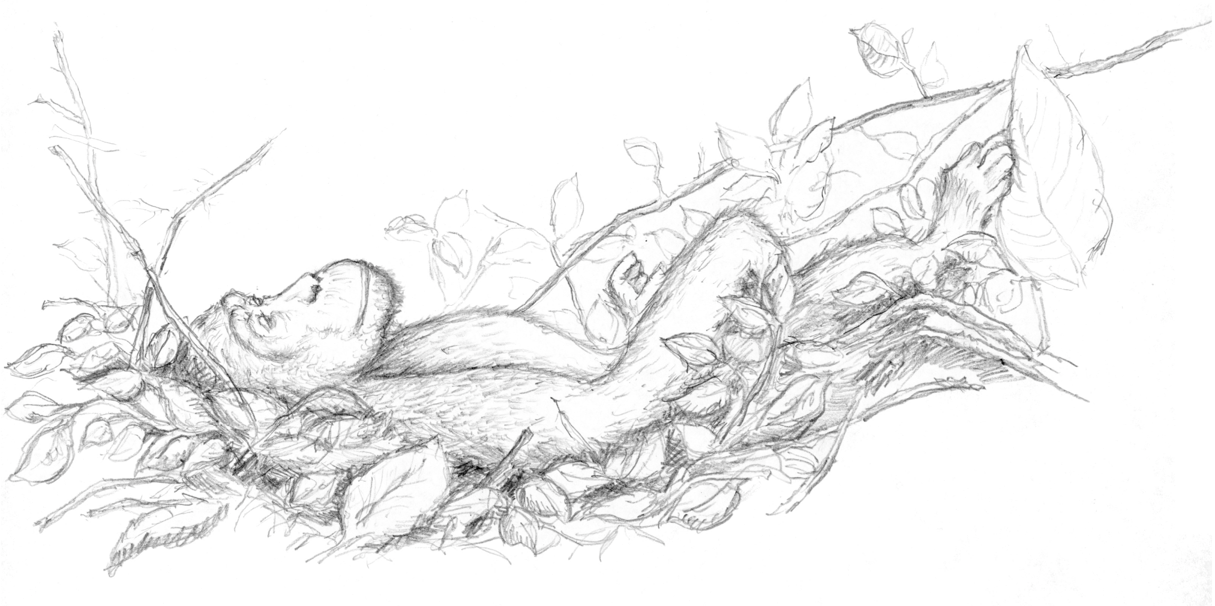
FACULTY OF SCIENCES – UNIVERSITY OF LIEGE

Department of Biology, Ecology and Evolution

Behavioral Biology Unit - Primatology Research Group

Ecology and Conservation of wild Chimpanzees *Pan troglodytes verus* in the Nimba Mountain (Côte d’Ivoire and Guinea).



A dissertation submitted by Nicolas Granier

with a view to obtaining the degree of Doctor of Science.

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Belgian Group for Primatology

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PROJET CHIMPANZES
BOSSOU-NIMBA

COOPERATION

GUINEE JAPON

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Cover-sheet sketch: “Chimpanzee in nest” by Odile Reboul

ABSTRACT

Great ape populations have alarmingly declined across their ecological range in the course of the past decades. In Africa, chimpanzees and gorillas do not elude this menace, which today appears primarily due to the loss, degradation and fragmentation of suitable habitat. African apes are our closest living evolutionary relatives, flagship and umbrella species playing important roles in ecosystem services and showing a great diversity of behavioral and ecological adaptations, as well as important cultural variations. In order to efficiently protect them, and at the same time to ensure the sustainability of a series of naturally co-occurring wildlife species, it is crucial to understand their specific ecological requirements in each place where they are subsisting. In the biodiversity hotspot of the Guinean Forests of West Africa, the World Heritage site of Mount Nimba was established in 2003 as one of the 5 exceptionally important areas for the conservation of West African chimpanzees. This scenic relief stretching over the tri-national border between Guinea, Côte d'Ivoire and Liberia harbors a particularly rich biodiversity with high level of endemism.

Striving to meet the above-described conservation objective, the present study proposes a detailed investigation of basic traits of wild chimpanzees' life history in the Nimba Mountain. Based on the results of preliminary surveys conducted in the eastern part of the Nimba Biosphere Reserve between 2006 and 2008, we established a 60 km^2 study area in the middle of the massif's southern slope, where chimpanzees were thought to permanently dwell. The central question was to understand why this population was apparently more frequently ranging in altitude habitat, particularly in the mountain forest of secondary vegetation type, and in places of high ground declivity. The formulated hypothesis was that this habitat type supplied food year-round to chimpanzees, while offering a reduced proximity to humans and a low probability of unforeseen encounter. To test this assumption, we monthly monitored 80 km of survey itineraries systematically set in the study area during 19 months between 2009 and 2011. We extensively described the structure and composition of habitat, the fruit phenology, seasonality and topography along these itineraries, while recording all signs of chimpanzee presence together with signs of other large mammals and human activity.

We used nest counts methods from line transect to estimate a population density that was included between 0.14 and 0.65 chimpanzee/km^2. Chimpanzees were highly selective in their choice of nesting-tree and nesting-site. Logistic regression indeed showed their preference for nesting in gallery and mountain forests rather than lowland forest, and in old-growth forest rather than secondary forests, preferentially in steep locations. Poisson regression with all non-nest signs of chimpanzee presence revealed a marked preference for mountain and gallery forests of old secondary type, particularly when feeding. General availability of fruit food was highly seasonal in the study area, with a soaring fructification peak during 4 dry months (Jan-Apr) and a clear, consistently scarcer availability during the 7-month rainy season. However, the abundance of 45 principal fruit foods of Nimba chimpanzees showed aseasonal monthly fluctuations with an opposite tendency: it was relatively low during the dry months and showed 3 peaks of increase during the rainy season. A second logistic model showed that non-nest signs of chimpanzee presence were linked to the abundance of seasonal fleshy fruits during the rainy season and to the fruit abundance of plants with lowly seasonal fructification pattern during the dry months. *Nauclea diderrichii* and *Grewia barombiensis* seasonally produced fleshy fruits we proposed as preferred foods. Two plants of lowly seasonal fructification pattern (*Solanum torvum, Rinorea oblongifolia*) and Marantaceae stems, which attracted chimpanzees only during fruit food scarcity, were considered as filler fallback foods. Furthermore, we established Zingiberaceae stems and fruits, which were eaten every month and attracted apes across seasons, as a staple fallback resource. In addition, both logistic and Poisson models revealed greater chimpanzee activity in the study area during the dry season

(Dec-Apr), and year-round preference for altitude habitats (between 770 and 975 m altitude). Chimpanzees avoided habitats exploited by artiodactyls and humans, and obviously selected the same habitats as 7 other primate species described in the study area.

Plotting observations of chimpanzee nest groups and signs revealed a clear gap in the middle of the study area. In the lights of findings on the ranging and grouping patterns, this result suggests that the approximately 40 chimpanzees dwelling in the study area would divide into 2 distinct communities. The Nuon River marking the border between Côte d'Ivoire and Liberia would be part of the core area of one community, and the Goué River at the Guineo-Ivorian border would be in the peripheral zone of the second community.

Taken altogether, these findings lead to general conclusions on the status and basic ecological requirements of Nimba chimpanzees, which can readily be used to enhance purpose-built actions for their conservation. In a broader viewpoint, we show how ecological research conducted on populations of chimpanzees and *Cercopithecus* monkeys can efficiently contribute to the sustainable conservation of forested ecosystems in the Nimba region. As a conclusion, we propose a holistic and cohesive outlook on environmental conservation in the tri-national Nimba. We expose the key features of a purpose-built general management plan, and discuss the opportuneness and efficiency of the different conservation tools that have been used in this extremely rich and diverse region.

TABLE OF CONTENTS

FIGURE INDEX

ACKNOWLEDGEMENTS

A Jean, et à Stéphane

I first visited Bossou at the invitation of Professor Matsuzawa. In addition to Bossou chimpanzees, I discovered with great amazement the neighboring Nimba Mountain, where I had the luck to observe wild and non-habituated chimpanzees in the forest of Seringbara. The same year, I met Marie Claude Huynen in Guinea through David Brugière. After several experiences in natural resources management in West Africa, in 2005, thanks to these persons I started conducting field research on chimpanzees of the Nimba region as a PhD student of the University of Liège. In the course of the past years, I actually spent more time in West Africa, and particularly in the Nimba region, than anywhere else. I was living there, working with different persons in changing places. Guinea, and particularly the Nimba region became somehow my home of adoption. Thus, it is difficult to acknowledge everybody here, but I would like to start by thanking you, who are reading these lines, sincerely hoping it will provide you as much pleasure and enrichement as it did to me.

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INTRODUCTION

I.1. The Mount Nimba

I.1.1. General presentation

I.1.1.1. Geomorphology and biogeography

The Mount Nimba is a 40 kilometers long wall, large of about 10 km, stretching in a northeastern-southwestern orientation at the tri-national border between Guinea, Côte d'Ivoire and Liberia. Rising abruptly more than 1,000 m above a surrounding plain covered by a ferruginous crust and culminating at 1,752 m, it is one of the highest West African mountains. Its steep slopes dug of deep and narrow valleys can exceed 75° inclination in some places, particularly in their higher part where they get steeper and delimit the sharpened ridge line of the massif (Fig. 1).

Fig. 1: The Nimba relief

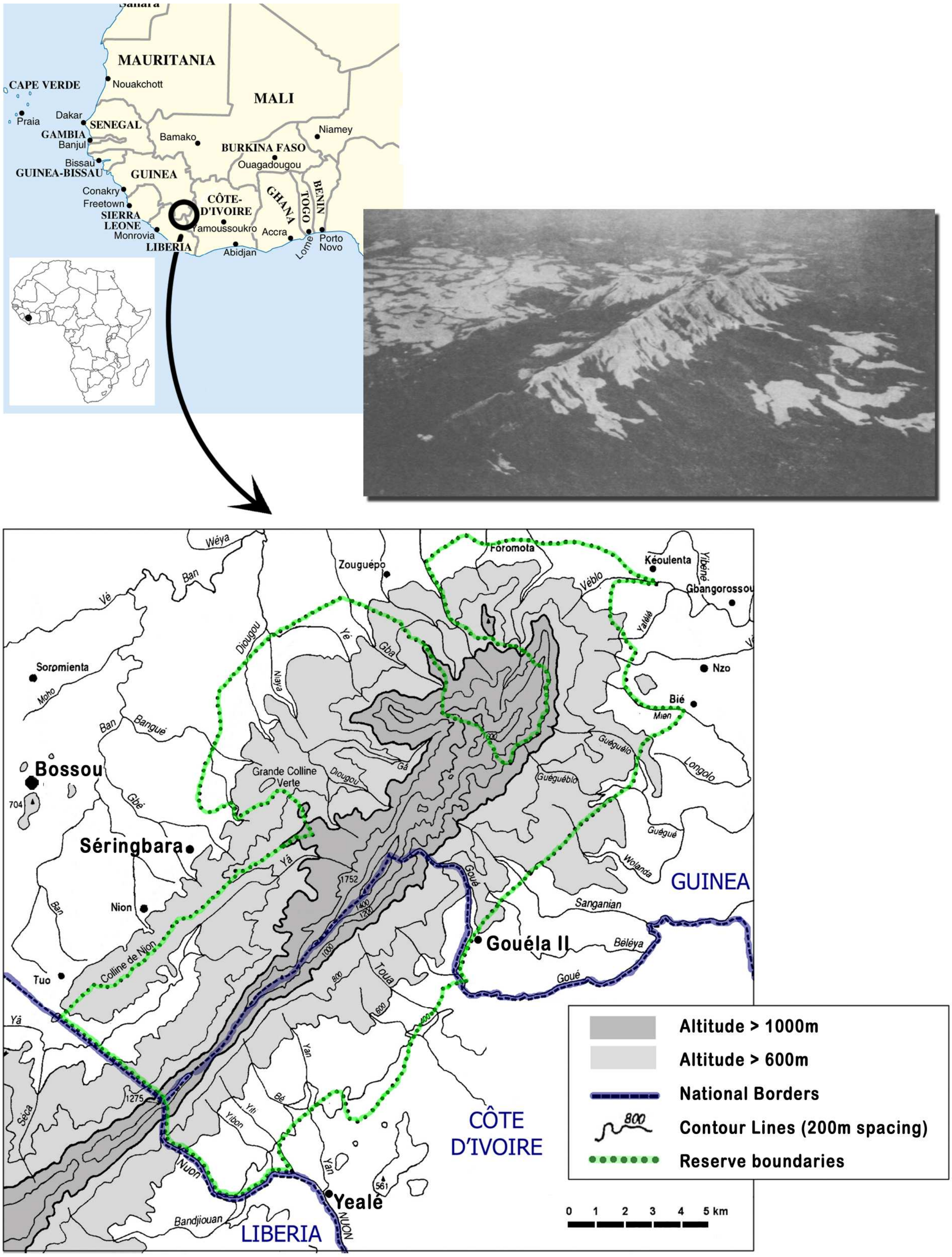
Photograph by J. Holden

The Nimba relief is a Precambrian formation of green schist based on a gneiss and granite bedrock, which has been formed from the folding of birrimian sediments (Leclerc et al. 1955). Its long and complex geological history has determined its harsh topography (Lamotte et Rougerie 1998) and the atypical presence on its top of emergent iron ore quartzite inlaid into a ferruginous mica-schist formation (Misra and Raucq 1986). The relatively large iron deposit (estimated to 600 millions tons), which is of very high quality (Fe 65%) and can be extracted by open-pit mining, has drawn the attention of mining industry for decades (Pascual 1988).

Watercourses of the important and regularly developed hydrographic network draining the Nimba Mountain have shaped deep and steep ravines (Lamotte and Rougerie 1998). The numerous streams originating in the massif feed three main rivers ending up in the Atlantic Ocean: the Cavally, flowing southwards into Côte d'Ivoire; the Ya, flowing south-eastwards into Liberia; and the Nuon, flowing south into Liberia (Fig. 2).

The Nimba mountain chain is located at the crossroads of three climatic domains (equatorial-guinean, libero-guinean and sub-sudanian) and of two major tropical winds (the humid monsoon blowing from the Gulf of Guinea, and the dry and hot trade wind, or Harmattan, blowing from the Sahara; Lamotte 1998a). The climate of Nimba results therefore from a mixture of these 3 climatic influences, with each likely to be predominant depending upon years. Similarly, the seasons are determined by the labile balance between the influences of the monsoon, dominant during the rainy season, and of the Harmattan prevailing during the dry season. Altitude reinforces the influence of Harmattan during the dry season and of rainfalls during the rainy season, creating a greater inter-seasonal contrast between the crest and foothill (White 1986). Although these highly original climatic conditions and topography ruggedness cause important fluctuations in temperature and rainfall pattern across places, seasons and years, the Nimba region is globally subject to an alternation of a dry season lasting in average from December to April, and a rainy season from May to November

Fig 2: Presentation of the Nimba Mountain



In the up-right picture from Lamotte and Rougerie (1998), which has the same orientation than the map below, savannas appear in white both on the top of the mountain and in the plain, while forest is in black. Altitude savannas covering the top of the mountain northeastern half stop briefly at the level of the Yan River, in Côte d'Ivoire.

(Lamotte 1998). The Nimba relief brutally emerging more than 1,000 m over the surrounding bedrock forms a climatic barrier exposed to, and constraining airflows, which despite its relatively small size, provides remarkable additional diversity in landscape and local climates. Such a complex climatic diversity, added to the variety of the existing edaphic conditions, has led to differentiation of a wide variety of vegetation formations and ecological niches populated by a highly diverse fauna.

I.1.1.2. Biodiversity and endemism

Located in the range of Guineo-equatorial evergreen rainforest, the low part of Nimba slopes is wooded. In the northeastern half of the massif, which is the highest, this forest is found up to 800 – 900 m altitude. A thin and rocky soil covered of low herbaceous vegetation is found from 900 m altitude to the top, broken by stretches of gallery forest extending along ravines up to 1,600 m altitude. In the occidental half of Nimba, which is of lower altitude and more exposed to humid winds, slope forests join up on the ridge forming a continuous afforestation. The demarcation between presence and absence of altitude grasslands in the massif is clearly materialized at the level of the Yan River (Fig. 2).

I.1.1.2.1. Flora

Almost all vegetation types of the Guineo-Congolese regional center of endemism (White 1986) are represented in Nimba, which led Schnell (1998) to describe the mountain as a “West African crossroads of floras”. His early study of Nimba flora has revealed 6 main vegetation types that have been - and still are - broadly used by scientists exploring Nimba (Schnell 1951). Lowland savanna covers the surrounding plain crossed by gallery forests, which extend the lowland forest encountered up to the lower part of slopes. Mountain forest stretches above with an important component ‘*Parinari excelsa* dominant’ found around

1,000 m altitude (Adam 1971; White 1986). Beyond, the herbaceous formations of superior regions present floristic variants linked to altitude and substrate nature/thickness. This altitude region constitutes the main biogeographical originality of Nimba: due to elevation, it is subject to the most important seasonal variations in rainfalls and temperatures of the massif, which have favored the differentiation of a particularly rich and diverse orophyte flora showing a high level of endemism (Schnell 1952; Adam 1971-1983). The sixth vegetation type encountered is the secondary vegetation, often described as a post-pioneer formation taking part to the healing process of rainforest after destruction and opening of the tree crown (Schnell 1951; Brugière et al. 2003; Fig. 3). It offers all the successive steps of reconstruction from clearing to shrubby thicket, secondary forest and then old-growth forest. In its first stages, the secondary vegetation is characterized by an abundant ground heliotropic vegetation (terrestrial herbaceous vegetation (THV) mainly composed of herbs of Marantaceae and Zingiberaceae), which smother ligneous species seedling (Brugière et al. 2003). In its later stages, the secondary forest contains lower density and diversity of wooded species than old-growth forest, and the canopy formed by the crown of the rare emergent trees is discontinuous (Schnell 1951). In the northeastern end of Nimba this kind of regrowth habitat is mainly found at forest edges with herbaceous ecosystems, where it seems to be favored by bushfires (Fig. 3). However, southwestern of the Yan River, where altitude grasslands are absent, patches of secondary vegetation are apparently randomly distributed across the slope: they mainly correspond to previous human settlements, plantations or result from windthrow or emergent trees cutting.

Bushfire constitutes an important ecological factor favoring the extension of herbaceous formations by inhibiting the installation and maintenance of ligneous species (Fournier 1987). Since ancient time in Nimba, fires burn the herbaceous vegetation each dry season, progressively encroaching on the adjoining forest edges (Schnell 1951). They occur as well in foothills savannas as in the altitude grasslands, but their impact is particularly destructive on the mountain forest because of its particular edaphic and topographic properties. Pascual (1988) evoked the destruction of soil humus caused by the recurrent annual fires as responsible of a significant decline of mountain forest, by unavoidably pushing their natural boundaries back (Fig. 3).

Fig. 3: Secondary vegetation at the mountain forest edge

Repetitive bushfires in altitude grasslands favor the expansion of savanna by progressively pushing back the mountain forest edge.

As a result, the constantly expanding edge of mountain forest consists of secondary vegetation habitat with low tree diversity/density, unclosed canopy, and colonized by THV and pioneer species (Schnell 1951; Brugière et al. 2003). These fires are most likely of anthropic origin as it is practiced across the tropics by cultivators, hunters or passer-by, even though the question of natural fires lit by thunder lightning or by rolling iron stones knocking each others and sparking, has been widely-evocated (Lamotte 1998).

I.1.1.2.2. Fauna

The floral richness and the diversity of ecological niches have permitted the development of a particularly diverse and rich fauna, which has been amongst the most studied in Africa (Lamotte and Roy 2003). In a literature review, Rondeau and Lebbie (2008) reported 3,500 animal species that have been described from Nimba, including over 500 taxa new to science and 200 endemics. Among the almost 600 inventoried species of mammals, birds and amphibians, 28% were classified in the IUCN red list of Endangered species (IUCN 2007). A well-known strict endemic to Mount Nimba is the Western Nimba toad (*Nimbaphrynoides occidentalis*, Fig. 4), the only viviparous bufonid described in the world, which lives at high elevation in the altitude grassland biotope (Rödel and Schiotz 2004, Hillers et al. 2008). Another strict endemic is the bat *Hipposideros lamottei*, only described in Nimba (Mickelburgh et al. 2008); both species being classified "Critically Endangered" in the IUCN red list of threatened species (IUCN 2014).

Fig. 4: The Mount Nimba viviparous toad

Nimba toad in the palm of J. Gamys' hand

The Nimba otter shrew (*Micropotamogale lamottei*) known only from Nimba for decades, before being describe 380 km away in the Putu range (Liberia), is listed as "Endangered", (Heim de Balsac 1954 in Vogel 2008). Several species of large mammals are also present, including some listed as threatened by the IUCN, like the Liberian Mongoose *Liberiictis kuhni* (“Vulnerable”; IUCN 2014), the recently re-discovered *Genetta johnstoni*, (“Vulnerable”; Gaubert et al. 2002), and artiodactyls which presence needs to be updated, particularly for duikers *Cephalophus jentinki* (“Endangered”) and *C. zebra* (“Vulnerable”). At least 11 primate species populate the forested ecosystems of Nimba (Galat-Luong and Galat 2000; Dufour 2007; personal observations). Two third of this important diversity face today serious menaces to its survival, including 2 “Endangered” species (*Pan troglodytes verus* and *Procolbus badius temminckii*), 3 “Vulnerable” (*Cercopithecus diana diana*, *C. nictitans martini* and *Colobus polykomos*) and 2 “Near Threatened” (*Cercocebus atys atys* and *Procolobus verus*).

I.1.2. Research and conservation

Scientific investigations of the Mount Nimba wildlife that revealed such an unusual level of unknown species started in the 1930s (Lamotte 1998; Brugière and Kormos 2009). In order to protect this rich biodiversity and favor its further exploration, the French colonial administration classified the Guinean and Ivorian parts of Nimba as a Full Nature Reserve in 1944 (JO-RF 1944), under the scientific management of the National Museum of Natural History of Paris (Fig. 5). From there, a long series of biological studies were carried out in the 3 countries of the Nimba range, providing considerable amount of data in all fields of biology and placing the Nimba amongst the most studied areas in Africa (Lamotte and Roy 2003).

In the 1980s, the UNESCO recognized the exceptional nature of Nimba by classifying its Guinean and Ivorian sections as a Natural World Heritage Site (World Heritage program), and by establishing an almost 13,000 ha-Biosphere Reserve in Guinea (Man and Biosphere Program, Fig. 8) (Hartley et al. 2008). The growing interest of the scientific community for biodiversity exploration and protection, and the menaces hanging over the Nimba Mountain have favored the diversification of funding sources and the multiplication of scientific missions supported by different NGOs, organizations or universities.

Fig. 5: Remains of the scientific station built in the 1940s.

Ziéla, northeastern end of Mont Nimba, Guinea.

As a result, today the Nimba wildlife is amongst the most renowned in West Africa, and numerous conservation statuses were superimposed on the mountain as discoveries occurred: IUCN Strict Nature Reserve category Ia, Center of Plant Diversity (Hartley et al. 2008), Important Bird Area (BirdLife 2008), priority area for the conservation of West African chimpanzees (Kormos et al. 2003).

I.1.3. Human populations and threats to biodiversity

Archeological tracks of lithic technology and pottery fragments indicate that human settlement in the Nimba region has been important between 600 BC and 1,000 AD (Mauny et Holas 1953). The first traces recorded after this period were dated from about 1750. Since that time, 3 main ethnic groups live in the mountain surroundings: the Mano and Yakuba, who have a common forest origin, and the Kono people who result from the mixing of these 2 groups with the Mandingo people coming from the north during the vast islamization movement of the seventeenth century (Germain 1984). This resident population has lived from sustainable exploitation of natural resources during centuries (forest products, game and small-scale agriculture). But the armed conflicts that occurred in the neighboring countries of Sierra Leone, Liberia and Côte d'Ivoire since the early 1990s have created successive fluxes of refugees, which are at the root of an important demographic increase (USCR 2002). In the mid 1990s, about 800,000 refugees were settled in Guinea, mostly in the forest region along the Liberian border (USCR 2002). Many of these people durably settled outside refugee camps to live from forest resources exploitation and find a piece of land to cultivate (Van Damme 1999). As a consequence, the pressures exerted on biotopes and fauna were considerably intensified, and the ecosystems were not able anymore to regenerate rapidly enough to fulfill the needs of the growing population (UNEP 2000; Fig. 6).

Fig. 6: Hunter with 3 putty-nosed and 1 moustached monkeys (Central Africa)

© National Geographic

Another critical conservation issue is related to the geological structure of Mount Nimba. Due to the high quality of its iron ore deposit and its open-air situation at the top of relief, mining prospects menace Nimba diversity since the 1960s. An open-pit mine was exploited between 1963 and 1992 on the Liberian crest of Nimba, at about 3 km from the border with Guinea and Côte d’Ivoire. Drillings occurred in the 1970s in the Guinean section of Nimba, and in 1993 the core area (integrally protected) of the Nimba Mountain Biosphere Reserve was withdrawn from a 1550 ha mining enclave (in the Guinean northeastern end, Fig. 8) (Hartley et al. 2008). Ten years later, a mining consortium signed an agreement with the Guinean government for iron exploitation in this enclave, and in 2012 a several-years phase of drilling ended (Fig. 7).

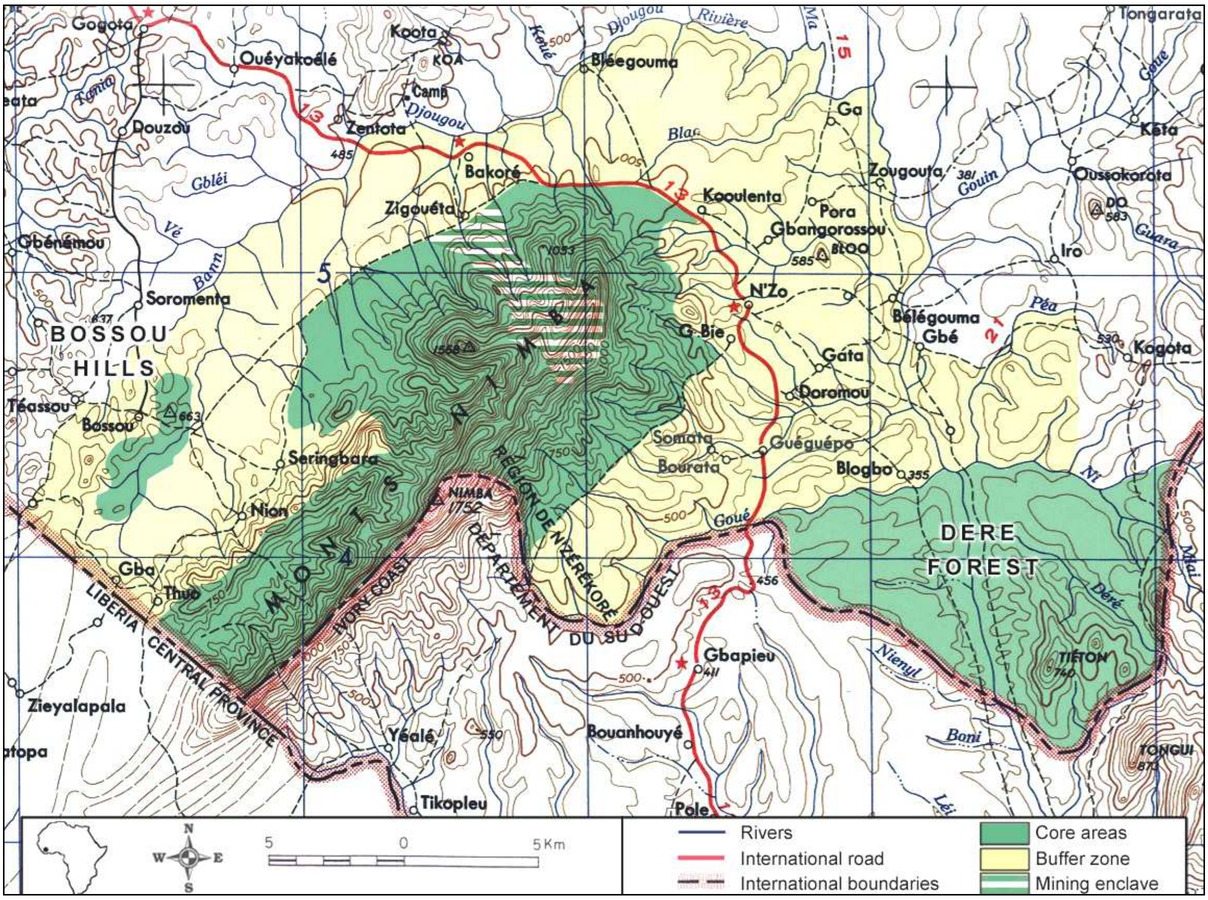
Fig. 7: Roads on the top of Nimba, in the mining enclave

March 2012.

Beside, we conducted in 2012 the baseline ecological studies on large mammals and chimpanzees in the framework of an environmental and social impact study of mining activity in the Nimba Mountain (Granier et al. 2012; 2012b; 2012c). The same year, another mining company started to drill for iron ore in the ferruginous plain located at the southern foothill of the Guinean Nimba, and created roads linking the international road between Guinea and Côte d'Ivoire to the limit of the integrally protected area (Fig. 8). In addition to habitat loss, degradation and fragmentation, mining activity also indirectly worsen the environmental problems by attracting people seeking employment and subsequently increasing the irrational exploitation of wildlife.

As consequences of these threats and as early as 1992, the Nimba Mountain was labeled as an Endangered Natural World Heritage Site by the UNESCO (Hartley et al. 2008). In 1993 the Biosphere Reserve was enlarged by inclusion of 2 additional integrally protected areas: the Bossou hills and the Déré Forest (Fig. 8).

Fig. 8: Map of the Nimba Mountain Biosphere Reserve



Background map from the US Army, 1953.

Overall, the conservation measures taken have been rather effective, and today forest biotopes within the fully protected part of the Nimba Mountain are still well preserved from cutting. However, they are noticeably retracting in favor of herbaceous biotopes due to the repeated and uncontrolled bushfires, and all Nimba ecosystems are exposed to constantly increasing pressures, particularly mining and subsistence activities of a growing local population.

I.2. The chimpanzee

The chimpanzee is human's closest living evolutionary relative (Kortland 1974), sometimes referred to as the "cultured chimpanzee" (McGrew 2004). He is an efficient seed disperser playing a key role in forest ecology and renewal, recognized as a good flagship, umbrella and environmental indicator species (Junker et al 2012). Thus understanding this ape species has gradually became a matter of prime importance for scientists from various domains of biology (including ecology, sociology, anthropology, behavior, psychology, cognition, evolution, genetics, archeology), and awareness of the necessity to act for ensuring its sustainable living has concomitantly grown.

I.2.1. Taxonomy

The chimpanzee shares a common ancestor with human being, which is estimated to have lived about 6 millions years ago (Groves 2001), and molecular studies haves shown that our genomes are almost 99% similar (Gunter and Dhand 2005). The chimpanzee belongs to the genus *Pan* of the primate order and the hominid super family (Fig. 9). Two species occur in equatorial Africa: the pygmy chimpanzee, or bonobo (*Pan paniscus*), which lives only below the Congo River in the Democratic Republic of Congo, and the common or robust chimpanzee (*Pan troglodytes*), divided into 4 sub-species. The West African chimpanzee (*Pan troglodytes verus*, Fig. 9) ranges from Senegal to Nigeria, the Nigeria-Cameroon chimpanzee

(*Pan troglodytes eliotti*) is found only in these 2 countries north of the Sanaga River, while the central chimpanzee (*Pan troglodytes troglodytes*) occurs south of the Sanaga River to the Congo River in DRC, and the Eastern chimpanzee (*Pan troglodytes schweinfurthii*) ranges eastwards to the great lake region (Oates et al. 2014).

Fig. 9: Young adult male from Bossou community

The alpha male is leisurely crossing the road

1.2.2. Long-term research sites

Chimpanzees have been studied at more than 40 locations across equatorial Africa, but seminal discoveries on chimpanzee biology, society, and culture were done in only 6 long-term study sites that started before 1980, and where research is still ongoing nowadays. In 1960, Jane Goodall began the first long-term study of wild chimpanzees on the shore of Lake Tanganyika in northwestern Tanzania (Fig. 10). Her research at Gombe Stream led to significant findings on the social relationships, tool-use, and warfare in chimpanzee societies (Goodall 1968). At another site located 140 km southerly in Tanzania, Toshisada Nishida began a long-term research project on the chimpanzees of the Mahale Mountains in 1965 (Fig. 10). He set a new standard for the analysis of primate social structure and brought in particular significant understanding of the organization of chimpanzee social groups (Nishida 1968). Chimpanzee research was also carried out at two other important Ugandan sites in the 1960s, where it was however stopped in the 1970-80s due to civil wars that raged in the country (Fig.10). The Budongo Forest project was restarted in 1990 by Vernon Reynolds, who had already conducted primatological studies there in 1962 (Reynolds 1965). After intermittently collecting data since 1976 on the Ngogo chimpanzee community of the Kibale Forest, Richard Wrangham officially established Kibale as a long-term research site in 1987.

Fig. 10: The 6 long-term research sites on chimpanzees in Equatorial Africa

These pioneer works were all conducted on East African chimpanzees (*Pan troglodytes schweinfurthii*) living in either savanna woodland mosaic (Gombe and Mahale) or tropical rainforest (Budongo and Kibale). The will to further understand and to conduct comparisons between different subspecies may have pushed Yukimaru Sugiyama to initiate in 1976 the long-term study on the West African chimpanzees of Bossou (*P.t. verus*) in Guinea (Sugiyama 1984). And in the same dynamic, Hedwige and Christophe Boesch initiated the Taï chimpanzee project in 1979 in the Taï Forest National Park in Côte d'Ivoire (Boesch and Boesch-Achermann 2000). The Taï Forest is located 230 km south of Bossou and constitutes the largest and one of the oldest remnants of tropical forest in West Africa (Fig. 10).

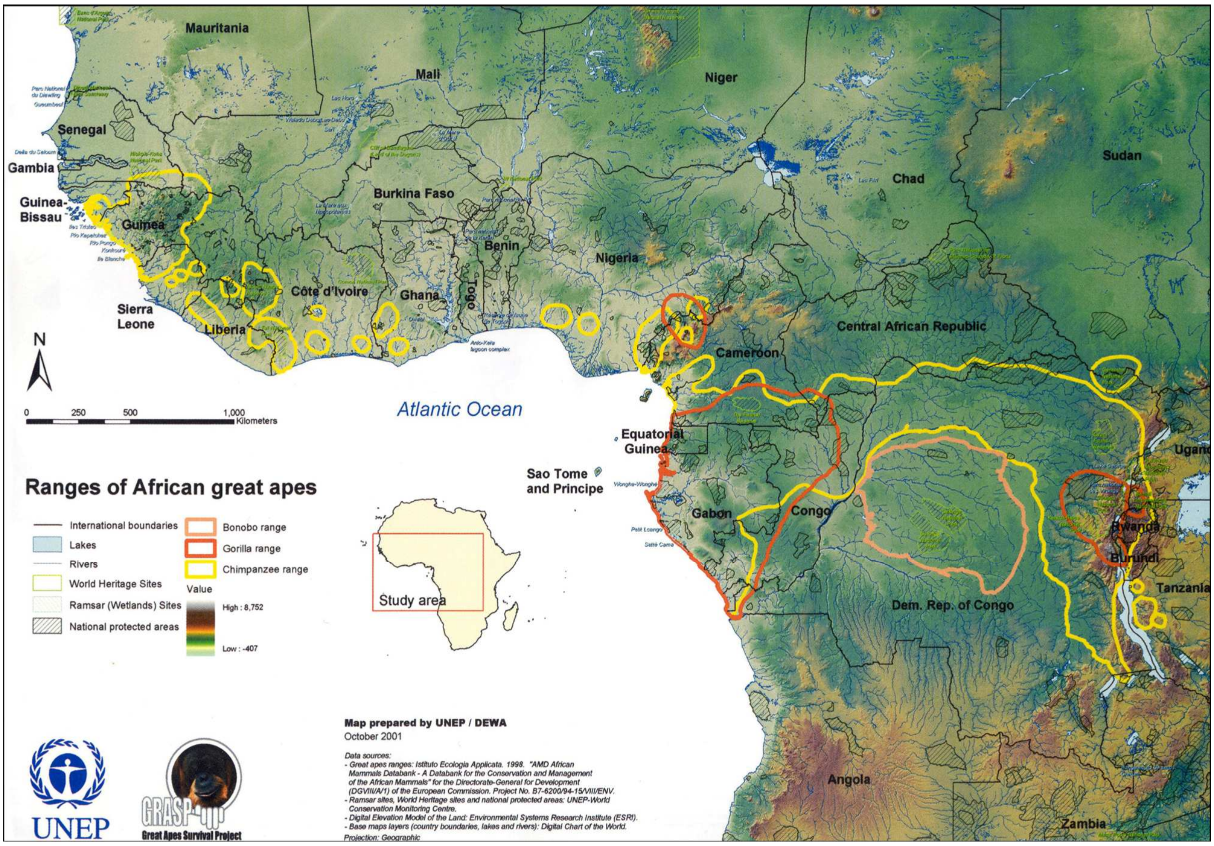
I.2.3. Ecology and behavior

Common chimpanzees have a broad but discontinuous distribution across tropical Africa (Butynski 2003; Fig. 11). They still occur in 22 countries chimpanzees and in a wide variety of habitat types including dry savannas, evergreen rainforests, montane forests, swamp forests, and dry woodland-savanna mosaics (Reynolds 1965; Goodall 1986; McGrew et al. 1981).

I.2.3.1. Ranging and social

Unlike most primate societies, organized in relatively stable and cohesive groups, chimpanzees live in communities of 5 to 150 individuals characterized by a fluid system of fission-fusion within a common home range (Nishida 1968; Sugiyama 1973). The size of the home range averages 12.5 km², but presents great variations strongly related to the nature of vegetation formations (from 6 km² in mixed forest to 300 km² in woodland forest mosaic; Sugiyama 1994; Baldwin et al. 1982). Within this home range, which is a territory defended against intruders, chimpanzees travel either alone or in loosely structured temporary parties that varies greatly in size, composition and persistence over time (Goodall 1986). They have excellent mental maps of their territory, which are achieved by learning, and use a precise spatial memory to locate their food resources repeatedly (Boesch and Boesch 1984; Normand et al. 2009; Tweheyo and Lye 2003). Their curious and explorative nature allows them to be attracted to new food sources by noisy group of animals, such as birds or other primates, or they may be led to a new resource by a foraging companion that has been there before (Goodall 1986).

Fig. 11: Map of the chimpanzee ecological range



Map prepared by UNEP / DEWA
October 2001

Data sources:
- Great apes ranges: Istituto Ecologia Applicata. 1998. "AMD African Mammals Databank - A Databank for the Conservation and Management of the African Mammals" for the Directorate-General for Development (DGVIII/A/1) of the European Commission. Project No. B7-6200/94-15/VIII/ENV.
- Ramsar sites, World Heritage sites and national protected areas: UNEP-World Conservation Monitoring Centre.
- Digital Elevation Model of the Land: Environmental Systems Research Institute (ESRI).
- Base maps layers (country boundaries, lakes and rivers): Digital Chart of the World.

Projection: Geographic

In addition to this fluid and dynamic social structure, they have a highly developed social system characterized by tight bonds between community members and capacities for cooperation, empathy, reconciliation and alliance formation (Nishida 1968, Byrne and Whiten 1988). Typically, in chimpanzees, females emigrate by the age of puberty (around 10 years old), and philopatric males remain within their natal community (Nishida 1968; Goodall 1986; Boesch and Boesch Achermann 2000). Large carnivores are the only predators that happen to attack chimpanzees. Fatal attacks from leopards *Panthera pardus*, have been reported in the Taï Forest (Côte d'Ivoire; Boesch and Boesch-Achermann 2000) and the Lopé Forest (Gabon; Henschel et al. 2005), and from lions *Panthera leo*, in the Mahale Mountains (Tsukahara 1993).

I.2.3.2. Nesting

Like all great apes, each weaned chimpanzee builds a new nest (also called bed or sleeping platform) every night, and occasionally a day-nest in which to rest, socialize or eat, most nests being built in trees and not reused (Plumptre and Reynolds 1996; Fig. 12). Arboreal nests are founded on a solid branch and made by bending, breaking and inter-weaving all surrounding smaller twigs. Nests constitute tangible and persistent evidences of chimpanzee presence and abundance that have been used to develop nest count methods (Plumptre and Reynolds 1997; Ancrenaz et al 2004), particularly useful to census non-habituated populations over wide areas (Tutin and Fernandez 1984). We provide further details on the nesting behavior of Nimba chimpanzees in chapter III.

Fig. 12: Chimpanzee nests

I.2.3.3. Diet

Chimpanzees are omnivorous, and their diet is highly variable according to communities and seasons. However fruit always comprises more than half of their diet, and leaves, bark, and stems are also important (Hladik 1977). They also happen to eat flowers, buds, roots and tubers, tree gum and insects, algae, mushrooms, honey and bird eggs (Sugiyama and Koman 1987). Mammals comprise a small but significant component of the diet of many communities (McGrew 1983; Stanford 1998; Boesch and Boesch Achermann 2000). As the feeding repertoire of chimpanzees is being compiled and expended at different sites, it is becoming apparent that differences in the foods eaten across sites can not be explained by differences in their biotic environments and rather reflect traditional and potentially cultural variants between communities (McGrew 1992; Boesch and Tomasello 1998).

I.2.3.4. Tool use and culture

Chimpanzees are the only primates with the exception of humans, who habitually make and use various sets of tools in their daily activities, to access their food, socialize, or explore their habitat (Whiten et al. 2003). The use of tools to obtain some foods has been documented across all the studied chimpanzee populations (Goodall 1964; Sugiyama 1993; Fig. 13). Sticks, rocks, grass, and leaves are all commonly used materials that are modified into tools and used to gather and eat honey, termites, ants, nuts or water (Yamakoshi and Myowa-Yamakoshi 2004).

However, this elementary technology shows important inter-community variations in the sets of tools that are used, and in the aim of their use (Sugiyama 1993). Converging research indicates that each community possesses a unique and proper repertoire of tool use behaviors, which does not depend on resource availability, passes down generations and shows evolutionary capacities (Whiten et al. 2003). In other words, different chimpanzee communities present significant cultural variations in their customary behavioral repertoires that are greatly influenced by their social structure and social context of transmission (Whiten et al. 1999).

Fig.13: Chimpanzee using a stick to expel food

Unknown source

Extensive studies have been conducted on the material culture of chimpanzees, especially on the nut-cracking and ant-catching behaviors, demonstrating great variations between communities in the techniques used and the species consumed (Collins and McGrew 1987, Sugiyama 1993, Humle and Matsuzawa 2001). For instance, chimpanzees crack-open nuts only west of the N’Zo-Sassandra River in Côte d’Ivoire, whilst nuts are available throughout their ecological range (Boesch et al. 1994; Joulian 1995; Fig. 14). Studies on different “cracking communities” detailed the numerous behavioral variants related to the 6 different nut species that are cracked (Joulian 1995), and to the materials used to reach their kernel (stones, woods or a combination of both, Boesch and Boesch 1984).

I.2.4. Conservation

In the past decades, large African mammals have suffered from the important and increasing global deterioration of both their living conditions and populations' status (Brashares et al. 2004), as documented for elephants (Bouché et al. 2011) and lions (Henschel et al. 2014). The growing human demography and economical issues cause an increased exploitation of natural resources resulting in significant degradation, loss and fragmentation of natural habitats. Local communities living in remote areas still containing rich wildlife need land to cultivate and game to hunt for feeding themselves, whereas mining and logging companies take over natural resources at commercial ends. Besides, political instability and armed conflicts negatively impact animal populations due to weapons spreading, derived product trade (ivory, horn…), bushmeat hunting to supply soldiers and refugees, and they do not facilitate implementation of sustainable management of natural resources.

Fig.14: Bossou chimpanzees cracking-open nuts of *Elaeis guineensis*

Photograph by E. Nogami

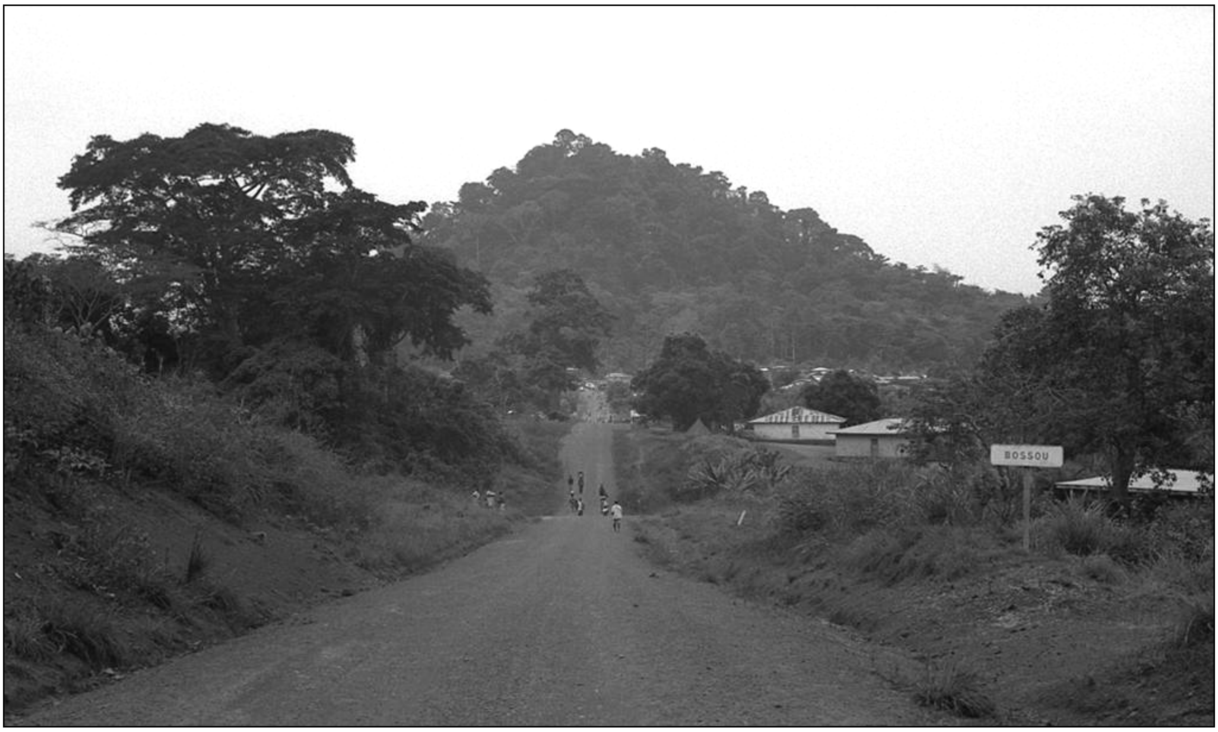
Primates do not elude from these menaces, and several African species are threatened with extinction (Oates 1996). Classified as "Endangered", the chimpanzee is amongst the most threatened primate of the continent (Oates et al. 2014). A large majority of the remaining population of common chimpanzees (about 2 thirds of 235,000 individuals) was estimated to belong to the Central African sub-species, and to occur in only 2 countries: Gabon and Congo-Kinshasa (Butynski 2003, IUCN 2014). The West African and the Nigeria-Cameroon chimpanzees are the less numerous and considered as the most threatened. At the dawn of this century, the population of *Pan troglodytes verus* was estimated to 38,000 individuals, with the Republics of Guinea and Côte d'Ivoire containing the most abundant populations (Butynski 2003). In 2 national censuses of chimpanzees in Côte d'Ivoire conducted at the end of the 1980s, Hoppe-Dominik (1991) estimated the nationwide population to 11,867 individuals, and Marchesi et al. (1995) to 11,676. The Marahoué National Park provided the highest national density estimate in both studies, and accounted for about a tenth of these relatively high values (N = 1,407 individuals). However, in an estimate they qualified as a guess, N'Goran et al. (2007) proposed the remaining population of the Marahoué to be of less than 50 individuals. It is a drastic decline already suggested in 2001 by Butynski (2003) that may have been worsened by the armed conflict that started in September 2002. In Guinea, the population was estimated to 12,000 individuals (Ham, 1998), and it is very likely that Guinea would currently be the West African country containing the highest density and abundance of wild chimpanzees (Kormos et al. 2003).

I.3. Chimpanzee research in Bossou and Nimba

I.3.1. The chimpanzees of Bossou

The Mano people, who live in the village of Bossou (Guinea) at 4 km from Mount Nimba northern foothill, are animists. In their world view, which is actually a form of totemism, each local group or family is mystically associated to 3 animal species representing its totems. In concrete terms, these totems consist of taboos or prohibitions hereditary transmitted that apply to all the family members (Germain 1984). Some individuals of the family (ancestor or contemporary) have metamorphosis ability and can turn into these totems (see Annex 4). The Zogbila family, who founded Bossou about 3 centuries ago near a small hill populated by chimpanzees (the Mont Gban; Fig. 15), has for main totem the chimpanzee. Zogbila welcomed all the people who wanted to settle with them at the only condition to respect their taboo. This belief is still lively today and villagers continue to make offerings to chimpanzees and to strictly prohibit their hunting, which explains the atypical coexistence of chimpanzees and human beings in Bossou. This remote village in the farthest reaches of southeastern Guinea offers a perfect example of traditional protection of wildlife that rose long before modern conservation became influential in the area (Holas 1952, Lamotte et Roy 2003).

Fig. 15: Bossou village at the foothill of Mont Gban



Photograph by JA. Lièvre.

This traditional protection of chimpanzees was first reported by Lamotte (1942) and mentioned by couple of researchers (Holas 1952, Adam 1971-1983). The Dutch ethnologist Adrian Kortland who visited Bossou twice in 1960 and 1965 was the first to explicitly describe direct observation of chimpanzees. He noted that “they did not seem to be shy and could easily be observed” (Kortland 1986). In 1967 and 1969, he organized 2 scientific expeditions (6-7 months in total) to observe Bossou chimpanzees using classical ethological methods of field experiments, in a context of investigation of the hominization process in hominids (Kortland 1974). These expeditions yielded the first estimates on the size of the community and individual identification of its members, their ability to manipulate objects in an antipredatory context (Fig. 16), and important baseline data on their ecology and behavior (Yamakoshi 2011). More systematic research on Bossou chimpanzees started in 1976 when Professor Yukimaru Sugiyama of Kyoto University (Japan) initiated their long-term study, which has been undergoing for almost 40 years. Continuous observation of known individuals has provided key discoveries on their life history, behavior and ecology, development, material culture and on the hominid evolution (Matsuzawa et al. 2011). Another remarkable and extensively studied feature of Bossou chimpanzees is the relatively large and diverse repertoire of tools they use in daily life. All the organic and lithic materials known to be utilized by wild chimpanzees are used in Bossou either as they are, modified or combined. These tools are mainly generated to fulfill their subsistence needs such as feeding and drinking, but they are also used in contexts of defense, communication, exploration, reaching or comfort (Sugiyama 1997; Hirata et al. 1998; Humle 2011). Amongst the 24 tool-use behaviors recorded since 1976, 8 are unique to this community (i.e. so far never observed elsewhere).

