDELS-JAMAR R., HUYNEN M-C. AND DOUCET J-L., 2013. Role of the western lowland gorilla (Gorilla gorilla gorilla) in seed dispersal in tropical forests and implications of its decline. Biotechnology, Agronomy, Society and Environment, 17(3), p. 517-526

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Focus on:

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

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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 fulfill 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, Africa.

Le rôle du gorille des plaines de l'Ouest (*Gorilla gorilla gorilla*) dans la dissémination des graines en forêts tropicales et les implications de son déclin. La dissémination des graines par les animaux participe significativement à la démographie, la dynamique et la 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 caractérisés 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, Afrique.

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) (IUCN, 2012).

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, we summarize 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. 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).

3. PRIMATES AS A KEYSTONE TAXON FOR TROPICAL FORESTS

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; Tutin et al., 1994; Poulsen et al., 2001; Poulsen et al., 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 colors, 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.

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:

- 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; 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 = 4,301 feces; Tutin et al., 1993). On average, one fecal clump was found to contain remains of three different fruit species;
- 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 *Cercopithecus nictitans nictitans*, the crowned guenon *Cercopithecus 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 per day per 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:

- 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 western lowland gorilla's 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;
- 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 h, with a mean of 47.1 h (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 favors 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);

- 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, 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., 1999). 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.

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) they often rely on large continuous habitat tracts, 3) they have slow reproductive rates, 4) they give birth to fewer offspring, 5) they are more valuable to hunters and 6) they 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 (IUCN, 2012); 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 subtler 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).

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 as the 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 available on western lowland gorilla seed dispersal, considered alongside the inherent biological and ecological traits of the gorilla, clearly lead 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.

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