

# Impacts of logging and hunting on western lowland gorilla (*Gorilla gorilla gorilla*) populations and consequences for forest regeneration. A review

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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*, primates, logging, ecosystems, tropical forests, biological interaction, Congo.

**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'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 : 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 ; 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*, primate, récolte du bois, écosystème, forêt tropicale, interactions biologiques, Congo.

## 1. INTRODUCTION

Ecological interactions between animal and plant species impact forest structure and composition (Beckman et al., 2007; Nuñez-Iturri et al., 2007; Wang et al., 2007; Wright et al., 2007a; Fa et al., 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; Nellemann 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 (Nellemann 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 et al., 2006). The bushmeat requirements of rural and urban human populations are increasing as a result of two main drivers (Bennet 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 (Bennet 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 et al., 2004; Morgan et al., 2007; Walsh et al., 2008; Clark et al., 2009; van Kreveld et al., 2009; Remis et al., 2010; Stokes et al., 2010).

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 et al., 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 (2008) because of the relevance of its subject. The 48 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<sup>-1</sup> (Rieu et al., 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 et al., 2007; van Kreveld et al., 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, 2012). 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 et al., 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 et al., 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:

- habitat alteration and fragmentation, linked to the road network;
- increase in human population density;
- increase in hunting (Nasi et al., 2012).

**Effects of habitat alteration and fragmentation.** Primate community structure is strongly influenced by natural factors, such as habitat structure and plant species composition (Peres et al., 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., 1992; Wilkie et al., 2000; Rieu et al., 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 et al., 2008; Clark et al., 2009; Remis et al., 2010). 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 et al., 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 et al., 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 et al., 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 et al., 2004; Arnhem, 2008; Clark et al., 2009; van Kreveld 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 et al., 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 et al., 2010). 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 et al., 2004). Under strict hunting regulation and anti-poaching control it seems that gorilla populations benefit from this growth of herbaceous vegetation (Wright, 2003; Matthews et al., 2004; Morgan et al., 2007; Walsh et al., 2008; Clark et al., 2009; van Kreveld et al., 2009; Remis et al., 2010; Stokes et al., 2010). 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., 1992; 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 et al., 2007). On the contrary, densities of chimpanzees (*Pan troglodytes troglodytes* Blumenbach 1799), which often live sympatrically with western lowland gorillas, have been shown to decrease during and after exploitation (Matthews et al., 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.

**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 (Wilkie et al., 1992; Tutin, 2001; Laurance et al., 2006; Van Vliet et al., 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 et al., 2007; van Kreveld et al., 2009) which might further increase disease distribution (Morgan et al., 2007; van Kreveld et al., 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 (Wilkie et al., 1992; Rieu et al., 2006; Clark et al., 2009; Poulsen et al., 2009), which is further facilitated by the use of logging vehicles for hunter and bushmeat transportation (Wilkie et al., 1992; Tutin, 2001; Rieu et al., 2006; 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 et al., 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 operations that could be converted into hunting camps (Rieu et al., 2006).

**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 et al., 2006; Wright et al., 2007a; Fa et al., 2009). As a result, a decline in mammal densities is generally observed (Wilkie et al., 2000; Walsh et al., 2003; Rieu et al., 2006; Morgan et al., 2007; Poulsen et al., 2009; van Kreveld et al., 2009). Hunting pressure affects mammal distribution more than logging activities *per se* (van Vliet et al., 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 et al., 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 et al., 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., 1992; Rieu et al., 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 et al., 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 et al., 2010; Linder et al., 2011).

Vulnerability to hunting notably depends on the degree of ecological specialization of the species, their anti-predator behavior and life history characteristics (Linder et al., 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 et al., 2006). Large-bodied species such as great apes are generally the most sensitive to hunting (Tutin, 2001; Bennet et al., 2007; Muller-Landau, 2007; Peres et al., 2007; Wright et al., 2007a; Fa et al., 2009; Holbrook et al., 2009; Vanthomme et al., 2010), notably because they allow higher investment returns to poachers (Wright, 2003; Linder et al., 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 et al., 2007). Specifically, hunting activities also affect the structure of primate communities and lead to a decrease in primate diversity (Linder et al., 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 et al., 2004; Mehlman, 2008; Stokes et al., 2010). Furthermore, gorilla trophy hunting exists: gorilla skulls are considered as 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; Nellemann 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 et al., 2006; Morgan et al., 2007; Mehlman, 2008; Stokes, 2008; Walsh et al., 2008; Fa et al., 2009; Linder et al., 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 et al.,

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 et al., 2007; Nuñez-Iturri et al., 2007; Wang et al., 2007; Wright et al., 2007a; Fa et al., 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 (Bennet et al., 2007; Fa et al., 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).

*Gorilla gorilla gorilla* is a highly frugivorous species. Fruit consumption is observed all year round and in large quantities: for example, Cipoletta (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 km<sup>2</sup>) 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 et al., 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 et al., 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 et al., 2009).

Studies have demonstrated dispersal distances of animal-dispersed plant species to be lower in fragmented forests (Wright, 2003) and in hunted forests (Wang et al., 2007; Wright et al., 2007b), and seed removal as being lower in hunted forests compared to undisturbed forests (Beckman et al., 2007; Wang et al., 2007; Holbrook et al., 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 et al., 2007; Muller-Landau, 2007; Nuñez-Iturri et al., 2007; Wright et al., 2007b; Fa et al., 2009; Vanthomme et al., 2010). Large-seeded plant species would be more indirectly affected by hunting because hunters target large-bodied animals (Bennet et al., 2007; Muller-Landau, 2007; Peres et al., 2007; Wright et al., 2007a; Fa et al., 2009; Holbrook et al., 2009; Vanthomme et al., 2010), which are more likely to be able to swallow large seeds (Holbrook et al., 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 et al., 2007; Wright et al., 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 (Nuñez-Iturri et al., 2007; Peres et al., 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 et al., 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 et al., 2006; Morgan et al., 2007; Mehlman, 2008; Stokes, 2008; Walsh et al., 2008; Fa et al., 2009; Linder et al., 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 et al., 2003; Matthews et al., 2004; Morgan et al., 2007; Walsh et al., 2008; Clark et al., 2009; van Kreveld et al., 2009; Remis et al., 2010; Stokes et al., 2010).

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 et al., 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., 1992; 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 et al., 2006; Bennet 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 foreign potential hunters (Morgan et al., 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:

- 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;

- 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;
- comparison of seed dispersal by gorillas before, during and after logging activities;
- 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.

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