The core area of this small chimpanzee community is constituted of 4 hills surrounding the village of Bossou, mainly covered by multi-stage secondary forest and encircled by cultivated fields, fallow lands with small remaining patches of secondary forest (Sugiyama and Fujita 2011). Chimpanzees exploit all vegetation types available in their home range, but are heavily relying on cultivars such as cassava, corn, papayas, bananas, mangoes, pineapples (Yamakoshi 1998).

Fig. 16: The leopard experiment

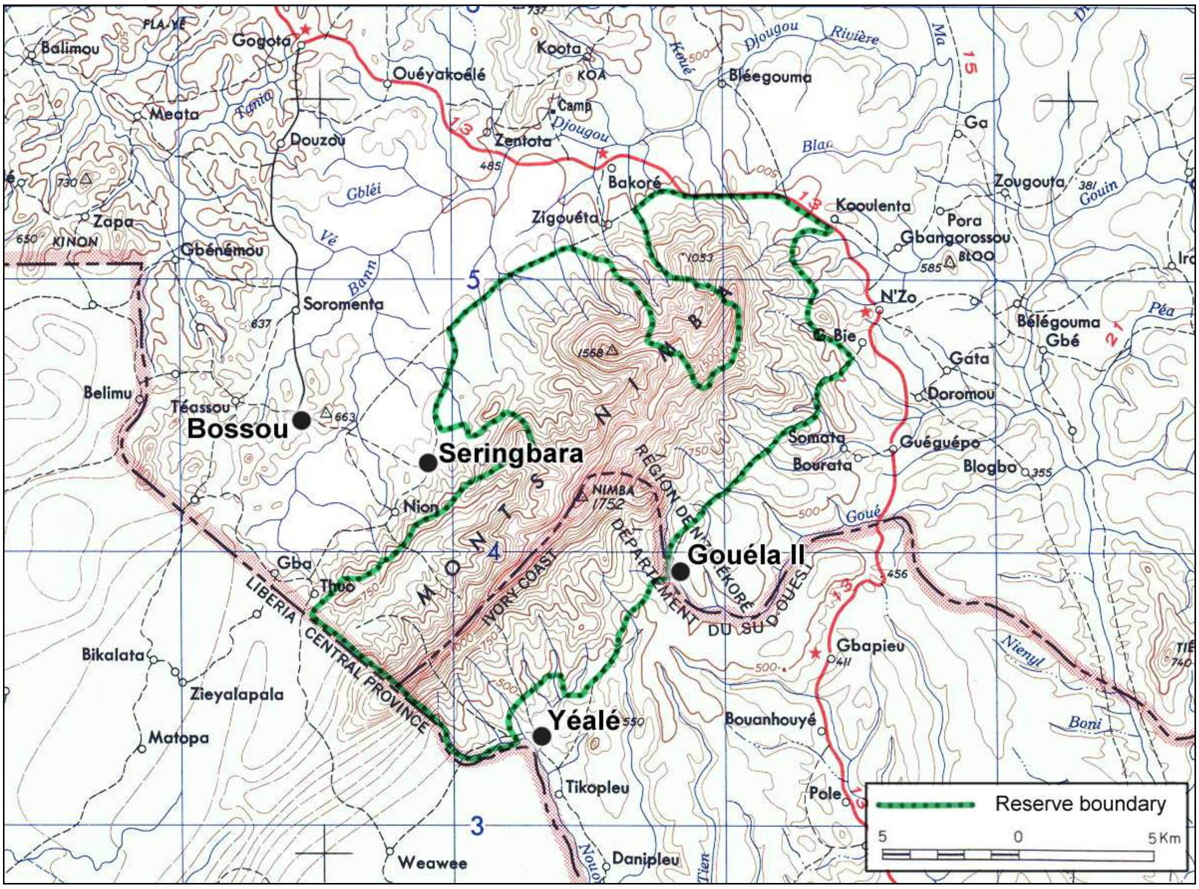
Photograph by A. Kortland, who introduced a plush leopard in the territory of Bossou chimpanzees and observed their reactions.

However, the growing human demography results in an increased encroachment on natural habitat, and local people who depend on agriculture for their survival express a decreased tolerance to crop-raiding (Hockings et al. 2009). Bossou chimpanzees are getting more and more isolated from other communities, and we deplore the absence of immigration into Bossou group since 1982 (Sugiyama 1984). A green corridor project was initiated in 1997, consisting of planting trees in the 4 km-stretch of savanna between Bossou and Nimba in order to favor chimpanzee immigration into Bossou group (Matsuzawa et al. 2011a). Studying adjacent chimpanzee communities populating the Nimba Mountain is interesting in itself to compare all aspects of behavior and cultural adaptations between different groups, but investigating whether Nimba chimpanzees could immigrate into Bossou group has also became a central issue of conservation in this strongly human-influenced context.

I.3.2. History of chimpanzee research in Nimba: Seringbara, Gouéla II and Yealé

Sugiyama has intermittently visited the Nimba Mountain since 1976 seeking to establish the presence of chimpanzees. He mainly focused on the Seringbara Forest located 6 kilometers southeast of Bossou on the northern slope of the massif (Fig. 17), where he concluded to their presence based on both field and interview surveys with the local people (Koops 2011).

Fig. 17: Chimpanzee study sites in the Nimba region



Shimada (2000) surveyed the area twice in 1999 and collected further evidences of their presence. During repeated visits in 2000, Humle and Matsuzawa (2001) have studied the tool-use behavior and medicinal use of plants of Seringbara chimpanzees to investigate their material culture in comparison to adjacent communities. And in 2003, Koops (2011) established a permanent research site at Seringbara to initiate a systematic research on the influences of habitat ecology on elementary technology use by chimpanzees.

Sporadic studies were carried out by several institutions in other areas of Nimba to survey different chimpanzee populations or address inter-community behavioral variations. Gouéla II is a centenary-old encampment for cultivation divided into small spread out settlements of less than 10 huts, inhabited by several families (about hundred people from the Kono and Mano ethnic groups) living from farming and hunting. It is located down the southern slope of Nimba, in Guinea, near the Goué River marking the border with Côte d'Ivoire and the reserve limit (Fig. 17, 18). A 3-hour walk departing either from N'Zo or Gouéla is needed to reach the site. Sugiyama (1995) and Shimada (2000) briefly surveyed the Gouéla II forest. They recorded nests, feeding related signs, use of vegetal wands to catch and eat ants, and concluded that chimpanzees may be periodically present in this area of the mountain.

Another important site is the Yealé village, located in Côte d'Ivoire at the border with Liberia, which is marked by the Nuon River (Fig. 17). This small village of less than thousand people, 2 kilometers south from the reserve limit, is remotely situated in a dead end, more than 50 kilometers from its prefecture Danané. Predominantly populated by the Yakuba and Mano people, the village mainly subsists on farming and hunting. Hoppe Dominik (1991) and Marchesi et al. (1995) who conducted national censuses of chimpanzees in Côte d'Ivoire, both visited the Yealé forest as a sample site and estimated densities of 0.5 chimpanzees / km^2 in the Ivorian section of Nimba. The national study of Marchesi et al. (1995) was also aiming at investigating the differences in the material culture of different chimpanzee communities, and seminal papers were published on this topic, particularly considering the nut-cracking behavior (Boesch et al. 1994, Joulian 1994).

Fig. 18: The southern slope of the Nimba Mountain

Wide-angle view on the northeastern half Nimba

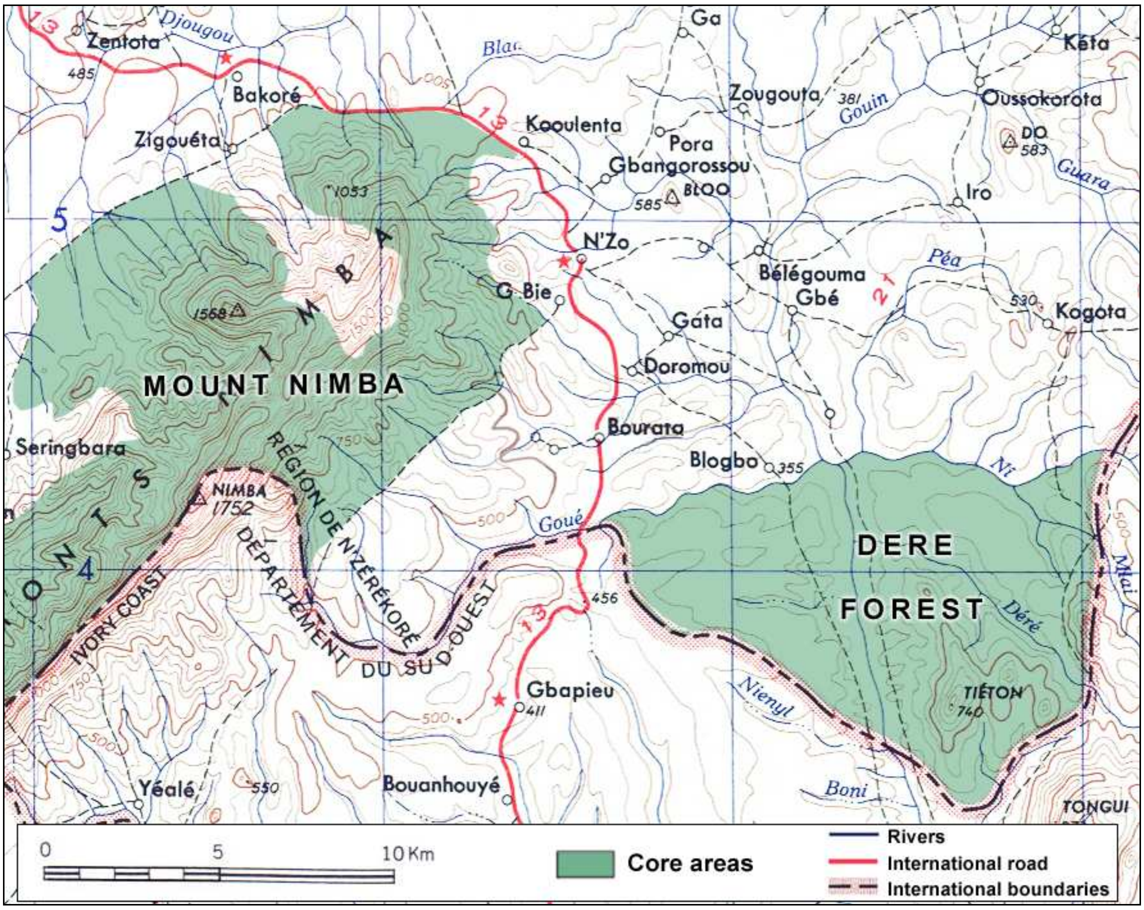
Matsuzawa and Yamakoshi (1996) also intensively surveyed the Nuon River area of the Yealé forest (Libero-Ivorian border) to investigate the tool-use and nesting behaviors of chimpanzees in comparison to those of Bossou. This research was pursued by Humle and Matsuzawa (2001) who visited Yealé several times between 1996 and 2001 in the framework of their comparative study between Bossou and Seringbara chimpanzees. The war that torn Côte d’Ivoire apart from 2002 has interrupted research activities, until we first visited Yealé in 2007.

I.4. Building and implementing the present study

I.4.1 Preliminary surveys in the eastern Nimba Mountain Biosphere Reserve

Between 2006 and 2008, we conducted 13 months of survey divided into 3 fieldwork periods in both the Gouéla II and Déré forests (Fig. 19; Granier 2011). The aim was to evaluate the status of chimpanzees in these 2 core areas of the Nimba Mountain Biosphere Reserve using interviews of local populations and scouting field surveys. The Déré Forest is separated from the forested slopes of Nimba by a 10 km gap of savanna, cultivated fields and roads, with sparkled fragments of secondary forest (Fig. 19). Despite it has been established as an integrally protected area of the Nimba Mountain Biosphere Reserve by the MAB program of UNESCO in 1993 (Hartley et al. 2008), no legal Guinean text was published to enforce this decision. Moreover, farmers took advantage of a logging company that exploited the forest in 1999-2001 to flood in the area from 2001, and established their encampment for cultivation. The settlement of Ivorian rebels in 2003 within the classified forest arrogating that it was belonging to Côte d’Ivoire has increased the agricultural and hunting pressures and made the socio-environmental problem more complex. As a result, the Déré Forest mainly consists today of farmbush with always reducing forested patches still harboring the marks of past rich, diverse and healthy forested ecosystem.

Fig. 19: Map of the eastern part of the Nimba Moutain Biosphere Reserve



Chimpanzee presence in the Déré Forest was reported in 3 interviews out of 32, and we observed a single sign of chimpanzee presence: a more-than 3 months old nest built over 20 m above the ground. Considering the extremely low prospects for chimpanzee research in the Déré forest, we concentrated further efforts on the Gouéla II area of Nimba, where we observed 730 signs of chimpanzee presence related to nesting, feeding, traveling and tool-using (Granier 2011). In Gouéla II, chimpanzees appeared to preferentially use the upper parts of the mountain forest and the adjoining secondary vegetation habitat. We observed 2 thirds of the signs in such habitats at the edge between mountain forest and altitude grassland (above 700 m altitude). The nests records represented almost half of the total observations and provided important information on the grouping and ranging patterns of these chimpanzees. These findings, added to the fact that their presence was temporally discontinuous, suggested the Gouéla II forest as a peripheral zone of a chimpanzee community territory.

I.4.2. New study area: Yealé – Gouéla II

Aside from that, chimpanzees were known to permanently live in the Yealé forest of Nimba, contiguously located southwest of Gouéla II in the southern slope of Nimba (Humle and Matsuzawa 2001; Fig. 17, 19). Matsuzawa and Yamakoshi (1996) indeed reported that the Nuon River area (Fig. 17) marking the border between Liberia and Côte d'Ivoire in the Yealé forest, hosted a resident chimpanzee community dwelling between 700 m and 1,000 m altitude. They also recorded an extremely high percentage of nests built on the ground (35.5% of N = 464 nests), including an important part used overnight, which was totally unusual. With the objective of re-centering the study area on the home range of one chimpanzee community, and to guarantee the collection of a large-enough data set to perform consistent statistical analysis, we decided to shift and enlarge our study area towards the Yealé forest of Nimba, as shown in Fig. 20).

I.4.3. Aims of the core research in the southern slope of Nimba

The founding question was to understand why in the southern slope of Nimba chimpanzees appeared to mainly exploit altitude habitats colonized by secondary vegetation and with relatively high ground declivity. Was this habitat selection due to preferences linked to the composition and structure of the vegetation, to the availability of food resources, to the lower rate of human frequentation? We formulated the hypothesis that the old secondary vegetation habitat was important for those chimpanzees, who exploited it year-round because it constantly harbors food resources, while providing enough-sturdy trees to build nests. In a broader perspective, understanding the ecological requirements of chimpanzees is interesting in a purely research-oriented purpose, perhaps even more exciting because of their evolutionary proximity with human beings, but we also conducted this research with strong prospects on general conservation of Nimba ecosystems.

The objective was to focus on chimpanzees as a good umbrella and environmental indicator species, to describe the basic ecological requirements of this specific population, estimate its home range and abundance, in order to implement in situ purpose-built actions of conservation that will ensure their living and thereby the sustainability of naturally co-occurring wildlife species. To enlarge the scope of this research and provide inter-specific comparisons related to habitat use, we also paid interest to the presence of other primates including humans, and artiodactyls. Collecting such baseline ecological data on chimpanzees and other large faunal species has became especially crucial in the current context of constantly increasing human pressures on Nimba ecosystems.

I.4.4. General field method and schedule of the core research

To reach this objective and shed light on basic ecological traits of chimpanzee life history, we implemented a mid-term ecological monitoring of its population in the Yealé and Gouéla II forests, in the southern slope of Nimba (60 km^2). With the help of local field assistants we set 80 km of permanent survey itineraries up in 2009 and 2010, systematically laid out into the newly defined study area (Granier et al. 2014; Fig. 20). We thoroughly described habitat along these itineraries in terms of tree composition, vegetation structure, food availability, topography and climate. Then we monthly monitored them for 19 months of fieldwork divided into 2 periods: from June to December 2009, we walked 7 times the 65 km of reconnaissance surveys (recces), and from May 2010 to April 2011, we surveyed these recces plus 12.5 km of line transects 11 times (Fig. 20). During each visit we systematically described, recorded and georeferenced all chimpanzee signs of presence, together with all the signs of other large mammals and human activity.

Fig. 20: Map of survey itineraries in the study area

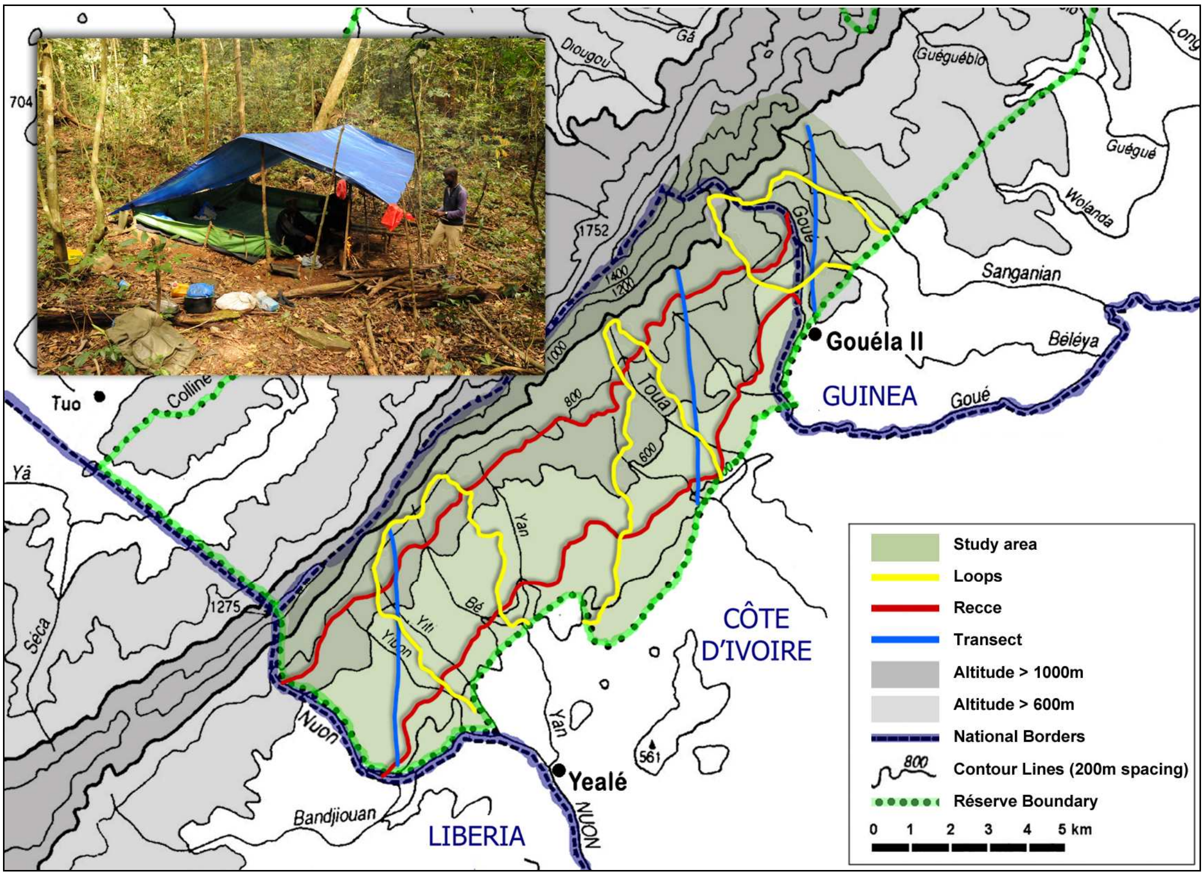


Photo shows our mobile camp set in the upper part of the Bé River on the southwestern recce loop

Survey itineraries were walked following a fixed sequence of 14 days, living autonomously in the forest with 3 field assistants and changing sleeping site every night (walking speed ≤ 1 km/h, progression rate = 5.7 km/day; Fig. 20).

I.4.5. Content

The first chapter deals with the issues related to great apes conservation at the scale of their entire African range, and draws out the complex problematic of chimpanzee protection in the tri-national Nimba Mountain. A continent-wide perspective on ape populations (Junker et al. 2012) shows that in the course of the 1990s, African ape populations have undergone significant decreases in distributional range due to a dramatic decline in suitable environmental conditions (SEC) and habitat fragmentation, rendering local populations more vulnerable to extinction. In order to efficiently maintain, and even favor the regrowth of ape populations in their natural living conditions, it is of critical importance to cumulate synergic efforts focused on each area, or geographical entity, where they are still present. In this perspective, the present research has focused on the chimpanzee population of Mount Nimba. In a holistic review of the recent history and conservation of this exceptional site, Granier and Martinez (2011) present this varied but single ecological and anthropological entity torn apart between 3 administrative and multiple protective statuses. The extensive research and conservation efforts carried out in the course of the past century did not prevent the rich Nimba biodiversity to be jeopardized by growing human pressures mainly related to subsistence of local people and mining activities. We emphasize the necessity for elaborating a global and coherent transnational program of natural resource management, which would devote special attention to alleviating the threats faced by chimpanzees.

To reach this objective, we investigated in details the status and the specific ecological requirements of Nimba ape population. We started with preliminary surveys in 2 lowly studied areas of the eastern part of the Nimba Biosphere Reserve: the Gouéla II and Déré forests. The second chapter offers a comprehensive presentation of these preliminary surveys (Granier 2011). We built on findings of this exploratory research to delimit a new study area centered on the southern slope of Nimba (including all the Ivorian section of the mountain), and sketch out the future orientation of the core research of this study by formulating working hypotheses. The third chapter presents a detailed analysis of the nesting behavior of chimpanzees in the Ivorian section of Nimba (Granier et al. 2014). We estimated their population abundance using nest count methods and investigated their criterions of nesting-site selection using logistic regression. This nest-based study also provided interesting findings on the general behavioral ecology of chimpanzees, particularly on their year-round ranging and grouping patterns. The fourth chapter thoroughly analyzes the criterion of habitat selection in chimpanzees (Granier et al, submitted). We used regression analyses to investigate their presence in relation to the fluctuating food availability, and to the structure of habitat, the altitude, and the presence of other primates, artiodactyls and humans. We found out that chimpanzees were significantly more dwelling in altitude habitats, particularly the mountain and gallery forests of old secondary type, and that THV was playing a leading role in their feeding strategy and habitat selection. Altogether, the achieved knowledge on the behavior and ecology of Nimba chimpanzees constitutes essential preliminary data to be increased and used for their conservation, and thereby the sustainability of the entire wildlife.

Finally, all findings is put together in the discussion to draw out general conclusions on the ranging, grouping, feeding, nesting behaviors of chimpanzees in the Ivorian Nimba. These conclusions are discussed in the lights of other researches, and we build on this achieved knowledge to formulate purpose-built actions of environmental conservation intending to enable perpetuation of this umbrella species in its exceptional environment. In a more general perspective, we expose the guidelines of a general management plan we propose for the

Nimba region, and discuss the opportuneness and efficiency of the various conservation measures that exist or have existed in this region.

CHAPTER I. Global issues and local perspectives of conservation

This chapter is composed of 2 subparts offering respectively a large-scale perspective on African great apes conservation, and holistic views on local chimpanzee conservation in the Nimba Mountain.

II.1. Recent decline in suitable environmental conditions for African great apes

This part is a paper published in the periodic journal “Diversity and Distribution” that was coauthored with 46 persons studying great apes in equatorial Africa (Junker J, Blake S, Boesch C, Campbell G, du Toit L, Duvall C, Ekobo A, Etoga G, Galat-Luong A, Gamys J, Ganas-Swaray J, Gatti S, Ghiurghi A, Granier N, Hart J, Head J, Herbinger I, Cleveland Hicks T, Huijbregts B, Imong IS, Kuempel N, Lahm S, Lindsell J, Maisels F, McLennan M, Martinez L, Morgan B, Morgan D, Mulindahabi F, Mundry R, N’Goran KP, Normand E, Ntongho A, Tiku Okon D, Petre CA, Plumptre A, Rainey H, Regnaut S, Sanz C, Stokes E, Tondossama A, Tranquilli S, Sunderland-Groves J, Walsh P, Warren Y, Williamson EA and Kuehl HS. 2012). It provides data on continental distribution and trends of ape population, and highlights the importance of large-scale, comparative analyses to effectively guide regional conservation efforts. This work has been done from the compilation of 68 local surveys data, centralized and standardized into the IUCN/SSC A.P.E.S. (Ape Populations, Environments and Surveys; http://apes.eva.mpg.de) database, through an initiative of the Max Planck Institute for Evolutionary Anthropology (Leipzig, Germany).

II.1.1. Abstract

Aim: To predict the distribution of suitable environmental conditions (SEC) for eight African great ape taxa for a first time period, the 1990s and then project it to a second time period, the 2000s; to assess the relative importance of factors influencing SEC distribution and to estimate rates of SEC loss, isolation and fragmentation over the last two decades.

Location: Twenty-two African great ape range countries.

Methods: We extracted 15,051 presence localities collected between 1995 and 2010 from 68 different areas surveyed across the African ape range. We combined a maximum entropy algorithm and logistic regression to relate ape presence information to environmental and human impact variables from the 1990s with a resolution of 5 x 5 km across the entire ape range. We then made SEC projections for the 2000s using updated human impact variables.

Results: Total SEC area was approximately 2,015,480 and 1,807,653 km2 in the 1990s and 2000s, respectively. Loss of predicted SEC appeared highest for Cross River gorillas (-59%), followed by eastern gorillas (-52%), western gorillas (-32%), bonobos (-29%), central chimpanzees (-17%) and western chimpanzees (-11%). SEC for Nigeria-Cameroon chimpanzees and eastern chimpanzees was not greatly reduced. Except for Cross River and eastern gorillas, the number of SEC patches did not change significantly, suggesting that SEC loss was caused mainly by patch size reduction.

Main conclusions: The first continent-wide perspective of African ape SEC distribution shows dramatic declines in recent years. The model has clear limitations for use at small geographic scales, given the quality of available data and the coarse resolution of predictions. However, at the large scale it has potential for informing international policymaking, mitigation of resource extraction and infrastructure development, as well as for spatial prioritization of conservation effort and evaluating conservation effectiveness.

II.1.2. Introduction

In recent years, thousands of species have declined dramatically, and many populations are close to extinction owing to anthropogenic impacts (Koh et al., 2004). The effects of this conservation crisis have been particularly severe in tropical regions, which support *c.* 50% of described species (Wright, 2005), including our closest living relatives, the great apes. Bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), gorillas (*Gorilla beringei*, *Gorilla gorilla*) and orangutans (*Pongo abelii*, *Pongo pygmaeus*) are particularly important for biodiversity conservation. They fulfill the multiple roles of charismatic flagship species, umbrella species and environmental indicator species (Wrangham et al., 2008). Focusing on ape populations and their habitats raises public awareness and funding for biodiversity conservation, overlaps with conservation priorities identified for many other tropical plant and animal species, and helps maintain tropical ecosystem services.

During the past 30 years, there have been alarming declines in great ape populations (Oates, 1996). Ape populations in Gabon were halved between 1983 and 2000 owing to outbreaks of Ebola and poaching for bushmeat (Walsh et al., 2003); an estimated 5000 gorillas died in the Republic of the Congo following an Ebola outbreak (Bermejo et al., 2006); 90% of chimpanzees in Côte d'Ivoire died between 1990 and 2007 (Campbell et al., 2008); in Senegal a formerly contiguous chimpanzee population was fragmented into three blocks with large unoccupied areas in between (Galat-Luong et al., 2000), and in south-western Nigeria, chimpanzee population size and distribution sharply declined over a decade (Greengrass, 2009). Even in areas with large intact ape populations, such as northern Democratic Republic of Congo, evidence of the sale of large numbers of chimpanzee orphans and carcasses testify to a rapid recent increase in illegal hunting (Hicks et al., 2010).

Much of the remaining African ape range, previously relatively intact, is now rapidly being converted to human-dominated mosaics (Laporte et al., 2007). In many ape range states this has created isolated remnants of prime ape habitat, often inside protected areas, within a landscape dominated by agriculture and agro-forestry (e.g. Plumptre et al., 2010).

Whether or not great apes will survive within these human-modified landscapes depends on whether protected areas are large enough and, more importantly, adequately protected (Tranquilli et al., 2011). Encouragingly, if poaching pressure is low, some ape taxa may survive in heterogeneous land-use mosaics that include extensive agricultural activity. For example, chimpanzees occur at low density throughout Sierra Leone, where only a small proportion of the original forest cover remains in a landscape dominated by traditional small-scale slash-and-burn agricultural fields (Brncic et al., 2010). Other studies report similar situations in Guinea (Hockings et al., 2009), Guinea-Bissau (Torres et al., 2010) and Uganda (McLennan, 2008).

At the other end of this spectrum lie the large and contiguous forest blocks of Central Africa. However, human population densities, hunting, logging and mining activities are now rapidly increasing, destroying ape habitat in their wake (Laporte et al., 2007; Hicks et al., 2010).

Recent site-specific or landscape-scale surveys have provided information on the effects of these threats on density and abundance (Morgan et al., 2006; Kuehl et al., 2009; Stokes et al., 2010; Campbell et al., 2008), and on spatial and temporal trends in ape populations (e.g. Hall et al., 1998; Blom et al., 2001; Reinartz et al., 2008). Surprisingly, only very few studies exist which have attempted to combine the wealth of available GIS and remote sensing information and data on ape populations in a predictive modeling context. Pintea et al. (2003) used data on chimpanzee presence in Tanzania and related it to multiscale remote sensing imagery; Bergl et al. (2010) used a set of Landsat imagery and other predictors to develop a habitat suitability model for Cross River Gorillas (*Gorilla gorilla diehli*) to assess dispersal corridors and available non-occupied habitat; similarly Torres et al. (2010) suggested a habitat suitability model for an area in south-western Guinea-Bissau and three distinct time periods to asses rates of change in available chimpanzee habitat.

However, effective conservation also requires range-wide information on spatial and temporal trends in ape distribution, to inform global policy-making (Norconk et al., 2010) and donor decisions, and to foresee and confront emerging threats, such as habitat destruction, large-scale infrastructure developments and resource exploitation projects, as well as increasing poaching pressure and climate change impacts (Kormos et al., 2003; Tutin et al., 2005; Oates et al., 2007; Plumptre et al., 2010; Morgan et al., 2011). Eventually this information will allow us to evaluate the effectiveness of ape conservation worldwide. The only attempt to provide a range-wide predictive model of African ape biogeography has been derived from behavioral observations at the several long-term field sites (Lehmann et al., 2008). This model uses information on body mass and climate conditions to first predict time allocation for key activities and subsequently for group size that is predicted across the entire range.

In an effort to further bridge the gap between local scale information and global ape population trends, we conducted a first continent-wide analysis of data compiled in the IUCN/SSC A.P.E.S. (Ape Populations, Environments and Surveys) database (http://apes.eva.mpg.de). A.P.E.S. serves to centralize and standardize all existing ape survey information, providing a universal platform from which these data may be accessed by the scientific and conservation community following a strict data access and release policy.

Despite differing data collection methods, confirmed ape presence is standard information available across all archived data sets. Species presence localities can be used to model suitable environmental conditions (SEC) (Pearce and Boyce, 2006). Applying such models simultaneously to different taxa, varying environments and spatial scales is a great challenge and limitations are likely to arise from the quality and resolution of available predictor variables. In this study we aim to (1) estimate the distribution of SEC for African great apes for two time periods, the 1990s and 2000s, to (2) assess the relative importance of factors influencing SEC distribution, and (3) quantify temporal rates of SEC loss, fragmentation and isolation. We define SEC as the probability of ape occurrence given certain environmental conditions.

II.1.3. Methods

To model SEC for African apes we combined a maximum entropy algorithm (MAXENT; Phillips et al., 2006) with logistic regression. We chose this approach for two reasons. First, we had confirmed ape presence localities but only few confirmed absence locations. Although presence-only modeling approaches are widely used (Pearce and Boyce, 2006), we also wanted to make use of the advantages of Generalized Linear Models (GLMs) (i.e. with regard to the inclusion of interactions and nonlinear terms) and multimodel inference, which is well developed for logistic regression (Burnham and Anderson, 2002). We therefore used MAXENT to generate pseudoabsences and then used logistic regression to build SEC models. Owing to lack of comparable ape presence data sets for the 1990s and 2000s, we modeled SEC for the 1990s and then projected SEC probability into the 2000s using updated predictor variables. We repeated the MAXENT analysis 50 times using different random selections of presence points for each taxon separately as test data. We generated 20 sets of pseudo-absences from each of the derived presence probability maps (i.e. a total of 1000 data sets), which we then combined with the presence localities and analyzed using logistic regression. The results reported here are the averages revealed by these 1000 analyses per taxon. Details of the analysis are described below and in Appendix S1 in Supporting Information which also includes a flowchart (S1-1) depicting the analytical process. The text passages are directly linked to the respective steps in S1-1.

II.1.3.1. Presence localities

We extracted 15,051 great ape presence localities from the A.P.E.S. database (defined as GPS positions of sightings, nest sites, vocalizations, dung, carcasses, trails, tracks, feeding and tool-use-sites) (step 1, Fig. S1-1 in Appendix S1). After referencing presence locality data to a 5 x 5 km grid, we eliminated all duplicates from the data set to reduce sample bias. The extracted and used presence points per (sub-) species were *Pan troglodytes verus*: 3033/325 extracted/used presence localities; *Pan troglodytes troglodytes*: 1317/272; *Pan troglodytes schweinfurthii*: 5866/537, *Pan troglodytes ellioti*: 477/143; *Pan paniscus*: 896/121; *Gorilla gorilla gorilla*: 2293/387; *Gorilla gorilla diehli*: 759/69; and *Gorilla beringei graueri*: 410/92 (Fig. S1-2 and Table S2–1 in Appendices S1 and S2). For areas with overlapping chimpanzee and gorilla range we did not use ape signs that could not be assigned to one or the other species. These presence localities were originally confirmed during ape and biodiversity surveys in 68 different areas. Survey areas ranged in size from a few km^2 to tens of thousands of km^2. We excluded localities for mountain gorillas as good estimates of this subspecies' population size and geographic range are available covering several decades (Guschanski et al., 2009; Gray et al., 2010). All ape presence locations used in this study were collected between 1995 and 2010 and are GPS-based. We dealt with obvious GPS errors by excluding all those points, which fell outside of the survey area defined for a particular survey data set. Additionally, because of the scale of the study, potential small-scale spatial error from GPS inaccuracies may not be significant.

II.1.3.2. Predictor variables

African apes are primarily forest dwelling species and many populations occur within the tropical forest belt, which is characterized by a humid climate, high rainfall and low temperature variability. However, at their range limits towards the Sahel zone in the north and east and in West Africa, chimpanzees range in drier woodland and savannah-dominated areas (Caldecott and Miles, 2005). Almost all ape populations are impacted to some degree by human activities in the form of habitat destruction and poaching (Kormos et al., 2003; Plumptre et al., 2003; Walsh et al., 2003; Caldecott and Miles, 2005; Reinartz et al., 2006; Campbell et al., 2008; Greengrass, 2009; Kuehl et al., 2009; Hicks et al., 2010). Therefore, we chose 13 predictor variables of three categories (climate, vegetation and human impact) to model SEC (Table 1; step 1, Fig. S1-1 in Appendix S1). This choice was also influenced by the limited availability of high quality range-wide GIS data sets.

Table 1: Variables used, their sources, the year(s) for which data were available and the time period for which each layer was included into the SEC model

ID	Category	Variable name	Reference	Year	Time
1	Climatic[*1]	Mean temperature (bio1)	Hijmans et al. 2005	1950-2000	Both
2		Mean precipitation (bio12)			Both
3		Range in temperature (bio4)			Both
4		Range in precipitation (bio15)			Both
5		Minimum temperature (bio6)			Both
6		Minimum precipitation (bio14)			Both
7	Human impact	Human population density[*2]	CIESIN	1990	1990s
			CIAT	2010	2000s
8		Human influence index	Fotheringham 1981	1990	1990s
				2010	2000s
9		Poverty index	Elvidge et al. 1997	1993	1990s
				2003	2000s
10		Distance to nearest road	DCW	1992	Both
11		Distance to nearest river	FAO	Undated	Both
12	Vegetation	Percentage forest cover[*3]	De Fries et al., 2000	1992-1993	Both
			Hansen et al., 2006	2000	Both
13		Forest in neighbourhood	De Fries et al., 2000	1992-1993	Both
			Hansen et al., 2006	2000	Both

[*1](WorldClim Bioclimatic Variables); **[*2]**(Gridded Population of the World, version 3 (GPWv3), 2); **[*3]**(1992/1993: GLCF AVHRR Continuous Fields Tree Cover Project); (2000: MODIS Vegetation Continuous Fields); **CIESIN**: Center for International Earth Science Information Network, Columbia University; **CIAT**: Centro Internacional de Agricultura Tropical; **DCW**: Digital chart of the World, **FAO**: Food and Agricultura Organization of United Nations

II.1.3.3. MAXENT analysis

We ran one MAXENT analysis per taxon using presence localities and seven environmental predictor variables, which were partially principal components analysis (PCA) scores (see Table 2, Table S1 in Appendix S1) derived for the 1990s (step 3 and 4, Fig. S1-1 in Appendix S1). We bootstrapped the models 50 times per taxon, and for each run we randomly selected 75% of the occurrence locality grid cells as training data with the remaining 25% reserved for testing the resulting model. We used recommended default values for the convergence threshold (105), maximum number of iterations (500) and regularization value (104), and let the program automatically select 'features' (environmental variables) following default rules according to the number of presence records (Phillips et al., 2006). Overall model performance was evaluated by means of the 'Area under the Curve' (AUC) determined by the Receiver Operating Characteristic Curves (ROC) analysis (Phillips et al., 2006).

For each taxon we used its broadly classified geographical range (provided by IUCN) to which we added a 100-km buffer where no obvious geographic barriers existed (for *G. g. diehli* we added a 10-km buffer because of their relatively small geographical range), to ensure that potential suitable habitat outside the defined distributional limit would be included in our analysis.

II.1.3.4. Absence localities

We generated pseudo-absences from the presence probability maps revealed by MAXENT (Engler et al., 2004) (step 5, Fig. S1-1 in Appendix S1). We derived pseudo-absences by randomly drawing cells from the range of the respective taxon whereby the probability of each particular cell to be drawn equaled one minus the cell's ape occurrence probability (as derived from MAXENT). For presence cells and cells directly neighboring them, the probability to be drawn was set to zero. The number of pseudo-absences generated (N_a) was determined as $N_a = (N_p \times H_{unsuitable}) / H_{suitable}$, where $H_{suitable}$ and $H_{unsuitable}$ were the number of pixels with MAXENT output values > 0.5 and < 0.5, respectively, and N_p was the number of presence cells for a taxon. Per cell, only one pseudo-absence could be placed. For the small range of *G. g. diehli* we selected as many pseudo-absences as there were cells with presence localities.

Table 2: Predictor variables used for the SEC model

Variable name	**After PCA analysis**	**Var. n°**	**Anticipated effect**
Human population density	Human impact (Factor 1)	1	Negative linear, potentially interacting with var. 4 & 5
Human influence index	Human impact (Factor 1)	1	
Poverty	Human impact (Factor 1)	1	
Precipitation driest	Climatic (Factor 2)	2	Negative quadratic – apes occur within an optimal climatic range
Seasonality precipitation	Climatic (Factor 2)	2	
Seasonality temperature	Climatic (Factor 2)	2	
Mean annual precipitation	Climatic (Factor 2)	2	
Minimum temperature	Climatic (Factor 2)	2	
Mean annual temperature	Climatic (Factor 3)	3	Negative quadratic
Distance to roads	Distance to roads	4	Positive linear (see var. 1)
Distance to rivers	Distance to rivers	5	Linear (see var. 1)
Percentage forest cover	Percentage forest	6	Positive linear
Forest in neighbourhood	Forest in neighbourhood	7	

The variables indicated in the first column were partly highly correlated and thus combined using a principal component analysis (**PCA**). Numbers in the third column label the derived principal components or original variables which entered our models as predictors.

As the number of pseudo-absences was usually small compared with the number of available cells, we expected large variability in the particular locations at which pseudoabsences would be placed. To avoid an undue influence of any particular selection of cells with pseudo-absences, we generated 20 sets of pseudo-absences for each of the 50 occurrence probability maps per taxon, creating 1000 data sets per taxon (step 6, Fig. S1-1 in Appendix S1).

II.1.3.5. SEC model

Based on the presence localities and the derived pseudoabsences we ran GLMs (McCullagh and Nelder, 1989) with binomial error distribution and logit link function (i.e. logistic regressions) to estimate (1) the relative probabilities of apes occurring at a specific location within their potential geographical range under past and current environmental conditions and (2) the relative importance of the predictor variables in explaining ape presence or absence (step 7 and 8, Fig. S1-1 in Appendix S1). Models were built using the predictors as derived for the 1990s and then projected to the 2000s using updated layers of human impact variables (step 9 and 10, Fig. S1-1). See Appendix S1 for details of the analyses, model specification and formal inference.

II.1.3.6. Temporal change in SEC

To determine changes in SEC between the 1990s and 2000s, we first converted the continuous prediction maps into binary suitability maps. We defined a given pixel as suitable for apes when the model average of predicted ape occurrence probability was above a certain threshold. For each taxon we used nine different thresholds which were the quantiles (10, 20, etc., up to 90%) of the average ape occurrence probabilities derived for those pixels on the 1990s map, in which each respective taxon was actually present (Pearce and Boyce, 2006). The same thresholds were then also used to determine SEC on the map with average ape occurrence probabilities projected for the 2000s (step 11 and 12, Fig. S1-1 in Appendix S1). The derived maps (total of 9 thresholds 9 2 periods 9 8 taxa = 144 maps) were then characterized as follows (step 13 and 14, Fig. S1-1 in Appendix S1).

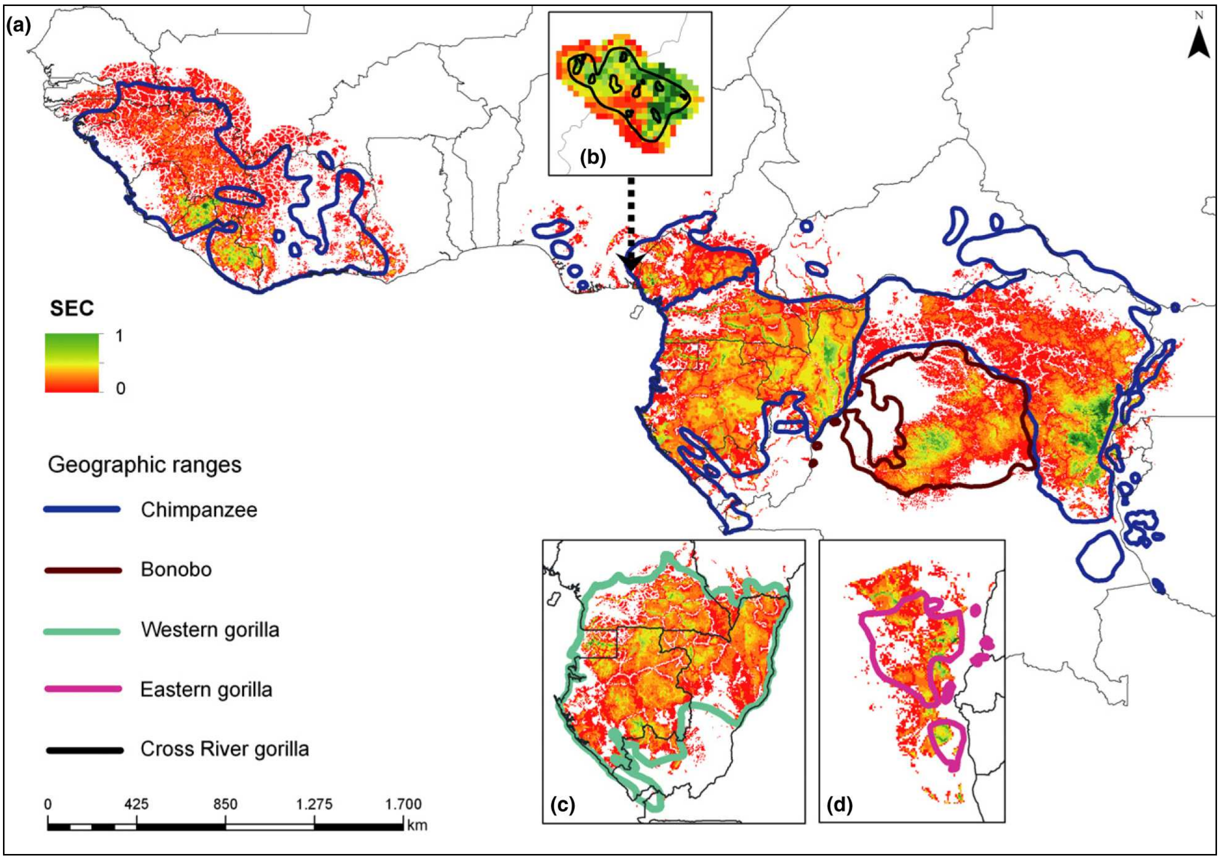
To estimate total ape range for the 1990s and 2000s and rate of change between the two decades, we first counted the number of pixels predicted as SEC for each map. Next, we determined patches of SEC. We defined a patch as a group of all SEC pixels directly neighboring one another. We then determined for each patch its size (number of pixels) and its degree of isolation (closest distance from its border to the nearest border of any other patch). Finally, we counted the number of patches. To estimate mean rates of change in SEC, SEC patch size and degree of isolation for each taxon, we averaged values across all nine thresholds. We calculated total extent of SEC for the 1990s and 2000s by converting SEC predictions into a binary map using a threshold, which we derived by maximizing the product of the true positive rate and the proportion of the area predicted as nonsuitable for the 1990s data set. We then applied the same threshold to the 2000s SEC predictions. All statistical analyses were done in R (R Development Core Team, 2010).

II.1.4. Results

II.1.4.1. Current SEC distribution

SEC showed a high degree of spatial heterogeneity both within and among taxa (Fig. 21). This resulted, for instance, in a highly variable SEC patch size distribution for the different taxa (Appendix S2). Although, the total number of SEC patches was dominated in general by very small patches, mean patch size and range differed considerably between taxa (Fig. S2-1 to S2-8). The largest SEC patches occurred in Central Africa within the ranges of *G. g. gorilla*, *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. Countries with SEC values predicted highest by our model were Democratic Republic of Congo (DRC), Gabon, Liberia and Republic of the Congo. Where environmental predictor variables contributed substantially to predicted SEC distribution (i.e. mean Akaike weight was larger than expected), our hypotheses about their effects on ape SEC were mostly confirmed (Tables 2 and 3). However, variable contributions to predictions of SEC differed considerably between taxa. Human impact had a clear negative effect on all taxa except *P. t. schweinfurthii*. Looking at all variables combined in the ‘human impact’ factor and the ‘human impact’ factor itself, clearly demonstrates the differences in human pressure on the different taxa with Central Africa having lower human impact values than in East and West Africa (Fig. 22).

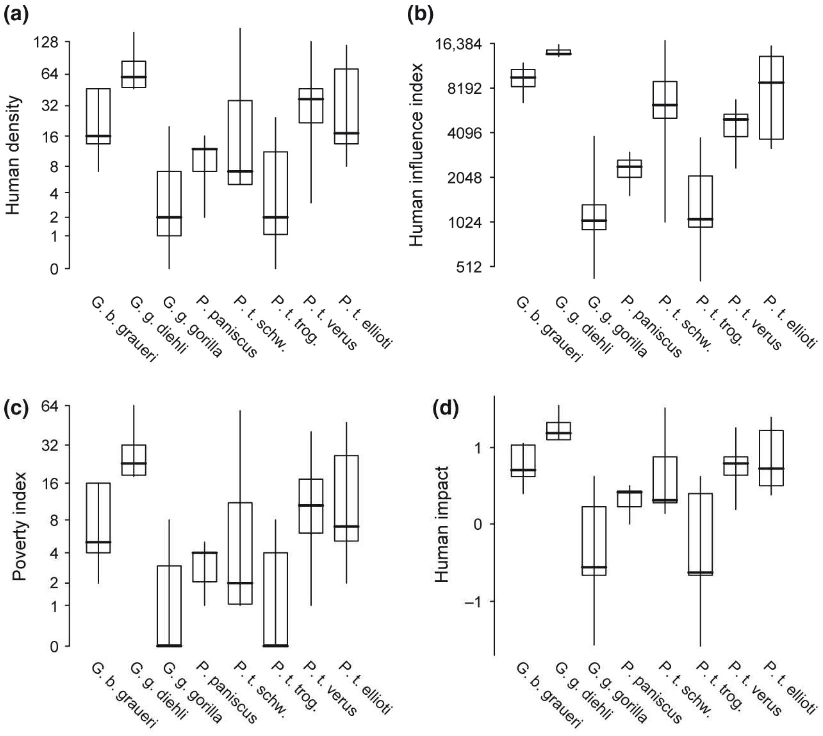
Fig. 21: Predicted distribution of SEC for the 2000s: (a) chimpanzee and bonobo, (b) Cross River gorilla (c) western lowland gorilla and (d) eastern lowland gorilla.



Colours indicate the gradient in SEC ranging from red to yellow to green, indicating low, intermediate and high values, respectively. White indicates unsuitable environmental conditions for great apes.

Model predictions of most taxa were influenced heavily by distance to rivers and distance to roads; for most taxa these two predictors interacted in their impact or distance to rivers interacted with human impact, making the direct interpretation of the results difficult. Climate variables heavily weighted models of all eight taxa. In this case, however, the coefficients did not always behave as expected [e.g. factor 2 squared (climate variables) had a positive impact on *P. paniscus* and *P. t. schweinfurthii*, implying these taxa would be least common at intermediate values of this factor].

Fig. 22: Values extracted for (a) human density, (b) human influence index, (c) poverty index and (d) human impact (PCA1) for all presence localities of the different taxa of great apes.



Shown are medians, quartiles and percentiles (2.5% and 97.5%).

II.1.4.2. Recent decline in SEC

Comparisons of SEC area between the 1990s and 2000s revealed much stronger declines for *P. paniscus* and the three gorilla taxa than for *P. troglodytes*. SEC declined by 59% for *G. g. diehli*, 52% for *G. b. graueri*, followed by 32% for *G. g. gorilla* and 29% for *P. paniscus*. For *P. troglodytes* SEC decrease was highest in West Central Africa (Figs. 23a and 24).

In West Africa, SEC levels decreased in areas previously predicted as very suitable for apes such as in Liberia (Fig. 21a) and similar decreases occurred in the Central African range (../..)

Table 3: Results of the taxon-specific logistic regression, indicated are the coefficients derived (average of 198–324 models; 468 in case of the intercept, weighted by Akaike weights), as well as summed Akaike weights, and these weights divided by their respective expected value (for details see Appendix S1). Variables in bold had Akaike weights considerably in excess of the expected value

Species	Variable name	Estimates	Wgt	Wgt/ exp	Species	Variable name	Estimates	Wgt	Wgt/ exp
Gorilla gorilla diehli	Intercept	−0.865			*Pan troglodytes schweinfurthii*	Intercept	−4.994		
	Distance to rivers	**2.297**	**0.999**	**1.444**		Distance to rivers	−0.056	0.675	0.975
	Distance to roads	0.395	0.532	0.865		Distance to roads	**0.471**	**1.000**	**1.625**
	Forest in neighbourhood	0.831	0.477	0.955		Forest in neighbourhood	**0.759**	**0.998**	**1.996**
	% Forest cover	**1.363**	**0.798**	**1.597**		% forest cover	**0.722**	**0.999**	**1.998**
	Factor 1 (human impact)	**−0.942**	**0.795**	**1.293**		Factor 1 (human impact)	−0.043	0.429	0.697
	Factor 2 (climatic)	**3.873**	**0.723**	**1.084**		Factor 2 (climatic)	**1.544**	**1.000**	**1.500**
	Factor 3 (climatic)	**−4.126**	**0.845**	**1.268**		Factor 3 (climatic)	**−1.912**	**1.000**	**1.500**
	Dist. rivers : dist. roads	0.676	0.177	0.768		Dist. rivers : dist. roads	**−0.736**	**0.293**	**1.270**
	Factor 1 : dist. rivers	0.783	0.247	1.072		Factor 1 : dist. to rivers	0.066	0.174	0.754
	Factor 2^2	0.353	0.299	0.897		Factor 2^2	**−0.069**	**1.000**	**3.000**
	Factor 3^2	1.464	0.360	1.079		Factor 3^2	0.527	0.382	1.146
Gorilla beringei graueri	Intercept	−6.504			*Pan troglodytes troglodytes*	Intercept	−5.068		
	Distance to rivers	**−0.387**	**0.981**	**1.417**		Distance to rivers	**−0.273**	**1.000**	**1.444**
	Distance to roads	**−0.320**	**0.687**	**1.116**		Distance to roads	**0.463**	**0.999**	**1.623**
	Forest in neighbourhood	**2.676**	**0.999**	**1.998**		Forest in neighbourhood	**0.811**	**0.994**	**1.988**
	% Forest cover	0.077	0.284	0.568		% Forest cover	0.057	0.293	0.586
	Factor 1 (human impact)	**−1.106**	**0.972**	**1.580**		Factor 1 (human impact)	**−0.253**	**1.000**	**1.625**
	Factor 2 (climatic)	**−2.225**	**0.946**	**1.419**		Factor 2 (climatic)	**0.353**	**0.903**	**1.355**
	Factor 3 (climatic)	−0.545	0.553	0.830		Factor 3 (climatic)	−0.221	0.695	1.043
	Dist. rivers : dist. roads	**−0.784**	**0.307**	**1.330**		Dist. rivers : dist. roads	**0.650**	**0.303**	**1.313**
	Factor 1 : dist. rivers	**0.158**	**0.295**	**1.278**		Factor 1 : dist. to rivers	**0.613**	**1.000**	**4.333**
	Factor 2^2	**0.620**	**0.765**	**2.295**		Factor 2^2	0.784	0.329	0.987
	Factor 3^2	0.732	0.320	0.960		Factor 3^2	0.891	0.199	0.597
Gorilla gorilla gorilla	Intercept	−4.397			*Pan troglodytes verus*	Intercept	−5.608		
	Distance to rivers	**−0.333**	**1.000**	**1.444**		Distance to rivers	**−0.151**	**0.947**	**1.368**
	Distance to roads	**0.713**	**1.000**	**1.625**		Distance to roads	**0.411**	**1.000**	**1.625**
	Forest in neighbourhood	**0.448**	**0.691**	**1.382**		Forest in neighbourhood	**0.429**	**1.000**	**2.000**
	% Forest cover	**0.416**	**0.738**	**1.476**		% Forest cover	**0.354**	**0.958**	**1.916**
	Factor 1 (human impact)	**−0.399**	**1.000**	**1.625**		Factor 1 (human impact)	**−0.146**	**0.731**	**1.188**
	Factor 2 (climatic)	**0.290**	**0.992**	**1.488**		Factor 2 (climatic)	**−0.436**	**0.999**	**1.499**
	Factor 3 (climatic)	**−0.652**	**1.000**	**1.500**		Factor 3 (climatic)	−0.129	0.572	0.858
	Dist. rivers : dist. roads	**−0.236**	**0.315**	**1.365**		Dist. rivers : dist. roads	**0.735**	**0.767**	**3.324**
	Factor 1 : dist. to rivers	**−0.048**	**0.977**	**4.234**		Factor 1 : dist. to rivers	**0.665**	**0.345**	**1.495**
	Factor 2^2	**0.658**	**0.968**	**2.904**		Factor 2^2	0.699	0.335	1.005
	Factor 3^2	**1.125**	**0.957**	**2.871**		Factor 3^2	0.704	0.195	0.585
Pan paniscus	Intercept	−5.956			*Pan troglodytes ellioti*	Intercept	−6.310		
	Distance to rivers	−0.110	0.485	0.701		Distance to rivers	**0.662**	**0.992**	**1.433**
	Distance to roads	**0.564**	**0.779**	**1.266**		Distance to roads	**0.372**	**0.987**	**1.604**
	Forest in neighbourhood	−0.128	0.310	0.620		Forest in neighbourhood	**0.305**	**0.926**	**1.852**
	% Forest cover	0.248	0.349	0.698		% Forest cover	0.122	0.332	0.664
	Factor 1 (human impact)	**−0.574**	**0.928**	**1.508**		Factor 1 (human impact)	**−0.122**	**0.964**	**1.567**
	Factor 2 (climatic)	**−0.350**	**0.940**	**1.410**		Factor 2 (climatic)	**1.618**	**0.990**	**1.485**
	Factor 3 (climatic)	**−0.947**	**0.931**	**1.397**		Factor 3 (climatic)	**−2.424**	**1.000**	**1.500**
	Dist. rivers : dist. roads	−1.632	0.123	0.533		Dist. rivers : dist. roads	**−0.634**	**0.704**	**3.051**
	Factor 1 : dist. to rivers	−0.767	0.136	0.589		Factor 1 : dist. to rivers	**0.412**	**0.945**	**4.095**
	Factor 2^2	**−1.136**	**0.908**	**2.724**		Factor 2^2	0.641	0.316	0.948
	Factor 3^2	0.265	0.284	0.852		Factor 3^2	**0.575**	**0.946**	**2.838**

countries, that is, Cameroon, DRC, Gabon and Republic of the Congo. Our model predicted much less SEC loss for other countries (Fig. 24).

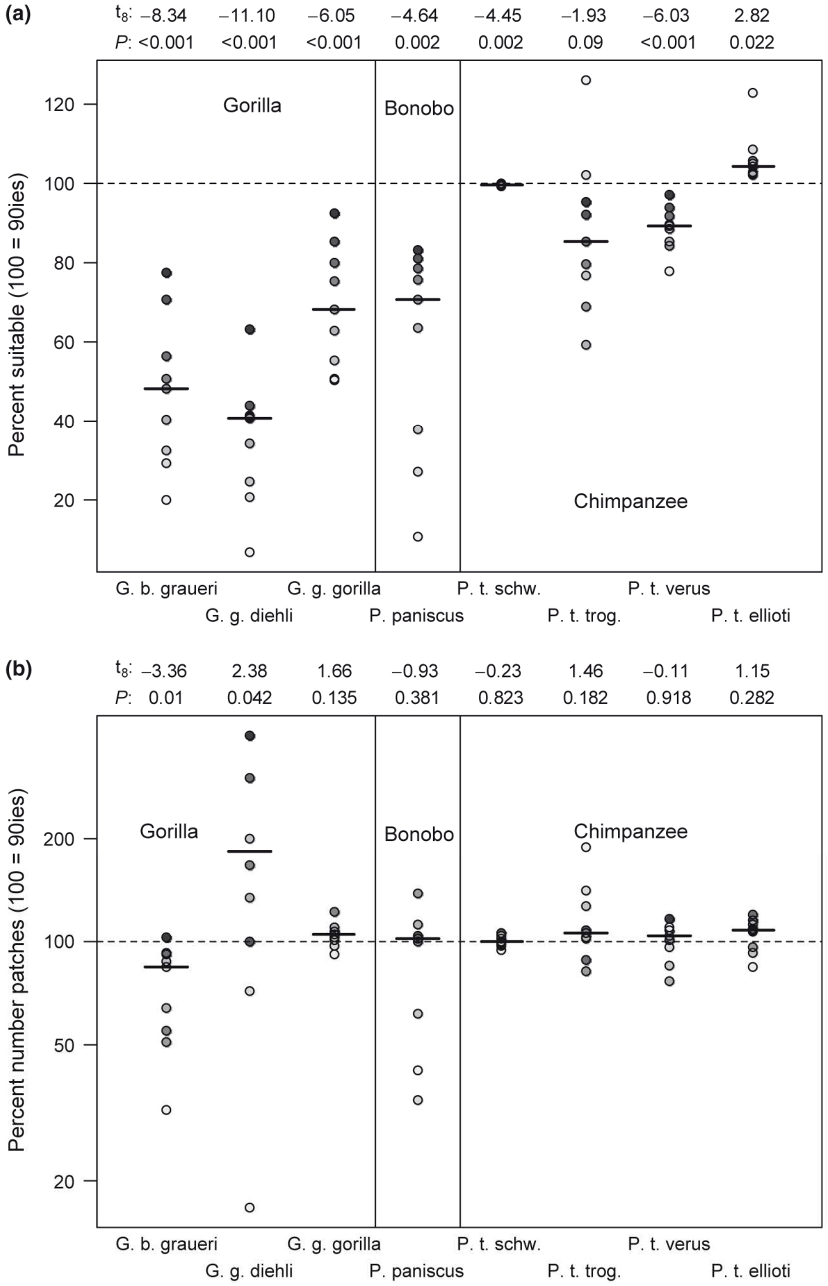
Comparing the number of SEC patches between the two time periods revealed that the total number of SEC patches declined significantly for *G. b. graueri* only (Fig. 23b). Furthermore, because patch size distribution was dominated by very small SEC fragments neither mean SEC patch size nor distance between SEC patches changed significantly over time (Appendix S2).

II.1.5. Discussion

This is the first range-wide study that attempts to quantify African ape SEC distribution and its changes over time. Between the 1990s and 2000s about 208,000 km² of SEC appeared to have been lost. In general, SEC for the three gorilla subspecies and bonobos was affected more than SEC for chimpanzees. SEC decline rates were as high as 59% and 52% for *G. g. diehli* and *G. b. graueri*, respectively, but showed almost no change for *P. t. schweinfurthii*.

The regions that experienced the greatest loss of SEC were central and eastern DRC, western Equatorial Africa and the upper Guinean forest in Liberia. Importantly, the lack of decline in other areas may reflect the fact that much SEC had already been lost before the 1990s (i.e. East and West Africa). Within the Central African forest block for example, the areas highlighted as having had the highest SEC loss are currently the remaining strongholds of the great apes, however, even in these areas, the vast, once-remote forest tracts have been interlaced with logging and mining roads, and subsequent human immigration (Laporte et al., 2007).

Fig. 23: (a) Percentage change in area of SEC between the 1990s and 2000s for all African ape taxa and (b) percentage change in number of SEC patches for all African ape taxa.



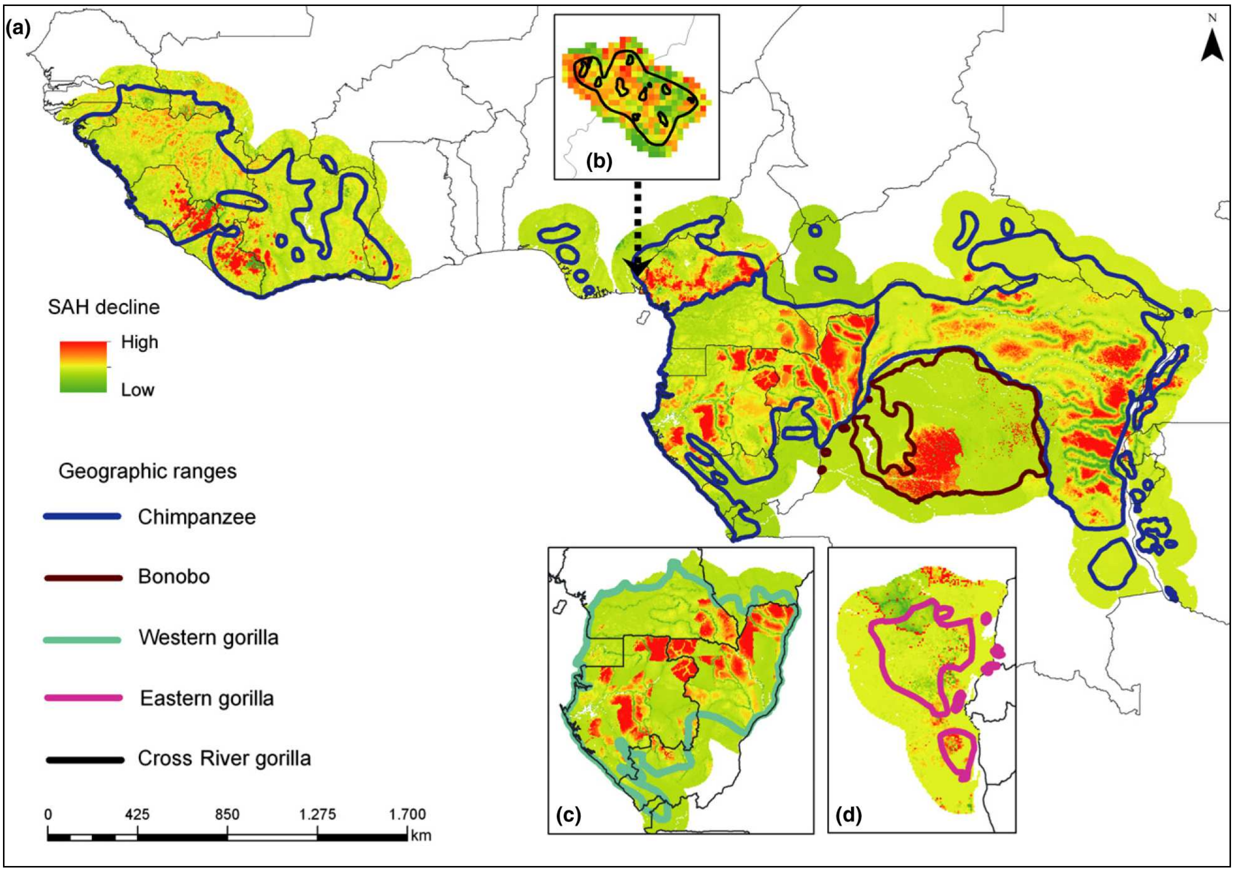
The points depict the different thresholds (quantiles 10, 20, etc., until 90%) used to define conditions as suitable, whereby darker points denote a lower threshold and hence a larger amount of area considered suitable. The short line represents the median. On top of the plots the results of one-sample tests (H0: average change = 0) are shown. However, these should be treated cautiously as the degrees of freedom are arbitrary (i.e. depend solely on the number of thresholds used).

To interpret our estimated SEC loss and its effect on ape populations, both the delay effects in population response and the potential counterbalancing of human pressure by conservation measures need to be considered. Increased human pressure does not necessarily lead to instantaneous extinction of wildlife populations. Rather there is a time-lag effect, during which populations still exist under increased human pressure and show decline only years later (Findlay and Bourdages, 1999). Great apes are particularly susceptible to such effects as they are long lived and have a low reproductive rate. Increased offspring mortality but relatively high adult survival may therefore mask critical changes before population decline becomes clearly evident. Our data set was presence-based and not density-based, so immediate decline will be less easy to pick up at the scale used. In some areas, effective conservation and/or an improved environmental awareness and attitude towards apes may counterbalance even relatively high human pressure and impact (Hockings and Humle, 2009; Tranquilli et al., 2011). Consequently, observed SEC decline rates cannot be equalized in a linear way with ape population decline, but could mean reduced long-term survival of ape populations.

II.1.5.1. Species and regions

There were clear regional differences in loss of SEC and among taxa. One striking pattern that emerged from our analysis was a difference in rates of SEC decline for gorillas and bonobos compared with chimpanzees. Likely explanations include (1) differences in species-specific ecological requirements, such as dietary preferences and niche specialization (Tutin et al., 1991), and (2) differences in vulnerability to poaching related to behavior and social structure (Caro et al., 2009). Chimpanzees show considerably more behavioral flexibility than gorillas, enabling them to survive in human-modified landscapes (McLennan, 2008; Hockings et al., 2009; Brncic et al., 2010). In contrast, the killing of a dominant male gorilla disrupts the whole group and reduces likelihood of infants survival if their mothers are obliged to join another male (owing to infanticide by a new dominant male) (Robbins, 1995). Additionally, variation in poaching pressure across Africa can partially explain the observed patterns, with little direct hunting of chimpanzees in East Africa and high poaching pressure in Central and parts of West Africa. It is likely that SEC for bonobos declines at similar rates to that of gorillas owing to the particularly heavy impacts of human land-use and poaching in DRC, where the human population is growing by 2.6% per year and an enormous commercial bushmeat trade is emptying huge forest blocks at an accelerating rate (e.g. Hart et al., 2008; Liengola et al., 2010).

Fig. 24: Estimated decrease in SEC between the 1990s and 2000s



for (a) chimpanzee and bonobo, (b) Cross River gorilla, (c) western lowland gorilla and (d) eastern lowland gorilla. Colours indicate the gradient in SEC decrease ranging from green to yellow to red, indicating low, intermediate and high decrease in SEC. Note that areas previously characterized by high values of SEC may experience high rates of SEC decline.

It is not surprising that rates of SEC loss are so marked in Central Africa, as this region experienced the greatest socio-economic changes during the 1990s and 2000s with, for example, previously remote forests being carved up by logging roads (Laporte et al., 2007; Blake et al., 2008; Stokes et al., 2010). By contrast, East and West Africa had already experienced relatively high human impacts. For a more detailed discussion of model results, please see Appendix S1.

II.1.5.2. Model evaluation

Unfortunately, we could not quantitatively evaluate our SEC model predictions with independent data across the ape range. The only exception is Liberia for which an independent survey data set was available, suggesting SEC to be a good predictor of chimpanzee density (Appendix S1). We made further qualitative comparisons using other published and unpublished sources that suggest a relatively good agreement with our SEC model predictions, although for some regions ambiguity remains (Appendix S1). In West Africa, the low SEC predictions for Côte d'Ivoire are supported by a recent nationwide survey (Campbell et al., 2008). Discrepancies between our SEC change projection and the results of Campbell et al. (2008) are owing to the lack of a suitable forest cover layer for the recent period in our study, thereby underestimating SEC destruction in recent years.

An on-going large-scale field survey in Western Guinea confirms a widespread chimpanzee population as suggested by the SEC model (S. Regnaut, pers. comm.). Similarly, Brncic et al. (2010) found an elevated chimpanzee density in the northern part of Sierra Leone. A study on a range-wide bonobo distribution model suggests the same for regions to which bonobo populations are now confined (J. Hickey, University of Georgia, Athens, et al., in prep.). For eastern chimpanzees a comparison with a distribution model by Plumptre et al. (2010) reveals obvious discrepancies. Solving these discrepancies will require an in-depth investigation of both models and more likely an independent data set. Ongoing fieldwork in the region, in particular northern DRC will provide this opportunity in the near future.

II.1.5.3. Limitations of SEC model

Although our results seem reasonable, it is important to keep in mind that our predictions represent only a rough approximation of the true distribution of SEC for African great apes. Development of our model was limited by the quality and resolution of available data: the non-random distribution of presence points and the lack of confirmed absence localities, the lack of consistent predictor variables at resolutions above 5 km, and the lack of comparable and detailed vegetation maps and other predictors for the two time periods at global scales. These issues and their effects on model predictions need to be investigated in more detail.

A large proportion of the presence points we used were collected in protected areas. This non-random distribution of presence localities may have biased our model, probably towards lower environmental suitability outside protected areas. In addition, the use of pseudo- instead of true absences certainly introduced more noise to the model predictions (Wisz & Guisan, 2009).

The use of predictor variables with a relatively coarse resolution of 5 x 5 km prohibits the use of model predictions at a local scale. This limitation is particularly relevant for taxa with particularly small ranges, such as *G. g. diehli*. The inevitable averaging of environmental conditions masks any small-scale variation of habitat and human impact that might be of particular importance for variation in ape occurrence.

Furthermore, because of the lack of comparable time-specific global GIS data sets, the variable ‘human impact’ was the sole predictor of change in SEC in our model. Although the variables combined in the ‘human impact’ factor can be interpreted as proxy for the impact of agriculture, logging, artisanal mining, commercial and subsistence poaching on apes, other factors such as infectious diseases (Walsh et al., 2003; Leendertz et al., 2004; Bermejo et al., 2006) and climate change are also important predictors of ape distribution. Cultural taboos and traditional proscriptions of eating apes in some ethnic groups and regions can impact ape SEC (Lahm, 2000; McLennan, 2008; Hockings et al., 2009; Brncic et al., 2010). Other factors may also have important roles in structuring human-ape interactions, including human warfare, land-use rights, indigenous hunting and farming traditions.

Because we lacked information on the attitudes of local people towards apes and because we modeled SEC on a global scale, we could not explicitly incorporate spatial differences in coexistence between humans and apes into our models. Here our results require particularly careful interpretation: our models usually detected only the generally negative correlation between human population density and ape presence. They are not representative of locations where apes and humans coexist in close proximity, such as parts of Guinea (Hockings et al., 2009), Sierra Leone (Brncic et al., 2010) and Uganda (McLennan, 2008). However, it remains to be seen whether these are stable situations or transitional phenomena in the process of habitat conversion and development of human-dominated landscapes. Including such scenarios would need a more fine-scaled analysis and additional predictors (e.g. local attitudes towards apes and long-term human impacts, such as the modification of food-plant distribution and historical development of land-use by humans). Similarly, our model does not take into account the effects of conservation activities aimed at mitigating human impact (Tranquilli et al., 2011). This is an obvious weakness, but could not be incorporated given the limitations of existing data.

Finally, we did not have two comparable vegetation maps to represent past and current habitat conditions, thereby underestimating the impact of continued habitat destruction on ape populations in Africa, although in the Central African forest blocks identified as the ape strongholds (Fig. 21) forest loss is still very low (Hansen et al., 2008, 2011) Additionally, the model did not distinguish between swamp and terra firma forest, nor between closed-canopy-open-understory forests and open-canopy-closed-understory forests, which affected the SEC maps produced for both central chimpanzees and western lowland gorillas. However, from our continental perspective this effect is less important than it would be from a regional perspective. Given the number of limitations discussed above, we consider our model and estimates of change in SEC distribution over the past 20 years as only the first attempt to provide a continent-wide perspective of the situation ape populations face and much work needs to be done to improve this model (see Conclusion and outlook).

II.1.5.4. Fields of application

The results presented in this paper may provide another source of information to support researchers, wildlife managers, funding agencies, industry and politicians when making decisions in identifying priority conservation areas, research gaps, potential wildlife corridors and future survey sites, within the limitations of the model outlined above. However, given the complexity of decision-making in conservation, involving national and international politics, local communities and economical interests, we do not make specific recommendations about specific locations that deserve greater attention. This process will require studying our results in the context of the respective question, location, region or taxon of interest. We also strongly recommend to overlay the SEC models with a series of other GIS layers, including expert based ape priority areas, confirmed presence locations, survey areas, as well as various contextual layers related to human activities, land-cover, topography, and conservation to help inform decisions (all available at http://apesportal.eva.mpg.de). This approach will help to identify obvious discrepancies between different sources of information (e.g. expert based priority areas and SEC model predictions) but at the same time provides a further source of information.

II.1.6. Conclusion and outlook

Our results represent the best available estimate of continent- wide African SEC distribution and change over the past 20 years. This is also the first study to have amalgamated data from numerous sites across the African ape range in an attempt to bridge the gap between local efforts in the field and a global perspective of the distribution of ape populations. This is one of the major goals of the IUCN/SSC A.P.E.S. project, from which the presence localities used in this study were extracted. We demonstrated dramatic declines in SEC for great apes, which strongly suggest that conservation efforts must be radically stepped up. It is also highly likely that many other species within the apes' range have experienced similar declines in SEC.

Future studies are needed to further develop the model presented in this paper and we suggest the following. (1) Evaluation of model: in principle every new field data set (transect, recce, genetic or camera trap survey) can be compared against our SEC model prediction (see Appendix S1 for example method), elucidating over which spatial scale and in which regions model predictions are reasonable. (2) Improving current model: development of models that use real absences, which are likely to be more easily available in the near future; and comparison of different modelling techniques. (3) Development of regional and local models of ape population status taking more finely scaled spatial information into account and compare predictions against the SEC model of this study; (4) Explicit modeling of ape-human coexistence to evaluate whether ape persistence in human-dominated landscapes is likely to be long-term; (5) Evaluation of ape population changes under different conservation management scenarios.

Our work is only the beginning of modeling ape populations in relation to their environments, threats and conservation effort. This is a wide and open field with many interesting avenues to pursue.

II.2. Conservation issues in the Nimba Mountain

This part is a holistic presentation of the tri-national Nimba, which aims at exposing the complexity of this site of exceptionally rich biodiversity by bringing together ecological and anthropological aspects, history, research and conservation. It has been published as a book chapter in “The Chimpanzees of Bossou and Nimba” (Granier N and Martinez L 2011). Such a contextual overview of Nimba, added to the findings of this study on chimpanzee ecology, constitutes essential knowledge to initiate in situ and purpose-built efficient actions of conservation.

II.2.1. Abstract

The Nimba Mountain consists of a 40km-long scenic mountain chain, which extends along the tri-national border between Guinea, Côte d'Ivoire and Liberia. Its unique biogeographical characteristics have led to the differentiation of multiple micro-climates and ecological niches, which have favored the emergence of highly diverse wildlife and landscapes. It forms a varied but single ecological and anthropological entity that is torn between different administrative and protective statuses. The Nimba Mountain has benefited from an early protective status, which was favored by the numerous scientific investigations initiated in the 1940s. Threats to biodiversity, including chimpanzees, are tightly linked to habitat destruction, which is mainly due to the increasing human pressures. The biggest challenge consists of dealing with the trade-off between biodiversity preservation and local development. This reinforced the necessity for elaborating a global and coherent transnational program of natural resource management.

II.2.2. A tri-national biogeographical and anthropological entity

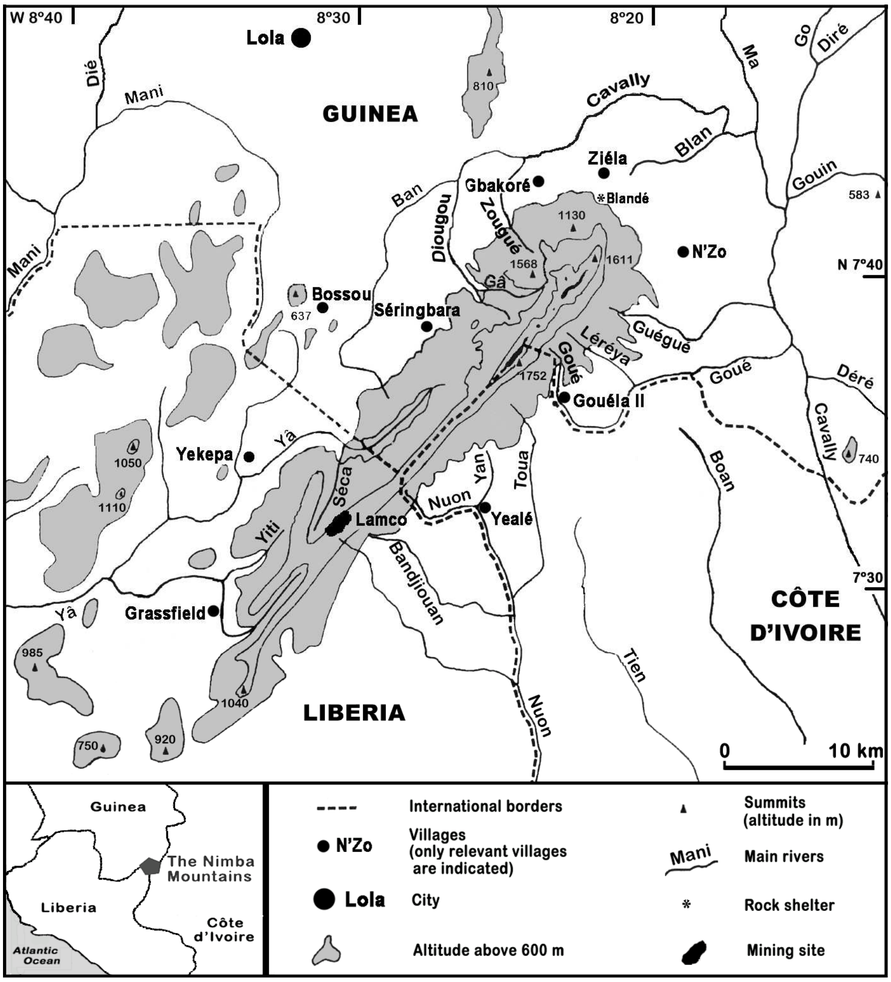
The Nimba Mountain exhibits a particularly rich and unique biodiversity, which is due to a highly specific conjunction of multiple biological factors and distinctive geographical, geological, climatological, and ecological patterns. Its tri-national location at the crossroads of several ethnic influences and migratory fluxes also contributes to their uniqueness. Yet, the Nimba Mountain can be defined as much by their intrinsic diversity as by their global homogeneity.

II.2.2.1. Biogeomorphology

The Nimba Mountain (7°25 N - 7°42 N and 8°20 W - 8°40 W) peaks at 1752 m, constituting the second highest relief in West Africa. The massif forms a 40km-long barrier oriented north-east/south-west, which marks the border between Guinea, Liberia, and Côte d'Ivoire (Fig. 25). Rising abruptly more than 1000 m above the surrounding plains, it presents a thin crest with steep and rocky slopes, which exceed 75 degrees inclination in some places. In its particular location at the crossroads of three climatic influences (Equatorial-Guinean, Libero-Guinean and Sub-Sudanian) and of two major tropical winds (the Monsoon – a humid wind blowing from the south, and the dry Trade wind, or Harmattan, blowing from the north), this relief constitutes an important climatic barrier. Pluviometry varies from 1500 to 4000 mm^3 across areas and years, with generally more rain at the highest altitudes and in the southeast (Lamotte 1998, Soropogui et al. 2008). These original climatological features added to the steepness of the relief, the complexity of the geological structure and peculiar edaphic characteristics, have favored the emergence of an important diversity of micro-climates and ecological niches populated by a highly diverse and endemic wildlife.

Almost all vegetation types of the West African region are represented, which led Schnell (1998) to describe the Nimba Mountain as a "West African crossroads of floras". In the north-eastern (Guinean) end, the massif's top is covered by altitude grasslands from 800 m high. This ecosystem, which harbors a highly endemic orophyte vegetation made of gramineae, terrestrial orchids, heathers and euphorbiaceae (…), is an essential component of the massif's uniqueness (Adam 1981). The slopes and foothills of the relief are covered by altitude and lowland Guineo-Equatorial rainforest, and the surrounding plain presents lowland forest with sprinkled stretches of savannas. A fifth habitat type described by Schnell (1998) is the secondary vegetation, which consists of a low tree density habitat with ground-heliotropic vegetal species. Mainly found at forest edges, it has a growing importance due to human activities and uncontrolled bush fires. Towards the south-western part of the mountain range (Liberian side), the ridge progressively descends from 1752 m to 1000 m and the forest rises over the crest to cover the entire massif. The floral and habitat type richness is accompanied by a particularly diverse and important fauna, which has been amongst the most studied in West Africa (Lamotte and Roy 2003).

Fig. 25: Map of the Nimba Mountain along the tri-national border between Guinea, Côte d’Ivoire and Liberia, West Africa



This map shows the main geomorphological patterns and hydrographic network of the Nimba region, as well as important human settlements surrounding the massif.

An important and regularly developed hydrographic network drains the Nimba Mountains with deep and steep ravines shaped by watercourses (Lamotte and Rougerie 1998). The numerous streams originating in the massif feed three main rivers: the Cavally, flowing southwards into Côte d’Ivoire; the Ya, flowing south-eastwards into Liberia; and the Nuon, flowing south into Liberia (Fig. 25). Finally, the substratum of the relief is composed of old granitic and gneiss formations, superimposed with layers of green schist inlaid with highly concentrated and pure iron ore (Pascual, 1988).

II.2.2.2. Cultural influences

The oldest traces of human settlements ever discovered around the Nimba Mountain were found in the northern-end foothill of the massif, in a rock shelter named Blandé cave (Fig. 25). The site was explored and studied from 1949 by French anthropologists (Holas 1952, Mauny and Holas 1953), who collected more than 2,000 pottery fragments and 100 lithic pieces such as rough flints (hatchets, knifes and points). According to them, occupation of Blandé cave would have approximately last from six centuries BC to 1000 AD, and would result from migratory influxes starting in the Sahara and the Sudan. Afterwards, knowledge of occupancy of the Nimba region from these dates relies more on oral tradition than on archeological data, and the first traces recorded after this period are reported from about 1750. Nowadays, the three main ethnic groups settled around the Nimba Mountain are the Mano, Kono, and Yakuba. An important feature that structures the social system in these animist populations is their clanistic organization. Each clan or family is composed of a group of individuals who possess a common ancestor and follow the same prohibitions. The most commons are the food prohibitions which concern proscribed animals or plants called totems. There is an intricate mixing between clans, some of them being absorbed or assimilated by others, alliances being formed, all of which result in a highly intertwined social network.

According to Germain (1984), the early creation legends of the Mano group say that the oldest unit was formed by the alliance of two clans: the Nia and the Ma. After the formation of this first nucleus in the Diecké area, the community was dispersed. One part of the Ma clan (whose totems are the chimpanzee, goat, and snail) emigrated to the region of Man in Côte d’Ivoire, and then moved to settle around N’Zo. The rest of the community walked around the

Nimba Mountain to the plain located north (Bossou region) passing either by the east (Vépo region) or the west (today constituting Liberian territories). Later, the vast Mandingo islamization movements of the 17th century forced the Mano people to limit their occupation to the Diecké and the Nimba Mountain regions. Mixing between the already established forest populations and the newly arrived Mandingos led to the creation of the Kono ethnic group. An alliance was later concluded between the Mano and Kono groups, reinforcing the cultural and genetic interconnections. In sum, while intra-group traditional characteristics have been preserved throughout generations, complex migratory fluxes have led to a continuous inter-group mixing.

II.2.3. Conservation keystones

II.2.3.1. Conservation statuses of the Nimba Mountain

The unique biological characteristics of the Nimba Mountain have led to the early protection of its Guinean and Ivorian parts in June 1944. Unlike the four national parks of Guinea (which were managed by local forestry administration), the Mount Nimba Full Nature Reserve was placed under scientific management of the Museum National d’Histoire Naturelle (MNHN, Paris) and the Institut Français d’Afrique Noire (IFAN, Dakar). The latter was in charge of scientific and anthropological studies in the former West African French Territories (Lamotte et al. 2003; Brugière and Kormos in press). After their independence, the administrations of both Guinea and Côte d’Ivoire maintained the massif under protective status in their legislations. Table 4 shows chronological landmarks of the Nimba Mountains in the three countries over the last 70 years.

In 1980, the Guinean side of Nimba was classified as a Biosphere Reserve by the Man and Biosphere (MAB) Program of UNESCO. In 1981-82, the Guinean part (8,520 ha) and Ivorian part (6,482 ha) were established as Strict Nature Reserves by the International Union for

Conservation of Nature (IUCN) and as Natural World Heritage Site (NWHS) by the WHS Program of UNESCO (Hartley et al. 2008, WHS-UNESCO 2008). The Nimba Mountain Strict Nature Reserve is assigned to IUCN category Ia, which corresponds to protected areas “managed mainly for science, possessing some outstanding or representative ecosystems, geological or physiological features and/or species, available primarily for scientific research and/or environmental monitoring” (IUCN 2007). In 1992, the Guinean part of the Nimba Mountain was labeled an “Endangered World Heritage Site” due to potential mining activity and the increasing human pressure caused by successive waves of refugees from Liberia and Sierra Leone. In 1993, the Biosphere Reserve was enlarged from 12,700 ha to 22,000 ha by inclusion of two additional core areas: the Bossou hills and Déré forest, with an extended buffer zone (Fig. 26). However, no Guinean legal text ratified the new protected status of these two core areas, leading to difficulties in protection and management. The same year, an enclave of 1,550 ha was withdrawn from the core area of the Biosphere Reserve in the Gbakoré region (north-east of the massif), to become an iron-ore mining concession (Debonnet and Collin, 2007).

The civil war that began in 2002 in Côte d’Ivoire has induced political instability, which put a complete stop to environmental research and management activities in the country. This situation facilitated many kinds of illicit activities such as poaching, deforestation and settlement of rebel forces. Today the armed conflict is over and the government shows a renewed interest in environmental issues.

The Liberian part of Nimba has suffered from extensive logging activities in the East Nimba National Forest, Grassfield region (Verschuren 1983), and from iron-ore mining in the Yekepa area. Finally, in 2003, the Liberian authorities showed their willingness to officially protect the Nimba Mountain by publishing a legal act establishing the Nimba Nature Reserve (13,500 ha) and stipulating their wish to include it in the NWHS complex. This reserve incorporates the former Nimba East National Forest extending up to the border with Guinea and Côte d'Ivoire (Act for the Establishment of the East Nimba Nature Reserve 2003, Beamont and Suter 2004).

Table 4: Chronological landmarks of the Nimba Mountain

Year	Guinea	Côte d'Ivoire	Liberia
1939	First visit of a scientific team to NM		
1942	Scientific studies of NM begin		
1944	Strict Nature Reserve		
1963			Mining launched
1976	Study Bossou chimps		
1980	NMBR		
1981	NWHS		
1982		NWHS	
1992	Endangered NWHS		Armed conflict begins
1993	Mining concession	Study Nimba chimps	
2001			Armed conflict
	Tri-national program for the protection of the NM		
2002		Armed conflict begins	
2003	Mining agreement		Nature Reserve
2004	PCBMN and drillings		
2010		Armed conflict ends	

NM: Nimba Mountain; NMBR: Nimba Mountain Biosphere reserve; NWHS: Natural World Heritage Site; PCBMN: Program for Biodiversity Conservation of the Nimba Mountain.

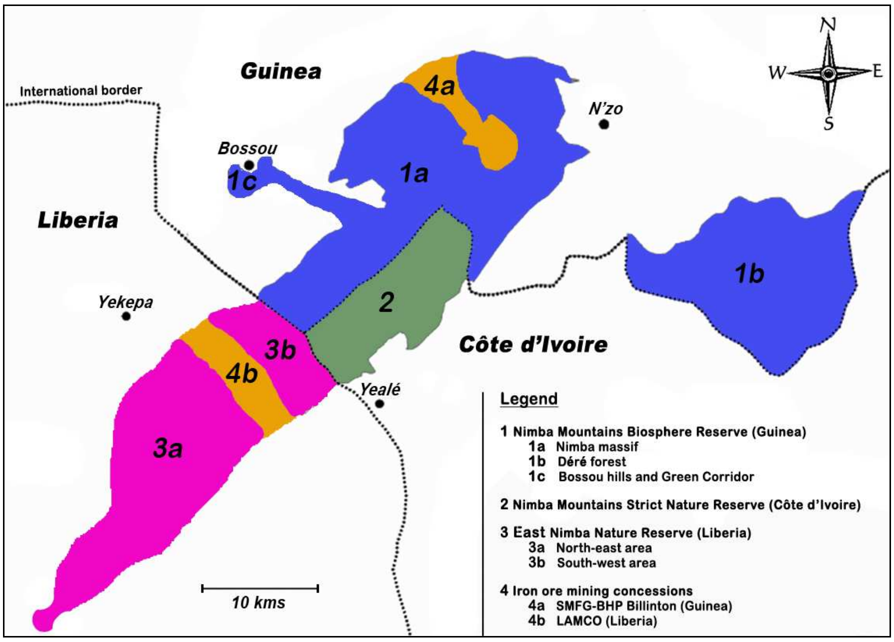
Taken together, the three countries cover over 31,000 ha of protected areas that would greatly benefit from being considered as a complete and single ecological unit.

II.2.3.2. Tri-national perspectives of conservation

Despite their formal conservancy status, the Nimba Mountain has suffered from a severe lack of law enforcement, rational utilization of forest resources, and global biodiversity management. As a consequence, the ecological entity of the Nimba Mountain is split into a mosaic of areas exhibiting different levels of preservation and statuses of conservation (Fig.

26). While large areas of well-preserved forest are still present in the three countries (e.g., areas 1a, 2, 3b in Fig. 26), others have been severely damaged by logging exploitation and subsequent habitat destruction (areas 1b, 3a). In the same way, while long-term conservation activities, such as the Primate Research Institute of Kyoto University's (KUPRI) efforts in the Bossou hills and the green corridor project (see Chapter 42), have permitted the protection, reforestation and connection of conservation key areas (areas 1c), iron-ore mining sites and their surroundings have already been heavily spoiled in Liberia, and we fear similar future developments around the Guinean mining enclave (areas 4a and 4b).

Fig. 26: Protected areas in the Nimba Mountain region



This map shows the mosaic of areas with different status of protection across the countries of Guinea, Côte d'Ivoire and Liberia. Despite an ecological continuum, the conservation status is 'discontinuous'.

Aware of this problematic situation, concerned authorities from the three countries initiated in 2001 a "Tri-national Program for the Protection of the Nimba Mountain". This program has two objectives. The first is to elaborate a legal context that would ensure consistency in the administrative rules and protective statuses of the Guinean, Liberian and Ivorian parts of the

Nimba Mountains. The second objective is to increase and update the scientific knowledge on Nimba wildlife and environment, by monitoring climate, hydrometry, fauna, and flora. Two meetings were organized in 2001 and 2002 to launch administrative and field activities in the three countries (Touré and Suter 2002), but the armed conflict that started in Côte d’Ivoire has frozen the whole initiative. It is to hope that the newly peaceful situation in the sub-region would favor the restoration of this tri-national initiative.

II.2.4. Contribution of scientific studies

II.2.4.1. History of scientific studies in the Nimba Mountain

The Nimba Mountain has been one of the most studied sites in West Africa, in terms of the number of scientific investigations (Lamotte and Rougerie 1998). In 1939, a first scientific mission explored the Nimba Mountain area on the border between Guinea and Côte d’Ivoire and reported an unusual level of unknown species as well as a spectacular landscape (Brugière and Kormos in press). To facilitate further investigations, a scientific station was established in the early 1940s in Ziéla (northern end of the massif, Fig. 25). Until 1957, long series of scientific studies were carried out from there by Maxime Lamotte, Roger Roy and many IFAN scientists on geology, geomorphology, fauna and flora, and climate (Lamotte et al. 2003). Later, another research station was built by miners in Grassfield, Liberia (Fig. 25), catering for a new study area, from where, among others, an extended floral description of Nimba was completed by Adam (1971-1983).

Since the 1980s, a number of scientific missions were supported by the UNESCO, mainly to assess anthropic pressures affecting Nimba biodiversity and to propose suitable conservation recommendations (Debonnet and Collin 2007). Different NGOs, organizations, and universities have also investigated this biodiversity. For example, the Royal Botanic Garden of Kew conducted botanical studies (Hawthorne and Jongkind 2006), Würzburg University studies on amphibians (Hillers et al. 2008), MNHN studies on carnivores (Gaubert et al. 2002), and Birdlife International ornithological surveys (Borrow and Demey 2001). In 1976, Yukimaru Sugiyama from KUPRI initiated the long-term research on wild chimpanzees in Bossou, and Tetsuro Matsuzawa extended the research on chimpanzees to the Nimba Mountain from 1993 onwards (Table 4; see Chapter 1).

Today, the recent increase in scientific studies designed and conducted by Guinean, Ivorian, and Liberian researchers and students, sometimes in collaboration with internationally recognized researchers, heralds a new era in Nimba biodiversity studies (e.g., Kourouma et al. 2008).

II.2.4.2. From research to conservation

Results of scientific studies can lead to the emergence of conservation measures. By providing ecological data and designing tools to evaluate biodiversity and endemism, systematic scientific accounts can constitute the best ally for setting-up concrete and adapted programs of biodiversity preservation.

The establishment of biodiversity hotspots is a good example of the great worldwide impact that can be reached through this kind of scientific work (Myers et al. 2000, Fa and Funk 2007). The Nimba Mountain is actually located in one of these hotspots called the Guinean Forests of West Africa (Conservation International 2008). In addition, identification of more than 2000 plant species including 16 endemics has contributed to the classification of the Nimba Mountain as a center of plant diversity (Hartley et al. 2008). In the same way, due to ornithologists' discoveries the site was classified as an Important Bird Area by BirdLife International (BirdLife 2008). A further example is provided by the ongoing long-term studies on chimpanzees, which have led to the classification of the Nimba Mountain, together with Bossou and Déré forests in Guinea and Tiapleu forest in Côte d'Ivoire, as one of the six exceptionally important priority areas for the conservation of West African chimpanzees in the IUCN/SSC/PSG-CI Action Plan (Kormos et al. 2003). Finally, the IUCN Red List of Endangered species is another example of conservation statements based on the long-term efforts undertaken by scientists. In a bibliographical study, Rondeau and Lebbie (2007) listed 3384 animal species in the Guinean ecosystems of the Nimba Mountains. More than 500 animal species new to science were discovered across Nimba, including 200 endemics amongst which 13 species of mammals, birds and amphibians are classified as Critically Endangered (CR), Endangered (EN) or Vulnerable (VU) in the IUCN Red List (Hartley et al. 2008; IUCN 2007). Endangered flagship species such as the viviparous Nimba toad (*Nectophrynoides occidentalis*-CR*)*, the only viviparous bufonid known in the world, the Mount Nimba otter shrew (*Micropotamogale lamottei*- EN) or the West African chimpanzee (*Pan troglodytes verus*-EN), by attracting focus of public opinion, can play important roles in fundraising and become weighty arguments in favor of Nimba wildlife preservation.

II.2.5. Threats to Nimba chimpanzees

Chimpanzee conservation is not dissociable from natural habitats and biodiversity protection. In Bossou, despite the long-term traditional and scientific protection, chimpanzees have become increasingly isolated from neighboring communities and are nowadays threatened by an intricate web of pressures (see Chapters 42 and 44). In Nimba, the two main kinds of threats exerted on biodiversity are anthropic pressures, characterized by a domestic and relatively limited environmental exploitation, and industrial pressures, characterized by a large-scale use of the environment. Both of these threats lead to habitat modifications, which jeopardize chimpanzee survival.

II.2.5.1. Anthropic pressures

Forest habitats supply an important part of local people’s domestic needs. Since the hunter-gatherer era, forester ethnic groups have been using forest by-products such as fruits, leaves, seeds, roots, and bark as food, medicine or construction materials. In the same way, the fauna of the forest has always constituted the main source of protein. More recently, small-scale agriculture has enlarged food resources by providing a staple diet based on cereals and tubers, especially rice and cassava. This way of exploiting natural resources has apparently been sustainable over centuries, but nowadays, the balance have been upset: the natural habitat cannot regenerate rapidly enough to continue fulfilling the needs of a growing resident population. The demographic overgrowth and increase in human densities in the Nimba region has been aggravated by the successive armed conflicts that occurred over the course of the past 18 years in Sierra Leone, Liberia, and Côte d’Ivoire. These conflicts have fostered important instabilities in the countries of the Mano River Union (MRU, i.e. alliance and economical collaboration between Sierra Leone, Liberia and Guinea, recently joined by Côte d’Ivoire), which pushed their residents to settle in Guinea.

As a result of the demographic increase, agricultural yield has been intensified in order to keep up with local needs. The slash and burn agricultural technique used in combination with a practice of fallowing land, always requires more arable land, pushing communities to deforest new parcels every year. As a consequence, the Nimba forests are becoming more and more isolated, surrounded by a fragmented habitat composed of deteriorated forest patches, perennial cultures (palm tree, coffee, cocoa, pineapple, and banana), seasonal cultures (rain-fed rice, cassava, tarot, yam, peanut, and corn), and fallow lands covered by grasses and shrub species.

Bushfires lit by villagers are amongst the most threatening pressures for Nimba ecosystems. People are accustomed to burning the herbaceous vegetation of savannas, altitude grasslands and secondary forests for purposes related to cultivation, poaching, the clearing of trails and the promotion of new growth for grazing cattle. Fires are central to the ecology of African tropical savannas and are commonly used as a tool for managing the tree-grass balance in protected areas (Clerici 2006). However, the excessive and uncontrolled use of fire occurring in Nimba has a strong negative impact on habitats (Granier in prep.). Every year during the dry season, fires lit in herbaceous ecosystems penetrate into the forest’s driest edges, leaving partially burned trees that finally fall down creating large holes in the canopy, favoring in this way the development of ground heliotropic vegetation. Natural regeneration of the forest is then particularly long and difficult.

Poaching and excessive hunting with guns and snares are reported across the whole Nimba Mountain Biosphere Reserve, despite international and national regulations. Hunting appears to be rather unselective and chimpanzee poaching is sometimes reported, although it seems to have greatly declined due to the long-term conservation efforts undertaken by KUPRI in the area (Granier in prep.). Several reasons can lead to the killing of chimpanzees. First, their meat is eaten, although traditional taboos in some ethnic groups, such as among the Mano people, appear to limit its consumption. Second, in certain ethnic groups, chimpanzee meat is believed to hold medicinal virtues and prized parts of the body can be sold at high prices. Third, seasonality in food availability, fragmentation, and reduction of habitat can conduct chimpanzees to feed on human cultivars (Hockings and Humle in review). Crop-raiding may drive cultivators to kill chimpanzees, as it happens to occur in other regions of Guinea (Granier and Martinez 2004). Fourth, non-selective snaring and trapping could also represent a fatal danger for chimpanzees owing to injuries that could cause infection and gangrene. One case of death from snare was recorded in the Tai forest (Côte d’Ivoire) over the past 29 years and four cases from both snare and trap in the Budongo Forest (Uganda) over the last 18 years (Boesch and Boesch-Achermann 2000, Reynolds 2005). Finally, pet-trade also represents a menace since capturing a baby chimpanzee necessitates killing members of the community who will protect their group. This menace can potentially cause much more severe damage to the population than poaching.

II.2.5.2. Mining and logging

Industrial views on iron exploitation have been the sword of Damocles hanging over Nimba biodiversity since the 1960s. Today we know that mining can indeed have significant local and regional negative impacts on ecosystems (habitat loss and quality decrease, waste discharge, pollution of rivers and soil, modifications of hydrographic regime and network…). In fact, an iron-mining project operated between 1963 and 1992 in the site of Yéképa, in the Liberian Nimba, just 10 km south-east of Bossou (Verschuren 1983) (Fig. 25). Exploitation was under control of a consortium called Lamco (Liberian-American-Swedish Minerals Company). Early 2007, the exploitation lease was bought out by another multinational company, ArcelorMittal, which is planning to reopen the exploitation site in the near future. In addition, the Guinean government signed in 2003 an agreement of iron exploitation in the Guinean side of the Nimba Mountain with EuroNimba, a consortium held by three companies: BHP Billiton, Newmont, and Areva. This consortium, in association with the Guinean government, has created the SMFG company (Société des Mines de Fer de Guinée), which operates the mining site. Aware of the irreversible negative impacts of Lamco mining and constraint by international lobbies, the SMFG program has taken environmental commitment, which includes long-term impact studies of mining on wildlife, hydrographic regime, and climate.

Logging also exists in the Nimba region. The example of Déré forest, which was logged in 1999-2000, shows how commercial exploitation of timber can be destructive even over a short timescale (see Chapter 32). In addition to deforestation and direct collateral damage caused by falling trees, the construction of infrastructure and roads in the forest has favored human settlement for cultivation and subsequently increased poaching. Similarly, the Liberian part of the Nimba Mountains (especially the southern and western ridges of the East Nimba Nature Reserve) has suffered from extensive timber exploitation by a company named Nimbaco, from the 1970s until at least 1983 (Verschuren 1983). Although exploitation has now stopped, this part of the forest is severely deteriorated and may contain lower faunal abundance than the northern area of the reserve (Fig. 26, areas 3a and 3b).

Highly recurrent demands of communities for local development cause that the financial spin-offs of industrial activities cannot be ignored nor simply rejected. Industrial companies judiciously invest in infrastructures (roads, schools, hospitals), create local employment, and favor local/national dynamism of the economy. Even if such activities are probably not sustainable and certainly harmful to the environment, majority of locals see the arrival of an industrial activity as a great opportunity. Thus, logging and mining companies easily benefit from support of local populations.

II.2.6. Towards integrated conservation

Many poor countries today are trapped in a cycle of poverty and environmental degradation (Ehmke and Shogren 2008). To turn the corner, they often concentrate efforts on the poverty problem to the detriment of the environmental issues. The biggest challenge for the conservation of the Nimba Mountain undoubtedly consists of dealing with the trade-off between biodiversity preservation and local development. A strong argument that could be put forward to meet this challenge is the potential long-term economic value of such an exceptional and unique natural heritage, if rigorously protected (Verschuren 1983, Debonnet and Collin 2007). However, threats leading to its degradation, such as the local anthropic pressures and industrial activities, perpetually keep this perspective off. Consequently, these threats should be considered as inescapable and difficult-to-change components of the complex matter of natural resource management. In Nimba, the problem is getting even more complicated due to the absolute necessity of a tri-national harmonization of approaches. In this context, the inability for conservation actions to be efficiently carried out without a collaborative and integrated multipartite approach is salient. Thus, we propose below some suggestions for a successful and sustainable conservation program of the Nimba Mountain.

Local populations are undoubtedly the key actors in the sustainable protection of their heritage (Bajracharya et al. 2005, Danielsen et al. 2005). Conservation programs may not be successful on the long run without integrating communities in a central position. Additional anthropological investigations are necessary to obtain a better understanding of local notions on natural heritage and human-wildlife coexistence, as well as of the ongoing changes in their beliefs consequent to environmental evolution. Progression of customary and legal environmental practices and laws also need to be more carefully examined and must be better taken into account in conservation programs.

Permanent collaboration between conservationists and researchers appears essential to enhance suitable actions of conservation. All conservation stakeholders should consider the most updated outcomes from scientific studies. To facilitate this process, researchers should be keen to present their work in easily comprehensible formats and to ensure that the potential conservation actions are coherent with their scientific findings. From the same perspective, researchers should keep in mind conservation issues when designing and conducting their studies. For example, the numerous threats jeopardizing the Nimba Mountain chimpanzees and the almost nonexistent management of the reserve may lead researchers to consider very carefully the benefits of habituating apes to the presence of human observers, since it is very difficult to guarantee proper protection to wildlife over the long-term (Jenkins 2008, Köndgen et al. 2008).

Bio-monitoring programs focusing on Nimba wildlife should be developed on a long-term basis. A perennial follow-up of flagship and good bio-indicator species appears to be the most appropriate strategy since it would afford information on global population and ecosystems evolution trends, which are still insufficiently known (Hortal and Lobo 2005).

The Nimba Mountain forms an essential water catchment area, which has great regional importance because it contains the headwaters of three major river systems flowing into the Atlantic Ocean: the Cavally, Ya and Nuon Rivers. These rivers irrigate vast zones of Guinea, Liberia and Côte d'Ivoire, where they constitute important water resources for domestic, agricultural and industrial needs. Thus, degradation of the Nimba ecosystems, by affecting the headwaters of these rivers, would have a long-term negative impact on their entire hydrographical networks, and sanitary/economic consequences in the three countries. Indeed, the sustained protection of the Nimba Mountain has important regional correlates.

As a conclusion, the biggest challenge for the sustainable conservation of the Nimba Mountain is to integrate all these issues in a tri-national coherent initiative, which would be thoroughly designed and strictly enforced. Such an attempt is embodied by a newly launched biodiversity conservation program, which unfortunately focus only on the Guinean part of the Biosphere Reserve (Programme de Conservation de la Biodiversité du Mont Nimba). Funded by the United Nation Environment Program and the Global Environment Facility, this program was initiated in 2004 for a 9-year period with the objective of conciliating research, conservation, mining activities and local development. Our biggest hope is to see this initiative backed, durably reinforced and enlarged to the entire massif so as to efficiently tackle the most critical conservation issues and to ensure a sustainable future for the Nimba Mountain's habitats, wildlife, chimpanzees, and humans.

CHAPTER II. Chimpanzees in the eastern part of the Nimba Mountain Biosphere Reserve: Gouéla II and Déré forest

This chapter thoroughly presents the preliminary surveys conducted in the eastern part of the Nimba Mountain Biosphere Reserve during 13 months between March 2006 and June 2008. We focused on 2 strictly protected areas of the Biosphere Reserve: the Gouéla II area in the southern slope of the Guinean part of Nimba and the Déré forest, which are separated by a 10 km gap of buffer zone covered by savanna and crossed by an international road (Fig. 27). It has been published as a chapter of the book “The chimpanzees of Bossou and Nimba” (Granier N 2011). A shorter version was earlier published in the newsletter “Pan Africa News” (Granier N, Huynen MC and Matsuzawa T. 2007). These surveys were determinant in defining an adequate study area and formulating the working hypotheses of the core research of the core research of this study.

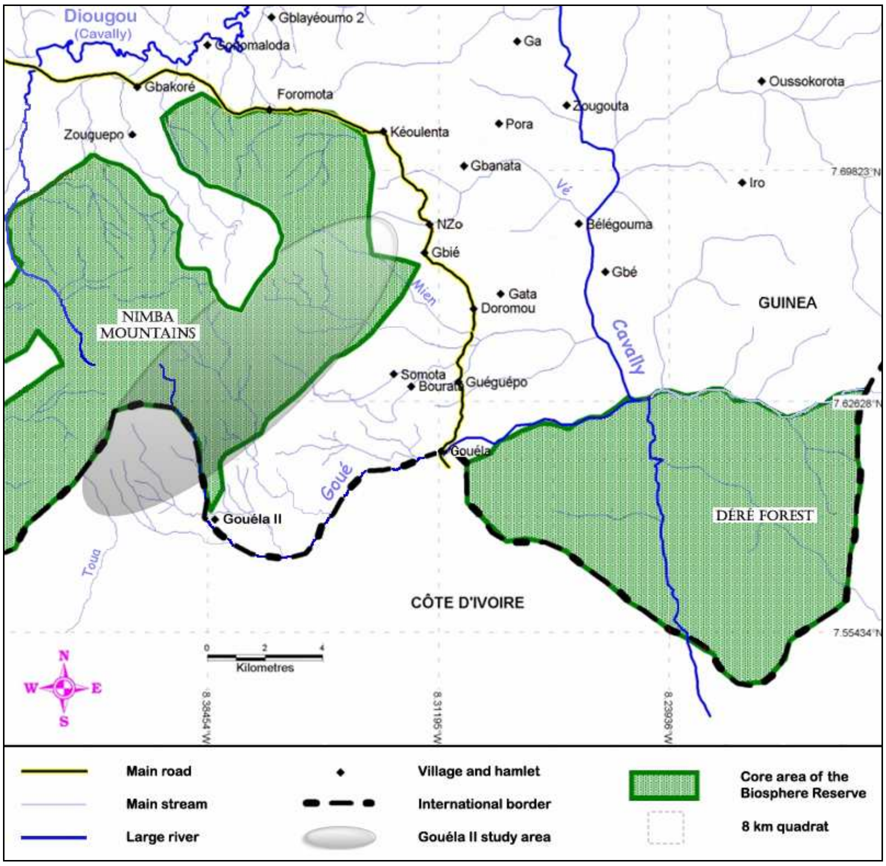
III.1. Abstract

The eastern part of the Nimba Mountain Biosphere Reserve is constituted of two strictly protected areas: the whole Guinean southern slope of the massif, called Gouéla II, and the Déré forest, which are separated by 10 km of buffer zone consisting of lowlands with high human encroachment. A behavioral and ecological study of non-habituated chimpanzees was initiated in this area to provide information on their habitat-use and ranging patterns. Data on chimpanzee presence were systematically and periodically collected between 2006 and 2008 using a combination of 3 survey methods. In Gouéla II, 75% of chimpanzee's presence indicators occurred above 700m high, in altitude forest, galleries and secondary vegetation habitats. In Déré, owing to an unclear protection status, the forest was logged in 1999-2000, and then swarmed in by cultivators. Today the Déré forest is critically damaged and only one chimpanzee track was observed during 29 days of survey. By offering new information on Nimba chimpanzees, this work also targets conservation perspectives of the species and its unique environment.

III.2. The eastern part of the Nimba Mountain Biosphere Reserve

The eastern part of the Nimba Mountain Biosphere Reserve (NMBR), called by local people the "Vépo region", refers to the Guinean territory localized "behind Vé river" (e.g. "south of Vé"). It contains two core areas of the Biosphere Reserve, which are the uneven southern slope and foothills of the Guinean Nimba range (hereafter Gouéla II) and the hilly Déré forest (Fig. 27). These 2 strictly protected areas are separated by ten kilometers of buffer zone consisting of lowlands covered by fields and fallow lands with small residual patches of damaged forest. Drained by the upper part of the Cavally River, the Vépo region presents fertile and arable soil attracting cultivators. As a consequence, it is nowadays one of the first rice production areas of the Lola Prefecture, and this to the detriment of the forest.

Fig. 27: The eastern part of the Nimba Mountain Biosphere Reserve.



This map presents the eastern part of the NMBR at the border between Guinea and Côte d'Ivoire. The two study areas, Gouéla II (gray shadow oval) and the Déré forest are represented, as well as the surrounding human settlements and hydrographic network, including the name of important rivers.

A road linking Guinea to Côte d'Ivoire crosses the eastern part of the Reserve's buffer zone. Several villages and settlements occur along this road, with two major poles of human concentration: N'Zo, the county town and Gouéla, the border village. Historically, the first humans to settle in the Vépo region were the Kono people (Germain 1984). Nowadays, it is also populated by other ethnic groups: forest people, in majority Guerzé, Mano and Yakuba, as well as exogenous populations found mostly in N'Zo and Gouéla, such as Mandingos and Fula. The recent soaring population growth and the inherent subsistence activities of local people generate important anthropic pressures upon surrounding ecosystems.

III.2.1 Gouéla II

Gouéla II is the name of a century old Guinean encampment for cultivation localized near the Goué River (which marks the border with Côte d'Ivoire) just at the limit of the Reserve's core area (N 07º35'49.8"; W 08º22'48.3"; Fig. 27). It is accessible only after more than 3 hours walking, departing either from N'Zo or Gouéla. By extension, the region under study, which corresponds to the transboundary part of the Nimba southern slope stretching between the Mien and the Toua Rivers, was named Gouéla II. This forest is strictly protected since 1944 like the whole Nimba Mountain (Lamotte 1998, see Chap. 43). In Guinea, crest and slopes of Nimba above 800 meters high are covered by altitude grasslands. The foothills of the Nimba relief present sprinkled stretches of savanna, which correspond to iron-bearing plains with thin soil and scattered shrubby species. Between these lowland and altitude herbaceous ecosystems, Guineo-equatorial rainforest covers the slopes of the massif (Fig. 28).

Fig. 28: View of the Nimba Mountain from Gouéla II encampment.

This picture illustrates the vegetation types present in the study area: altitude grassland, Guineo-equatorial rainforest and plain savanna (photograph by N. Granier).

A fifth habitat type described by Schnell (1998) is the secondary vegetation, made of heliotropic ground plants with a relatively low density of wooded species. It occupies a growing space at the limit between altitude grassland and altitude forest, due to the negative impact of uncontrolled and repetitive bushfires.

A footpath links N'Zo (Guinea) to Yealé (Côte d'Ivoire) through Gouéla II, following the Reserve's limit. Along this path stands a network of human settlements interconnected by secondary trails and populated by remote communities living of farming, hunting and natural resources exploitation. Despite a good preservation status of Gouéla II core area of the NMBR, the adjacent forested buffer zone suffers from annual clearance for cultivation, which increases the isolation of Nimba ecosystems. A relatively significant poaching pressure using both guns and snares is exerted on the fauna inhabiting this core area. Amongst some 29 mammal species surveyed, Granier et al. (2007) reported the presence of the emblematic African buffalo and 10 primates species, half of them being listed in the IUCN red list of endangered species: the chimpanzee *Pan troglodytes* (Endangered), *Cercopithecus diana diana*, *C. nictitans martini* and *Colobus polykomos* (Vulnerable), and *Cercocebus atys atys* (Near Threatened, IUCN).

III.2.2 Déré forest

This triangular-shaped forest at the border between Guinea and Côte d'Ivoire is contiguous to the Ivorian Tiapleu and the "massif des Dans" forests (Fig. 27). Jealously protected by local villagers, it was called 20 years ago the "black forest" because of its close canopy, as well as the traditional ceremonies and initiation rites that took place within. To address the small-scale agricultural colonization that started in the early 1990s, the Man And Biosphere (MAB) program of UNESCO has established the Déré forest as a core area of the NMBR in 1993. However, no Guinean legal text has yet enforced this decision, and a logging company named

Valauris S.A., took advantage of the situation by building roads and cutting timber inside the forest between 1999 and 2001. The resulting land settlement has favored the immigration of hundreds of farmers seeking arable land to cultivate rain-fed rice using slash-and-burn techniques. Thus, an important part of this Reserve's core area is nowadays made up of farmbush, while the remaining patches of forest, which includes large and diverse tree species, always get smaller. Since 2002, the settlement of Ivorian rebels arrogating that the Déré forest belongs to Côte d'Ivoire has worsen this environmental problematic.

The last mammal survey carried out in the Déré forest by Granier and colleagues (2007) has reported the presence of 17 species including one primate species (*Cercopithecus nictitans*) and 1 artiodactyl quoted in the IUCN red list of endangered species: the pygmy hippopotamus, *Hexaprotodon liberiensis* (IUCN, 2007).

III.3. Chimpanzee research

III.3.1 History

The presence of chimpanzees in the southern slope of the Nimba Mountain was reported more than sixty-five years ago by Lamotte (1942). However, particular interest for the species in this region truly began in 1993 with the establishment by Matsuzawa of Yealé research site in Côte d'Ivoire (Matsuzawa and Yamakoshi 1996, Humle and Matsuzawa 2001; see Chapter 30). In Gouéla II forest yet, only 2 short-term surveys were conducted to estimate the status of chimpanzees (Sugiyama 1995, Shimada 2000) and both confirmed the presence of the species. In the Déré forest, the only primatological data came from a Rapid Assessment Program conducted by Conservation International on several taxonomic groups of wildlife (McCullough et al. 2006). The presence of chimpanzees was not reported during their 3-days survey.

III.3.2 Present study

III.3.2.1. Objectives

A behavioral and ecological study of non-habituated chimpanzees' habitat-use was initiated in the eastern part of the NMBR in 2006. The general aim of this still undergoing work is to describe the ranging and grouping patterns of the species in this region. Specifically, it aims to understand how seasonality in food availability and anthropic pressures leading to habitat modifications influence the spatio-temporal distribution of chimpanzees (Sugiyama and Koman 1992; Chapman and Peres 2001; Basabose 2005). It is nowadays commonly admitted that different chimpanzee communities have different cultural traditions, which express through behavioral variations in material skills, know-how, habitat-use or resources exploitation (Boesch 1996, Matsuzawa and Yamakoshi 1996, Whiten et al. 1999, Humle and Matsuzawa 2001). Consequently, the study of an unknown community always presents important issues, which brought me to investigate the chimpanzees of the eastern part of the NMBR. This study also has conservation-oriented objectives consisting of achieving accurate data on this endangered species in its exceptional and peculiar environment in order to be able to efficiently protect it (Kormos et al. 2003, IUCN 2007).

III.3.2.2. Methods

To reach these objectives and get a preliminary overview of chimpanzee presence, I first conducted interviews of local communities in March 2006. Thirty-two were performed in 18 human settlements located between the two focal core areas of the NMBR. Interviewees were all hunters and/or cultivators, contacted either individually or in group, in a random and opportunistic manner. However, a systematic questioning procedure was repeatedly used, with questions addressing chimpanzee presence, abundance, distribution and relationships with humans.

Then, during 3 fieldwork periods (March-April 2006, December 2006-May 2007 and February-June 2008), field studies of chimpanzees' habitat-use were carried out in Gouéla II and Déré forests. Evidences of chimpanzee presence were recorded from 3 types of survey (transect, recce and scouting survey). These itineraries were systematically positioned across the study areas, and walked (Table 5). All chimpanzee presence indicators, including nests, feces, trails, footprints, traces, feeding remains, tool-use sites and vocalizations, were thoroughly recorded and geo-referenced together with changes in habitat types encountered during walks.

Table 5: Sampling effort from the 3 survey itinerary types

	Gouéla II			**Déré Forest**		
Survey type and number	T (n=12)	R (n=4)	S (n=51)	T (n=0)	R (n=3)	S (n=18)
Number of passage	8	4	1	0	3	1
Walk distance (km)	28.8	96	225	0	79	84
Total distance (km)		349.8			163	
Total number of day		165			29	

This table shows the number of each survey itinerary type in Gouéla II and in the Déré forest. The number of passages and the walked distance per site on each type of survey itinerary and in total are also figured, as well as the number of days it required. **T**: Transect; **R**: Recce; **S**: Scouting survey.

Sampling effort was lower in Déré than in Gouéla II, with respectively 163 km and 350 km walked (Table 5). Twelve parallel transects of 300 m long were established in Gouéla II. Their origins were systematically located 10' apart (309 m), starting in plain savanna and heading upwards to the north, going through all vegetation types. Each transect was walked 8 times. Four recces set in Gouéla II consisted of loops with a mean length of 5.9 km (± 0.7 SD), stretching between the plain and altitude herbaceous ecosystems; each was walked 4 times. Both transects and recces were periodically walked to record data, with a passing frequency of three weeks for transects and of one month for recces. In Déré, 3 recces were set as loops rising perpendicularly from the Cavally River to the limit of the classified forest (mean length

= 8.7 km ± 1.3 SD). They were walked 3 times, without any temporal regularity. Scouting surveys consisted of opportunistic walks covered just once following chimpanzee tracks. Fifty one were walked in Gouéla II and 18 in Déré.

III.4. Preliminary results in Gouéla II

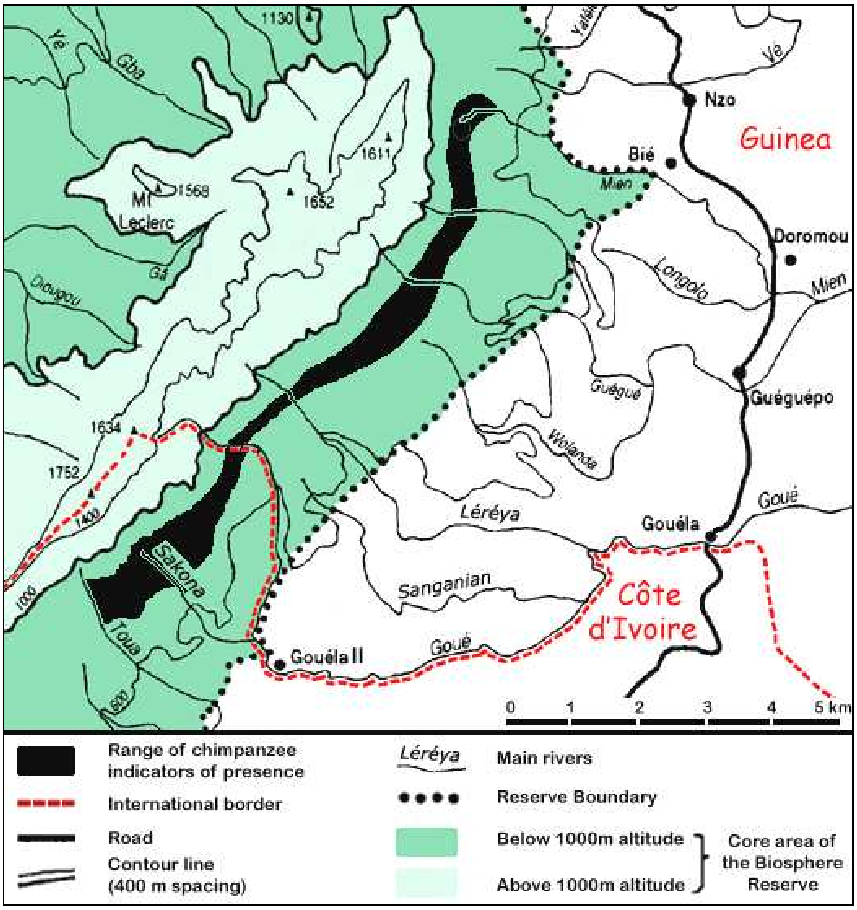
III.4.1 Selective use of altitude forest and irregular presence

Numerous animal trails roughly following the contour lines of the Nimba range were observed at the limit between altitude forest and grassland, between 700 and 800 m high. These trails crossed large expanses of secondary vegetation and surprisingly revealed numerous chimpanzee presence indicators: 1.14 seen per kilometer (n = 87 km walked on such trails). Almost two thirds of all the recorded evidences were in altitude forest and adjoining secondary vegetation (61% of all presence indicators; N = 393), whereas the sampling effort in these 2 habitat types represented 43 % of total. In addition, vocalizations heard (n = 18) always came from the higher parts of the forest. Chimpanzee tracks recorded in the lower parts of the forest (above 700 m; n = 97), stood for a quarter (24.7%) of all the recorded indicator of presence. Interestingly, the presence of ripe edible fruits was recorded in the vicinity of 87% of these low altitude records. Finally, the collected chimpanzee feces contained seeds of tree species such as *Harungana madagascarensis*, *Musanga cecropioïdes*, *Trema guineensis*, *Aframomum sp.* and *Ficus sp.*; plants species widely represented in the secondary vegetation of Nimba, most of which fruit during the period of fruit scarcity (March - June). Further investigations are undergoing to provide enlightenments on the potential relationship between chimpanzee’s use of secondary vegetation and food availability of this habitat type.

III.4.2. Nesting behavior

A total of 337 nests was seen and recorded. The total number of nesting groups could not be identified since several nesting sites are periodically re-used by chimpanzees, and discrimination of different-age nests is not reliable enough to determine group composition. However, a mean size of 5.4 nests per group was calculated from the fresh and unequivocally identified nesting groups (n = 23). Groups of 2 or 3 nests were frequently observed, and the largest one was composed of 22 fresh items in the higher part of Sakona River (Fig. 29). This area seems to be an important nesting site since large groups of fresh and recent nests were twice observed and new nests seen at each visit.

Fig. 29: Spatial distribution of chimpanzee presence indicators in Gouéla II.



This map shows details of Gouéla II study area at the border between Guinea and Côte d'Ivoire, including the name of all rivers and the nearest human settlements. The range in which all chimpanzee indicators of presence were observed appears in black.

Nesting sites were located between 649 and 843 m altitude, mostly in galleries (36% of total nest number) and altitude forest (34% of total). Nests were often built in very steep places with a ground declivity superior to 22.5% (63% of total). The mean height of nests from the ground was 7.8 m ± 4.6 SD. Both ground declivity and nest height were measured using a clinometer and calculated post-hoc.

These preliminary results altogether strengthen the assumption that the plant food availability would be a determinant factor of chimpanzee's spatio-temporal distribution in Gouéla II. The higher part of Gouéla II transboundary area would be part of the home range of at least one community of chimpanzees. It may constitute a peripheral zone of its (their) habitat(s), punctually visited by small parties or solitary individuals, although no periodicity has yet been revealed.

III.4.3. Tool-using behaviors

Eight ant-catching sites were observed on the ground in the altitude forest (mean altitude 784 m). The wands used by chimpanzees were systematically identified and measured. *Aframomum sp.*, *Dacryodes sp.*, *Microdesmis keayana*, *Mareya micrantha* were the most commonly used species to catch ants, seen in at least two collection sites. Tool length was included between 18 and 73 centimetres (N = 44; mean = 46.8 ± 15.5 SD) with a diameter ranging from 0.2 to 0.8 centimetres (mean = 0.4 ± 0.1 SD). Both Sugiyama (1995) and Shimada (2000) also reported evidence for ant-catching during their short-term surveys in Gouéla II. It is assumed that Gouéla II chimpanzees may crack-open nuts using stones, since nut trees (*Elais guineensis* and *Coula edulis*) occur in the Mien River catchment area (northern end of Nimba), and this behavior was reported from interviews. However, I have not yet uncovered any evidence of nut-cracking in the area. Lastly, four interviewees have reported chimpanzee fishing in little streams; behavior which was corroborated by an observation made by Michel Zogbélémou, my guide from Gouéla II. Chimpanzees would build a dam with trees and leafy branches in a narrow part of the stream, and use their hands to catch fishes from the upstream water. Mention of an individual from Bossou chimpanzee community eating fish was also made by Sugiyama (1987).

III.5. Preliminary results in the Déré Forest

It emerges from interviews with local communities that before the logging exploitation chimpanzees were present in the black forest. However, only 3 reports of a present chimpanzee occurrence in the Déré forest were made from the same interviews (n = 32). These affirmations were nonetheless corroborated in March 2006 by observation of a very old nest built in an *Aningueria altissima* tree near the Ivorian border, in the south eastern part of the forest (Granier et al. 2007). A farmer settled in this area of the classified forest, reported that chimpanzees would annually visit the place at the end of the rainy season, coming from the “Massif des Dans” just across the border. Although the age of the nest seemed to correspond to the end of the rainy season, I could not confirm this assumption. Still, it is highly plausible that the presence of chimpanzees and of other large fauna in the Déré forest has largely decreased during the last decade, mainly due to the negative influence of human activities and habitat destruction. Given the actual high rate of forest clearance, prospects for chimpanzee research in Déré are extremely poor, unless huge and long-term efforts of environmental conservation are urgently undertaken.

III.6. Perspectives on future chimpanzee research and conservation

III.6.1. Research perspectives

Further data collection is still necessary to provide a detailed picture of factors influencing habitat-use of chimpanzees in the eastern part of the NMBR. Up to now, data collection occurred exclusively during the dry season, consequently the rainy season 2009 will be spent collecting missing data. Then, botanical and fruit phenology information will be integrated to the spatial analysis of chimpanzee indicators of presence to obtain a year-round image of seasonality. Further investigations have also been initiated to understand the influence of food availability and human/predator presence on chimpanzees' choice of nesting in difficult-to-reach places.

It is well known that chimpanzees from the Bossou community regularly travel to the Nimba Mountain and to Liberia (Sugiyama 1999, Ohashi 2006). Yet, very scarce data are available regarding intercommunity exchanges and encounters between Bossou and Nimba communities. Since the chimpanzee is a highly mobile species, which exploits very large habitat regardless of national borders and shows individual migrations, it would be of great interest to implement a large-scale study of the variables driving chimpanzee's ranging and grouping patterns. The objective is to put forward tri-national perspectives on Nimba chimpanzee's habitat use, inter-community exchanges and material cultures, by working from an overall point of view.

After analysis of the above-presented preliminary results, it appeared essential to amend the study area in order to obtain a more cohesive area, in keeping with research objectives. That is how I decided to exclude Déré forest and to focus exclusively on an enlarged part of the Nimba range by including Yealé (Côte d'Ivoire, south-east from Gouéla II), where previous chimpanzee research has been carried out (see Chapter 30). However, aware of the huge conservation issues of Déré forest, I decided to maintain contact with its resident populations.

III.6.2. Conservation perspectives

Chimpanzee conservation is tightly connected to the problematic of habitat and biodiversity sustainable preservation. In addition, there is growing evidence suggesting that the alleviation of threats facing Nimba chimpanzees requires an integrated collaboration between research and conservation. Consequently, the challenge facing nowadays chimpanzee protection is to provide coherent conservation policy and measures that would integrate the different political, socio-economical and protective statuses of the Nimba Mountain in each of the three countries, plus the known elements of chimpanzee life history and ecology. Such integrative perspectives are consistent with the above-proposed approach of research.

The current very poor conservation status of Déré forest is due to an intricate mix of almost all the critical threats facing nowadays biodiversity conservation: industrial activities (logging in this case) and human-related activities such as human politics (soaring population growth, migrations, war, difficulties in cross-border management…) or community subsistence activities (slash and burn agriculture with perpetual lack of arable land, non-rational hunting or poaching, fishing, gathering, uncontrolled use of fire…) (see Chapters 43-44). It emerges from this situation that the eastern part of NMBR does not constitute a cohesive unit, mainly because of the different conservation statuses, problems and needs of its two core areas. It would be rather consistent to apprehend it in two distinct parts: Gouéla II linked to the problematic of research and conservation in the NMBR core area, and the Déré forest, which has concretely became more related to the buffer zone management issue. Such a differential management would emphasize the dissimilarities of these two focal areas, while improving efficiency of conservation measures in the single but diversified entity of the Nimba Mountain Biosphere Reserve.

CHAPTER III. Density estimates and nesting-site selection in chimpanzees of the Nimba Mountain, Côte d’Ivoire and Guinea

Following the findings of preliminary surveys, from 2008 we focused our efforts on the southern slope of the Nimba massif, shifting the study area southwesterly to encompass the entire Ivorian section of Nimba, where chimpanzee populations were thought to live permanently and at higher densities (Matsuzawa and Yamakoshi 1996, personal observations). The central question was to understand why chimpanzees in this region of Nimba apparently selected more the secondary vegetation habitat located in the altitude part of the mountain and gallery forests. The working hypothesis was that the secondary vegetation located at the edge between mountain forest and altitude grassland was constantly harboring food resources, while providing enough-sturdy trees to build nests and a reasonable distance to humans. In collaboration with 8 local field assistants, we opened 80 kilometers of survey itineraries (transects and recces) in the study area (Fig. 30), and monthly monitored them during 19 months between 2009 and 2011. We described habitat along these itineraries according to the composition in woody species, to the phenology of fruits, and to 12 variables of vegetation structure, topography and seasonality. During each passage we systematically recorded and georeferenced all chimpanzee signs of presence together with signs of other large mammal’s presence including humans.

This third chapter presents an extensive study of the nesting behavior of chimpanzees populating the Ivorian part of Nimba, which has been published in the American Journal of Primatology (Granier N, Hambuckers A, Matsuzawa T, Huynen MC. 2014). We estimated chimpanzee abundance using nest count methods from line transects, providing knowledge of high conservation value as the only published estimates dated from the early 1990s (Hoppe-Dominik 1991, Marchesi et al.1995). We also investigated in details the selection criterions of chimpanzees for nesting site and nesting-tree, and drawn out general conclusions on their ranging patterns in this large area.

IV.1. Abstract

We investigated nesting behavior of non habituated chimpanzees populating the Nimba Mountain to document their abundance and their criterions of nesting-site selection. During a 19-month study we walked 80 km of transects and recces each month, and recorded 764 nests (mean group size = 2.23 nests) along with characteristics of vegetation structure and composition, topography and seasonality. Population density estimated with two nest count methods ranged between 0.14 and 0.65 chimpanzee/km^2. These values are lower than previous estimates, emphasizing the necessity of protecting remaining wild ape populations. Chimpanzees built nests in 108 tree species out of 437 identified, but 2.3% of total species comprised 52% of nests. Despite they preferred nesting in trees of 25-29 cm DBH and at a mean height of 8.02 m, we recorded an important proportion of terrestrial nests (8.2%) that may reflect a cultural trait of Nimba chimpanzees. A logistic model of nest presence formulated as a function of 12 habitat variables revealed preference for gallery and mountain forests rather than lowland forest, and old-growth forest rather than secondary forests. They nested more frequently in the study area during the dry season (December-April). The highest probability of observing nests was at 770 m altitude, particularly in steep locations (mean ground declivity = 15.54%). Several of the reported nest characteristics combined with the existence of 2 geographically separated clusters of nest, suggest that the study area constitutes the non-overlapping peripheral areas of 2 distinct communities. This nest-based study led us to findings on the behavioral ecology of Nimba chimpanzees, which constitute crucial knowledge to implement efficient and purpose-built conservation.

IV.2. Introduction

Chimpanzee societies are organized in a fission-fusion system in which individuals of a same community frequently gather together and split into sub-groups that vary greatly in size, composition and duration [Lehmann and Boesch 2004]. Grouping patterns considerably vary across communities and years, which is interpreted as resulting from a delicate balance between ecological (food availability, presence of danger-predators) and social parameters (demography, community size and sex ratio, presence of receptive females) [Doran 1997, Lehmann and Boesch 2004], but also activity or cultural behaviors (e.g. cooperative hunting) [McGrew 2004]. Such an adaptive community organization, in addition to the particularly elusive behavior of non-habituated chimpanzees and their relatively low population densities, explain the difficulty of conducting censuses based on social group counts [Ghiglieri 1984]. However, each weaned chimpanzee builds a new nest (also called bed or sleeping platform) every night, and occasionally a day-nest in which to rest, socialize or eat, most nests being built in trees and not reused [Plumptre and Reynolds 1997]. Nests constitute tangible evidence of chimpanzee presence and abundance used to develop nest count methods [Ancrenaz et al 2004]. These methods are particularly well adapted to census non-habituated populations over wide areas [Tutin and Fernandez 1984], such as the Nimba Mountain, a 40 km long and 10 km wide massif stretching along the border between Guinea, Côte d'Ivoire and Liberia (Fig.1). Despite early report of chimpanzee presence in Nimba forests [Lamotte 1942], data on population abundance of this endangered species are still strikingly lacking, which is of foremost conservation concern. Understanding chimpanzee habitat preference and particularly criterions of sleeping-site selection is another crucial conservation issue [Anderson 1984, McGrew 2004]. Earlier studies have shown that selection of nest implantation (nesting-site, nesting-tree and situation within nesting-tree) can be influenced by a myriad of factors such as vegetation structure and composition [Tutin and Fernandez 1984, Furuichi and Hashimoto 2004], location and physical characteristics of trees [Hernandez-Aguilar et al. 2013], seasonality and food resources [Doran 1997, Basabose and Yamagiwa 2002], predator and human avoidance [Marchesi et al. 1995, Stewart and Pruetz 2013], thermoregulation

[McGrew 2004, Koop et al. 2012], comfort [Stewart et al. 2007], topography [Furuichi et al. 2001] or parasite avoidance [Samson et al. 2013]. Thus, studying nest distribution and characteristics over time provides valuable scientific information on the behavioral ecology of chimpanzees, particularly on their habitat-use, grouping patterns, diet, and on seasonal variation of these behaviors [Anderson 1984]. This knowledge is an essential prerequisite to leading further inter-community comparisons, and implementing efficient and purpose-built in situ conservation.

Preliminary investigations we conducted on non-habituated chimpanzees of the Nimba southern slope in 2006-2008 suggested that their presence was seasonal and preferentially in altitude habitats [Granier 2011]. In the present study, we used recent and solid methodologies to go further and achieve a twofold objective. We first aimed at filling the knowledge gap on chimpanzee abundance [Kormos et al 2003] by applying and comparing two techniques of nest count from line transects: the standing crop and marked nest count methods [Hashimoto 1995]. We then aimed at characterizing the ecological factors that best predict nesting-site distribution of this particular population. Building on our preliminary findings, we formulated the hypotheses that chimpanzees would nest more frequently in the study area during the dry season, that they would prefer nesting at high altitude, in places with high ground declivity, and in gallery or mountain forests of either old-growth or good-quality secondary types. We used logistic regression to model nest presence as a function of 12 ecological variables characterizing vegetation structure, topography and seasonality.

IV.3. Methods

IV.3.1. Study site

The northeastern part of the Nimba Mountain ridge culminates above 1500 m. It is covered by altitude grasslands from 800-1000 m high, tightly intertwined with various formations of evergreen rainforests on slopes and foothill. The crest progressively descends to 1000 m altitude towards the southwestern part of the mountain, and forest rises over the top to cover the entire massif from the Yan River (Fig. 30). This particular vegetation mix and the harsh topography fostered the emergence of multiple ecological niches with rich biodiversity and notable endemism [Lamotte and Roy 2003]. To ensure sustainability of these exceptional ecosystems, the Guinean and Ivorian sections of Nimba (180 km^2) were integrally protected in the early 1940s, and today benefit from several other conservation statuses [Granier and Martinez 2011].

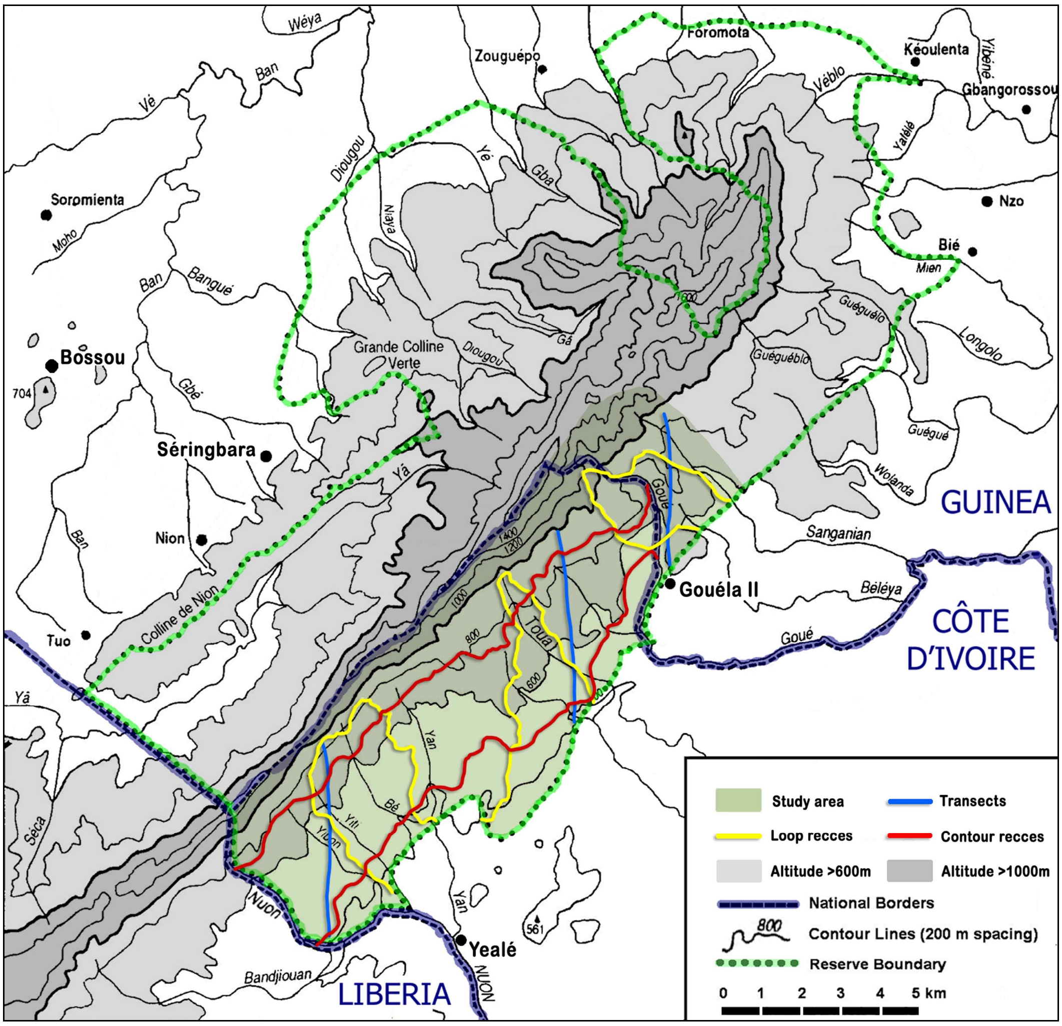
Since 1976 sporadic studies have been carried out to survey Nimba chimpanzee populations or address inter-community behavioral variations [Marchesi et al. 1995, Matsuzawa and Yamakoshi 1996, Shimada 2000, Humle and Matsuzawa 2001, Granier 2011]. More systematic research was initiated in 2003 with the establishment of a permanent research site at Seringbara (Nimba northern slope, Fig. 30) where Koops et al. [2012] study the influences of habitat ecology on elementary technology use by chimpanzees. The present study has focused on the lesser-studied southern slope of Nimba, centered on its Ivorian section (50 km^2) and extending beyond the Guinean border (10 km^2). The southwestern part of our study area was named ‘Yealé area’ (following the name of Yealé village), and the northeastern part ‘Gouéla II area’ (in keeping with the small settlement of Gouéla II; Fig. 30).

IV.3.2. Data collection

IV.3.2.1. Surveying method

This research adhered to the American Society of Primatologists principles for the ethical treatment of primates. We used 3 types of survey itineraries to monitor the study area (Fig. 30). (1) Three parallel line transects drawn from where the 3 main rivers outflow from the reserve following the north azimuth, up to altitude grasslands, or as high as topography allowed (mean length = 4.15 ± SD 0.27 km). (2) Two contour recces stretching between the Liberian and Guinean borders following the contour lines 750 and 450 (mean length = 17 ± SD 0.71 km); and (3) three loop recces starting where the 3 main secondary rivers outflow from the reserve, extending up to the altitude grassland edge and back down in a large “u-turn” forming a loop (mean length = 10.90 ± SD 2.27 km).

Fig. 30: Study area and survey itineraries in the Nimba Mountain



When opening these approximately 80 km of itineraries in 2009-2010, we measured distances with a hip-chain (topofil) and tied tapes every 100 m on transects – 500 m on recces. Surveying effort was spread over 19 months divided into 2 field survey periods. From June to

December 2009, we walked contour and loop recce each month (7 visits), and from May 2010 to April 2011, we walked all itineraries every 24 days following a fixed sequence of 14 days, except in December (11 visits).

IV.3.2.2. Vegetation and nests

Survey itineraries were used to describe the structure and composition of vegetation, and to record nest data. The composition of woody species was assessed on a 10 m-width strip along the 3 transects, identifying and measuring diameter at breast height (DBH) of all trees > 10 cm DBH. Vegetation structure was described according to 9 variables characterizing the different vegetation strata (Table 6): forest type, forest disturbance, canopy closing, plus 6 dichotomous non-exclusive variables describing understory: open understory and/or understory containing sapling, liana, Marantaceae, Zingiberceae and/or Chromolaena species [Marchesi et al 1995, Duvall 2008]. As each survey itinerary was opened, we continuously recorded the levels of these 9 variables. Each observed nest was georeferenced and we systematically noted the following information: (1) location; (2) height above ground; (3) age-class following Tutin and Fernandez [1984] criteria; (4) species and DBH of nesting-tree; (5) size of nest group, defined as nests of the same age-class within 20 m; (6) vegetation structure according to the above-described criteria; (7) altitude and ground declivity under the nest; and (8) season of nest construction – rainy (May-November) or dry (December-April). For nests seen on transects, we also recorded the perpendicular distance (PD) between transect and nest.

IV.3.3. Data analysis

IV.3.3.1. Chimpanzee density estimates

We used Distance 6.0 software to estimate chimpanzee density from the standing crop (SCNC) and marked nest count methods (MNC), based on both nest groups and individual nests [Plumptre and Reynolds 1996, Furuichi et al 2001]. Nest density d is the ratio of the number of detected nests n, to the area surveyed multiplied by the probability of detecting a randomly chosen nest [Tutin and Fernandez 1984]. A detection function $g(x)$ is created as the probability of detecting a nest at distance x of transect, and characterized by the effective strip width, μ, or distance for which the number of nests detected beyond equals the number of nests missed within [Buckland et al 1993]. Nest density d is given by the formula, where L is the transect length:

$$d = n / 2 \mu L$$

Post-hoc determination of μ was made on the basis of lowest Akaike's Information Criterion (AIC) by selecting between 4 mathematical keys available in Distance, the model of $g(x)$ that fitted the best our distribution of PD frequency [Buckland et al. 2010]. We set truncation distance w at PD = 20 m, considering that beyond this point measures were not accurate enough [Buckland et al 2010]. Given that some day-nests may have been counted as night-nests and that contrarily, some night-nests could have been reused, we assumed the chimpanzee daily nest production rate to be 1 nest/chimp/day [Hashimoto 1995]. In the SCNC method, which requires just one census per transect, nest density is corrected by the average length of time nests remain visible to obtain the total number of nest builders [Ghiglieri 1984]. We used the nest life-span estimated in Taï forest National Park (Côte d'Ivoire) by Kouakou et al. [2009]: 91.22 ± SE 5.89 days. All nests collected during the 11 passages on transects were included to increase sample size [Plumptre and Reynolds 1996]. Repeated counts on each transect were processed as non-independent replicates by pooling line data following Buckland et al [1993]. In the MNC method only new nests are counted, which allows getting rid of the nest life-span [Plumptre and Reynolds 1996]. Density of new nests is corrected by the number of day elapsed between two consecutive passages (which must be shorter than the minimum nest life-span) to obtain the density of nest-building chimpanzees [Hashimoto 1995, Plumptre and Reynolds 1997]. During the opening of transects and the first passage we marked all nests, and used only new nests recorded during the 10 ensuing passages to estimate density. For both methods we calculated individual nest density using the PD frequency, and nest group density using the mean PD of nests belonging to a same group, plus group size [Marchesi et al. 1995, Kouakou et al. 2009].

IV.3.3.2. Nesting-tree selection

We used a G-test for goodness-of-fit to compare distributions of tree species used for nesting to overall tree availability [Sokal and Rohlf 1995]. Overall tree diversity and abundance recorded on the 3 transects were used as theoretical values to generate the expected sample. We excluded from this analysis nests recorded in tree with DBH < 10 cm and nests for which we did not record theoretical value. Our data set was then truncated in such a way as to respect the assumption of having 80% of expected values > 5 [Agresti 2002]. Similarly, we used G-test for goodness-of-fit to compare the DBH distributions of trees used for nesting to trees sampled on transects, grouped in classes of 5 cm DBH. In order to interpret chimpanzee selectivity for each tree species and each DBH class, we calculated the adjusted (normalized) Pearson's residuals for each cell of a two-way table according to the following formula:

$$Res. = \frac{(O - E)}{\left[E\,(1 - P_i)\,(1 - P_j)\right]^{1/2}}$$

With O the observed frequency, E the standardized expected frequency, P_i the proportion of line i and P_j the proportion of the observed column [Agresti 2002]. The farthest is residual value from 0, the most preferred (positive value)/avoided (negative value) is the tree species/DBH.

IV.3.3.3. Nesting-site selection

We used logistic regression to model influences of habitat structure, topography and seasonality on nesting-site selection by chimpanzees. Initial variable selection was made of 16 effects produced by 12 predictor variables sensed to influence nesting-site choice (Table 6) according to our preliminary reconnaissance results [Granier 2011] and literature analysis [Tutin and Fernandez 1984, Furuichi et al. 2001, Basabose and Yamagiwa 2002].

Table 6: Variables and effects used to model nest presence, with their levels

Categories	*Variables* and effects		Levels
Vegetation structure	*Forest type*		Lowland forest Montane forest Gallery forest
	Forest disturbance		Old-growth forest Old secondary forest Young secondary forest
	Canopy closing		Closed (75-100%) Partially closed (50-75%) Light (25-50%) Open (0-25%)
	Understory	*Open* *Woody species (sapling)* *Liana species* *Marantaceae* *Zingiberaceae* *Chromolaena odorata*	Presence / Absence
Seasonality	*Season alternation*		Dry (December to April) Rainy (May to November)
	Season * forest type Season * forest disturbance		6 levels
Topography	*Altitude*		Range: 509-1,076 m
	Altitude^2		Continuous
	Declivity		Range: 0-85%
	Declivity^2		Continuous

The 16 effects of *12 habitat variables (italic)* used to build up model of nesting-site selection; all variables and effects characterizing **vegetation structure** and **seasonality** are categorical, the 2 variables and 2 effects describing **topography** are continuous (range of recorded values provided). In data analysis, 3 and 4 levels qualitative variables were recoded using binary dummy variables to produce the appropriate level numbers.

We used all nests as presence data, together with double number of absence data randomly selected amongst habitat description data. Spatial autocorrelation estimated with the Moran’s I test in ArcGIS 9.3 showed highly clustered data. A generalized linear model with a logit link function and binomial error distribution generated in Statistica 10 revealed that residuals were also spatially autocorrelated. We consequently used a generalized linear mixed model, which takes into account spatial autocorrelation of dependant variable [Bolker et al. 2009]. The glmmPQL function of the R free software MASS package was used [Venables and Ripley 2002], including a random effect of the dependent variable with an exponential spatial correlation structure, according to Dormann et al. [2007]. Model building strategy followed the hierarchical backward elimination procedure for sequentially removing non-significant variables on the basis of Wald t test P-value (P) [Kleinbaum and Klein 2010]. Variable removal was stopped when all P-values were inferior to 0.20, in order to minimize the type II error risk (accepting false null hypothesis). We evaluated the discriminatory and predictive performances of each generated model by introducing their estimated values into ROC_AUC software to calculate the Area Under the ROC-Curve (AUC) [Schröder 2006]. Finally, estimated parameters of the most parsimonious model were used to compute the odds ratios (OR), which are measures of the association strength between the dependent and explicative variables [Kleinbaum and Klein 2010]. In our study, the probability of observing nest in inappropriate conditions has been considered close to zero, which allowed interpreting OR in terms of probability [Schmidt and Kohlmann 2008] (for analysis in epidemiological context). We calculated OR by comparing two levels of each explanatory variable, following Kleinbaum and Klein [2010]:

$$\mathrm{OR}_{\mathrm{a\ vs.\ b}} = exp \left[\sum_{i=1}^{k} (a_i - b_i)\, \beta_i \right]$$

for one or several variables of two or more-than-two levels (a_i compared to b_i level), of k effects and β_i coefficients. OR of continuous variables were calculated for discreet values: we empirically set a 25 m increment for altitude, compared to altitude 500 m which was the lowest nest observed. In the same manner we calculated OR by 5% increment of ground declivity under nest, in comparison to a null declivity.

IV.4. Results

IV.4.1. Sampling effort, vegetation structure and composition

Sampling effort per vegetation category and per survey itinerary is presented in Table 7. Mountain forest was the most represented formation with 42% of sampling effort; 2 thirds of habitat sampled were old-growth forest and 2 other thirds had a closed canopy. Understory of most crossed habitat contained woody species (92.6%), 2 thirds contained lianas, and 52.4% contained Marantaceae.

Table 7: Sampling effort per vegetation category and per itinerary

	Vegetation structure																
	Forest type			Forest disturbance			Canopy				Presence in understory						
Itinerary	LF	MF	GF	Old growth	Old 2ry	Young 2ry	Cl	P	L	O	S	L	M	Z	Chr	O	Total (km)
T Nuon	1.85	1.46	1.02	3.37	0.96	0	2.48	1.45	0.32	0.08	4.22	2.89	2.31	0.57	0.14	1.03	4.33
T Toua	0.74	2.5	1.08	2.95	0.86	0.51	2.29	1.35	0.31	0.37	3.46	1.97	2.8	0.92	0.1	1.6	4.32
T Goué	1.2	1.08	1.57	2.58	1.27	0	2.6	1.23	0.02	0	3.81	2.67	1.82	0.46	0	1.84	3.85
Loop Yiti	2.95	4.45	4.78	8.7	3.08	0.4	8.32	3.3	0.41	0.15	10.93	8.28	7.09	1.9	0.27	3.91	12.18
Loop Yan	3.73	4.96	3.54	8.31	3.34	0.58	8.43	2.67	0.81	0.32	9.8	5.71	7.40	3.16	0.32	4.05	12.23
Loop Sakona	2.4	3.52	1.94	5.44	2.37	0.05	5.72	2.02	0.09	0.03	7.54	5.58	4.42	0.97	0.06	3.39	7.86
H Recce	0	13.84	3.1	8.88	7.27	0.79	11.17	4.15	0.9	0.72	16.56	9.84	7.56	3.5	1.02	7.08	16.94
L Recce	12	1.15	3.35	12.52	3.6	0.38	12.35	3.46	0.47	0.22	16.1	13.1	7.58	0.97	0.04	7.75	16.50
Total (km)	24.87	32.96	20.38	52.75	22.75	2.71	53.36	19.63	3.33	1.89	72.42	50.04	40.98	12.45	1.95	30.65	78.21
Total (%)	31.8	42.1	26.1	67.4	29.1	3.5	68.2	25.1	4.3	2.4	92.6	64.0	52.4	15.9	2.5	39.2	

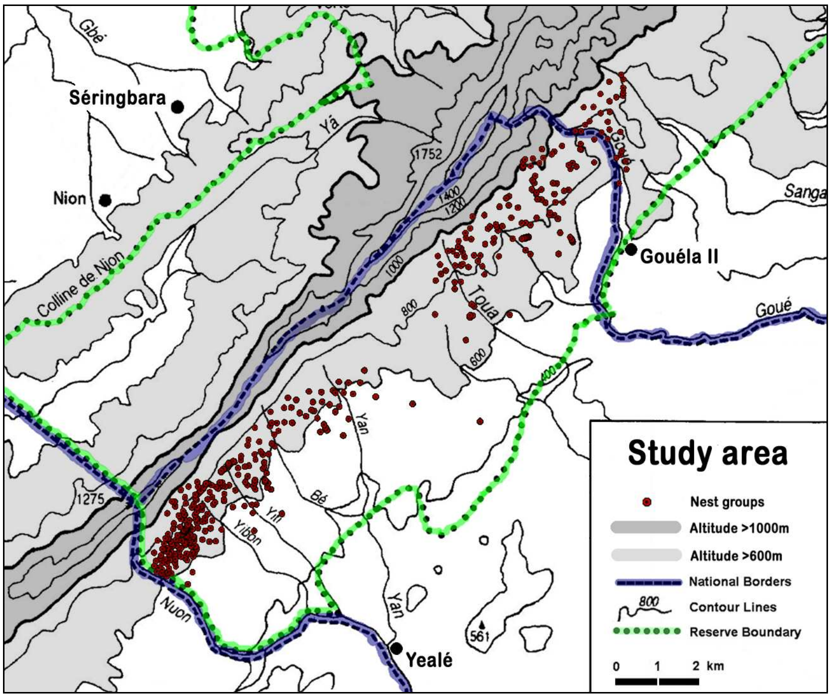
Vegetation structure: LF, lowland forest; MF, mountain forest; GF, gallery forest; Old growth, old-growth forest; Old 2ry, old secondary forest; Young 2ry, young secondary forest. Canopy was Cl, closed; P, partially closed; L, lightly closed or O, open. Presence in understory (non-exclusive) of S, sapling; L, liana; M, Marantaceae sp.; Z, Zingiberaceae sp.; Chr, Chromolenae odorata and/or O, open understory. Itinerary: T, transect; Loop, loop recce; H Recce, higher contour recce; L Recce, lower contour recce.

DBH of 8,463 trees measured along the 12.5 km of the 3 transects ranged between 10 and 625 cm (mean = 24.61 ± SD 26.81 cm; median = 16 cm). Amongst these, we identified 8,403 trees belonging to 368 species and 64 families, and classified 60 as “undetermined”. Sixty-eight additional species were identified on recces, bringing the total tree diversity to 437 species. Transects contained 84% (368/437) of the tree species identified in this study, and all levels of the 9 variables of vegetation structure.

IV.4.2. Nests

Overall N = 764 nests were observed in 338 groups constituted of 1 to 11 nests (mean group size = 2.23 ± SD 1.57 nests; 85% of groups constituted of 1 to 3 nests). Nests were mainly observed in the upper part of transects and loop recces, and in the higher contour recce (mean altitude = 757 ± SD 83.9 m; 50% of nests between 706 and 789 m), preferentially in steep locations (mean ground declivity = 15.54 ± SD 10.81%; 50% between 6.5 and 23.5%).

Fig. 31: Spatial distribution of nest groups



Nest groups were observed in the upper section of the study area. They were divided in two distinct clusters—a bigger one on the left (Yealé area, N=227 groups), and a smaller one on the right (Gouéla II area, N=111 groups).

Fig. 31 shows the distribution of nest groups spread out in 2 distinct clusters: a larger one in the Yealé area (N = 227 groups, 529 nests), separated by a gap west of Toua River from the Gouéla II area cluster (N = 111 groups, 235 nests).

Nests were constructed between 0 and 26 m above the ground, half of them between 5 and 10 m high in trees (mean = 8.02 ± SD 4.57 m). We observed 63 ground nests (8.2% of total) distributed in both clusters, including 17 particularly elaborated nests made of saplings – sometimes mixed with terrestrial herbaceous vegetation (THV) – which were recorded as night-nests. The 46 others, mainly composed of THV and often reduced to simple leaf-cushions [Matsuzawa and Yamakoshi 1996], were considered as day-nests (rest-nests) and discarded, bringing the total number of nests considered for analyses to N = 718 distributed in 322 groups.

IV.4.3. Density estimates

A total of N = 66 nests partitioned in n = 34 groups were observed on transects and used for density estimations with SCNC; for the MNC method we used N = 53 new nests grouped in n = 28 groups. The negative exponential curve was the model fitting the best our PD distributions. Results presented in Table 8 show values of density included between 0.14 (range: 0.04-0.53) and 0.65 (range: 0.32-1.33) chimpanzee/km^2.

Table 8: Chimpanzee density estimates

	Individual nests				**Group of nests**			
	D	CV	ESW	AIC	D	CV	ESW	AIC
SCNC	*0.19*	0.46	11.45	312.99	*0.14*	0.56	15.34	169.05
MNC	*0.65*	0.37	10.73	247.02	*0.46*	0.47	15.23	139.18

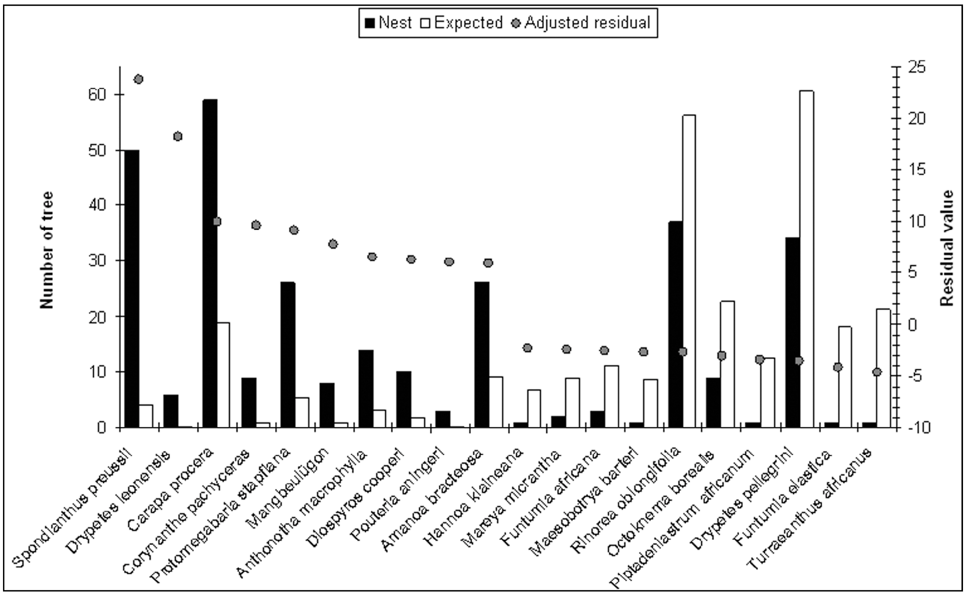
D: density of nest-building chimpanzees, CV: coefficient of variation, ESW: effective strip width and AIC: Akaike information criterion. Estimates were computed using the standing crop nest count (SCNC) and the marked nest count (MNC) methods with both individual nests and group of nests.

Based on lower AIC, the MNC method applied to nest group gave the most reliable estimate which is 0.46 chimpanzee/km^2 (range: 0.19-1.11). More generally, estimations based on nest group had a lower AIC than those based on individual nest, so did those obtained with the MNC in comparison to SCNC. Extrapolations of density estimates to the entire study area (60 km^2) gave a population of nest-building chimpanzees included between 8 and 39 individuals; the most reliable estimate being 28 individuals.

IV.4.4. Nesting-tree selection

One hundred fourteen vegetal species were used for nesting (108 woody, 3 Marantaceae and 3 Zingiberaceae), but 10 tree species accounted for 52% of the total N = 718 nests. Whereas 40% of nests (287/718) were made of vegetal species at least occasionally consumed by chimpanzees, 17% of nests (124/718) were recorded in tree species producing fruits eaten by chimpanzees, and just 0.7% (5/718) in food trees bearing ripe fruits.

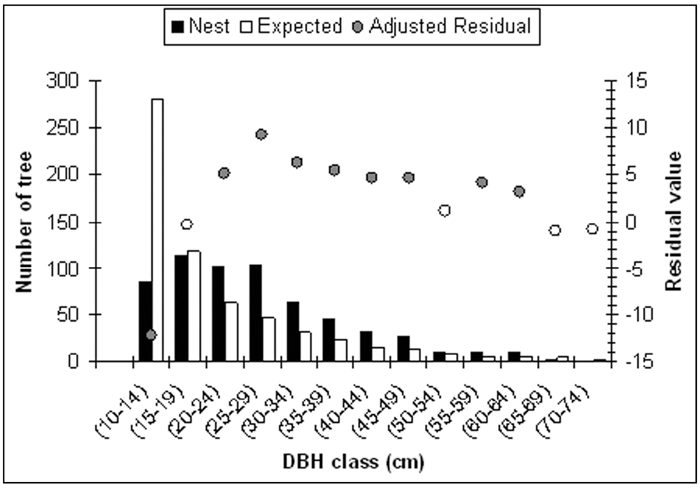
Fig. 32: Preferred and avoided nesting-tree species



The 10 most preferred (and avoided) nesting-tree species contained more (fewer) nests than expected from general availability, they have the highest (lowest) residual values. All absolute values are >2, indicating that they constitute the most relevant differences between observed and expected frequencies [Agresti 2002].

We used 635 nests recorded in 95 tree species (and N = 5,468 trees identified on transects as theoretical sample) to compute the expected sample, then truncated to 438 nests and 42 species for G-value calculation. Chimpanzees highly significantly selected their nesting-tree species independently of overall species availability (G = 577.49, df = 41, P < 0.00001). We identified 21 preferred nesting-tree species (residual value > 2) and 15 species significantly less used than expected (avoided species, residual value < -2). Fig. 32 plots the 10 most preferred species and the 10 most avoided sorted out per decreasing residual values. Three preferred nesting-tree species (*Carapa procera*, *Mangbeulügon*, *Anthonotha macrophylla*) and 5 avoided (*Funtumia elastica*, *Hannoa klaineana*, *Maesobotrya barteri*, *Piptadeniastrum africanum*, *Rinorea oblongifolia*) are components of chimpanzee diet, strengthening the idea that nesting-tree selection did not depend on the edible characteristics of species.

Fig. 33: Preferred and avoided nesting-tree DBH



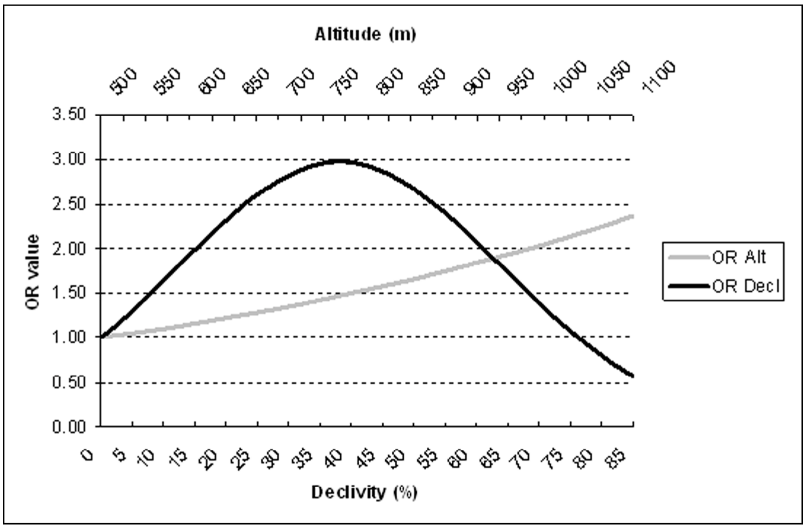
Grey dots indicate absolute values of residual >2 (signing lack of fit (P<0.05) between observed and expected frequencies), that is, the most preferred nesting-tree DBH(classes between 20– 49 and 55–64 cm) and most avoided DBH (10–14 cm). White dots indicate absolute values of residual <2, which designate the non significantly preferred and avoided nesting-tree DBH [Agresti 2002].

DBH of nesting-trees ranged between 1 and 235 cm (mean = 27.9 ± SD 24.01 cm; median = 23). The expected sample was computed for 13 classes of 5 cm DBH (range: 10-74 cm) with 642 nests and N = 8463 trees as theoretical sample. DBH distributions of nesting-trees and of overall trees differed in a highly significant manner (G = 366, df = 12, P < 0.00001), showing that tree DBH influenced chimpanzees' choice of nesting-tree regardless of the general availability. Trees of 10-14 cm DBH were rather avoided to build nests (Fig. 33), whereas trees of DBH included between 20 and 64 cm were preferred (except DBH 55-59 cm), with highest selectivity for the 25-29 cm class.

IV.4.5. Nesting-site selection

A total of N = 2210 nest data (718 presence, 1492 absence) were used to build up the logistic model of nest presence. The selected model contained 8 variables/effects with P < 0.05 (forest type, forest disturbance, altitude and altitude^2, ground declivity, presence/absence in the understory of woody species, of lianas and season alternation), and 1 variable with P < 0.2 (presence/absence of Zingiberaceae in the understory). Evaluation of this model's performance by means of the AUC indicated an acceptable capacity of discrimination (AUC = 0.746) [Hosmer and Lemeshow 2000].

Fig. 34: Variations of OR of continuous variables



Bell-shaped curve of altitude odds ratio (OR Alt) showing the maximum probability of nest presence at altitude 770 m. Ground declivity odds ratio (OR Decl) increasing in a curvilinear manner with steepness.

On the basis of OR value it appeared that forest type was the variable having the strongest influence on nesting-site choice (Table 9): chimpanzees overwhelmingly nested more in gallery forest (OR = 6.83) and montane forest (OR = 6.73) in comparison to lowland forest. Altitude was the second most influent factor. Nest presence likelihood varied as a function of altitude in a bell-shaped curve, with a maximum at 770 m and an OR approaching 3 (Fig. 34). Over altitude 1050 m, the probability of observing nests fell below initial level (OR < 1). Fig. 34 also shows the curvilinear positive influence of ground declivity on nest presence. The steeper was the ground, the greater was the probability of observing nests, with maximum OR value of 1.99 for the steepest slope encountered (85%). Probability of finding nest was higher in old-growth forest than in young secondary (OR = 1.36) and old secondary forests (OR = 1.24, Table 9). Old secondary forest was slightly preferred compared to young secondary forest (OR = 1.1).

Table 9: OR of categorical variables

		Forest type		
		MF	*GF*	*LF*
	MF		1.01	0.15
compared to	*GF*	0.99		0.15
	LF	6.73	6.83	
		Forest disturbance		
		Old growth	*Old 2ry*	*Yg 2ry*
	Old growth		0.81	0.74
compared to	*Old 2ry*	1.24		0.91
	Yg 2ry	1.36	1.10	
		Understory		
	Presence of	*Sapling*	*Liana*	*Zingib.*
compared to	*Absence*	1.28	0.93	1.06
		Season		
			Dry	
compared to	*Rainy*		1.28	

Comparison between **forest type** levels (*MF*: mountain forest, *GF*: gallery forest, *LF*: lowland forest); Comparison between **forest disturbance** levels (*Old growth*: old-growth forest, *Old 2ry*: old secondary forest, *Yg 2ry*: young secondary forest); Comparison between **understory** containing *sapling*, *liana* and/or *Zingib.*: Zingiberaceae species, and understory from which they are absent; Comparison between *dry* **season** and *rainy* season.

Two components of forest understory (out of 6) significantly explained the observed nest distribution (Table 9). Presence of lianas rather prevented chimpanzees from nesting (OR = 0.93), whereas understory containing saplings constituted a preferred nesting-habitat (OR = 1.28). Finally, comparing expected values of dry season to rainy season gave an OR = 1.28: chimpanzees nested more frequently in the study area during the dry than during the rainy season.

IV.5. Discussion

During a survey conducted around the Nuon River in the Yealé area of Nimba, Matsuzawa and Yamakoshi [1996] recorded 35.4% of ground nests (164/464), all above 800 m altitude. They distinguished 2 categories: some ground nests exclusively made of saplings, and others mainly composed of THV with a cushion-like appearance. In this study we recorded 8.2% of terrestrial nests (63/764), including 62% (39/63) exclusively composed of THV. Koops et al. [2012] reported 9.5% of ground nests (144/1520) from the Seringbara region of Nimba with only 13.8% (15/108) exclusively made of THV. The low predation pressure reported in Nimba is a necessary condition to have such a relatively high proportion of terrestrial nests, but it is insufficient to explain what motivate chimpanzees to nest on the ground. Further studies are needed to sort out and describe influences of the intermingled ecological and socio-cultural factors shaping this behavior [Matsuzawa and Yamakoshi 1996, Koops et al. 2012]. On average, nests were built slightly lower in the Ivorian Nimba (mean height = 8.02 ± SD 4.57 m) than in Seringbara (mean height = 11.3 ± SD 6.3 m), but both values are in the range of those reported from most research sites. However, mean size of nest groups was relatively low in our study area (2.23 ± SD 1.57 nests/group) compared to Seringbara (3.7 ± SD 3.96 nests/group) [Koops et al. 2012], Kalinzu Forest Reserve in Uganda (mean = 3.68 nests/group) [Furuichi and al. 2001], or Kahuzi-Biega National Park in Democratic Republic of Congo (4.31 nests/group) [Basabose and Yamagiwa 2002]. In a study of 3 habituated communities of the Taï forest (200 km south from Nimba), Kouakou et al. [2009] showed that chimpanzees tend to travel in smaller parties in peripheral parts of their home range in comparison to core areas. The small size of nest groups suggests that our study area constitutes the peripheral part of a community territory.

IV.5.1. Density estimates

Despite the small sample of nests recorded from transects, our density estimates are noteworthy in that they fill the knowledge gap on this priority area for the conservation of *Pan troglodytes verus* [Kormos et al 2003]. Two former studies published estimates of chimpanzee abundance in Nimba based on the SCNC method. Marchesi et al. [1995] have sampled 2 sites located at both edges of our study area, and extrapolated their data to the forested surface of the entire Ivorian Nimba; they reported a density of 1.31 chimpanzees/km^2 (for 59 weaned individuals). Hoppe-Dominik [1991] estimated a density of 0.5 chimp/km^2 (50 individuals) in a zone restricted to the Libero-Ivorian border. The limited sampling effort (in time and space) of these surveys combined to the seasonal variation of chimpanzee presence could explain the high values reported in comparison to ours based on the SCNC method (0.14-0.19 chimp/km^2, 8-11 individuals). Nevertheless with the MNC method, we obtained densities close to Hoppe-Dominik's result (0.46-0.65 chimp/km^2, corresponding to a smaller population of 28-39 individuals partly because our study area was larger). Based on SCNC and MNC methods from 3 known communities of the Taï forest, Kouakou et al. [2009] estimated densities of 2.19 chimps/km^2 in core area of territories, and 0.15 chimp/km^2 in peripheral area. Our estimates are comparable to density value of peripheral area of chimpanzee territory, suggesting that our study area is a peripheral part. In this respect, our results need to be refined with broader scale censuses before being extrapolated to the entire Nimba.

IV.5.2. Nesting-tree selection

In many research sites, chimpanzees appear to select nesting-tree species independently of their availability. In Kalinzu, this selectivity was characterized by the fact that chimpanzees constructed nests in 43 of 111 tree species [Furuichi and Hashimoto 2004], including 14 species harboring over 90% of nests. Stanford and O'Maley [2008] found that chimpanzees of the Bwindi Impenetrable forest (Uganda) were using 38 tree species out of 163 available to build nests, with 72.1% of nests built in just 4 tree species. In Kahuzi-Biega, nests were observed in just 28 tree species, with 90% of them made in 17 tree species, all bearing fruits eaten by chimpanzees [Basabose and Yamagiwa 2002]. Koops et al. [2012] reported that chimpanzees of Seringbara Nimba were using 115 of 216 available tree species for nesting, with 56% of nests in 10 tree species. In the Ivorian Nimba, chimpanzees used 108 tree species out of 437 described (52% of nests in 10 tree species). Both studies on Nimba chimpanzees report the use of 10 tree species to build slightly more than half of nests, and evoke that nesting-tree selectivity is independent of species and fruit availability. They also suggest that the relatively high tree diversity of Nimba favors the use of a larger panel of species than in other sites. Despite important variation in DBH of nesting-trees, chimpanzees in this study showed highest selectivity for trees of 25-29 cm DBH. The low predation pressure may enable them to nest at low height (mean nest height = 8.02 m) in sufficiently sturdy and stable medium-sized trees, while reducing thermoregulation constraints and climbing efforts [Stanford and O'Malley 2008, Stewart and Pruetz 2013].

IV.5.3. Nesting-site selection

In the Ivorian Nimba chimpanzees markedly nested more in gallery and mountain forests than in lowland forest. They also favored old-growth forest compared to old secondary forest, and avoided young secondary forest. In Seringbara Nimba and Kahuzi-Biega alike, chimpanzees preferred nesting in primary forest compared to secondary forest [Basabose and Yamagiwa 2002, Koops et al. 2012]. We found that altitude strongly influenced nesting-site selection as well, with a maximum probability of observing nests at 770 m altitude. Koops et al. [2012] reported that chimpanzees in Seringbara preferred nesting above 1000 m and avoided nesting below 800 m (range: 681-1169 m). Despite the discrepancy in altitude values, both these results show preference for nesting in altitude habitats, as those reported from the Nuon River area of Nimba by Matsuzawa and Yamakoshi [1996]. The altitude discrepancy may result from the higher elevation of the mountain in Seringbara compared to Yealé, and higher forest edge. The fact that chimpanzees nested more frequently in the study area during the dry season implies greater habitat-use, which may be explained in part by seasonal variation in food resource availability. As Doran [1997] showed, ranging patterns of chimpanzees in the Taï forest varied seasonally in relation to food availability. Chimpanzees adapted to the fruit scarcity of the dry season by spending more time feeding, reducing their day range and party size, and spending more time solitarily than during the rainy season.

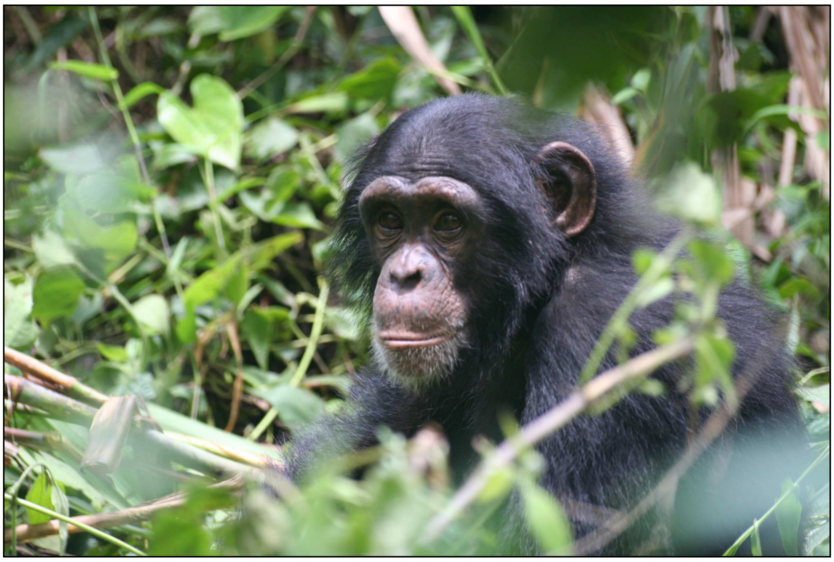
IV.5.4. General views on chimpanzee populations

Small size of nest groups (mean = 2.23 nests), seasonality detected in nest presence, and low chimpanzee density estimates (D = 0.46 indiv/km^2), constitute converging arguments for peripheral area of chimpanzee territory. Furthermore, the gap in nest presence between Yealé and Gouéla II areas (Fig. 31) suggests a zone chimpanzees avoid. We hypothesize that our study area is actually located at the junction of 2 distinct chimpanzee communities. These preliminary findings do not support Matsuzawa and Yamakoshi [1996] conclusions, that 3 chimpanzee communities populate the Ivorian section of Nimba. However, our results bring new evidence to support their idea of one community's core area located behind the Nuon River (in Liberia). They also suggest that most of the Yealé area constitutes the peripheral zone of this territory. The Gouéla II area would then be part of the peripheral zone of another community whose core area would be located in the upper Mien and Guégué Rivers (upright corner in Fig. 31) where we observed large nest groups at each visit during preliminary surveys.

IV.5.5. Conservation perspectives

If these findings are verified, Nimba chimpanzee populations, which have proven to be particularly well adapted to their specific habitat, would be less abundant than previously estimated. This would have major conservation implications, since even if chimpanzees are not hunted in Nimba, their survival is critically jeopardized by habitat loss and fragmentation under increasing pressures from local population livelihood (slash and burn agriculture, uncontrolled use of fire, non-sustainable use of resources), and iron ore mining in the Liberian and Guinean sections. More joint efforts between research and conservation are needed to mitigate and find alternatives to this complex multi-layered issue. Applied studies aiming to achieve a tri-national cohesive view on Nimba chimpanzees' status are an essential preliminary step in the elaboration and implementation of an efficient site-specific conservation policy.

CHAPTER IV. Importance of secondary vegetation in feeding strategy and habitat selection of Nimba chimpanzees (Côte d'Ivoire and Guinea): implications for conservation



Photograph by T Humle

This chapter proposes detailed analyses of the influences of monthly food availability, habitat structure, altitude and occurrence of signs of other primates including humans and artiodactyls, on chimpanzee presence in the Ivorian Nimba. It has been submitted in August 2014 for publication in the periodic journal "Biodiversity and Conservation", by Granier N, Huynen MC, Matsuzawa T, and Hambuckers A. We investigated in details the feeding strategy of chimpanzees and identified some of their preferred and fallback resources. We also qualified their habitat selection in relation to their different activities/behaviors. An ecological research on the primate population of the Nimba Mountain implemented with conservation views on this taxon is presented as an efficient strategy to sustainably preserve the whole Nimba forested ecosystems.

V.1. Abstract

The Nimba Mountain (West Africa) is remarkable for its sharp relief sheltering an outstandingly diverse wildlife. Assessing the ecological requirements of its rich primate population containing umbrella and flagship species is approached as an efficient strategy to ensure the sustainability of all Nimba ecosystems. With this objective, we investigated the feeding strategy and habitat selection of chimpanzees. We modeled their signs of presence as function of monthly fruit abundance and Marantaceae/Zingiberaceae availability using logistic regression. We used Poisson regression to model the annually cumulated signs as function of habitat structure and presence of other mammals/humans. During the rainy months (May-Nov), the overall number of fruiting plants was low but fruit food was periodically abundant, and chimpanzee presence was linked to Zingiberaceae and seasonal fleshy fruits. During the dry season (Jan-Apr), the overall number of fruiting plant species peaked but fruit food was scarce: chimpanzees were drawn to Zingiberaceae, Marantaceae and lowly seasonal fruits of 11 tree/shrub species. Our findings suggest that two of these species, together with Marantaceae, constitute filler fallback resources with wide spatiotemporal distribution, which attracted chimpanzees only during fruit food scarcity. Zingiberaceae however constitute staple fallback foods: eaten every month, they attracted apes across seasons. Chimpanzees were more active in the study area during the dry season, and exhibited a year-round preference for altitude habitats (mountain and gallery forests of old secondary type), particularly when feeding. They avoided habitats exploited by artiodactyls and humans, and obviously selected the same habitats as the 7 other primate species described.

V.2. Introduction

Chimpanzee populations have dramatically declined (> 66%) over the past 30 years, due to a combination of habitat loss, bushmeat hunting, pet trade and disease epidemics (Butynski

2003). The chimpanzee is human's closest living evolutionary relative, a seed disperser playing a key role in forest ecology and renewal, recognized as a good flagship, umbrella and environmental indicator species (Junker et al 2012). Understanding the specific requirements of each chimpanzee community in terms of diet, habitat and nesting is a crucial step in implementing purpose-built conservation actions of this ape, and thereby favoring the sustainability of Afrotropical ecosystems (Lambert 2010). Unlike most primate societies, organized in relatively stable and cohesive groups, chimpanzees live in communities characterized by a fluid system of fission-fusion within a common home range (Sugiyama 1973). Individuals may travel either alone or in loosely structured subgroups that vary greatly in size, composition and persistence over time (Goodall 1986). In such social organization, the grouping and ranging behaviors of an adult chimpanzee more likely reflect its personal decisions rather than a group compromise (Bates and Byrne 2009). Previous studies have identified a synergy of ecological and social factors influencing this decision-making: quantity and quality of food resources (White and Wrangham 1988; Doran 1997), predation pressure (Boesch 1991), community size and composition (Goodall 1986; Lehmann and Boesch 2004), intra-group aggression patterns (Doran 1997), territorial defense (Bates and Byrne 2009) and cooperative behaviors (Sakura 1994; McGrew 2004). Evidence from several chimpanzee research sites showed that food availability influences subgroup size, feeding time and habitat-use pattern, and suggested that fission-fusion grouping may reduce feeding competition within the community (Sakura 1994; Hashimoto et al 2003; Lehmann and Boesch 2004). Although omnivorous, chimpanzees depend on ripe fruits as preferred food (Hladik 1977). Fruits are of high nutritional value and easy to process, but in most ecosystems their availability greatly fluctuates across seasons and from year to year (Tutin et al. 1997). To cope with periods of fruit scarcity, chimpanzees have developed various socio-ecological strategies consisting of reducing energy expenditure, splitting into smaller subgroups and traveling further in the community territory to exploit more productive areas, or shifting the diet to lower quality but more abundant fallback foods such as leaves, stems, piths and terrestrial herbaceous vegetation (THV) (Wrangham et al. 1991; Doran 1997; Chancelor et al. 2012). Marshall and Wrangham (2007) define fallback foods as resources whose use negatively correlates with the availability of preferred food, a preferred food being a resource chosen more often than expected given its spatio-temporal abundance in a habitat. Fallback foods are higher in fiber, lower in energy and harder to process than ripe fleshy fruits, but more uniformly distributed in the habitat and available year-round (Yamakoshi 1998). The type of fallback resources and their use vary across chimpanzee communities: a fallback food at one site can be a preferred food at another (Harrison and Marshall 2011).

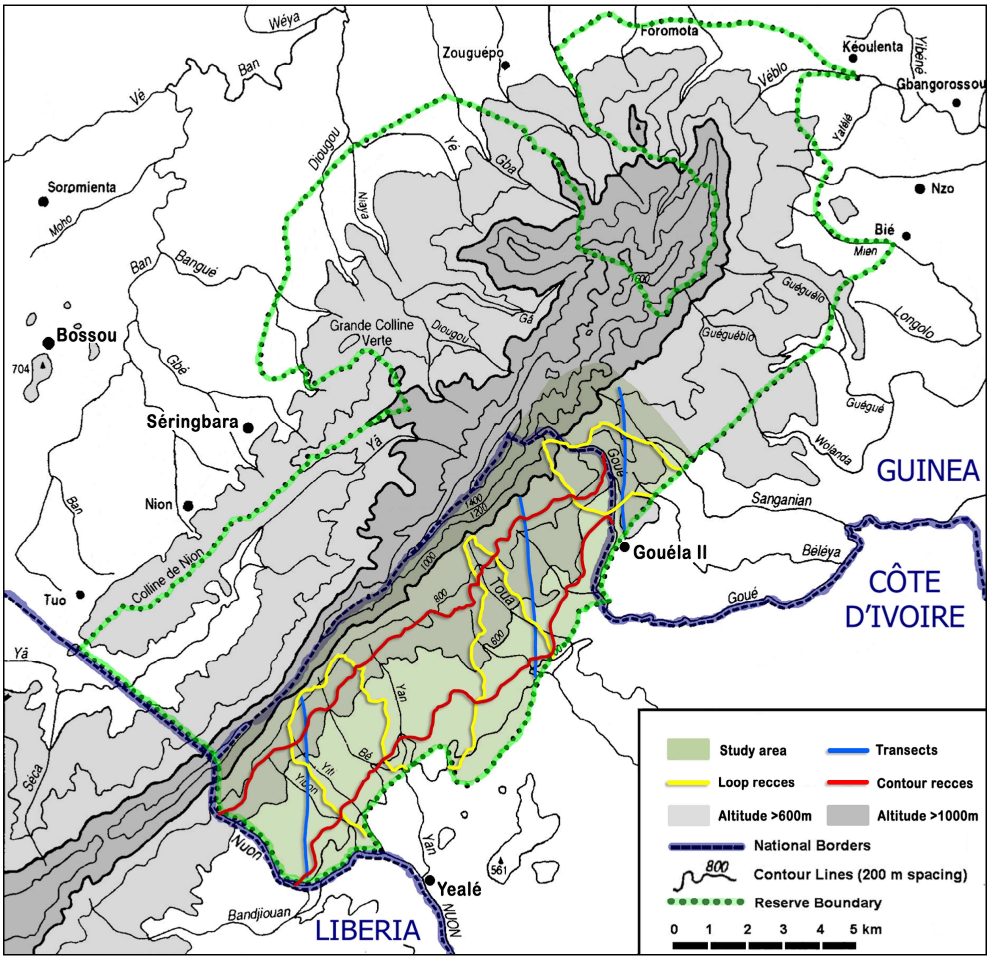
Located in the biodiversity hotspot of the Guinean Forests of West Africa (Myers et al. 2000), the full reserve of the Nimba Mountain exhibits a particularly rich and diverse wildlife with a high level of endemism, which is particularly marked in altitude habitats (Lamotte 1942; Schnell 1951). We aimed at shedding light on the feeding strategy and habitat selection of Nimba chimpanzees in relation to the seasonal distribution of vegetal foods, vegetation structure and faunal/human presence. We expected the overall recruitment of fruiting plants in the Nimba forest to be highly seasonal (Yamakoshi 1998). Since chimpanzees tend to dwell more often in the altitude part of the massif, particularly in secondary habitats found in mountain forest’s range, we raised the hypothesis that secondary vegetation would continuously supply them with fallback foods (THV and lowly seasonal fruits). On the assumption that foraging behavior basically aims at finding preferred foods, which we hypothesized to be fleshy fruits in Nimba, we expected chimpanzees to select secondary habitats more often during periods of general fruit scarcity. We assumed that the unhabituated chimpanzees of Nimba would avoid humans, and we investigated their behavior toward other mammal species for conservation purposes (Lambert 2010). We monitored 80 km of survey itineraries every month over a 12-month period, and tested the above hypotheses by analyzing our dataset in 2 ways. We used logistic regression to model the monthly presence of chimpanzee in relation to fruit abundance and THV availability, and Poisson regression to investigate the annually cumulated presence of chimpanzee signs as function of habitat structure and faunal/human presence. Lastly, we discussed our findings in light of other studies, and integrated them into conservation prospects.

V.3. Methods

V.3.1. Study site

The Nimba Mountain forms a 40 km-long relief culminating at 1,752 m, and stretching between Guinea, Côte d'Ivoire and Liberia (Fig. 35). At the crossroads of 3 West African climatic influences, the massif is subject to a 7-month rainy season (May-November) and a 5-month dry season (December-April) (Schnell 1951). Altitude grasslands cover the top of its northeastern half from 800-1,000 m high, tightly intertwined with various formations of evergreen rainforest on slopes and foothills. Towards the southwestern part of the mountain, the crest progressively descends to 1,000 m altitude and forest rises over the top to cover the entire massif from the Yan River. Since ancient times, bushfires lit in altitude grasslands each dry season repeatedly enter the mountain forest, progressively pushing its limit back. The expanding edge of mountain forest consists of secondary vegetation habitat characterized by low tree diversity/density, unclosed canopy, and colonized by pioneer species and THV, mainly herbs of the Marantaceae and Zingiberaceae families (Schnell 1951; Brugière et al. 2003). Southwesterly of the Yan River, where altitude grasslands are absent, patches of secondary habitat appear to be randomly distributed across the slope; they are marks of previous human settlement and cultivation, or sometimes result from windthrow or the cutting of emergent trees.

Fig. 35: Study area and survey itineraries in the Nimba Mountain



The present study focused on the southern slope of Nimba, including the entire Ivorian Nimba (50 km^2), and extended beyond the Guinean border (10 km^2); its southwestern part was named 'Yealé area' and northeastern part 'Gouéla II area' (Fig. 35). The research fit into a decennial agreement concluded between the Guinean authority and Kyoto University, and respected laws for conducting research on endangered species in an integrally protected area.

V.3.2. Data collection

V.3.2.1.Survey itineraries

We used 3 types of survey itineraries to monitor the study area (Fig. 35). (1) Three parallel line transects drawn from where the 3 main rivers outflow from the reserve following the north azimuth, up to altitude grasslands, or as high as topography allowed (mean length = 4.15 ± SD 0.27 km). (2) Two contour recces stretching between the Liberian and Guinean borders following the contour lines 750 and 450 (mean length = 17 ± SD 0.71 km). (3) Three loop recces starting where the 3 main secondary rivers outflow from the reserve, extending up to the altitude grassland edge and heading back down in a large “u-turn” (mean length = 10.90 ± SD 2.27 km). We present here the data collected between May 2010 and April 2011, period during which we surveyed all itineraries (total length = 78.21 km) every month (except December, 11 visits) following a fixed sequence of 14 days (walking speed $\leq$ 1 km/h, progression rate = 5.7 km/day).

V.3.2.2. Vegetation structure, fruit phenology, faunal and human signs of presence

We described vegetation structure along all survey itineraries according to 9 variables characterizing the different strata: forest type (lowland, mountain or gallery forest), forest disturbance (old-growth, old secondary and young secondary forest), canopy closing (4 classes by 25% increment), plus 6 dichotomous non-exclusive variables describing understory: open understory and/or understory containing saplings, lianas, Marantaceae, Zingiberaceae and/or *Chromolaena* species. While opening survey itineraries, we made continual records of the levels of these 9 variables, and of the distances they covered (Granier et al. 2014). During the 11 ensuing walks, we identified all plants that dropped their fruits on a 10 m-wide strip centered on our paths, and monitored their fruit phenology by assigning them a fruiting score on a scale of 1 to 5 (1: fruits start forming in tree - 5: all fruits on the ground). We systematically noted the presence of Marantaceae (*Hypselodelphys* sp., *Marantochloa* sp., *Megaphrynium macrostachyum*, *Sarcophrynium* sp., *Thaumatococcus daniellii*) and Zingiberaceae (*Aframomum* sp.), of which fruit, shoot, stem or pith are known to be eaten by chimpanzees (Sugiyama and Koman 1992; personal observations). On transects, we additionally measured the diameter at breast height (DBH) of all fruiting plants > 10 cm DBH. On all survey itineraries we systematically recorded and georeferenced all evidence of chimpanzee presence: trails or routes, footprints, feces, feeding remains, ant-dipping sites, wadges, leaf-cushions, hairs, resting/playing sites with ground tracks and flattened/broken vegetation, and direct observations. Each of these 10 different types of chimpanzee signs was assigned to one of the 4 following categories: feeding, moving, resting or feces. We also thoroughly recorded and georeferenced all signs of primate and artiodactyl presence, and identified the corresponding species, as well as evidence of human activity (hunting, fishing, exploiting vegetal products, traveling/camping).

V.3.3. Data analysis

V.3.3.1. Fruit abundance

We selected 45 species of tree, shrub and liana grouped in 38 genera, among the 128 plants producing fruits eaten by the neighboring Bossou chimpanzees (Sugiyama and Koman 1992). These 45 plants, called principal species, were concurrently the most recorded on all itineraries as feeding signs or through the macroscopic analysis of feces, and the most represented along the 3 transects (Table 10).

Table 10: Characterization and fruiting pattern of the 45 principal species

Principal species	**Plant type**	**BA**	**Fruiting**		
			AFAI	**Month**	**Season**
Alchornea cordifolia	Shrub	0.03	0.15	4	High
Alstonia boonei	LTree	13.78	4.22	2	High
Antiaris toxicaria	LTree	3.36	4.63	4	High
Blighia welwitschii	LTree	9.93	4.68	4	High
Canarium schweinfurthii	LTree	0.52	0.97	3	High
Chrysophyllum giganteum	LTree	17.22	51.79	5	High
C. perpulchrum	LTree	8.07	31.15	5	
Cola caricaefolia	STree	0.05	0.19	3	High
Coula edulis	LTree	2.17	11.26	4	High
Dacryodes klaineana	Tree	1.59	0.64	2	High
Diospyros mannii	Tree	1.19	0.71	3	High

Principal species	**Plant type**	**BA**	**Fruiting**		
			AFAI	**Month**	**Season**
Drypetes pellegrini	Tree	8.9	4.42	5	High
Elaeis guineensis	LTree	2.30	2.28	7	Low
Ficus eriobotryoides	Tree	0.42	3.37	6	Low
F. mucuso	LTree	1.86	1.58	4	
F. sur	STree	1.02	1.98	8	
F. thonningii	Liana	1.34	0.19	2	
Garcinia kola	Tree	1.49	2.20	5	High
Grewia barombiensis	Shrub	0.15	0.47	4	High
Hannoa klaineana	LTree	4.24	0.87	2	High
Irvingia gabonensis	LTree	2.63	28.01	3	High
Landolphia dulcis	Liana	0.25	0.57	3	High
L. hirsuta	Liana	0.08	0.43	4	
L. incerta	Liana	0.19	0.52	2	
L. owariensis	Liana	0.14	1.84	5	
Mammea africana	LTree	2.45	10.64	4	High
Microdesmis keayana	STree	1.29	3.27	6	Low
Milicia excelsa	LTree	6.82	4.45	3	High
Musanga cecropioides	Tree	3.88	4.04	8	Low
Napoleonaea vogelii	Tree	0.48	0.60	2	High
Nauclea diderrichii	LTree	5.48	100.20	5	High
Octoknema borealis	Tree	10.73	18.85	4	High
Ongokea gore	LTree	2.10	1.72	3	High
Panda oleosa	Tree	0.15	0.41	2	High
Parinari excelsa	LTree	22.96	66.73	4	High
Parkia bicolor	LTree	34.02	94.82	4	High
Pouteria altissima	LTree	8.95	10.99	3	High
Pycnanthus angolensis	LTree	8.51	6.43	3	High
Rinorea oblongifolia	STree	6.08	4.98	7	Low
Solanum torvum	Shrub	1.27	2.90	9	Low
Synsepalum afzelii	Tree	4.12	9.86	4	High
Tabernaemontana africana	STree	0.43	0.55	7	Low
Trema guineensis	STree	0.46	1.66	8	Low
Trichilia heudelotii	STree	1.52	0.92	3	High
Uapaca guineensis	Tree	6.47	0.69	1	High

Plant was Shrub, LTree: large tree, STree: small tree, Tree: medium-sized tree, or Liana; BA: Total basal area (m^2); AFAI: Annual Fruit Abundance Index; Month: number of month fruiting; Season: Seasonality was high for seasonal species (< 6 months fruiting), and Low for the lowly seasonal (> 6 months fruiting).

We divided transects into 64 sections of 200 m following Furuichi et al. (2001) and calculated for each month *m* of the study, the fruit abundance index of each principal species *k* in each section *s* (FAI) (Albert et al. 2013):

$$\mathrm{FAI}_{ksm} = D_{ks}\, B_{ks}\, P_{km}$$

with D_{ks} the density and B_{ks} the basal area [π (1/2DBH)^2] of species k in section s, and P_{km} the mean fruiting score of species k in month m. Summing the FAI of all species in a given 200 m-section gave the monthly fruit abundance index per section (SFAI):

$$\mathrm{SFAI}_{sm} = \sum_{k=1}^{n} \mathrm{FAI}_{ksm}$$

We distinguished the highly seasonal species (mainly large trees producing fleshy fruits once a year and for less than 6 months), from the lowly seasonal species (fruiting several times a year and for more than 6 months; Table 10). We computed SFAI_{sm} using total fruiting species, "$\mathrm{SFAI}_{\mathrm{sm}}$ seasonal" using the highly seasonal species and "$\mathrm{SFAI}_{\mathrm{sm}}$ low-seasonal" using lowly seasonal species. Due to data over-dispersion, FAI_{ksm} and both SFAI_{sm} were transformed in discrete variables by creating classes of 0.1 increments numbered by a continuous sequence of integer values starting from 0, and replacing class values by their numbers. We investigated the seasonality of fruit availability and abundance with the Mann-Whitney U-test (rank test), by testing whether the monthly numbers of fruiting plants during the dry and rainy seasons were drawn from identical distributions. The alternative hypothesis was that fruiting plant numbers were higher during the dry season (one-sided test).

V.3.3.2. Influence of fruit abundance and THV availability on chimpanzee presence

We used logistic regression to investigate influence of the monthly fluctuations of fruit abundance and Marantaceae/Zingiberaceae availability on chimpanzee presence. Moran's I test performed in R free software using the ape package (Paradis et al. 2004) revealed that presence data (sightings of chimpanzee sign per transect section) were spatially autocorrelated. To take into account this autocorrelation of the dependant variable, we utilized a generalized linear mixed model (Bolker et al. 2008). We used the glmmPQL function of R MASS package (Venables and Ripley 2002), including a random effect of the dependent variable with an exponential spatial correlation structure, according to Dormann et al. (2007). For each month, we systematically tested two models of chimpanzee presence. The first one tested the effects of the FAI_{ksm} of the 5 principal species that produced more fruits, plus the presence/absence of Marantaceae and Zingiberaceae. The second model tested the effects of $SFAI_{sm}$ seasonal and $SFAI_{sm}$ low-seasonal, plus Marantaceae and Zingiberaceae. Model building strategy followed the hierarchical backward elimination procedure for sequentially removing non-significant variables based on Wald t test p-value, and variable removal was stopped when all p-values were < 0.20, in order to include a low type-II error (Kleinbaum and Klein 2010). We performed F-test for goodness-of-fit to evaluate the overall fit of each model (Dougherty 2011), by comparing the residuals' variance of a constrained model (all parameters, but the intercept and the random effect, set to 0) to the unconstrained model. More formally, we tested the null hypothesis that all model parameters were equal to zero against the alternative that at least one was not, using the following statistic:

$$F_{(j-2,\, n-j)} = ((SSR_c - SSR_u) / SSR_u) * ((n-j) / (j-2))$$

with SSR_c and SSR_u the sum of squared residuals of the constrained and unconstrained models, n the sample size, and j the total number of coefficients of the tested model (intercept, random effect plus explanatory variables) (Bolker et al. 2008). $F_{(j-2,\, n-j)}$ asymptotically follows a Fisher distribution with $j-2$ and $n-j$ degrees of freedom, which were used to compute the corresponding p-values with a 10% confidence interval to reject the null hypothesis. We also evaluated the discriminatory and predictive performances of the generated models using pROC package in R, which calculates the Area Under the ROC-Curve (AUC) (Robin et al. 2011). Finally, we used the selected models to compute the odds ratios (OR), which measure the association strength between dependent and explicative variables (Kleinbaum and Klein 2010). We calculated OR by comparing two levels of each explanatory variable:

$$OR_{\text{a vs. b}} = exp \left[\sum_{i=1}^{k} (a_i - b_i)\, \beta_i \right]$$

for variable of two or more-than-two levels (a_i compared to b_i level), of k effects and β_i coefficients. OR > 1 (< 1) indicates greater odds of observing chimpanzee signs in level b_i (a_i); and OR = 1 points to an equally likely chimpanzee presence in the 2 levels.

We used the same statistic tool to search for potential confounding factors linking fruit abundance and THV availability, and statute on the models' validity. For this purpose, we considered $SFAI_{sm}$, Marantaceae and Zingiberaceae as dependent variables, assuming they followed negative binomial distribution. We consecutively modeled them as function of the 9 habitat structure variables, after recoding categorical variables of more-than-two levels using binary dummy variables to produce the appropriate level numbers. We then followed the procedure described above to successively build these 3 models for each month, and evaluate their performances. In the building process, we maintained in the model all dummy variables coding for a given explicative variable, as long as at least one of them presented a p-value < 0.20 (Kleinbaum and Klein 2010).

V.3.3.3. Influence of habitat, fauna and human and chimpanzee signs counts

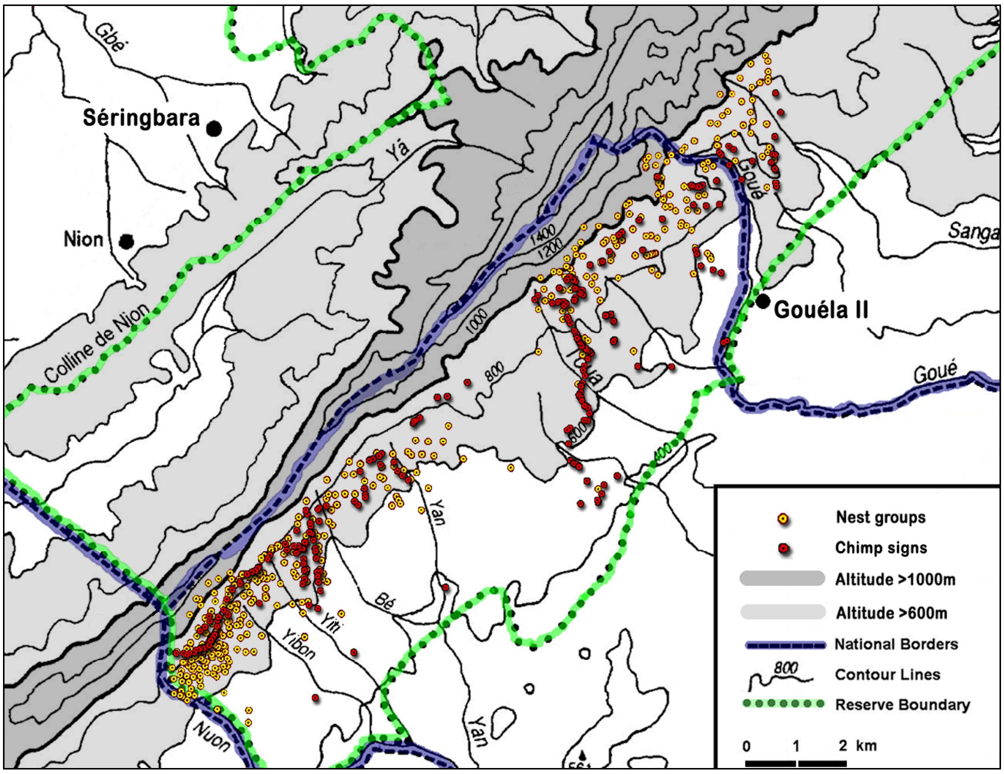
We divided all survey itineraries into 787 sections of 100 m, and modeled chimpanzee presence as function of the 9 variables of vegetation structure, altitude, plus signs of human, primate and artiodactyl presence. Observations of chimpanzee signs cumulated for each section over the 11 passages constituted the count data. To take into account visible overdispersion, we build models using a quasi-Poisson distribution (Zeileis et al. 2008). After positively testing spatial autocorrelation with Moran's I test, we used the same procedure described above (Dormann et al 2007), with the 3 and 4 levels explicative variables recoded in binary dummy variables. We used altitude values recorded in the middle of each 100 m-section with linear and quadratic effects, and the most represented level of qualitative variables in each section. To investigate influence of chimpanzee activity on habitat selection, we successively modeled in the same way the feeding-related, traveling-related, resting-related signs and the feces. We used the obtained models' coefficients to compute OR like in logistic regression. However in Poisson models, OR is also called occurrence rate of and corresponds to a multiplicative effect of the expected counts, when all other explicative variables are kept constant.

V.4. Results

V.4.1. Chimpanzees

We observed N = 455 chimpanzee signs during the 11 passages on all survey itineraries, including 166 feeding-related, 194 moving, 62 resting and 33 feces. THV feeding remains (n = 85) represented 51% of feeding-related observations: feeding remains of Zingiberaceae fruits and piths were seen every month (n = 56), and Marantaceae stems and piths were not seen in February, April, May (n = 29). We observed most signs in altitude parts of the study area (mean altitude = 771 ± SD 84 m), 100 m higher than the mean altitude of survey itineraries (675 ± SD 146 m). We recorded N = 222 chimpanzee signs during the late dry season (January to April; mean = 56 signs / month), and N = 233 during the 7-month rainy season (mean = 33 signs / month), that is, 59% more observations per month during the dry season. Even considering that signs of presence may fade away quicker during the rainy months, this large inter-seasonal difference in observation numbers suggests that chimpanzees were more active in the study area during the dry months. The cumulated distributions of chimpanzee signs and nest groups (Granier et al. 2014) show that observations occurred mainly above 600 m altitude (Fig. 36). They were spread out in 2 distinct clusters separated by a gap west of the Toua River, which constituted an important feeding site. The Yealé cluster contained N = 430 densely distributed observations, and the Gouéla II cluster N = 363 sparsely distributed observations, more widely distributed across the altitudinal gradient.

Fig. 36: Spatial distribution of chimpanzee signs and nest groups



Chimpanzee signs (red) and nest groups (orange) were observed in the upper part of the study area divided in 2 distinct clusters. The Yealé cluster down left contained slightly less signs (n = 203) but 2 times more nest groups (n = 227), than the Gouéla II cluster on the top right (n = 252 signs and n = 111 nest groups)

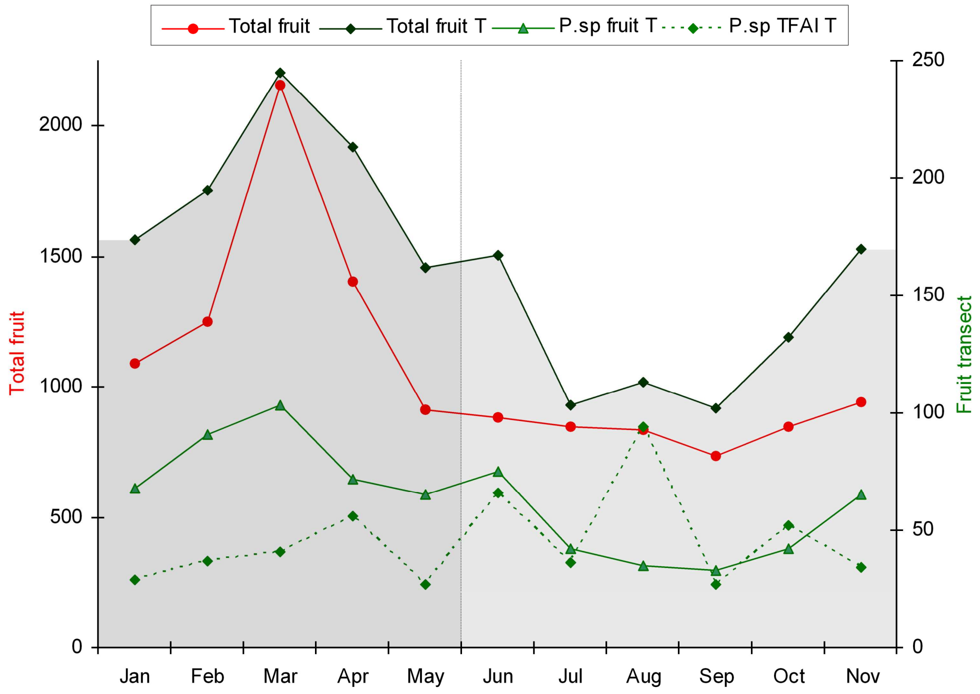
V.4.2. Seasonality and fruit availability

We identified a total of N = 11,898 fruiting trees, shrubs and lianas corresponding to 437 species belonging to 69 families. We recorded 49.6% of these during the late dry season (January-April), which presented the highest annual recruitment of fruiting species (Fig. 37). The number of fruiting species regularly decreased from May to September, the month with the lowest number of plants producing fruits.

Mann-Whitney U-test revealed that monthly numbers of fruiting plants on all itineraries were significantly higher during the dry season than during the rainy season ($U_{obs} = 0$, $P < 0.01$, N=11), indicating a markedly seasonal fruiting pattern. On transects, we recorded N = 1,776 fruiting plants > 10 cm DBH belonging to 368 species. Monthly numbers of fruiting plants observed on transects show the same discrepancy between the dry and rainy seasons ($U_{obs} = 0$,

$P < 0.01$, N=11), indicating a similar seasonal year-round recruitment of fruiting plants on transects than in the overall forest. However, fluctuation of the monthly numbers of principal species bearing fruits on transects were not influenced by seasons ($U_{obs} = 2$, $P < 0.01$, $N = 11$). Homogeneity between the 2 seasons' distributions was greatest when considering the monthly total fruit abundance index (sum of all $SFAI_{sm}$; $U_{obs} = 13$, $P < 0.05$, $N = 11$), pointing out that in principal species, fruit abundance was more strongly aseasonal than fruiting plant numbers. This discrepancy was due to large emergent trees punctually producing important amounts of fleshy fruits at different periods (*Canarium schweinfurthii* (Oct-Dec), *Chrysophyllum giganteum* (Jan-May), *Nauclea diderrichii* (Jun-Sep), *Parinari excelsa* (Nov-Feb), *Parkia bicolor* (Jan-Apr) *Pouteria altissima* (Jun-Aug)).

Fig. 37: Year-round patterns of fructification



Seasonal variation of fruit availability between the dry (dark gray) and rainy (light gray) seasons appears in red with the monthly numbers of overall fruiting plants recorded on all itineraries (Total fruit), and in dark green with the monthly numbers of all fruiting plants on transects (Total fruit T). The green line shows the non-seasonal variation of the monthly numbers of principal species fruiting on transects (P.sp fruit T), and the dotted green line the aseasonal variation of principal species fruit abundance index on transect (P.sp TFAI T)

V.4.3. Influence of fruit abundance and THV availability on chimpanzee presence

We used a total of 83 chimpanzee signs distributed along the 3 transects as presence data. We were able to build models for the months of January (2 models), February, March, April, June and July. AUC ranged between 0.798 and 0.943 (Table 11), indicating models with acceptable to very good discrimination capacities (Hosmer and Lemeshow 2000). F-test for goodness-of-fit confirmed these results.

Table 11: Fit monthly models of chimpanzee presence as function of food resources

Model	AUC	F	p-value	Variable	Coeff.	p-value
Jan 1	0.942	9.28	2.4 e^{-04}	(Intercept)	-3.37457	0.0001
				SFAI low-seasonal	0.41173	0.0335
				Zingiberaceae	2.8031	0.0005
Jan 2	0.943	10.38	2.3 e^{-06}	(Intercept)	-5.70269	0.0014
				FAI *Rinorea oblongifolia*	1.81613	0.0169
				FAI *Solanum torvum*	3.87149	0.0079
				Marantaceae	-2.34248	0.0532
				Zingiberaceae	2.52027	0.0290
Feb	0.817	27.17	8.3 e^{-07}	(Intercept)	-3.81534	0.0009
				Zingiberaceae	2.60026	0.0418
Mar	0.927	0.84	5.3 e^{-02}	(Intercept)	-4.77149	0.0005
				FAI *Solanum torvum*	1.91851	0.0584
				Marantaceae	1.57246	0.1305
				Zingiberaceae	3.56989	0.0035
Apr	0.798	19.22	1.9 e^{-05}	(Intercept)	-2.41174	0.0978
				FAI *Solanum torvum*	0.34660	0.0759
Jun	0.834	6.65	1.4 e^{-03}	(Intercept)	-2.11167	0.0026
				FAI *Nauclea diderrichii*	0.17323	0.0051
				Zingiberaceae	1.26907	0.0520
Jul	0.819	8.56	4.2 e^{-04}	(Intercept)	-2.37172	0.0336
				FAI *Grewia barombiensis*	1.01721	0.1170
				Zingiberaceae	1.14260	0.0681

AUC: Area Under the ROC Curve; F: value of F-test for goodness-of-fit; p-value: p-value associated to F; Variable: variables were fruit abundance of principal species and THV availability with FAI: fruit abundance index per section of the considered species, SFAI low-seasonal: sum per section of the FAI of all lowly seasonal fruiting species, and presence/absence of Marantaceae and Zingiberaceae per section; Coeff.: model estimated value; p-value: Wald t test p-value.

Zingiberaceae presence appeared as the most influential factor related to chimpanzee presence, as it was present in 5 out of the 6 models (all but April), with always the highest OR value.

OR of Zingiberaceae reached its maximal value in March (OR = 35.51), was high in June and July (3.56 and 3.13 respectively) and even higher in January (12.43 and 16.5) and February (13.47). Marantaceae and chimpanzee presence were negatively linked in January (OR = 0.09) and positively in March (OR = 4.82). During the late dry season (January, March, April), chimpanzee presence was also positively linked to the abundance of *Solanum torvum* fruits, a lowly seasonal shrub that fruited during 9 months of the study. The effect was strongest in January, and decreased in March to reach its lowest value in April. In January, fruit abundance of another lowly seasonal understory tree, *Rinorea oblongifolia*, strongly attracted chimpanzees. These findings were confirmed by the second January model which gave $SFAI_{sm}$ low-seasonal positively linked to chimpanzee presence with a curvilinear-shaped increasing OR. During the early rainy season, chimpanzees were attracted by fleshy fruits abundance of seasonal species (emerging tree *Nauclea diderrichii* in June, and shrub *Grewia barombiensis* in July) with the same OR shape. For all the 6 months where models of chimpanzee presence were fit, $SFAI_{sm}$ was controlled by different habitat structure variables than Marantaceae and Zingiberaceae. Despites monthly fluctuations, $SFAI_{sm}$ was always controlled by forest disturbance level and often by canopy closing, while Marantaceae and Zingiberaceae were systematically linked to forest type and understory lianas. This confirmed that fruit abundance and THV availability were not linked by any confounding factor, and validated the hypothesis that $SFAI_{sm}$ was a genuine predictor of chimpanzee presence.

V.4.4. Influence of habitat structure on chimpanzee signs counts

We used the total N = 455 chimpanzee signs as presence data. We excluded the feces model due to a very low number of feces observations (n = 33) preventing reliable statistical analysis. The 4 other tested models were successfully built. The overall model had the best fit (highest F value), and the model based on moving signs had the weakest (Table 12).

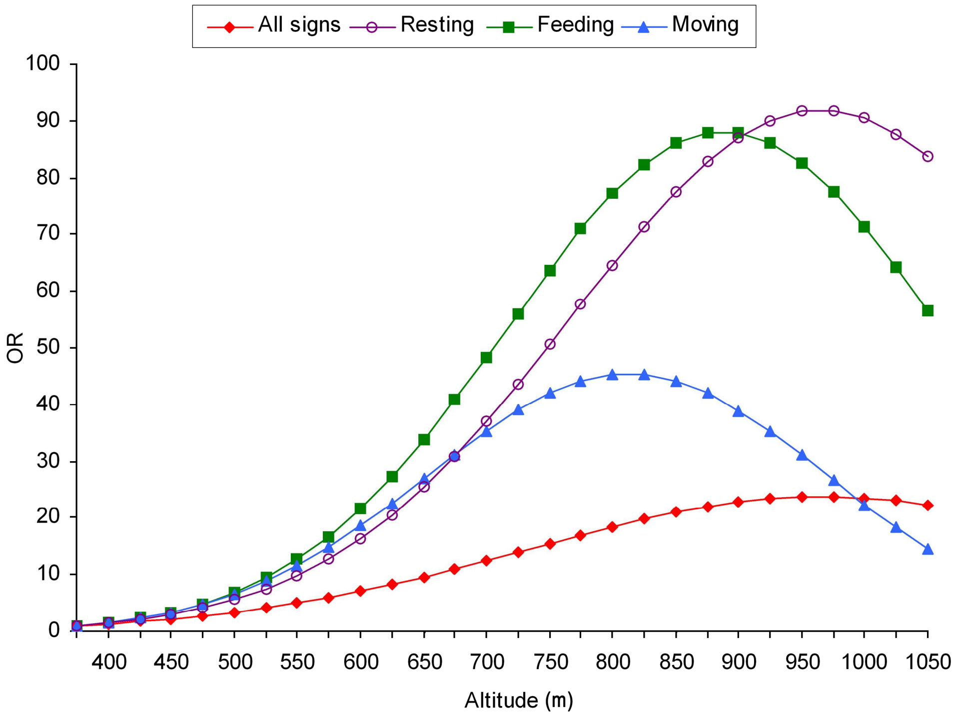
Table 12: Fit annual models of chimpanzee signs counts as function of habitat structure and mammals

Model	F	p-value	Variable	Coeff.	p-value
All signs	18.30	$< 10^{-4}$	(Intercept)	-8.24167	0.0007
			Type 1	0.44004	0.0002
			Type 2	0.16106	0.1651
			Disturb. 1	0.10384	0.3940
			Disturb. 2	0.20508	0.0629
			L	-0.12772	0.1609
			Alt.	0.01742	0.0069
			Alt^2.	-0.00001	0.0267
			Human	-0.25215	0.0742
			Primate	0.71576	0.0000
			Artio.	-0.59779	0.0000
Feeding	8.42	$< 10^{-4}$	(Intercept)	-14.08372	0.0003
			Type 1	0.63953	0.0025
			Type 2	0.07045	0.7491
			Disturb. 1	0.06547	0.7513
			Disturb. 2	0.60740	0.0018
			S	-0.33188	0.0964
			L	-0.29701	0.0485
			O	-0.28855	0.1039
			Alt.	0.03020	0.0024
			Alt^2.	-0.00002	0.0061
			Primate	0.52932	0.0009
			Artio.	-0.76139	0.0000
Moving	2.02	0.0837	(Intercept)	-15.028394	0.0000
			Type 1	0.495028	0.0055
			Type 2	0.148090	0.4101
			Disturb. 1	0.629769	0.0049
			Disturb. 2	0.206017	0.3110
			Chr	0.548903	0.0789
			O	-0.390872	0.0202
			Alt.	0.032469	0.0007
			Alt^2.	-0.000020	0.0019
			Human	-0.310866	0.1746
			Primate	0.610198	0.0002
			Artio.	-0.245744	0.1110
Resting	5.83	$< 10^{-4}$	(Intercept)	-14.462899	0.0392
			S	0.785908	0.1612
			L	-0.681562	0.0483
			Z	1.050815	0.0040
			O	0.989679	0.0044
			Alt.	0.025082	0.1664
			Alt^2.	-0.000013	0.2637
			Artio.	-0.671649	0.0388

F: value of F-test for goodness-of-fit; p-value: p-value associated to F; Variable: Type 1 and Type 2: binary dummy variables coding forest type, Disturb. 1 and Disturb. 2: binary dummy variables coding forest disturbance level, S, L, Z, *Chr*: presence of saplings, lianas, Zingiberaceae, *Chromolaena* in the understory, O: open understory, Alt. and Alt^2.: altitude with quadratic effect, Human, Primate, Artio.: presence of human, primate, artiodactyl signs; Coeff.: model estimated value; p-value: Wald t test p-value.

Altitude was the strongest factor influencing chimpanzee habitat selection (Fig. 38). The overall model predicted a maximum number of chimpanzee sign observations at 975 m altitude (OR_{max} = 23.67), like for the resting-related evidences (OR_{max} = 91.76). Highest numbers of traveling and feeding-related signs were expected at lower altitude (OR_{max} = 45.23 at 800 m altitude and OR_{max} = 87.99 at 900 m altitude respectively).

Fig. 38: Variations of altitude odds ratios for each category of chimpanzee signs



Maximum numbers of chimpanzee sign were expected between 800 and 975 m altitude, which northeasterly of the Yan River roughly corresponds to the limit between mountain forest and altitude grassland

Forest type was the second most determinant factor of chimpanzee habitat use. Overall expected counts were noticeably greater in the mountain and gallery forests in comparison to the lowland forest (OR = 2.83 and 2.14 respectively; Table 13), with more signs expected in the mountain than in the gallery forest (OR = 1.32). This clear habitat preference was also found for the traveling-related signs, and was the strongest for feeding-related observations.

Table 13: Odds ratios of categorical habitat variables computed from each of the 4 fit models of chimpanzee sign counts.

		All chimp signs			**Feeding**			**Moving**			**Resting**		
		MF	**GF**	**LF**	**MF**	**GF**	**LF**	**MF**	**GF**	**LF**	**MF**	**GF**	**LF**
	MF		0.76	0.35		0.57	0.26		0.71	0.32			
compared	**GF**	1.32		0.47	1.77		0.46	1.41		0.45			
	LF	2.83	2.14		3.86	2.18		3.12	2.21				

		All chimp signs			**Feeding**			**Moving**			**Resting**		
		Old	**2ry**	**Yg**	**Old**	**2ry**	**Yg**	**Old**	**2ry**	**Yg**	**Old**	**2ry**	**Yg**
	Old		1.11	0.66		1.72	0.48		0.66	0.23			
compared	**2ry**	0.90		0.60	0.58		0.28	1.53		0.35			
	Yg	1.51	1.67		2.01	3.6		4.33	2.83				

		All chimp signs	**Feeding**			**Moving**		**Resting**			
		L	**S**	**L**	**O**	**Ch**	**O**	**S**	**L**	**Z**	**O**
compared	**absence**	0.88	0.72	0.74	0.75	1.73	0.68	2.2	0.5	2.8	2.7

		All chimp signs			**Feeding**		**Moving**			**Resting**
		Hum	**Prim**	**Artio**	**Prim**	**Artio**	**Hum**	**Prim**	**Artio**	**Artio**
compared	**absence**	0.78	2.05	0.55	1.7	0.47	0.73	1.84	0.78	0.51

Comparison of chimpanzee signs counts between sections with different forest type levels: mountain forest (MF), gallery forest (GF), lowland forest (LF); Comparison between sections with different forest disturbance levels: old-growth forest (Old), old secondary forest (2ry), young secondary forest (Yg); Comparison between sections where understory contained sapling (S), liana (L) and/or *Chromolaena odorata* (Ch) and sections where they were absent, Comparison between open understory (O) and non-open understory; Comparison between sections that contained human (Hum), other primate (Prim) and artiodactyl (Artio) signs of presence and sections where they were absent.

Forest disturbance level also influenced chimpanzees' habitat selection. They always avoided young secondary forest, and overall preferred old secondary compared to old-growth forests (OR = 1.11). This tendency was particularly marked for feeding-related signs (OR = 1.72), but was not confirmed for traveling-related signs, which were more expected in old-growth than in old secondary forest (OR = 1.53). In their general pattern of habitat-use, chimpanzees rather avoided understory with liana (OR = 0.88). They fed more in habitat with non-open understory (OR = 0.75) free of saplings (OR = 0.72) and lianas (OR = 0.74), while they rather used habitat offering non-open understory with *Chromolaena odorata* when traveling. Resting-related signs were noticeably more expected in open understory containing sapling and Zingiberaceae (all OR > 2) and no liana (OR = 0.5).

V.4.5. Influence of other species on chimpanzee signs counts

We observed n = 387 signs related to the presence of 7 other primate species, including guenons (*Cercopithecus campbelli campbelli*, *C. diana diana*, *C. nictitans martini* and *C. petaurista buettikoferi*), black and white colobus (*Colobus polykomos*), sooty mangabey (*Cercocebus atys atys*) and dwarf galago (*Galagoides demidovii*). We also recorded n = 940 signs revealing the presence of 8 artiodactyl species, including duikers (*Cephalophus dorsalis*, *C. maxwelli*, *C. niger*, *C. rufilatus*, *C. silvicultor*), bushbuck (*Tragelaphus scriptus*), forest buffalo (*Syncerus caffer nanus*), and red river hog (*Potamochoerus porcus*). We finally recorded N = 151 human-related observations. Chimpanzee presence turned out to be positively influenced by the presence of other primates species (OR = 2.05), particularly when feeding and traveling (OR = 1.7 and 1.84 respectively). The presence of artiodactyl had an unequivocal negative effect on chimpanzee presence (in all models, with 0.47 < OR < 0.78), and chimpanzees also avoided habitats marked by human presence, particularly when traveling (OR = 0.78 and 0.73 respectively).

V.5. Discussion

V.5.1. Seasonality and food availability

Our results confirm that the overall recruitment of fruiting plants in the Nimba forest was highly seasonal, with the numbers of fruiting plants peaking in the late dry season and remaining consistently low during the rainy season (Fig. 37). However, fruit abundance of the 45 principal species (the most eaten by Nimba chimpanzees as well as the most represented along the 3 transects) showed aseasonal monthly fluctuations. In the late dry season (Jan-Apr), period of overall fruit abundance, the numbers of lowly seasonal species that were fruiting reached their highest annual rates and chimpanzee fruit foods were relatively low. On the contrary, during the rainy season (May-Nov) overall fruits were scarce, and the abundance of fruit foods showed 3 peaks of increase on a 2-month frequency, which were mainly due to fleshy fruits of large emerging trees.

V.5.2. Feeding strategy

Nimba chimpanzees consumed fruits year-round, but the nature and abundance of this food fluctuated majorly between seasons. During the dry months (general fruit profusion and relatively scarce fruit foods), chimpanzee presence was linked to Marantaceae and Zingiberaceae availability and to the fruit abundance of lowly seasonal species (*Rinorea oblongifolia* and *Solanum torvum*, together with *Elaeis guineensis*, *Ficus* sp., *Microdesmis kaeyana*, *Musanga cecropioides*, *Tabernaemontana Africana*, *Trema guineensis*). During the rainy season (general fruit scarcity and periodic abundance of fruit foods), chimpanzee presence was still linked to the existence of Zingiberaceae, but also to the abundance of fleshy fruits of *Nauclea diderrichii* (June) and *Grewia barombiensis* (July). Unfortunately, we could not fit any model for the other rainy months (Aug-Nov), presumably because the sample sizes of both chimpanzee signs and fruiting plants were too low, but the macroscopic analysis of feces indicated that chimpanzees were actually consuming fleshy fruits of tall emergent trees (*Canarium schweinfurthii*, *Parinari excelsa*, *Pouteria altissima*) during these months.

V.5.3. Preferred and fallback resources

Chimpanzees possess a precise spatial memory enabling them to remember the location of numerous resources and to select the most attractive ones (Normand et al. 2009). Our findings suggest that when overall fruits were scarce, Nimba chimpanzees used their spatial knowledge to locate and reach singular large trees producing fleshy fruits, like *Nauclea diderrichii*. We consider this actively sought resource, together with fleshy fruits of the shrub *Grewia barombiensis*, as preferred foods. When traveling between these feeding spots, chimpanzees would opportunistically feed on fallback resources. THV feeding remains accounted for half of total feeding-related observations, and we fit models showing that edible THV presence increased the probability of observing chimpanzee signs during months of relative fruit food scarcity (Jan, Feb, Mar, Jul). Based on Marshall and Wrangham (2007), we propose the Zingiberaceae to function as staple fallback foods because they were available and eaten throughout the year, and represented a significant part of the diet during months of lowest abundance of fruit foods (May, Jul, Sep). The Marantaceae, and the fruits of *Solanum torvum* and *Rinorea oblongifolia*, which were more widely distributed than Zingiberaceae, but less strongly linked to chimpanzee presence, would rather function as filler fallback foods that were avoided during periods of fruit food abundance. Fallback resources (especially Zingiberaceae) hold an important place in the annual feeding strategy of Nimba chimpanzees, which is different from Bossou (fig. 1) where chimpanzees eat THV very occasionally and cope with fruit scarcity by relying on 3 keystone resources neglected the rest of the year: nut and pith of *Elaeis guineensis*, and *Musanga cecropioides* fruit (Yamakoshi 1998).

V.5.4. Habitat selection

Prediction of the highest number of sign observations at 975 m altitude confirms that chimpanzees make year-round preferential use of altitude habitats, with higher habitats selected for resting than for feeding or traveling. Although Nimba orophilous wildlife is a major source of biodiversity (Lamotte 1942; Schnell 1951), chimpanzees selected the old secondary habitats found in the mountain and gallery forests, especially when feeding. During the late dry season (Jan-Apr), which was the period of highest activity recorded for chimpanzees, the abundance of fruit food was relatively low. Selecting mountain forest's edge or patches of old secondary vegetation ensured chimpanzees access to abundant and widely distributed fallback resources like lowly seasonal fruits of *Solanum torvum* and *Rinorea oblongifolia*, and herbs of Zingiberaceae. The emerging question is to understand whether this strong affinity for altitude secondary vegetation, and the fallback food-oriented diet, constitutes an optimal situation for Nimba chimpanzees, or rather strategic feeding adaptations to changing habitat.

V.5.5. Chimpanzee communities in the Ivorian Nimba

Superimposing spatial distributions of signs of chimpanzee presence and nest groups provides an image of chimpanzees' overall pattern of habitat use. As suggested by nest group characteristics and low population density estimates, we previously proposed that our study area would straddled the peripheral areas of 2 distinct community territories (Granier et al. 2014). The spacing between observations of chimpanzee signs in Gouéla II and their seasonality confirm this area as a peripheral part of one community territory (Fig. 2). However, considering the high concentration and the permanence of signs observed in the Yealé area, as well as their overlap with nest groups, we now propose the Nuon River area (Libero-Ivorian border) as an integral part of the core zone of this second community territory.

V.5.6. Research and conservation

Chimpanzee presence was positively linked to the presence of 7 species of monkeys and prosimians, and negatively by the presence of artiodactyls and humans. Amongst the 8 primate species confirmed in Nimba, 5 are classified in the IUCN red list of threatened species due to hunting and habitat loss through deforestation for timber and agricultural land (IUCN 2013). The chimpanzee *Pan troglodytes* is an Endangered species, *Cercopithecus diana diana*, *C. nictitans martini* and *Colobus polykomos* are classified as Vulnerable, and *Cercocebus atys atys* as Near Threatened. Though facing the same threats, the 3 other primates and the 8 artiodactyls species are still relatively common and widespread at the scale of their African range.

Fimbel (1994) showed that at Tiwai Island in Sierra Leone, *Pan troglodytes*, *Cercopithecus campbelli, C. petaurista* and *Cercocebus atys*, despite commonly using old-growth forest, were selecting regrowth forest more often than expected. Our findings similarly emphasize the importance of regrowth habitat in wildlife management. In functional terms of seed dispersal, Lambert (2010) proposed guenons to be the best umbrella taxon – a group of species whose conservation confers protection to several naturally co-occurring wildlife species – among primates of the Kibale forest in Uganda. Moreover, the chimpanzee, which functions well as a flagship in conservation tactics, is often observed in sympatry with at least one species of guenon. We believe that holistic research aiming to assess the ecological requirements of chimpanzees and guenons in their full range of habitats, constitutes a critical next step toward developing a “primate-oriented” conservation strategy which would guarantee protection to a wide range of wildlife species, and by extension ensure the sustainability of Nimba forest ecosystems.

DISCUSSION

VI.1. General views on the ecology of chimpanzees in the Ivorian Nimba

The detailed analyses conducted on the behavior and ecology of Nimba chimpanzees have provided central information on the abundance and distribution of their populations, as well as on their requirements related to the fulfillment of basic behaviors such as nesting, feeding, traveling, resting or socializing. We particularly investigated their criterions of habitat selection for the fulfillment of basic behaviors in relation to the structure of habitat, topography and seasonality, food abundance and availability, human and other mammals' presence. In this first part of the discussion chapter, we put these findings altogether to provide a better understanding of basic traits of chimpanzee's life history that could be pertinent to ensure their sustainable living in the Nimba region.

VI.1.1. Methodological considerations

Choice was actively made to work on non-habituated chimpanzees and to make all efforts to avoid any habituation effect. Though habituation allows conducting detailed research on the mechanisms and adaptive processes of behavior, ecology and sociology, it is also a huge responsibility for the observers (Williamson and Feistner 2011). Indeed the habituation process may have drawbacks on the studied population like impairing the chimpanzees, creating stressful situations and modifying the behaviors under study, increasing the possibilities of inter-specific diseases transmission, or by reducing their wariness it can draw chimpanzees to humans, which can be dangerous for them (poaching) or create conflicting situations (crop-raiding) (Kappeler et al. 2012; Hockings and Humle 2009). Moreover, chimpanzees are large and social mammals ranging in large territories and who possess a material culture producing long-lasting tracks. They consequently leave numerous signs of presence behind them, which provide precise information on their behavior, ecology and life history in general. Inscribing in a naturalistic perspective with great respect and admiration for wilderness, we made a point of having the smaller impact possible on both chimpanzees and habitat. We consequently focused on the monitoring of their signs of presence in relation to habitat characteristics, and did not search to establish direct contact with them.

For purposes of methodological consistency with Junker et al. (2012), we used the same regression analyses to relate chimpanzee presence to environmental and human impact variables. This methodological homogeneity allows further comparisons with general trends of African ape population, while affording for key knowledge on the behavioral ecology of Nimba chimpanzees. However, a sizeable sample of chimpanzee data collected in the southern slope of Nimba prior to 2009, or recorded in an opportunistic manner during displacements outside survey itineraries from 2009 were not used in these analyses. The fact remains that they constitute important information, congruent with the findings presented in the previous chapters on the abundance, ranging, habitat selection and diet of these chimpanzees that were taken into account to draw out a general overview of their life history.

VI.1.2. Habitat description

VI.1.2.1. Vegetation

We identified and measured diameter at breast high of 8,403 tree, shrub and liana species belonging to 368 species along the 3 transects. Sixty eight additional species were identified on recces, which added to the 60 plants that were not named on transects bring the total plant diversity recorded in the Ivorian Nimba to a minimum of 437 species distributed into 64 families (Annex 3). In an extensive study of the tri-national Nimba flora, Adam (1971-1983) reported 138 families of ligneous plants. The limited study area of the present research in relation to the transversal differences existing in the structure and composition of Nimba vegetation (Schnell 1998; see below) may not be sufficient to explain such an important variation in the number of ligneous plant families reported between these 2 studies. This statement enlightens the necessity of conducting further detailed botanical studies on vegetation composition in relation to chimpanzee ecology. Similarly, the continuous record of vegetation structure along the 80 km of survey itineraries has provided a dataset of 1,800 entries, which would greatly benefit from being enlarged to the entire southern slope of Nimba. Annual updates of this knowledge are also of crucial interest to document the rapid habitat changes undergoing in some Nimba ecosystems, particularly to investigate the labile relationship between altitude savannas and mountain forest, and monitor the evolution of secondary vegetation covering their edge (Schnell 1951; Adam 1971).

The vegetation of Nimba offers major transversal differences, which led Schnell (1952; 1998) to distinguish 2 parts in the massif. The northeastern half culminates higher (between 1,300 m and 1,752 m altitude) and its top is covered by altitude herbaceous vegetation, while the southwestern half is lower (between 1,000 m and 1,300 m altitude), and forest rises over the crest to cover the entire massif (Lamotte 1998). Due to the thin soil covering an emerging ferruginous cuirass, this forest at the top of Nimba is different from the slopes' mountain forest, and has in particular a lower canopy.

Fig. 39: The Yan River, clear cut in vegetation formations

Photograph taken from the Yealé village, Côte d'Ivoire

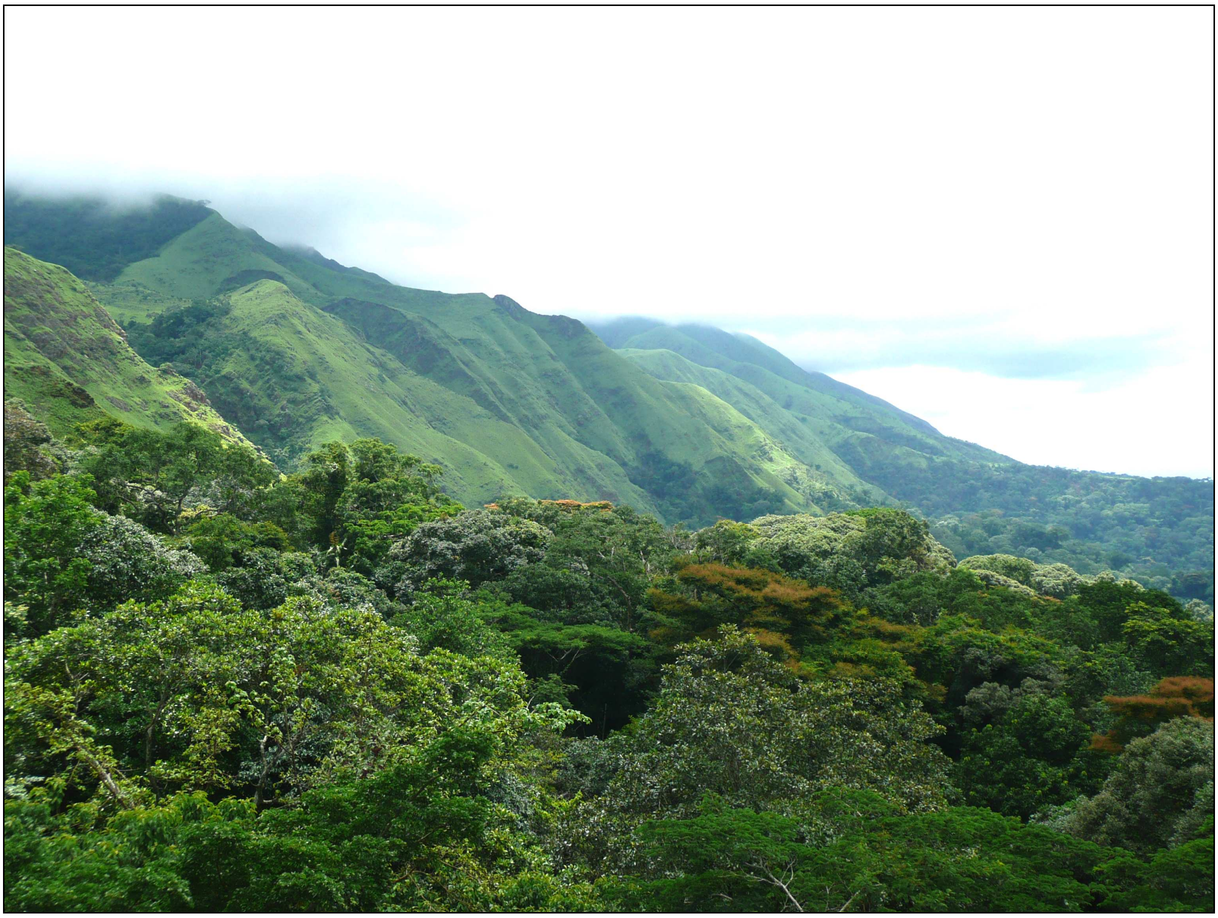
The Yan River marks a clear-cut in this ecological partitioning of the Nimba range (Fig. 39, 44). Its right bank is covered by mountain forest up to the crest, which there culminates around 1,300 m altitude, while on the left, after a thin band of gallery forest clinging on the slope of the top part of Yan gully, extends the altitude herbaceous vegetation covering all the top of Nimba northeastern half. Due to the topological and climatic differences existing between the oriental and occidental parts of the mountain (Lamotte 1998a), this vegetation partitioning is also found in lower altitude forest covering the slopes. More abundant rainfalls in the southwestern part have favored the development of rather ombrophilous forest, whereas the drier northeastern half offers forest of more mesophile type (Schnell 1951; Adam 1971).

VI.1.2.2. Fruit phenology

Although the Nimba flora has been extensively studied (Adam, 1971-1983; Schnell 1998), little quantitative knowledge is available on the phenology of its forests. The few quantitative analyses conducted were focused on the biomass of altitude herbaceous ecosystems (Fournier 1987). The present study provides a preliminary overview of forest phenology related to chimpanzee ecology in the middle of the southern slope of Nimba (Fig. 40). During one year, we systematically collected each month data on the distribution, abundance and fruit phenology of all fruiting plants observed along survey itineraries. However, fruit abundance was estimated solely from the 12 km of transects, because data on the diameter of fruiting trees were only available from them. Transects were assumed to, and revealed to be representative of the entire study area in terms of vegetation structure and composition, but they constituted a relatively small sample in regard to the average size of chimpanzee territory in tropical rainforest (5 - 40 km^2; Tutin et al. 1983). We emphasize the necessity of conducting a broader scale study aiming at monitoring and quantifying the fruit phenology in all types of forested habitats for both chimpanzee research and biodiversity conservation (Vogel and Janson 2011).

The record of fruit phenology along all survey itineraries constituted a dataset of 11,898 entries that was analyzed both in general terms of overall fruit availability and in particular terms of abundance of chimpanzee fruit foods on transects. Overall fruit availability in this part of Nimba forest was highly seasonal, showing a fructification peak during 4 dry months (Jan – Apr) and a consistently low availability during the rainy season (May – Nov). This result is congruent with previous studies on the phenology of tropical forests (Van Schaik et al. 1993) and on the seasonality of fruit availability in the habitat of neighboring Bossou chimpanzees (Yamakoshi 1998). However our study introduced a nuance of prime importance regarding the feeding behavior of chimpanzees.

Fig. 40: The southern slope of Nimba



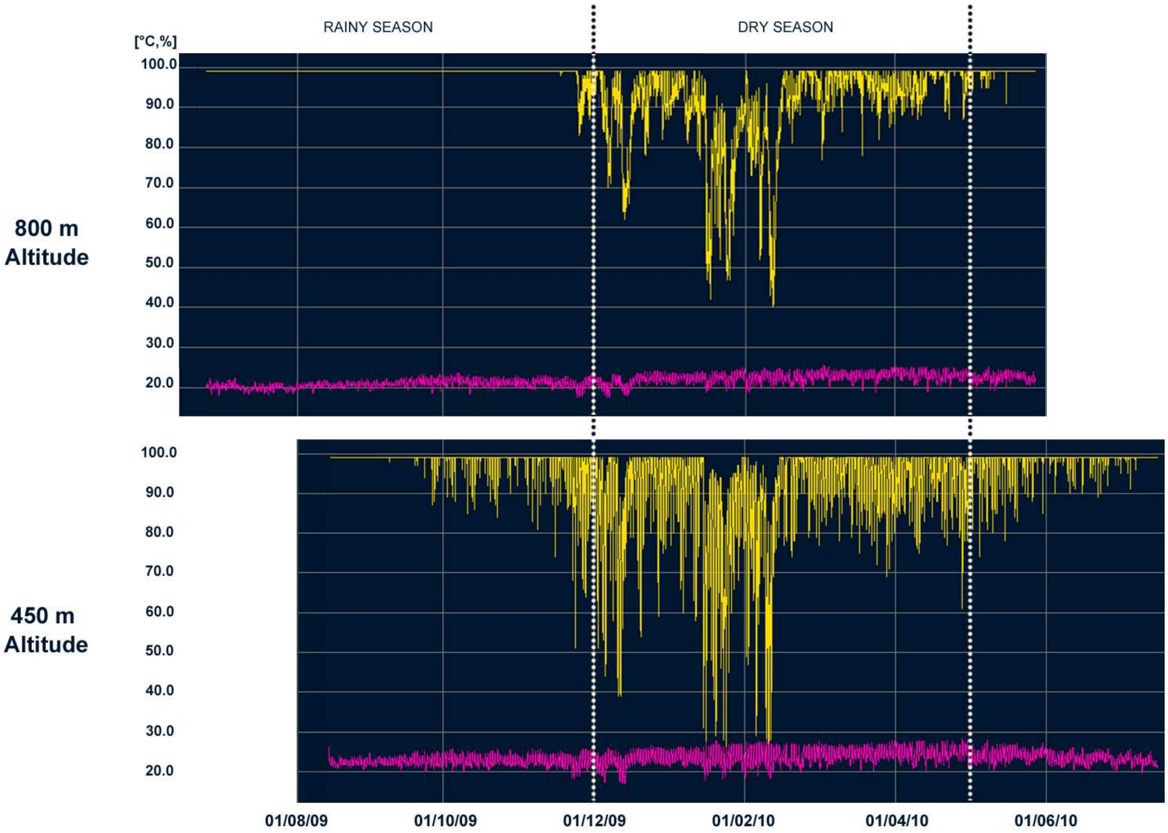
Photograph taken from Gouéla II moutain forest, looking towards northeast

According to Marshall and Wrangham (2007) preference for a given resource is defined as the relationship between its availability and its usage. Since we did not have information on the general availability of chimpanzee fruit foods in the Nimba forest, we were not able to determine what their preferred fruit foods were. To overcome this lack, we based on results from preliminary surveys in the southern slope of Nimba to search the fruits that were the most frequently eaten by chimpanzees. For methodological considerations inherent to logistic modeling, we needed to have a minimum ratio of presence/absence data of 1/6. We consequently based on woody species composition recorded from the 3 transects, to extract among the most eaten fruits, the 45 species that constituted the largest populations in the study area. We called them principal (fruit food) species, since they constituted an important portion of chimpanzee diet, and were largely available in the habitat. The point of interest is that the fruit abundance of these 45 principal species showed non-seasonal monthly fluctuations, which evolved with a tendency opposite to the overall pattern of fruit availability in the study area: it was relatively low during the 4 dry months (including however a small fructification peak in April, Fig. 37), and showed 3 peaks of increase during the rainy season (Jun, Aug, Oct). The fact that the abundance of chimpanzee principal fruit foods varied non-seasonally with no prolonged periods of scarcity rises important questions on the ecological and evolutionary adaptations of chimpanzees to Nimba environment that are developed in the following paragraphs.

VI.1.2.3. Temperature and humidity

We used two-channel temperature and humidity data logger (T&D Thermo Recorder TR-72Ui) to record and measure the annual variations of temperature and humidity within Nimba forest. The objective was to evaluate whether differences in climatic conditions between lowland and mountain forests could participate to explain the preferential use of altitude habitats by chimpanzees. We consequently put 2 thermo recorders in the middle of the study area (between the Yan and Toua Rivers), one at 450 m altitude in lowland forest and another at 800 m in mountain forest. Frequency of data acquisition was set to 60 minutes and both recorders were placed in large patches of primary forest with open understory and closed canopy, in wooded niches at 2 m above the ground on buttresses of large *Alstonia boonei* trees.

Fig. 41: Temperature and humidity recorded at 450 m and 800 m altitude.



Recording period at 450 m altitude was 2009, August 16th – 2010, July 12th; at 800 m altitude it was 2009, June 25th – 2010, May 24th.

Considering only data captured during the overlapped recording periods of the 2 units, which stretched from the heart of the rainy season to the end of the dry season (2009, August 16th to 2010, May 24th), the average nyctohemeral temperature was 1.6 °C cooler in altitude than in lowland forest (Fig. 41). It is however interesting to note that amplitude of temperature variation was greater in the lowland forest (average = 23.3 °C; temperature amplitude = 11.4 °C; range: [16.9° - 28.3°]) than in the mountain forest (average = 21.7 °C; temperature amplitude = 8.4 °C; range: [17.2° – 25.6°]). The minimal temperatures are almost similar between the 2 recording spots, and the difference in amplitude of temperature variation is mainly due to maximal temperature, which is almost 3 degrees higher in lowland forest. Though there is probably a bias in the recorded minimum temperature (we would have expected a lower value in altitude forest), this record is not incongruent with the fact that altitude decreases temperature. Furthermore at 800 m altitude the temperature was netly lower during the rainy season than during the dry season (Fig. 41). Lamotte (1998a) reported the greatest temperature variations in Nimba from the altitude grasslands, which are directly exposed to airflows due to the absence of forest cover. The multilevel closed canopy, under which the 800 m altitude thermo recorder was placed, certainly reduced airflows producing less temperature variation compared to altitude grasslands (and lowland forest). Our records on nyctohemeral variations of hygrometry are also in line with Lamotte (1998a) showing that the air was less humid in the lowland than in the mountain forest, with respectively 82.1% of average water saturation and 90.8% (Fig. 41). In addition, the number of days during which the air was not 100% water-saturated was about 2 times greater in the lowland compared to the mountain forest. During the rainy months, the air was 100% water-saturated and the temperature fluctuated less radically in comparison to the dry season, when air humidity varies of more than 50%. As a main conclusion of our records and congruently with previous climatological studies (Lamotte 1998a): the contrast between the dry and rainy season in both temperature and hygrometry was greater in mountain forest compared to lowland forest.

VI.1.3. Feeding strategy

VI.1.3.1. Importance of secondary vegetation

The secondary vegetation of Nimba has been presented as mainly resulting from human activities, especially to the joint effects of farming and uncontrolled bushfires (Schnell 1998). Before the classification of the Nimba Mountain in 1943, local people were living and cultivating in the lower parts of its slopes (Mauny and Holas 1953). They used slash and burn techniques of nomad farming, in which a land is deforested, burned and cultivated during few years before being abandoned to fallow land. After the swift installation of herbaceous species (including Marantaceae and Zingiberaceae) and at the favor of ligneous seedlings, fallow land rapidly evolves into scrubland, shrubby scrubland, and thicket (Schnell 1998). The characteristic pioneer ligneous species are all heliotropic (Schnell 1951), and we here mention the most common ones which fruits are also eaten by Nimba chimpanzees: *Alchornea cordifolia, Harungana madagascariensis*, *Macaranga hurifolia, Musanga cecropioides, Solanum torvum*, *Trema guineensis, Vismia leonensis*. In the later stages of secondary vegetation, thicket progressively evolves towards secondary forest. The young secondary forest is characterized by the settlement of arborescent species seedlings, which grow higher and start forming the almost-closed emergent canopy characteristic of old secondary forest (Brugière et al. 2003). At the end of the growth process the old secondary forest has the structural aspect of a primary forest, from which it can be recognized by the presence of secondary tree species, like *Elaeis guineensis*, *Lophira alata*, *Pycnanthus angolensis,* or *Terminalia* sp. (Van Steenis in Schnell 1998).

We recorded feeding signs in regrowth forests every month; they were mainly consisting of Zingiberaceae and Palmaceae stems leftovers, and fruit feeding remains of plants with lowly seasonal fructification pattern, such as *Alchornea cordifolia*, *Rinorea oblongifolia*, *Solanum torvum* and *Trema guineensis*. Furthermore, Poisson models gave the strongest rate of sign occurrence for feeding observations in old secondary forest, showing that the link between secondary forest and chimpanzee diet is very tight. In the Gouéla II side, chimpanzees were significantly selecting more often the old secondary vegetation located at the edge between mountain forest and altitude grassland, and we did more observations in this habitat type during the dry season, period of relative fruit food scarcity. In the Yealé side of the study area where altitude grasslands are absent, the secondary vegetation does not have the same clear spatial partition, but chimpanzees also strongly relied on it with the same seasonal pattern of use. These statements, added to the fruit phenology records, validate the working hypothesis that chimpanzees in the study area often selected the altitude habitats and particularly the old secondary forest because this biotope continuously provided them with foods. They additionally suggest that the secondary vegetation plays an important role in shaping the global feeding strategy of these chimpanzees.

However, chimpanzees systematically avoided all the early stages of secondary vegetation, categorized in this study under the unique term of ‘young secondary forest’. We have seen that secondary vegetation constitutes a dynamic habitat subject to perpetual evolution under regulation of a subtle balance between natural regrowth and decline due to bushfires. Unlike climax forests, secondary biotopes are perpetually and rapidly changing, and the unpredictable patterns of fire, which are slowing down the regrowth process, also considerably complicate the possibility of foreseeing how a previously known secondary biotope would have evolved. In this context, the teasing questions are to understand how chimpanzees manage to select the old secondary forest while discarding the young stages, and do they use their spatial memory to precisely locate a previously exploited feeding spot in the secondary vegetation? We rather believe that chimpanzees would select known large areas of secondary vegetation (for example the mountain forest edge in Gouéla II), and then randomly navigate within these patches in their search for foods. Even if secondary vegetation rapidly and unforeseeably evolves, such a way of foraging ensure chimpanzees to find fallback foods (Zingiberaceae and trees of lowly seasonal fruiting pattern), and to reach old secondary habitat with other fruit food resources.

VI.1.3.2. Preferred and Fallback foods

The chimpanzees of Bossou eat 156 different plant foods (Sugiyama and Koman 1992). Fruit and seeds constitute more than half of their diet whereas leaves, shoots and stems constitute about 1 third. In the woodland of the Mahale Mountains (Tanzania), chimpanzees eat a greater diversity of plants (198 different species), but fruits and seeds represent just 1 third of the diet

(Nishida and Uehara 1983). In this study we identified 87 species of plant foods as part of the chimpanzee diet, most of which consisted of fruits (chapter VI.2.2.1.). This preliminary list is mainly based on indirect observations (feeding remains and macroscopic analysis of feces; Fig. 42), and would greatly benefit from further investigations (Vogel and Janson 2011).

The main food sources find in old secondary habitat are the Marantaceae and Zingiberaceae, denominated under the generic term of THV, and the fruits from plants of lowly seasonal fructification pattern – i.e. fruiting more than 6 months per year –, which are mainly pioneer tree species. Chimpanzees eat the soft basal part of the stem and/or the fruit of several Marantaceae and Zingiberaceae species. THV constitute a common fallback resource in chimpanzees that has been reported from several research sites (Wrangham et al. 1991; Malenky et al. 1995; White et al. 1995; Marshall and Wrangham 2007). In Nimba, it was available year-round with low monthly variations: the Marantaceae were continuously present in more than half of habitat sampled (52.4%), principally in the gallery forests and secondary vegetation, whereas Zingiberaceae covered only 15.9%, mainly in the secondary vegetation. We identified the genus *Aframomum* of the Zingiberaceae family as a staple fallback resource, which was eaten every month of the study with a higher frequency during the period of relative fruit food scarcity (Jan–Apr), and that attracted chimpanzees across seasons (Marshall and Wrangham 2007). *Aframomum* sp. may be a keystone resource for chimpanzees of the Ivorian Nimba. Five Marantaceae genera (*Hypselodelphys* sp., *Marantochloa* sp., *Megaphrynium macrostachyum*, *Sarcophrynium* sp., *Thaumatococcus daniellii*), more widely distributed than Zingiberaceae but not eaten every month, attracted chimpanzees in March and were avoided in January (both during relative fruit food scarcity). In accordance with Marshall and Wrangham (2007), we proposed this plant family to function as filler fallback resource. The fact that Marantaceae and chimpanzee presence were negatively linked in January could be partly explained by the high availability of fruits from 11 plant species of lowly seasonal fruiting pattern at that time (*Elaeis guineensis*, *Ficus* sp., *Microdesmis kaeyana*, *Musanga cecropioides*, *Rinorea oblongifolia*, *Solanum torvum Tabernaemontana Africana*, *Trema guineensis*), that may have preferentially attracted chimpanzees due to their higher palatability and/or energy content. In particular, we identified the fruits of *Rinorea oblongifolia* and *Solanum torvum* as other filler fallback resources that had a wide spatio-temporal distribution but were linked to chimpanzee presence only during the dry season, and particularly strongly in January.

Fig. 42: Identifying fruits eaten by Nimba chimpanzees

Anatole Gogo and David Bilivogui identify trees during botanical surveys. Naming trees and fruits was not always obvious, and we recorded several specimens that remained unidentified

We additionally identified 2 preferred foods as the fleshy fruits of *Nauclea diderrichii* and *Grewia barrombiensis*, which seasonal abundance in the early rainy season were attracting chimpanzees. Unlike fallback foods, these two preferred resources were mainly found in old-growth forest and exhibited a scattered distribution. *Nauclea diderrichii* is a large emergent tree which does not form large populations in the forest of Nimba and provide large fleshy fruits constituting a highly palatable and energetic resource that is actively searched by chimpanzees. Chimpanzees may resort to acute spatial and temporal memory processes to locate the places where the resource is abundant and to visit them specifically during the fruiting period (Tweheyo and Lye 2003; Marshall and Wrangham 2007; Normand et al. 2009). Marshall and Wrangham (2007) proposed the preferred foods to shape harvesting adaptations (detecting resources and navigating between them), whereas fallback foods would rather enhance processing adaptations (extracting the edible part and digesting it). Yamakoshi (1998) indeed showed that during the period of fruit scarcity chimpanzees from the neighboring Bossou community increased their tool-use activity to fulfill their subsistence needs. In particular, they augmented their nut-cracking activity, providing typical illustration of a processing adaptation oriented towards feeding (Matsuzawa et al. 2011). During fruit scarcity, Bossou chimpanzees were also more heavily relying on human impacted habitats (secondary forest, scrub, orchards and cultivated fields) that provided numerous important fallback foods such as palm tree nut and pith, *Musanga cecropioides* fruits and cultivars). We highlighted the same pattern of habitat exploitation in Nimba chimpanzees, who fed more frequently and intensively in the old secondary forest during the period of low fruit food availability. These results are congruent with those of most research sites on chimpanzees (Takemoto 2000; Furuichi et al. 2001a; Chancelor et al. 2012). Thought chimpanzees in the Ivorian Nimba use tools (personal observation), such as stones to crack-open nuts of different species, sticks to dip for ants or leaves as a cushion to seat on the wet ground (Matsuzawa and Yamakoshi 1996; Humle and Matsuzawa 2001; personal observations), our ecological monitoring did not provided a large-enough dataset to investigate for seasonal difference in the frequency or spatial distribution of the different tool-using behaviors.

VI.1.4. Nesting behavior

We mainly observed nests in the higher altitude parts of the study area (78% of nests above 700 m altitude; highest probability of observing nests at 770 m), preferentially in steep locations (mean ground declivity = 15.5%). Like in most of research sites on this ape species, chimpanzees were highly selective of their nesting-tree species (Basabose and Yamagiwa 2002; Furuichi and Hashimoto 2004; Stanford and O'Maley 2008): 10 tree species representing 2.3% of the overall species diversity recorded contained 52% of nests. We also showed that they markedly nested more in gallery and mountain forests than in lowland forest, and favored old-growth forest compared to old secondary forest, while always avoiding the first stages of secondary vegetation which did not offer enough-sturdy trees.

An interesting behavioral feature of Nimba chimpanzees is the large amount of nests they build on the ground. Primatologists have long believed that wild chimpanzees almost always built their night nests in trees (Goodall 1968; Baldwin et al. 1981; Fruth and Hohman 1994). Matsuzawa and Yamakoshi (1996) reported an exceptionally high proportion of ground nest in the Ivorian Nimba (more than 1 third of 464 nests), all located above 800 m altitude. Recognizing that chimpanzees happen to construct terrestrial nests to rest during the day, they estimated that an important portion of these were night nests (because they observed tree nests of the same age in their direct vicinity). Furthermore, they distinguished 2 categories of ground nest regarding their structure and complexity. The first category was constituted of thick and elaborated nests that had the same appearance than tree nests, and the second of ground nests that were mainly composed of grasses with a cushion-like appearance. Few years later Hirata et al. (1998) observed Bossou chimpanzees using leaves as cushions to sit on wet ground. We based on these findings and on our personal observations in the Ivorian Nimba to discriminate between the day and night terrestrial nests: the more sophisticated ones were considered to have been used overnight, whereas the cushion-like ones were regarded as day rest nests. Amongst the 764 nests we observed, 8.2% were ground nests, which corresponds to a relatively high rate (Tagg et al. 2013). But regarding the complexity of their structure we classified 6% of total as day rest nests, and considered 2.2% of total as unequivocal ground night nests. Such a proportion of ground night nest is in the range of what has been observed in other communities (Tagg et al. 2013), and lead us to wonder on ground nests significance.

Fig. 43: Ground nest

A ground nest made from the elaborated interweaving of small branches and saplings belonging to 3 different ligneous species that has apparently been moved around and used like a cushion. It was however more structured than the numerous leaf cushions we recorded.

Ground nests used during the day most of the time consisted of very simple structures really comparable to cushions that were apparently used exactly the same way as humans, in an objective of comfort, to isolate the body from the ground (humidity, dirt, insects…) during few minutes or few hours of low activity. Night ground nests are used during a period of high vulnerability that confers them the additional vital function of protecting an unconscious organism from predators, parasites, or cooler night temperatures, but to some extent they deserve the same function (Koops 2012). Although we reported the existence of 2 the categories of classically recognized ground nests, we believe important to free ourselves from such a dichotomic approach of ground nesting, to study the cultural adaptation underlying this behavior. Fig. 43 illustrates a terrestrial nest difficult to categorize because it was relatively thick and structured, but has apparently been used as a cushion, displaced between different places around.

In the Seringbara region (northeastern part) of Nimba, a distinct chimpanzee community built 9.5% of ground nests (144/1520), but only about 1% of total were exclusively made of THV and considered as day rest nests (Koops et al. 2012). Despites differences in the rates of day and night ground nests, these studies emphasize the unusual habit of Nimba chimpanzees to build an important proportion of their nests on the ground. The vegetation and climatic conditions associated to the harsh topography of high altitude habitats (steep slopes and deep/narrow valleys), where good materials for tree nests are absent, are ecological factors favoring this behavior. The predation pressure exerted on Nimba chimpanzees is expected to be low (Granier et al. 2012a, 2012b), which is a necessary condition to have such a relatively high proportion of terrestrial nests. Nevertheless, these ecological characteristics of habitat remain insufficient to explain what motivate chimpanzees to nest on the ground. Further studies are needed to investigate the intermingled factors shaping this behavioral variant of Nimba chimpanzees, which seem to reflect a cultural trait proper to some Nimba chimpanzees.

VI.1.5. Abundance

Density was estimated using the standing crop and the marked nest count methods from line transect utilizing either individual nests or nest groups (Tutin and Fernandez 1984; Plumptre and Reynods 1996; 1997). Provided estimations were ranging between 0.14 and 0.65 chimpanzees per km^2, which corresponds to a population of 8 to 39 individuals in the entire study area (60 km^2). In the Taï Forest National Park in Côte d'Ivoire, which is situated 230 km southerly from Nimba and presents relatively similar habitats (exepted orophilous ecosystems), Kouakou et al. (2009) estimated a global density included between 0.69 and 1.76 chimpanzees per km^2. It is interesting to note that 14 years ago Marchesi et al. (1995) evaluated a density of 1.7 chimp per km^2 in all the protected areas of Côte d'Ivoire. Thought their estimates remain of the same order of magnitude than ours, the comparison of extreme values between Kouakou et al. (2009) and our study, shows a density 3 to 4 times lower in Nimba compared to Taï. Our results may be particularly low for methodological considerations exposed in chapter III, but we acknowledge that the total transect length (12.5 km) may have been slightly insufficient to reliably represent the entire study area in regards of the exigeant chimpanzees criteria of nesting-site selection.

The marked nest count method using nest groups, which gave a density of 0.46 chimpanzees per km^2, emerged as our most reliable estimates (Tutin and Fernandez 1984; Hashimoto 1995; Kouakou et al. 2009). Such a density would correspond to 28 individuals, which is a relatively small community in regards to the study area size and to the forested nature of habitat (Baldwin et al. 1982). Indeed, chimpanzees are known to live in communities of 5 to 150 individuals (Nishida 1968; Sugiyama 1973) sharing a territory whose size is correlated to the type of habitat, with larger ranges in more open (less-wooded) habitat (Tutin et al. 1983). Nevertheless, 9 research sites on forest- and woodland-dwelling chimpanzees produced home range estimates of fewer than 40 km^2, and averaging 12.5 km^2 (Tutin et al. 1983, Pumptre et Reynolds 1996). Our density estimates provide a snapshot of the status of chimpanzees dwelling in a limited area of Nimba, during one year in 2010-2011, but they constitute solid baseline data achieved through strict field and analysis procedures. They would however greatly benefit from implementation of a long term monitoring program aiming at following the population trends. The example of the Marahoué National Park in Côte d'Ivoire, where populations have dramatically declined of more than 97% between the early 1990s and 2007 (Marchesi et al. 1995, N'Goran et al. 2007) illustrates the importance of following the population dynamics while viable groups are still remaining in their natural habitats.

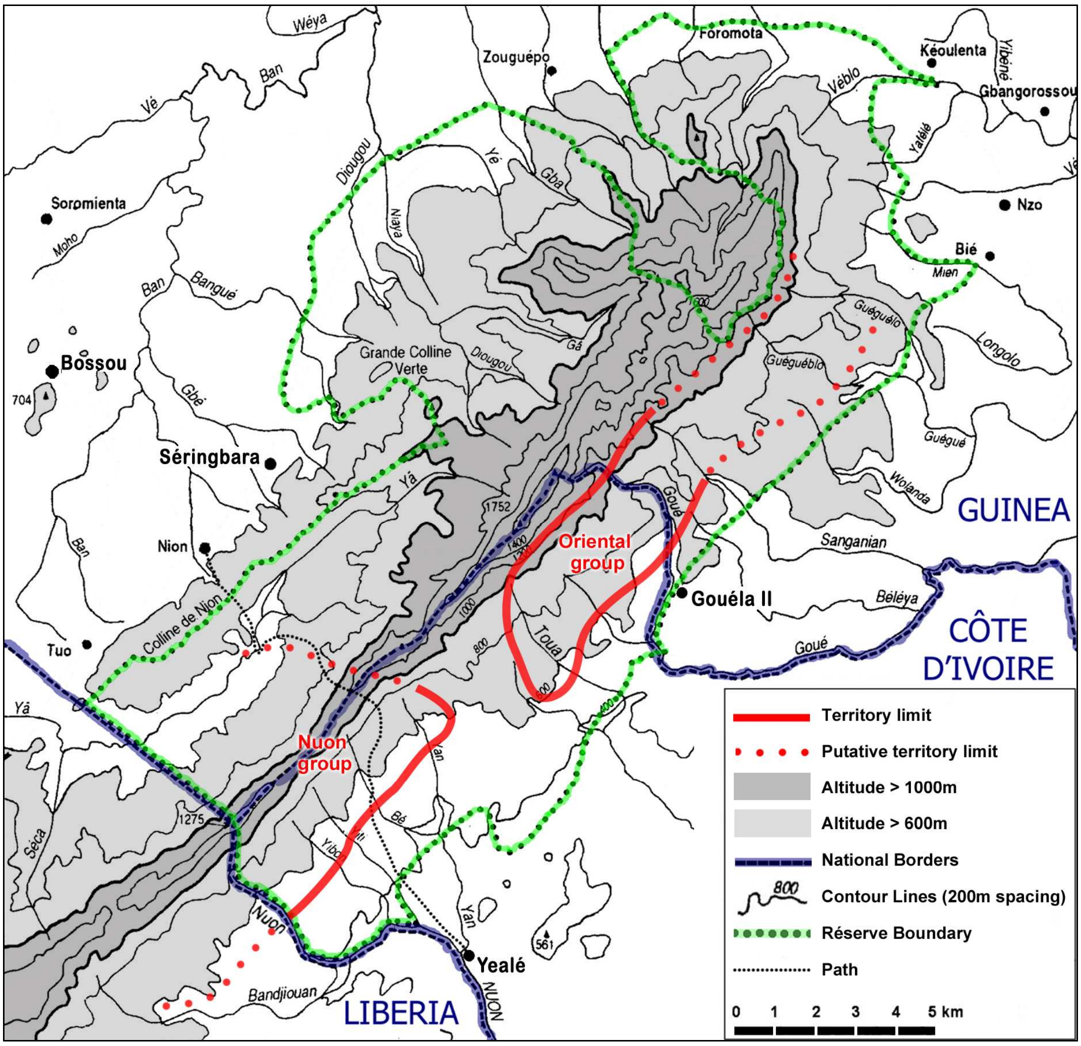
VI.1.6. General ranging patterns

Plotting all evidences of chimpanzee presence (including nests) revealed 2 clearly separated clusters suggesting the existence of 2 distinct communities in the study area. This finding confirms Matsuzawa and Yamakoshi (1996) assumption of having one chimpanzee community permanently dwelling in the Yealé forest of Nimba. We regularly observed numerous chimpanzee signs of all nature during each visit in altitude habitats around the Nuon River, suggesting this area as included in the core area of what we will call the Nuon River chimpanzee community (Fig. 44). The observed signs and nests of this Nuon community were particularly massed between 700 and 1000 m altitude with apparent seasonal variability which was not statistically significant. We did not conduct frequent surveys in the Liberian side of Nimba, explaining that we will not formulate here any hazardous hypothesis on the extent of the home range of this community behind the Nuon River. However, we often heard chimpanzees vocalizing in the very highest part of the relief slope, and local people walking on the path linking Yealé to Nion villages (Fig. 44) also reported such acoustic observations near the ridge, in very steep slopes exceeding 70% in declivity covered of low-forest. This development aims at reporting the possibilities for the territory of the Nuon community to extend either southwesterly on the same slope of the mountain, or northwesterly, embracing both slopes of Nimba (Fig. 44). Further detailed studies targeted on this Nuon community will allow characterizing its home-range with more precision. However that may be, individuals of this community also exploited the upper parts of the Yibon, Yiti, Bé and Yan Rivers located northeasterly from Nuon, where we observed a continuum of densely distributed signs of their presence. Matsuzawa and Yamakoshi (1996) indeed located a main chimpanzee track in the range of the Nuon River community that was roughly following the 800 m altitude contour line. They observed all the ground nests (n = 164) above this track, in steep mountainside covered by zones of small trees, bushes and grassland. Although we did not observe such a high proportion of ground nests, our altitudinal analysis of the different types of chimpanzee signs corroborated the idea that chimpanzees selected higher altitude habitats for resting (maximum expected number of resting-related signs at 975 m altitude), than for feeding or traveling. Feeding behavior was more likely to occur at 900 m altitude, and chimpanzees were prone to traveling at 800 m altitude. This latter altitude interestingly corresponds to the altitude of the main chimpanzee track reported by Matsuzawa and Yamakoshi (1996).

Very few chimpanzee sign observations were done between the Yan and Toua Rivers located in the middle of the study area (Fig. 36), suggesting this zone as a buffer between the territories of 2 communities. This zone apparently avoided by chimpanzees corresponds to the ecological limit of vegetation partitioning reported by Schnell (1998), between the presence and absence of altitude grasslands and between forests of more ombrophilous or more mesophile type (chapter VI.1.1.1.). In other words, the ranges of the 2 community territories interestingly appeared superimposed to the ecological partitioning of Nimba vegetation.

We called the second chimpanzee community dwelling in the Ivorian part of Nimba the oriental group (Fig. 44). In a general manner, we observed more signs and nests over 1,000 m altitude in this oriental community compared to the Nuon group, which may at least partly be explained by the highest altitude of the mountain. In addition, the spacing between observations of their signs and nests was more important than in the Nuon group. This dispersion appeared to result from seasonal variations in habitat-use mainly related to feeding behavior. We collected numerous feeding signs around 600 m altitude between June and October revealing that chimpanzees of the oriental group were sensibly going lower to feed themselves during the rainy season compared to the dry season. However, throughout the year nests were consistently built higher than all other signs, showing that chimpanzees of the oriental community made a clear differential use of habitats for feeding and nesting.

Fig. 44: Putative ranges of the 2 chimpanzee communities in the Ivorian Nimba



The ecological limit of vegetation partitioning marked by the Yan River, happened to be also the limit between the territories of 2 distinct chimpanzee communities. The Nuon community could range either southwesterly on the southern slope of Nimba, or northwesterly embracing both slopes of the mountain. Due to the herbaceous vegetation, the higher altitude and steep slopes of the northeastern half of Nimba, chimpanzees from the oriental group are more likely to exploit principally the southern slope of the relief (thought exchanges between both sides of the ridge remain possible).

The Toua River, the stream of the Ivorian Nimba originating from the highest altitude, presents important flow rate and power, and is flanked by a large healthy gallery forest. On both banks of Toua we observed a relatively high density of chimpanzee signs, which were closer from the limit of the Reserve than in the Nuon community, but with roughly the same lower limit of altitude (around 600 m asl; Fig. 36). The Toua River area was apparently an important feeding spot for the oriental chimpanzee community, more frequently used during the rainy months. Numerous trees producing fleshy fruits eaten by chimpanzees were indeed recorded in June, August and October between 500 m and 900 m altitude on the Toua transect and the central recce loop (*Blighia welwitschii*, *Bussea occidentalis*, *Canarium schweinfurthii*, *Chrysophyllum* sp., *Drypetes* sp., *Grewia barombiensis*, *Nauclea diderrichii*, *Octoknema borealis*, *Parinari excelsa*, *Thurraeanthus africanus*…).

The core area of this oriental community would be located northeasterly in the upper Mien or Guégué Rivers (Fig. 44), where we observed large nest groups at each visit during preliminary surveys. The largest group of nests was observed in March 2006 in a forest remnant of the upper gallery of Guéguélo River and was including 24 fresh nests. Guéguélo is located between the Guéguéblo and Mien Rivers, about 10 km away from the important feeding spot of the Toua River. If this oriental community was actually ranging between the Toua and Mien Rivers, it would have a territory of about 40 km^2, which corresponds to the superior limit of what has been reported at other sites (Hashimoto 2005; Plumptre and Reynolds 1996).

VI.1.7. Cultural variations

Chimpanzee research also provides interesting insights on the understanding of early hominids' adaptations, and on the emergence and transmission of cultural knowledge in a group of social primates (Boesch and Tomasello 1998). Unfortunately, we collected scarce data, in both spatial and temporal terms on the tool use behavior of chimpanzees in the Ivorian

Nimba, preventing further description of the mechanism of cultural transmission between neighboring communities. However, such studies conducted on different chimpanzee groups in Nimba, showed intercommunity behavioral variations that were not linked to environmental differences and demonstrated the existence of different material cultures (Humle and Matsuzawa 2001). For example chimpanzees in Seringbara have never been observed cracking-open nuts, whereas in the Nuon community they have developped 2 different cracking techniques to extract and eat at least 3 different nut species (*Elaeis guineensis, Coula edulis*, *Carapa procera*; Matsuzawa and Yamakoshi 1996; Humle and Matsuzawa 2001; Fig. 17, 45). Nevertheless, Seringbara chimpanzees were more recently observed using a new percussive technology consisting of a combination of 2 tools - stone and wooden cleavers - based on a lithic substrate, to divide the large and hard fruits of *Treculia africana* into manageable sized pieces (Koops et al. 2009).

Fig. 45: Nut-cracking in Bossou chimpanzees

Nut-cracking requires precise motor coordination combining at least 3 elements. Such a skill is not mastered before the adolescence in young chimpanzees, and results from a long learning process, which can also involve active teaching.

Studying chimpanzee’s ranging patterns, as well as intercommunity movements and migrations, is also crucial in understanding how these cultural behaviors are transmitted and do evolve. For example chimpanzees of Bossou customarily crack and eat nuts of *Elaeis* *guineensis*, and are unfamiliar with 2 other nut species cracked by chimpanzees of the Ivorian Nimba (*Coula edulis*, *Carapa procera*), which do not occur in their habitat. Matsuzawa has provided nuts of *Coula edulis* to Bossou chimpanzees, who discarded them (Matsuzawa 1994). However, one female of about 30 years old readily cracked-open the coula nuts and ate their kernel. In the following days two juveniles who had observed the scene also cracked these nuts, tasted their kernel, but did not ate them. Matsuzawa proposed the coula-eating female to have been born in the neighboring Nuon community and immigrated to Bossou, where she transmitted the cultural tradition of cracking coula nuts to young members of the community. His study emphasizes the importance of social interactions and individual characters in such mechanism of cultural transmission between communities and across generations of chimpanzees. It also constitutes a very good illustration of the necessity of investigating chimpanzee material cultures in a comparative approach focused on all communities dwelling in the Nimba region.

VI.2. Conservation perspectives

The distribution of suitable environmental conditions for African great apes have shown dramatic decline in the recent years. This study inscribing in a continental perspective of African apes conservation has particularly targeted the West African chimpanzees, who have experienced a loss of –11% in their suitable habitat (see chapter I.1.).

We put together important findings on the ecology of Nimba chimpanzees and analyze them in the lights of other studies with strong perspective on the species' conservation. By doing so, we realized that the knowledge achieved during this study allowed us to reach a broader objective than initially set. Our expertise on Nimba and its primate populations indeed allowed us drawing out priority actions for monkeys/ape conservation that will concomitantly ensure the protection of Nimba forested ecosystems. As a conclusion, we offer a holistic and cohesive outlook on the sustainable protection of the tri-national Nimba region, which aims at putting all elements of expertise we acquired together, and at presenting them from a chimpanzee perspective. We also expose the key features of a purpose-built general management plan of the region, while discussing in broader perspectives of the different tools that have been used to protect the exceptional biodiversity of Mount Nimba.

VI.2.1. General context and conservation issues

The distribution of suitable environmental conditions for African apes have shown dramatic decline in the recent years (see chapter I.1.). This loss was very strong for gorillas (between –59% and –32%) and more mixed for chimpanzees (from –29% to no significant reduction). Globally, this decline was not due to disappearance of habitat patches offering suitable environmental conditions, but rather to the reduction of the size of these patches. In this alarming context, it appears particularly crucial and urgent to preserve all the patches of suitable habitat for great apes, and even to favor their increase in size or to interconnect them by creating corridors.

Chimpanzees are our closest living relatives in both biological and behavioral terms, which in itself justify studying them and ensuring their sustainable protection. We have seen that they were also good flagship, umbrella and environmental indicator species (Junker et al. 2012), which gives good reason to protect them and thereby ensure the living of numerous co-occurring wildlife species. Furthermore, DNA studies have shown that West African chimpanzees were genetically rather different from those of Central and East Africa (Vigilant 2003). It consequently appears of crucial interest to make concerted efforts to protect the West African chimpanzees, and preserve in this way the genetic diversity currently existing among the *Pan* taxa. Researchers and conservationists conducting fieldwork on this subspecies have estimated that more than half of the populations were surviving outside designated protected areas (Kormos et al. 2003; Oates 2006), indicating the urging need for developing the protected area networks of the 3 countries bordering Nimba, which are still relatively weak, particularly in Guinea (Brugière and Kormos 2009).

We focused on the exceptional biodiversity haven of the Nimba Mountain, which is one of the oldest pieces of the protected area networks in West Africa (Brugière and Kormos 2009). The reserve harbors an important chimpanzee population and was classified as one of the five priority sites for the protection of *Pan troglodytes verus* (Kormos et al. 2003). However, the Nimba is split between 3 countries (Guinea, Côte d'Ivoire and Liberia), and has a complex history presented in chapter I.2., which complicates the implementation of global actions of research and conservation. We present below how in this multifaceted context, our local scientific contribution aiming at describing basic traits of Nimba chimpanzee's life history and assessing their specific ecological requirements, can readily and efficiently be applied to their sustainable protection.

Fig. 46: The labile relationship between savanna and mountain forest in the Zié valley

Photograph of the northern more part of Nimba

VI.2.2. Findings on chimpanzees of the Ivorian Nimba

VI.2.2.1. Tree species of particular interest for conservation

We collected numerous and important baseline data on the general ecology of chimpanzees in the Ivorian Nimba. The achieved knowledge has enlightened the preponderant importance of

53 ligneous species in the daily life of chimpanzees. Throughout the year, these species of trees and lianas were significantly more selected than expected from their general availability to build nests or eat fruits. We established them as of particular concern for chimpanzee conservation (Table 14). We note that *Parinari excelsa* and *Pouteria altissima* were used for both feeding and nesting, and should consequently be subject to particular attention. All the more because *Pouteria altissima* is classified in the IUCN red list of threatened species (IUCN 2014; Table 14). Eight other species are also listed by the IUCN, including *Nauclea diderrichii* (a preferred food for chimpanzees), which is listed as 'Vulnerable' (Table 14). Indeed in Nimba, local people exploit both ligneous and non ligneous products of some of these species to eat, treat themselves or build their huts, fences and benches, make pestles, mortars, percussions and many other things of the daily life. Some of these tree species of commercial value are moreover exploited by logging companies across Africa, as it has been the case in the Déré forest at the end of the 1990s.

Chimpanzees used a total of 114 vegetal species for nesting, including 108 woody plants, 3 Marantaceae and 3 Zingiberaceae. We considered the 10 most used nesting-tree species, added to 11 other species that were clearly more actively searched for nesting in regards of their general availability, as the 21 key nesting-trees of prime importance for chimpanzee conservation in the southern slope of Nimba (Table 14).

Table 14: The 53 tree species of particular interest for chimpanzee conservation

Species	**Chimp use**	**Family**	**IUCN**
Alchornea cordifolia	Food	Euphorbiaceae	n/a
Alstonia boonei	Food	Apocynaceae	n/a
Amanoa bracteosa	Nest	Euphorbiaceae	Vulnerable
Anthonotha fragrans	Nest	Leguminosae-Caes.	n/a
Anthonotha macrophylla	Nest	Leguminosae-Caes.	n/a
Antiaris toxicaria	Food	Moraceae	n/a
Blighia welwitschii	Food	Sapindaceae	n/a
Bussea occidentalis	Nest	Leguminosae-Caes.	n/a
Canarium schweinfurthii	Food	Burseraceae	n/a

Carapa procera	Nest	Meliaceae	n/a
Chrysophyllum africanum	Nest	Sapotaceae	n/a
Chrysophyllum giganteum	Food	Sapotaceae	n/a
Chrysophylum	Food	Sapotaceae	n/a
Cola caricaefolia	Food	Malvaceae	n/a
Corynanthe pachyceras	Nest	Rubiaceae	n/a
Coula edulis	Food	Olacaceae	n/a
Dacryodes klaineana	Food	Burseraceae	n/a
Diospyros cooperi	Nest	Ebenaceae	n/a
Diospyros mannii	Food	Ebenaceae	n/a
Drypetes inaequalis	Nest	Euphorbiaceae	n/a
Drypetes leonensis	Nest	Euphorbiaceae	n/a
Drypetes pellegrini	Food	Euphorbiaceae	Vulnerable
Garcinia kola	Food	Guttiferae	n/a
Grewia barombiensis	Food	Malvaceae	n/a
Gilbertiodendron limba	Nest	Leguminosae-Caes.	Near Threatened
Hannoa klaineana	Food	Simaroubaceae	n/a
Heritiera utilis	Nest	Malvaceae	Vulnerable
Irvingia gabonensis	Food	Irvingiaceae	Near Threatened
Landolphia dulcis	Food	Apocynaceae	n/a
Landolphia hisrsuta	Food	Apocynaceae	n/a
Landolphia incerta	Food	Apocynaceae	n/a
Landolphia owariensis	Food	Apocynaceae	n/a
Mammea africana	Food	Guttiferae	n/a
Mangbeulügon	Nest	n/a	n/a
Milicia excelsa	Food	Moraceae	Near Threatened
Napoleonaea vogelii	Food	Lecythidaceae	n/a
Nauclea diderrichii	Food	Rubiaceae	Vulnerable
Neostenanthera gabonensis	Nest	Annonaceae	n/a
Octoknema borealis	Food	Olacaceae	n/a
Ongokea gore	Food	Olacaceae	n/a
Panda oleosa	Food	Pandaceae	n/a
Parinari excelsa	Nest,	Chrysobalanaceae	n/a
Parkia bicolor	Food	Leguminosae-Mim.	Least Concerned
Pouteria altissima	Nest,	Sapotaceae	Near Threatened
Pouteria aningeri	Nest	Sapotaceae	n/a
Protomegabaria stapfiana	Nest	Euphorbiaceae	n/a
Pycnanthus angolensis	Food	Myristicaceae	n/a
Spondianthus preussii	Nest	Euphorbiaceae	n/a
Synsepalum afzelii	Food	Sapotaceae	n/a
Tetracera alnifolia	Nest	Dilleniaceae	n/a
Trichilia heudelotii	Food	Meliaceae	n/a
Uapaca guineensis	Food	Euphorbiaceae	n/a
Xylopia villosa	Nest	Annonaceae	n/a

Although our preliminary findings on chimpanzee diet resulted in the identification of 87 vegetal foods, we considered only the 45 principal species of this study as the most important food resources. As a reminder, these principal species were selected as the ones producing fruits that were the most frequently eaten year-round by chimpanzees in the southern slope of Nimba, and that were simultaneously the most represented along the 3 transects. However, these 45 species do not all have equivalent conservation significance: in particular, the pioneer tree species and certain large species characteristic of secondary forest, which are permanently expanding under the facilitation of fire (see chapter VI.2.2.2.), are rather considered as invasive species. We consequently excluded 11 widespread species that constituted large and colonizing populations which were not threatened of extinction in Nimba nor globally (neither classified in the IUCN red list and CITES), and that were found in different types of habitat.

VI.2.2.2. Importance of secondary vegetation and altitude habitats

Though secondary vegetation is not at first sight of great conservation value, it sustained chimpanzees all year round in the southern slope of Nimba, and with more intensity during the period of relative fruit food scarcity (the dry season, from December to April; Fig 47). At Tiwai Island in Sierra Leone, this secondary vegetation has been proved to also constitute an important habitat for several species of large mammals, such as primates and artiodactyls, which used it more than expected from general availability (Fimbel 1994). Such regrowth habitat appeared particularly more valuable to primates in period of general fruit scarcity. These findings corroborate ours concerning the distribution of monkeys and prosimians species in Nimba, enlightening the central role of regrowth habitat in the diet of several primate species, and its importance for the conservation/management of wildlife.

Secondary vegetation may be beneficial for various animal species, but it remains extremely important to maintain and encourage tracts of old growth forest, which support a greater diversity and biomass of primates per unit area than secondary forest (Fimbel 1994). High forest remnants also act as refuges and re-population centers for surrounding degraded habitats (Struhsaker 1972).

Fig. 47: Old secondary forest

Concerning chimpanzees, it is of crucial importance to understand if their preference for secondary forest represents an optimal situation they actively chose – i.e. a condition of optimal fitness between the species and its environment -, or if it expresses an adaptation to a changing habitat in which mountain forest is declining. To achieve this understanding, further studies are needed in lights of chimpanzee ecology, to investigate how the secondary vegetation evolves in Nimba under the conflicting influences of natural regrowth process and bushfires. It is of particular interest to monitor this evolution at the edge between altitude forests (mountain and upper parts of galleries) and grasslands, where bushfires act as a catalyst of savanna extension to the detriment of forest (Schnell 1951). At several occasions, the local field assistants indeed testified of the colonization phenomenon of altitude herbaceous vegetation on altitude forest (White 1986). They showed places that presented a closed canopy when Matsuzawa and Yamakoshi (1996) first visited the Nuon River area in 1994, and where no tree remained at the time of this study (personal observations). The emerging question that the conservationist willing to address forest loss should ask before starting his efforts, is to understand what exactly do chimpanzees need in the secondary vegetation, and whether they can find it in other habitat or not. Stopping the decline of mountain forest, for example by enforcing the law related to the rational use of fire, should progressively reduce the extent of secondary forest under the dominant influence of natural regrowth. But we should first wonder if chimpanzees will be able to find an alternative strategy to compensate for the lack of resources they are currently finding in such regrowth habitats.

VI.2.2.3. Primates as umbrella species

Most primates are primarily frugivorous, and they represent 25 to 40% of the frugivore biomass within the tropical forest they exploit (Chapman 1995). Their relatively large-bodied size makes them particularly efficient seed dispersers, and numerous evidences of their implication in the diversity, demography and recruitment of plant species in forest ecosystems are now available from throughout the tropics (Lambert 2010). However, about half of world’s extant primate species are of conservation concern (IUCN 2014). Limited funding and time in regards of the great extent of wildlife diversity do not allow developing research and conservation efforts targeting each plant and animal species. A conservation shortcut applied by Fleishman et al. (2000) consists of selecting particular taxa as representative of a given biocenosis, and focusing all efforts on these ‘umbrella’ taxa. All the difficulty of applying this tactic lies in the selection of these umbrellas. Following Roberge and Angelstam (2003) definition of umbrella species: “a species whose conservation confers protection to a large number of naturally co-occurring species, and the important mutualisms among them”, Lambert (2010) defined 3 criterions to select a relevant umbrella taxon. First, it should exhibit greatest richness and co-occurrence with taxonomically similar species; second it should be neither extremely rare nor extremely common; and finally be moderately sensitive to human disturbance - i.e. neither completely extirpated nor able to exploit heavily human-modified landscapes. On this basis, Lambert (2010) selected the *Cercopithecus* monkeys (guenons), which are the most efficient seed dispersers among the important diversity of frugivorous species dwelling in Afrotropical forests, as the best umbrella taxon of the Kibale Forest in Uganda.

Our results showed that Nimba chimpanzees in the southern slope of Nimba were clearly selecting the same habitats than the 7 other primate species (including 4 *Cercopithecus* species), and we sometimes observed polyspecific associations between *Pan* and *Cercopithecus* species (personal observations). Such sympatry between chimpanzees and guenons are moreover known to be relatively common (Gautier-Hion et al. 1999; Russak and McGrew 2008). The chimpanzee also functions as an umbrella species (Junker et al 2012), though less accurately than guenons (Lambert 2010), however great apes are amongst the best flagship species. These statements lead us to the conclusion that a mixed approach of research and conservation targeting the *Cercopithecus* monkeys and the chimpanzee, would be a very efficient way to raise funds and efficiently act for the preservation of a large range of wildlife species, and thereby ensuring the sustainability of all Nimba forested ecosystems.

VI.2.3. Global Threats to chimpanzees

Wild chimpanzee populations across Africa are facing general threats to their survival, which are extensively presented in chapters I.2.4. and II. We rapidly mention the agriculture and hunting as subsistence activities of local people, logging and mining, which all induce habitat loss, degradation and fragmentation. In addition, the deadly outbreaks of infectious diseases represent a growing menace, with more than 140 viral, bacterial, fungal or parasitic identified pathogens shared between humans and the great apes (Formenty et al. 2003). At the time of writing this dissertation, a violent epidemic of Ebola hemorrhagic fever is hitting Guinea, Sierra Leone and Liberia. Reaching for the first time West Africa, the virus, first identified in January 2014 at 150 km northwesterly from Nimba, belongs to a new strain of the *Zaire ebolavirus* (Baize et al. 2014), a particularly virulent form which is at the origin of the worst epidemic ever known on human beings. However no information is available yet concerning its impact on the chimpanzee population and investigative surveys are needed as soon as possible. The pet trade also seriously jeopardizes chimpanzees throughout equatorial Africa (Carter 2003), but this activity does not seem to occur in Nimba presumably due to the long-term presence of researchers who also participate in local development. The 2 most threatening menaces hanging over the sustainable living of chimpanzees and wildlife in the tri-national Nimba are the subsistence activities of local people associated to the non-rational use of fire, and the mining activity. They are presented in the paragraph below together with propositions to mitigate their impact.

VI.2.4. Holistic approach of biodiversity conservation in the nimba region

– A chimpanzee perspective –

The raison d’être of this study was to provide an applied research that could readily be used to lead actions for the conservation of great apes across Equatorial Africa. We made the choice of focusing on chimpanzees in the Nimba Mountain as such a large and multifaceted objective can only be achieved by the collaborative and cumulative efforts of all researchers and conservationists working in each site where apes are still present. Aware that an essential preliminary step to efficiently protect something is to achieve good knowledge and holistic understanding of it, it rapidly became highly tangible that it was not possible to consider a species separately from its environment. We enhanced the thorough description of the ecological environment of Nimba chimpanzees in the early moments of the present study, with the will to achieve the most complete view and embracing disciplines as varied as geology, topography, climate, botany and forestry. But in the course of this (relatively) long experience in the Nimba region, we felt a growing interest for the historical, anthropological, political and socio-economical contexts, which constitute inherent environmental characteristics with direct consequences on the life history of chimpanzees. Aware that a single person could not rightly embrace all these topics, we humbly realized that all the knowledge achieved on the Nimba region since 2002 has allowed us to attain broader objectives not limited to great ape conservation, but rather addressing the general thematic of natural resources sustainable management. This part offers a holistic and cohesive outlook on the sustainable protection of the tri-national Nimba region. It aims at putting together all the elements of expertise we acquired on this extraordinary biodiversity area, and to present them from a chimpanzee perspective. We expose the key features of a purpose-built general management plan of the Nimba region, while discussing in broader perspectives the different tools that have been used to protect its natural habitats.

VI.2.4.1. General measures

We present in this part the measures that should be taken at the scale of the entire Nimba sub-region to alleviate the impact of subsistence activities of local people, and refine our understanding of natural habitats. To be efficient, these activities should be implemented on a permanent basis in collaboration with local people.

VI.2.4.1.1. Subsistence activities of local people

The nomad technique of slash and burn farming associated to the overgrowth of human population has considerably increased the need for arable land. A larger local population also draws more intensively on the wild faunal resource to fulfill its protein needs. It is of high importance to collaborate with local people on the reduction of the hunting pressure exerted on fauna. Sources of proteins alternative to bushmeat should be identified and sustainably set up, for example by favoring the development of animal breeding or fish farming. Furthermore, research is definitely needed to develop ecologically sound, low-input farming processes with improved agricultural techniques and better production rates. It is of prime importance to work with local people on integrating agriculture and forest management to maintain the long-term health of West Africa's forests. An increase in the amount of old-growth forest will benefit to the forest wildlife populations, but also to the human populations that rely on plant and animal products present in these ecosystems (Davies and Richards 1991).

VI.2.4.1.2. Ecological monitoring

To refine our understanding of the natural habitats, their evolution and trends, it is critical to study the forest phenology at broader spatial and temporal scales than what we did in the present study (chapter VI.1.2.2.). The Nimba region is too vast and too rich to imagine implementing a monitoring program targeting all plant species. It should consequently uppermost focus on the plants of critical conservation value for the ecology of the *Cercopithecus* monkeys and chimpanzees considered as umbrella species. Such a long-term program of ecological monitoring of primates will at the same time provide data indirectly enabling the sustainable protection of the exceptional biodiversity of the Nimba Mountain. The ecology of *Cercopithecus* monkeys should be further investigated in the Nimba region, in order to obtain an accurate view on their most important resources and habitat selection across seasons. Once available, these results will be integrated to data available on chimpanzees to complete the list of species and range of habitats of important conservation concern for primates. This ecological monitoring should focus on all kinds of forest habitat in the region, since primates actually exploit all of them. However, a particular interest should be paid at understanding how the secondary vegetation evolves (chapter VI.2.2.2.), and this should be achieved should be done through a GIS approach allowing to map this evolution, for example annually.

Concerning only chimpanzees, for which data are already available, this monitoring activity should primarily focus on fruit phenology of the 34 important food species which constitute the most eaten and vulnerable fruit resource of this ape in the southern slope of Nimba (Table 14). It will also aim at mapping the spatial distribution of these important foods together with the 21 most important nesting-tree species. This follow up will be concurrently conducted on a selection of important large trees producing fleshy fruits eaten by chimpanzees throughout the Nimba region (*Antiaris toxicaria*, *Canarium schweinfurthii*, *Nauclea diderrichii*, *Parinari excelsa*…) in order to evaluate the quantity of suitable habitat for the species and study the population movements. This action will be conducted following Balcomb et al. (2000), who showed the existence of a positive relationship between chimpanzee abundance and the density of large, fleshy-fruit trees in the Kibale Forest, Uganda. They combined 2 techniques of forest reconnaissance method to identify the presence/absence of chimpanzees, and perform quick density estimates of large, fleshy-fruits trees, to provide an effective and efficient mean of determining appropriate chimpanzee habitat to which allocate conservation efforts.

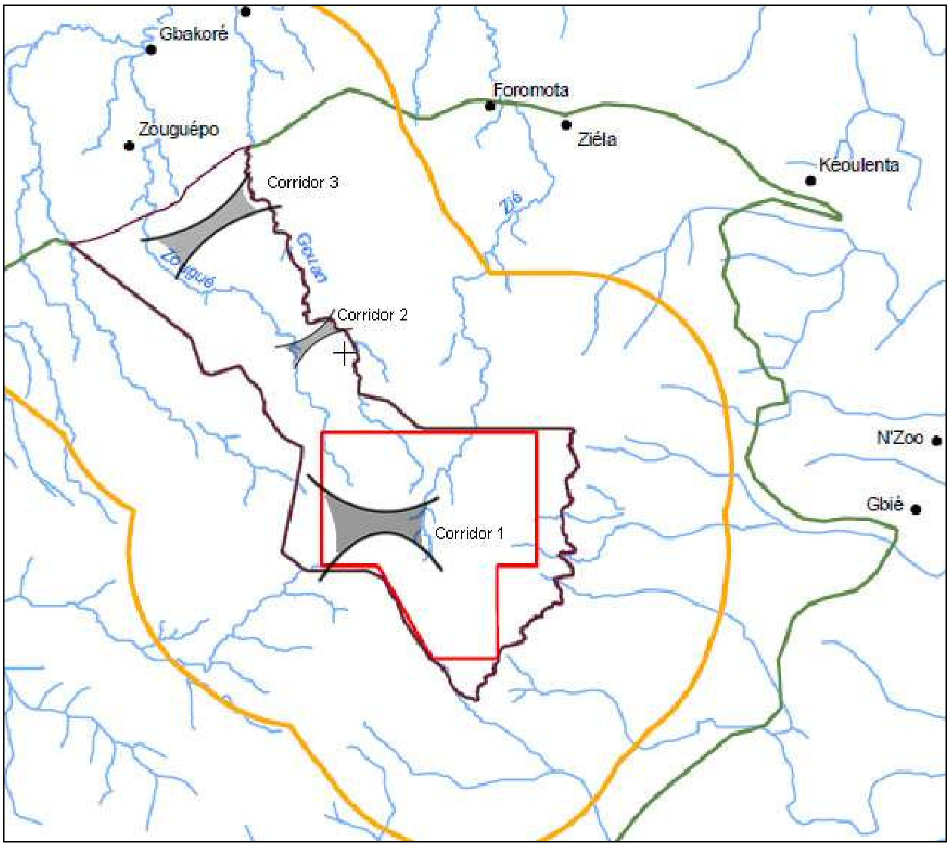
VI.2.4.2. Mount Nimba

Due to its very particular biogeomorphological characteristics, the relief of Mount Nimba is the biodiversity reservoir justifying all past, present, and future efforts of research and conservation in the area. Adamantly protected since 70 years, it is relatively low-impacted by agricultural activities of local people who settled outside the reserve limit after being chased in the early 1940s (JO-RF 1944). More recently, the extractive industry probably used more convincing arguments to obtain the declassification of a mining enclave within the reserve limit (Fig. 48). In 2012, an 8-year drilling phase aiming at designing its exploitation plan was completed. Mining in Liberian Nimba lasted 29 years and has left indelible scares in landscape and ecosytems. This perspective, which has been very seriously hanging over the Guinean section of Nimba, has been avoided several times since the 1960s before finally being concretized in 2003.

VI.2.4.2.1. Mining mitigation

The socio-political opening of Guinea since the years 2000s has favored a considerable increase of activities from the extractive industry throughout the country. The declassification of the 1,550 ha mining enclave in the northeastern end of the Nimba World Heritage site in 1993 was anticipation to this development (Hartley et al. 2008). This enclave almost reaching 4 km in its largest part constitutes a clear-cut in the oriental part of the massif’s northern slope, which extends beyond the crest on the altitudinal part of the southern slope (Fig. 48).

Fig. 48: The mining enclave and the 3 proposed corridors



Schematic map of the mining enclave (appearing in burgundy) and mining concession (in red), with the limits of the study area in orange and of the reserve in green.

In the framework of an environmental impact assessment of mining activity in the Guinean Nimba, we conducted 2 baseline studies on the large mammals populating the mining enclave and surroundings (Granier et al. 2012b). In this northeastern part of Nimba, the mountain forest of old secondary type also appeared as an important habitat for all primate species (Granier et al. 2012a). To mitigate the effects of such a clear-cut in the northern slope of Nimba, we proposed among other things the creation of three corridors to allow and favor faunal exchanges between the left and right sides of the enclave (Fig. 48). The apical corridor (1) stands in the altitude grasslands within the mining concession, interconnecting the upper and forested parts of 3 major valleys of the massif’s northeastern end: the Gâ, Gba and Zié Rivers. These valleys all contained numerous signs of chimpanzee presence and nests, as well as signs of multiple primate, artiodactyl and carnivore species. They have indeed been known for long to contain a rich and diverse fauna (Lamotte 1942, Lamotte and Roy 2003), but it is less known that the Zié River is sacred for the Manon people living in the village of Ziéla located downstream near the reserve limit. Mining consequences will simply be catastrophic for both human and wildlife living along the Zié River. The corridor 2 was proposed to enable the safe crossing of an important population of buffalos (*Syncerus caffer*) that we described on 2 large plateaus bordering both sides of the enclave. And the corridor 3, located in the low altitude evergreen rainforest was proposed for species dwelling in lowland forest, in particular the numerous primate and artiodactyls species we observed.

VI.2.4.2.2. On the value of biodiversity sanctuaries

Our results provided an update confirming the high richness and conservation value of the Nimba fauna and these despite the 8-year existence of a noisy mining camp, as well as the large and numerous drilling engines. In contrast with the negative perspectives of conservation associated to mining, we here report a positive side-effect: mining seems to have improved the enforcement of environmental protection laws. The start of the mine was associated to the reinforcement of the control of human displacements in the mining enclave. Initiated at the beginning for security reasons, this effort resulted in a more efficient enforcement of the interdiction to enter the enclave than in the adjoining full nature reserve. Granier et al. (2012b) surprisingly reported that in the zones of the enclave where the only activity consisted of vehicles going back and forth without stopping – i.e. in the lower part of slope forest –, the large fauna population appeared to be more abundant than in the Biosphere Reserve. The enclave would have constituted a faunal shelter or refuge attracting bovids and primates, living there at higher densities, possibly due to the absence of poaching. This preliminary findings need to be confirmed on the long-term, but they already show the importance of creation and enforcement of faunal sanctuaries for wildlife conservation.

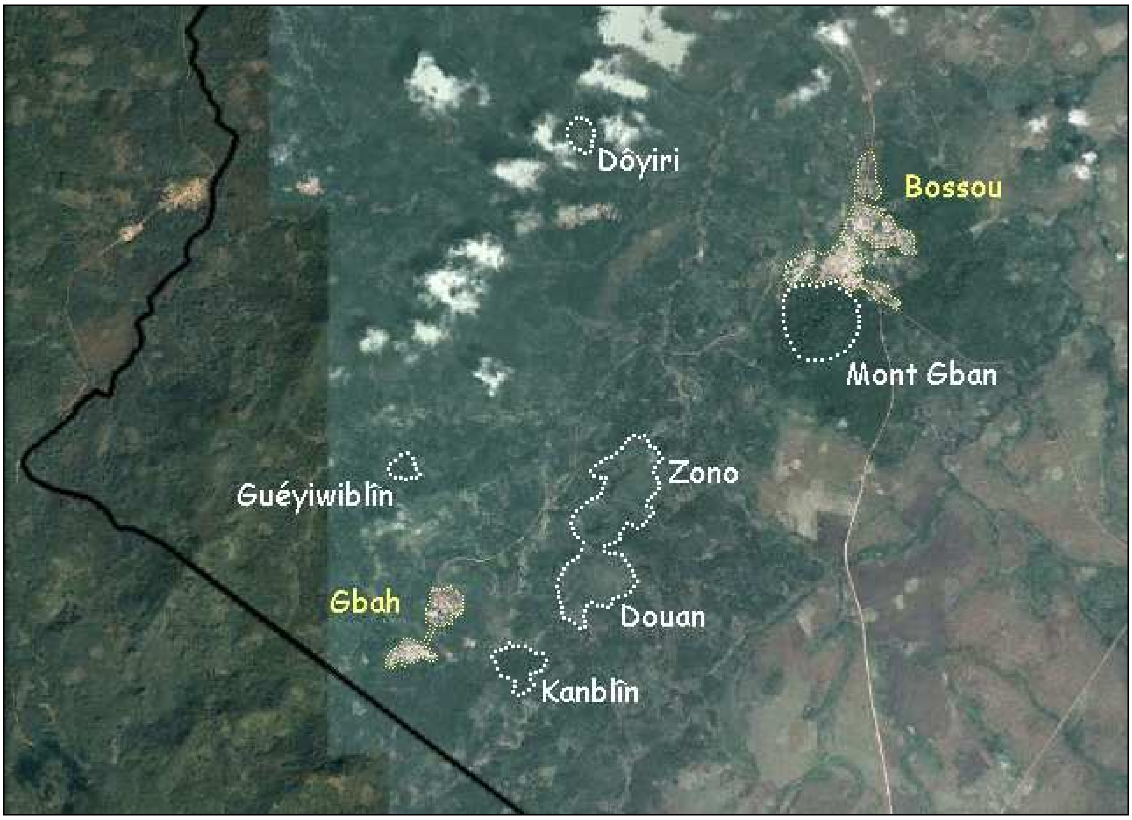
Establishing a fully protected area has always been controversial because other people always had other plans for the designed area. It poses further ethical questions in the case 'exogenous' people impose this choice to native populations. On the other hand, we have to admit that presumably very few of the Nimba forest and fauna would have survived to the growing human pressures of the past 2 decades without their sanctuarization (Hartley et al. 2008). To fully preserve a zone as a reservoir for the regeneration of wildlife has indeed proved to be particularly efficient in terms of resource sustainability (Chardonnet 1995; Lamotte 1998).

It was of course not respectful for the local people of 1943 to chase them from the current Nimba reserve, but today the persistence of this unique biodiversity, its rich fauna and flora, and the abundant water flowing down its steep slopes are still ensuring the living of a large local population. The Nimba relief is drained by a dense and highly branched hydrographic network containing the sources of 3 large rivers flowing to the Atlantic Ocean, which fulfill the water needs of hundred thousands people in Guinea, Côte d'Ivoire and Liberia. We believe important to continue collaborating with local people in the preservation of Nimba forests to limit soil erosion and thereby ensure the perpetual water flow of these rivers.

VI.2.4.3. Bossou hills and chimpanzee research

Due to the long research history on Bossou chimpanzees, considerable knowledge were achieved on many aspects of these chimpanzees' life history and habitat (Matsuzawa et al. 2011), which will not be developed here. However, we conducted systematic surveys of the large mammals populating the Bossou hills in 2007 (Granier et al. 2007), and surveyed chimpanzees throughout the sous-prefecture of Bossou in 2012 to evaluate their presence farther from the village (Granier et al. 2012c). The large fauna revealed to be relatively poor (due to a high human encroachment), and no other chimpanzees were observed. The only, but huge potential of faunal conservation in the entire sous-prefecture emerged to be the well-studied Bossou chimpanzees. But despite the long term efforts of research and conservation on this community, it is also facing serious menaces putting its survival at risk (Fujita 2011; Matsuzawa et al. 2011a; Humle 2011a). The community becomes more and more isolated from other groups of the Nimba forest, and is facing a serious inbreeding problem due to the absence of immigration since 1982 (Sugiyama 1984; Sugiyama and Fujita 2011). In order to favor chimpanzee immigration into Bossou group, a green corridor project was initiated in 1997, planting trees on a 4 km long and 300 m wide strip in the middle of the savanna stretching at the Nimba foothill (Granier and Martinez 2011; Matsuzawa et al. 2011a).

Fig. 49: Important places for chimpanzees between Bossou and Liberia.



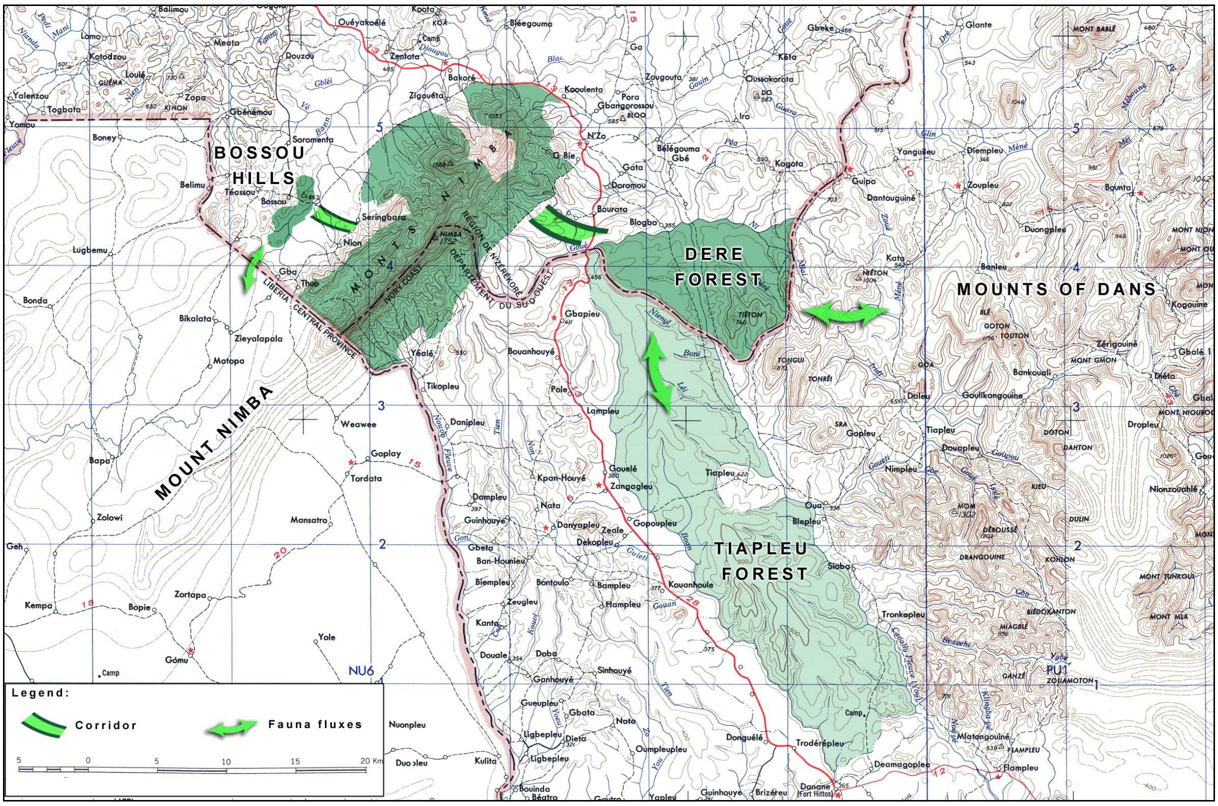
Chimpanzees go down the Mont Gban to rejoin the Zono and Douan hills, and then continue to the Kanblîn traditionally protected forest where we observed numerous recent Dôyiri et Guéyiwiblîn sont are other sacred forest, and though we did not recorded chimpanzee signs there, we believed important to mention them.

Some members of Bossou group periodically visit the Nimba Mountain located southerly or the forest of the neighboring Liberia located westerly (Ohashi 2006). The suggestion we did was to favor the crossing of Bossou chimpanzees to Liberia (Granier et al. 2012c; Fig 49), and that the setting of this route may favor the immigration of exogenous individuals. However the creation of a corridor, which would be more useful for foreign chimpanzees than for Bossou chimpanzees, is difficult to envisage in this place almost entirely devoted to agriculture (Fig. 50). The local farmers, who were chased from the Bossou hills in 1993, need land to cultivate and we do not have reliable data available on potential chimpanzees that could immigrate from the Liberian side.

VI.2.4.4. Déré Forest and mining offset

According to local people the Déré Forest still existed in the late 1980s, and harbored a continuously closed canopy throughout the 8,000 km^2 of its range. It was firmly protected under the local custom and laws, and was serving for traditional ceremonies such as sacrifices and initiation rites usual in animist societies. This type of traditional protection measures (which relate to both forest and fauna) are found in many African countries, and have been existing long before modern conservation became influential (Yamakoshi 1998). They are efficiently enforced by all local people, who are actors of these classifications, and have direct interest in respecting the associated prohibitions. But persons with other beliefs or priorities can be more inclined to infringe such local laws, and as the result of complex sociological, economical and political factors intermingled between the 3 countries, in less than 30 years the Déré Forest has been almost entirely replaced by crop fields. The pigmy hippopotamus (*Hexaprotodon liberiensis*, Endangered in the IUCN red list of threatened species; IUCN 2014) has fled downstream the Cavally River in the neighboring classified forest of Tiapleu, in Côte d’Ivoire, whereas the chimpanzee was pushed back to the Mounts of Dans in Côte d’Ivoire, though he was still occasionally entering the Déré Forest in 2006 (Granier et al. 2007; Fig 50). The Mounts of Dans is a very large stretch of forested hills and mountains extending westerly of the Déré forest towards the city of Man in Côte d’Ivoire. It is not classified but do contain chimpanzee populations (personal observation).

Fig. 50: Green network for chimpanzees and large fauna of the Nimba region



This map sums up the propositions of this dissertation to ensure a sustainable environmental management of the Nimba region and the persisitence of the Nimba massif as a faunal reservoir.

Things ran out of control in Déré from 1999, when the logging company started to operate in the forest and in 2001 after the departure of loggers, when many farmers settled within its limits. So it is actually relatively recent. Considering the very high past conservation value of the Déré Forest (Wright et al. 2006), as well as the will of the Guinean government to enlarge its protected area network and to particularly recover this forest, we believe that something should definitely be done. With the conviction that it is not possible to continue losing biodiversity at such a frenetic rate, and in accordance with the emerging concept of “no net loss”, we would like to see the mining company operating in Nimba invest efforts in the re-establishment of the Déré Forest as a wildlife sanctuary.

Fig. 51: The Nimba Mountain from the Déré Forest

Picture taken from a freshly burned field within the Déré Forest, and aiming at illustrating the feasibility of a corridor project between Déré and Nimba.

No net loss is one of the answers to curb the current loss of biodiversity. It can be defined as the “point where biodiversity gains from targeted conservation activities match the losses of biodiversity due to the impacts of a specific development project, so that there is no net reduction overall in the type and amount of biodiversity present, over space and time”. With the firm will to reverse the balance of the perpetual biodiversity loss, we prefer substituting the concept of “net gain” to the no net loss presented above. To reach this objective in the Biosphere Reserve of the Nimba Mountain, the mining company should as an offset measure for the loss, degradation and fragmentation of the exceptional ecosystems of the Mount Nimba, financially support the Guinean government in its effort of ratifying the classification of the Déré Forest as a fully protected area, enforcing this conservation status and establishing a participative management program favoring the wildlife regeneration. A corridor linking Déré to the southern slope of the Nimba should also be created to favor exchanges between these two zones of high conservation value, and particularly to ensure a connection between the Dans Mounts, the Tiapleu classified Forest and the Mont Nimba, which all contain chimpanzee populations (Fig 50).

VI.2.5. Outlook on conservation strategies

Each of these 3 core areas of the Nimba Mountains Biosphere Reserve have been protected for different reasons and benefit from different conservation statuses. The colonial administration fully protected the Nimba Mountain 70 years ago to preserve and further explore its unique diversity. In the early hours, this sanctuarization imposed on local people was not accepted, and was rather firmly enforced. Over the successive scientific discoveries and the socio-political struggles, multiple international conservation statuses were superimposed on the different sections of Nimba, which somehow reinforced the legitimacy of this site for local people. In particular, many of them are today proud to live near a ‘World Heritage’ site, and in Yealé they feel as the guardians watching on a humankind natural treasure. In other words, after an early and difficult start due to the imposition of the full protective status, today a sufficient part of the local population feel invested and concerned with it, and despite problems, it works.

In Bossou, local people have been protecting chimpanzees for generations, and this traditional conservation measure still holds good today. We believe the fact that Bossou villagers were the instigators of this measure as the main reason explaining its success. The arrival of the chimpanzee research was not conflicting with this prohibition, and has been well accepted. Some potentially contentious situations emerged to some extent when researchers pushed for the full protection of the Bossou hills as a chimpanzee habitat in 1993. The unease was coming from the growing population of the village, which always needs more land to cultivate, and was not contented with the interdiction of entering the forest as the freshly cut rainforest provides a very fertile soil if correctly burned. But this problem was overcome and despite problems, today the full protection of the remaining forested parts of the Bossou hills is effective.

We similarly believe that the traditional protection of the Déré Forest has been functioning for centuries because it was the initiative of local people. We like to imagine that Déré would still be a dense forest if a logging company did not make it accessible and started destroying it. The lack of arable lands due to the impossibility of cultivating in the Nimba Reserve has been intensified by the population overgrowth caused by successive waves of refugees that lasted 20 years from the early 1990s as the result of civil wars in the neighboring Sierra Leone, Liberia and Côte d'Ivoire. It was particularly tough at the end of the 1990s, and local people (mixed to 'exogenous' refugee population), who mainly live from farming and hunting, experienced a critical period of survival. In such moments, nothing was more pressing than fulfilling the subsistence needs of their families, and the conservation, whether traditional or modern, was relegated to a position of secondary importance. But this matter may certainly not be inextricable. We are convinced that alternative can be found between local population, local government, researchers and conservation actors to favor the revival of the Déré Forest as a key piece of a green network connecting the Nimba Mountain to the Tiapleu Forest and the Mounts of Dans (Fig. 50).

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ANNEX 1: Appendix S1

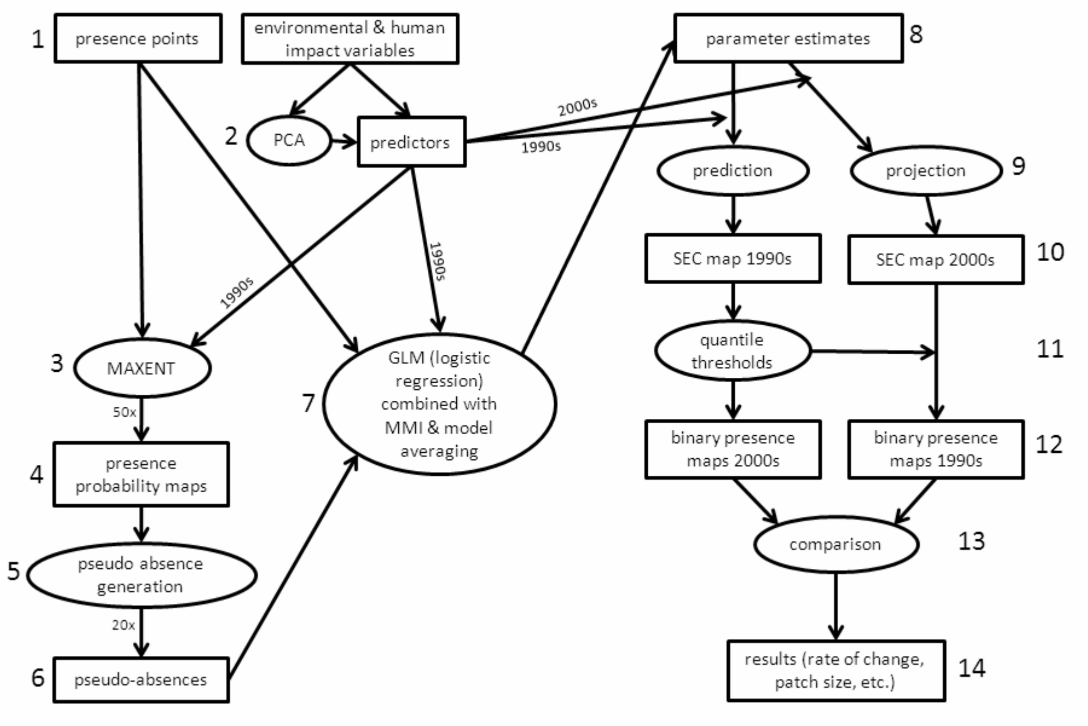

Fig. S1-1: Flowchart depicting the process of the analysis and the flow of data. Rectangles denote data (in- and output of analytical steps) and ellipsoids denote analytical steps and processes. Arrows pointing at arrows denote that data were combined. Note that the entire process was conducted separately for each taxon. Note that some of the environmental variables entered the process directly others as Principal Component Factor scores combining several of them. Note also that the entire model was derived from environmental and human impact variables as they were in the 1990s, and that human impact variables from the 2000s were only used to project the model to this period. Numbers refer to text passages in the main text. Abbreviations: GLM, Generalized linear model; MMI, Multi model inference, PCA, Principal component analysis.

Ape presence localities

Presence localities of eight African great ape taxa were included in the model (Fig. S1-1).

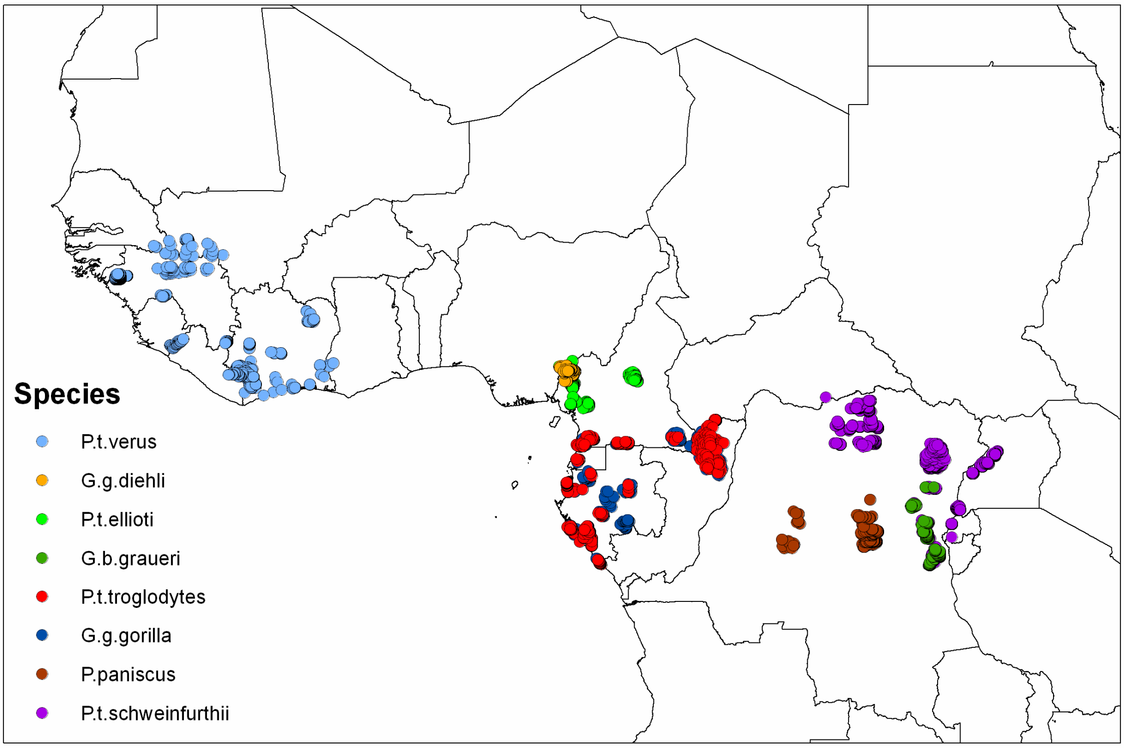

Fig. S1-2: Great ape presence localities available at the time of the study extracted from the A.P.E.S. database (http//:apes.eva.mpg.de) and used as input for the ape habitat model.

Predictor variables

For vegetation, we used two measures of forest cover: percentage of forest cover at each sampling location, and the proportion of forest cover within an 8-km radius. Originally, we planned to include these measures separately for both time periods, the 1990s and 2000s. However, a random probe test showed that the two available layers were incompatible due to different classification methods (see below), which did not allow us to reliably estimate change in vegetation cover. Therefore we averaged the available percentages of forest layers of the periods 1992/1993 and 2000 and included them as a single predictor into our model (Table 1).

We characterized human impact using five proxy variables for human populations, socio-economics and infrastructure (Table 1). We included human density as the number of individuals per km². The human influence index (HII), we calculated for each 5x5 km pixel as the inverse distance weighted average of human density in all pixels (Fotheringham, 1981). Poverty index was calculated as human population density divided by a measure of intensity of night time light, which has been proposed as a proxy for socio-economic status (Elvidge *et al.*, 1997).

Roads have been shown to have a detrimental effect on wildlife in Africa (*e.g.*, Lahm *et al.*, 1998; Laurance *et al.*, 2006, Yackulic *et al.*, 2011), because uncontrolled roads provide access for poaching and forest encroachment. Therefore we included distance to roads as an additional predictor. Lastly, we included distance to rivers. Navigable rivers are widely used as transportation routes, particularly in regions with low road density; thus they can have similar detrimental effects as roads.

To reduce the redundancy inherent in our sets of predictor variables, we ran two separate Principal Component Analyses (PCA; see below).

We extracted or derived all predictor variables from a grid of approximately 5x5 km resolution. GIS layers for all variables were prepared in R v. 2.10.1 (R Development Core Team 2009-2011) or ESRI® ArcMap™ v. 9.2, respectively.

Comparison of vegetation layers

We extracted twenty-five values of percentage forest cover from both forest layers (GLCF AVHRR Continuous Fields Tree Cover Project; MODIS Vegetation Continuous Fields) for areas that did not change in percentage forest cover from the 1990s to the 2000s. We used satellite images from the 1990s and the 2000s (https://zulu.ssc.nasa.gov/mrsid/) to identify areas for which percentage forest did not change noticeably. We extracted values approximately evenly distributed across the range in values of percentage forest cover. We then compared values from the 1993 AVHRR and the 2000 MODIS layer (Fig. S1-2) and concluded that values extracted from the two forest cover layers varied considerably and, thus, should not be included in our analysis as separate layers for the two time periods, but rather as an average representing both time periods.

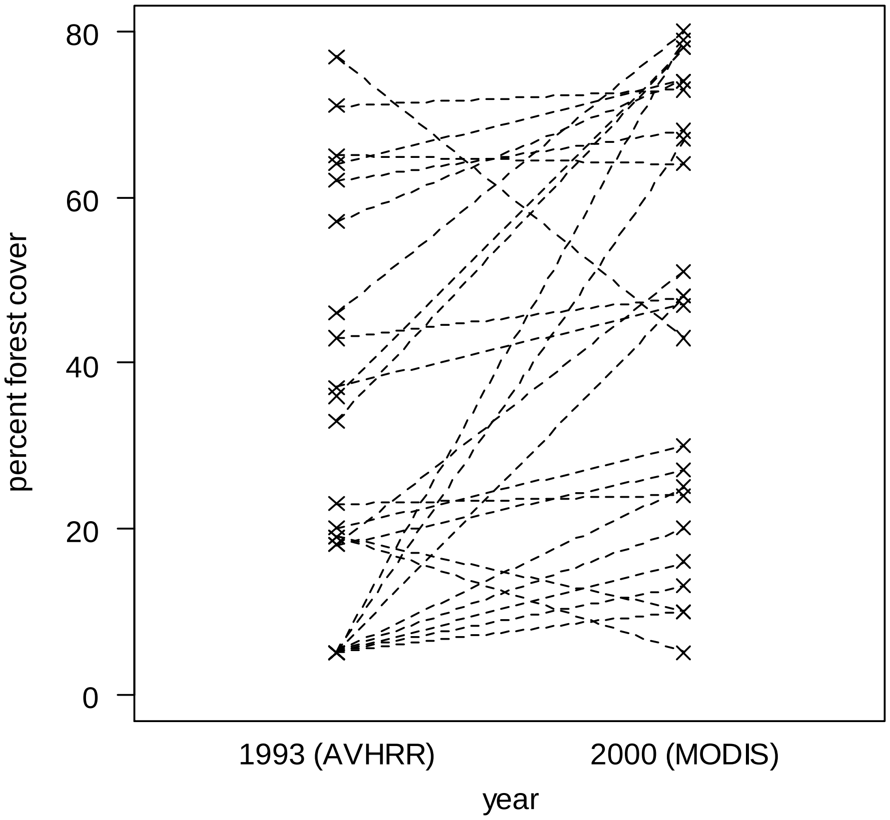

Fig. S1-3: Percent forest cover for twenty-five sites where forest cover did not change between 1993 and 2000 (assessed from satellite images) extracted from two different vegetation layers, namely GLCF AVHRR Continuous Fields Tree Cover Project and MODIS Vegetation Continuous Fields. Due to high variance between the two layers, we included the averaged percent forest cover, rather than using both layers as separate predictors for both time periods in our model.

Protected area

Our initial analysis also included each area's protection status (IUCN categories one and two only) as one of the predictor variables for ape occurrence, because we expected higher ape occurrence probabilities inside than outside protected areas (*c.f.* Hall *et al*., 1998). However, since the majority of presence localities included in our model was collected inside protected areas, we decided to exclude this variable after visual inspection of our probability maps, as it biased the model results and considerably under-estimated ape occurrence probability outside protected areas.

Ebola

Although disease - specifically Ebola - is an important predictor of ape occurrence probability (Walsh *et al*., 2003; Bermejo *et al*., 2006), we excluded this factor from our analysis. Accurate and detailed spatial information on Ebola outbreak sites for the 1990s is very limited (although more information is available for the 2000s) meaning that we could not use Ebola outbreak sites as predictor variables to fit our models using Ebola outbreak sites for the 1990s as predictor variables. Consequently, results of SEC for *G. g. gorilla* and *P. t. troglodytes* do not include the devastating effects Ebola, so our estimates of SEC decline are conservative.

Spatial resolution

In ArcMap, we standardized each variable’s grid extent and cell size and, where necessary, adjusted grid resolution by re-sampling from the original finer resolution. All maps with covariate values thus finally had a pixel size of ca. 25 km^2, yielding a 1392*923 grid with 1,284,816 pixels.

Principal Components Analysis

To reduce redundancy inherent in the set of predictor variables we ran two separate Principal Component Analyses (PCA): PCA 1 included all variables that had different values for the two time periods (Human population density, Human Influence Index, poverty); PCA 2 included all variables for which we did not have separate datasets for the two time periods (six climatic variables, distance to roads and distance to rivers). Prior to this, we visually ensured that all predictor variables had approximately symmetric distributions and transformed variables if necessary (Table S1-1). We used Varimax rotation to rotate factors such that each variable loaded strongly on one Principal Component (PC) and weakly on the others (Quinn & Keough, 2002; Field, 2005).

Table S1-1: Transformations used to reveal approximately symmetric distributions of all predictor variables.

Variable name	**Transformation**
Human population density	$x^{1/8}$
Human influence index	$x^{1/3}$
Poverty	$x^{1/6}$
Distance to rivers	$x^{1/3}$
Distance to roads	$x^{1/4}$
Precipitation driest	$x^{1/4}$
Seasonality temperature	$x^{1/2}$
Mean annual precipitation	$x^{1/2}$
Mean annual temperature	x^4

Percentage forest cover, forest in neighbourhood and distance to roads correlated only weakly with any other variable and also did not load strongly on the same PC as any other variable, so we excluded these from the PCA and included them as separate predictor variables in our model. Last, we also excluded the variable distance to rivers, as we expected an interaction between this variable and distance to roads and factor 1 (human impact), which would be difficult to specify, if distance to rivers loads strongly with other variables on the same PC.

PCA 1 revealed one PC with an Eigenvalue > 1, explaining 87% of the total variance. After Varimax rotation, all three human impact variables (human population density, human influence index and poverty) loaded strongly on this PC (Table S1-2).

Table S1-2: Loadings for the variables included in PCA 1 on the single Principal Component revealed.

Variable name	**PC1**
Human population density	0.95
Human influence index	0.82
Poverty	0.93
Eigenvalue	1.62
% variance explained	87.0

PCA 2 revealed two PCs with an Eigenvalue ≥ 1, together explaining 89 % of the total variance. After Varimax rotation, all climatic variables loaded most strongly on the first PC and mean annual temperature loaded most strongly on the second PC (Table S1-3).

Table S1-3: Loadings of the variables included in PCA 2 on the two Principal Components. Figures in bold indicate the largest absolute loading of a variable.

Variable name	**PC2**	**PC3**
Precipitation driest	**0.72**	-0.40
Seasonality precipitation	**-0.66**	0.49
Seasonality temperature	**-0.88**	0.40
Mean annual precipitation	**0.87**	-0.34
Minimum temperature	**0.92**	0.22
Mean annual temperature	-0.12	**0.99**
Eigenvalue	2.05	1.06
% variance explained	69.8	18.9

MAXENT analysis

We repeated the MAXENT analysis fifty times per taxon, and for each run we made random partitions of the occurrence locality grid cells. Each partition was created by randomly selecting 75% of the occurrence locality grid cells as training data, with the remaining 25% reserved for testing the resulting models. We used recommended default values (Phillips *et al.*, 2006) for the convergence threshold (10^{-5}), maximum number of iterations (500) and regularization value (10^{-4}) and let the program automatically select 'features' (environmental variables or functions thereof), following default rules according to the number of presence records (Phillips *et al.*, 2006). Overall model performance was evaluated by means of the ‘Area under the Curve’ (AUC) determined by the Receiver Operating Characteristic Curves (ROC) analysis (Phillips *et al.*, 2006).

MAXENT model fitting procedures for eight great ape taxa yielded models with a good fit, with the ROC plots for both the training and the test datasets revealing mean AUC values between 0.857 and 0.966 and 0.790 and 0.932, respectively (Table S1-4).

As the probability of pseudo-absences being selected near actual presences was higher for taxa with a small geographical range, maximum occurrence probabilities were higher for models of taxa with larger ranges than for taxa with relatively small ranges.

Table S1-4: Training and test AUC values (mean and range) and from fifty MAXENT models for eight great ape taxa.

Species name	**training**	**test**
G. gorilla diehli	0.857 (0.837-0.878)	0.790 (0.742-0.848)
G. beringei graueri	0.931 (0.917-0.950)	0.914 (0.832-0.963)
G. gorilla gorilla	0.916 (0.902-0.929)	0.885 (0.847-0.920)
P. paniscus	0.966 (0.952-0.977)	0.929 (0.860-0.974)
P. t. schweinfurthii	0.945 (0.938-0.951)	0.929 (0.912-0.944)
P. t. troglodytes	0.947 (0.938-0.960)	0.922 (0.875-0.958)
P. t. verus	0.898 (0.863-0.924)	0.858 (0.806-0.894)
P. t. ellioti	0.966 (0.960-0.970)	0.932 (0.894-0.964)

Details of the model of suitable environmental conditions (i.e., logistic regression)

The response variable was the confirmed presence localities of the particular taxon combined with a set of pseudo-absences. The Number of pseudo-absences selected from within the different taxa’s geographical limits ranged between 1,163 and 9,169. The model included the seven predictors described above (with distance to rivers and distance to roads transformed as shown in Table S1-1) as they were derived from the 1990 dataset. In addition to these predictors, we included the two-way interactions between distance to rivers and human impact on the one hand (Table 2), and distance to roads, on the other hand, assuming that the effect of distance to rivers might be stronger with smaller human impact and larger distances to roads. We also included the two climatic factors as squared terms since we assumed that for those factors an optimum value for ape habitat suitability might exist. Prior to fitting the models and deriving squared terms and interactions, we z-transformed all seven main effects to a mean of zero and standard deviation of one.

To avoid depending on a single (and potentially unduly complex) model, and to avoid overfitting and bias, we used multimodel inference (Burnham & Anderson, 2002). Specifically, we evaluated all of the possible models that could be built out of the set of main effects, non-linear terms and interactions. Models were constructed such that whenever a squared term was included, the corresponding linear term was included as well and that whenever an interaction was included, the two main effects involved were included, too. Hence, the total number of models was 468 (including the null model with no predictors). In each of the models we further included an autocorrelation term to account for potential spatial non-independence in the residuals (see below).

To derive predictions for a particular data set, we first determined Akaike weights (Burnham & Anderson, 2002) for each of the 468 models, and then averaged their predicted occurrence probabilities per cell with the contribution of the individual models being weighted by their Akaike weights. After this was completed for all 1,000 datasets, we averaged the predicted occurrence probabilities per cell across all 1,000 predictions.

Projections to the 2000s were made using the parameter estimates from the 1990s model, and environmental and human impact layers for the 2000s. These projections were made for each of the 1,000 sets of coefficients derived from the 1,000 data sets and then averaged. Per data set, we averaged the coefficients revealed from the 468 models with the contribution of the individual models being weighted by their Akaike weights. Predictions were made per cell.

Drawing inference based on summed Akaike weights

To make inferences about the importance of each of the terms in the models (main effects, interactions and non-linear terms) we determined for each of the terms the sum of the Akaike weights of the models in which they were comprised. However, due to interactions and squared terms being in the full model, the number of models per term varied considerably (i.e., terms were presented in 23–69% of the models with the intercept being in all models), and hence summed Akaike weights were no more comparable between different terms. Nevertheless to make them comparable, we first divided summed Akaike weights per term by the respective expected value, which we assumed to be the proportion of models the respective term was included in. Furthermore, to come up with an estimate of what could be regarded as a 'considerable' deviation from this expected value, we took the following approach. First, we ran a simulation with models based on pure random data. This revealed that the distribution of Akaike weights per model very closely followed a log-normal distribution. Based on this, we ran 10,000 simulations, each of which first generated 468 (i.e., the number of models in our set) log-normally distributed values summing to a total of one. We then summed these generated weights as we did for the original results, and hence came up with a distribution of summed Akaike weights, as expected given no impact of a particular term on the response. Finally, we determined the upper 2.5 percentile of the resulting distribution per term and considered a term as having considerable impact on the response when its actual summed Akaike weight was above this threshold.

Spatial autocorrelation

Presences and pseudo-absences modelled were likely to show spatial autocorrelation unexplained by the predictors included in the models, leading to non-independent residuals, which is an essential assumption of the analysis we conducted. We hence explicitly included autocorrelation in the model. We did this by first running the full model (i.e., the one with all main effects, squared terms and interactions included) and then deriving the residuals from it. We then determined, separately for each cell, the weighted average of the residuals of all other cells whereby the weight equalled

$w_{ik} = \frac{e^{(\frac{d_{ik}}{\sigma})^2}}{\sigma\sqrt{2\pi}}$ (*i.e.*, a Gaussian distribution), with d_{ik} being the distance between the two cells i and k, and σ being set to 10 km. We then included the resulting values as an ‘autocorrelation term’ in all models for the respective taxon.

Model comparison and evaluation

Since we could not evaluate the SEC models with independent data (except for Liberia, see below) we here provide a list of references and other studies in preparation and compare them with our model predictions.

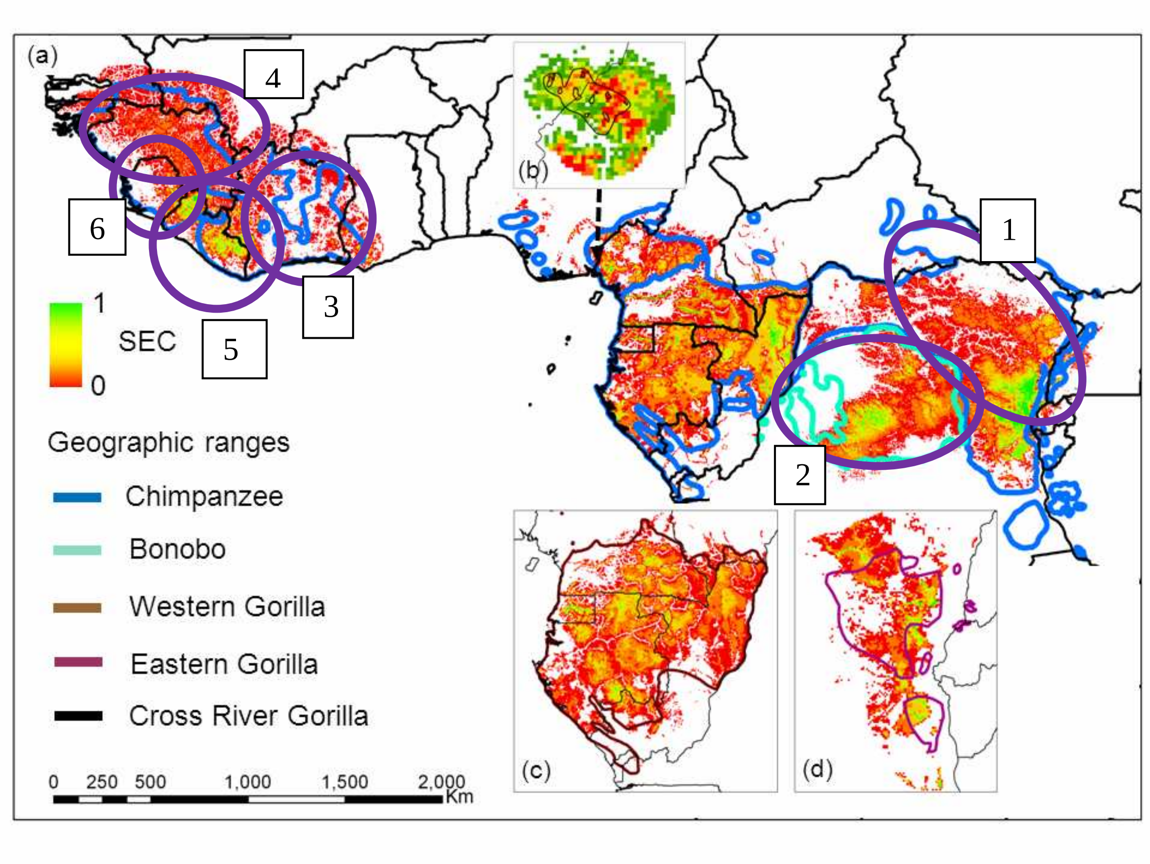

Figure S1-4: SEC map with regions highlighted (purple line) for which a quantitative or qualitative comparison with results with another study was possible.

1. Eastern chimpanzees

To examine model accuracy, we visually compared predictions of current suitable ape habitat distribution with those published by Plumptre *et al.* (2010). For eastern chimpanzees, models generally agreed, except for an area at the southern tip of their distribution in the DRC and Tanzania (Fig. S1-5). Here, our model predicted low suitability, whereas Plumptre *et al.* (2010) considered this area as one of the most suitable for eastern chimpanzees. Second, our model predicted suitable habitat for eastern chimpanzees east of the Congo River in the DRC along the border to Uganda, Burundi and Rwanda. However, Plumptre *et al.* (2010) predicted only low to intermediate suitability values for this area. These inconsistencies may be due to differences in presence localities, spatial resolution, environmental predictor variables and methodology. Our model results concurred with those of Plumptre *et al.* (2010) in that rainfall and temperature variables seemed to be important predictors of habitat suitability in this species (Table 3).

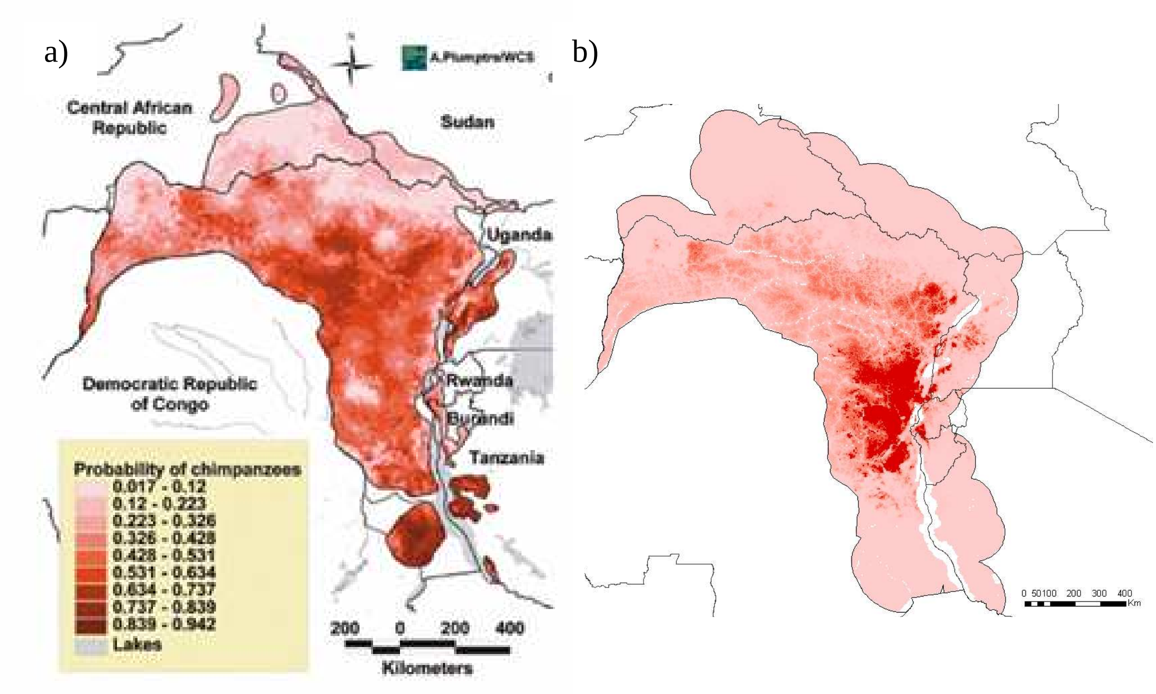

Fig. S1-5: Predicted distribution of suitable chimpanzee habitat in DRC, Central African Republic and Sudan by (a) Plumptre *et al.* (2010) and (b) this study. Chimpanzee habitat suitability ranges from light- to dark red, indicating low to high suitability, respectively.

2. Bonobo

A study in preparation by Hickey *et al.* (in prep.) suggests very similar regions with high and low occurrence probabilities of bonobos as predicted by our SEC model. Bonobos seem to be largely confined to the Salonga region, the Tshuapa-Lomami region, the Maringa-Lopori region and the Lac Tumba Lac/ Mai-Ndombe region. Areas in-between have low probability values. This coincides very much with our SEC model predictions.

3. Ivory Coast

The West African chimpanzee SEC model predicts very low probability values for Ivory Coast, in particular in the central regions. Only in the Tai region, the North-West, North-East and South-West of the country small SEC patches remain. This overlaps very much with recent surveys that have been conducted in the country (Comoe region: Campbell *et al.*, 2008, WCF 2009; Cavally: WCF 2009; Goin-Débé: 2009)

4. Guinea

An on-going field survey in the Fouta-Djallon regions indicates a widespread distribution of chimpanzees (Regnaut pers. comm.). The West African chimpanzee SEC model predicts intermediate to low SEC values for this region, but also suggest a widespread distribution of chimpanzees.

5. Liberia

During a recent nationwide survey in Liberia 118 sampling locations were visited where line transect nest counts were conducted. This survey was based on a completely systematic design using a grid with a cell size of 9x9km. Groups of two transects were placed in every third grid cell (27km spacing). This survey dataset we used to evaluate the Liberian part of the SEC model for *Pan troglodytes verus*. First, we extracted for each transect the SEC value of the 5x5km pixel, in which the transect was located. We then used SEC as the sole predictor of the transect nest observations in a Generalized Linear Model (GLM). We ran two GLMs, one with the raw nest counts on each transect, a negative binomial error term and an offset term to account for differing transect length, and one with a binary response (nests present or absent). Both models showed a good correlation between transect nest counts and the SEC model.

Table S1-5: GLM results from comparison of transect nest survey in Liberia with SEC model prediction for West African chimpanzees. The values given are the parameter estimates (p-values).

Model	intercept	SEC
Binomial	-1.7796 (7.96e-09)	2.9704 (0.0254)
Negative Binomial model	-0.8775 (0.0193)	3.9659 (0.0258)

6. Sierra Leone

In Sierra Leone, signs of chimpanzees encountered by Brncic *et al*. (2010) generally matched with areas predicted suitable for chimpanzees by our model, with the exception of an area in the east, near the border to Liberia, for which our model appears to have over-estimated habitat suitability, as well as in western and central Sierra Leone, for which our model predicted only low to intermediate habitat suitability, but in which survey teams found signs of chimpanzee presence (Fig. S1-6). These discrepancies may be due to the fact that our model only included presence localities from Gola Forest, a forest block located in the southeast of the country on the border to Liberia. However, survey results reported by Brncic *et al*. (2010) showed that chimpanzees in Sierra Leone survived in areas inhabited by relatively high human densities and impacted by subsistence farming – habitat previously thought of as unsuitable for chimpanzees and for which we had no presence data at the time of our study. This may explain the relatively low suitability values predicted by our model and emphasizes the need for more survey data from different areas over the whole range of environmental conditions to improve model accuracy.

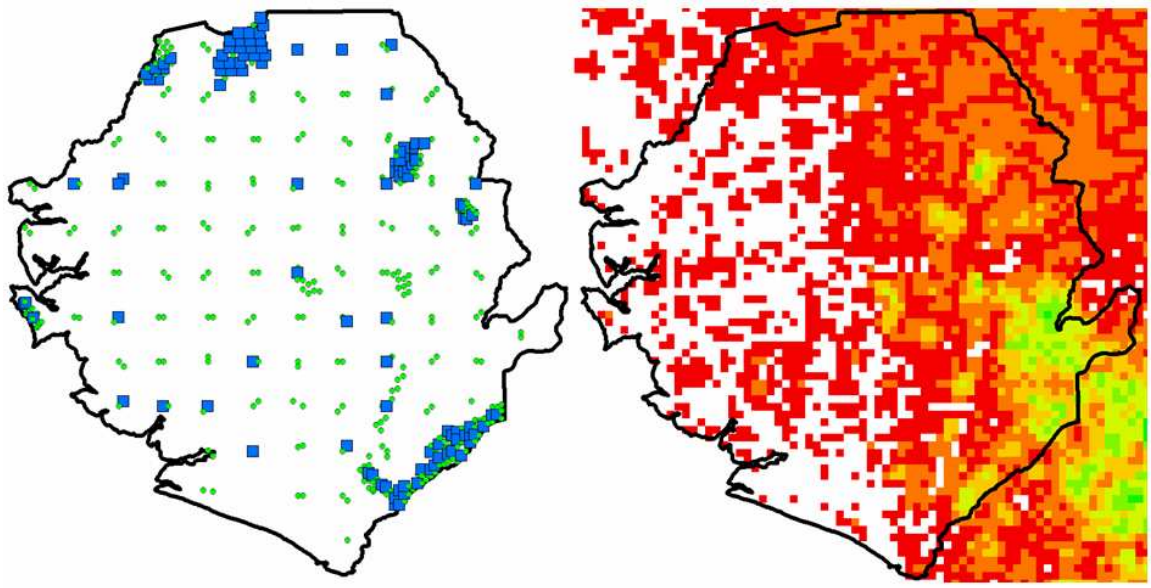

Fig. S1-6: (a) Distribution of signs of chimpanzee presence (blue squares) along transects, transect without signs of chimpanzee presence in green, data were recorded during a nationwide survey in 2008/2009 (Brncic, unpublished data), (b) chimpanzee habitat suitability in Sierra Leone predicted by our model (colours range from red over yellow to green, indicating low, intermediate and high SEC, respectively). White indicates unsuitable habitat.

Discussion of modelling results (table 3 main document)

Variables used in the models differ considerably across species in their estimated coefficients and overall importance. For instance parameter estimates for ‘distance to rivers’, which may indicate different suitability due to either a natural gradient of riverine vegetation or routes of transportation and access for hunters, were negative for six of the eight taxa (*G.g.gorilla, G.g.graueri*, *P.t.troglodytes*, *P.t. schweinfurtii*, *P.t. verus*, *P. panicus*). This suggests that hunting pressure potentially emanating from rivers may be less elevated for these taxa, than for *G.g. diehli and P.t.ellioti*. Rather, habitat conditions *(i.e.* vegetation) may be particularly suitable along watercourses. However, for *P. panicus* and *P.t. schweinfurthii* variable weights are only moderate suggesting a much weaker effect than for the other species.

As shown in many previous studies (e.g., Lahm *et al.*, 1996, Laurance *et al.*, 2006) roads often have a detrimental effect on wildlife, as they provide easy access to hunters. This is also what we find for all, but one taxon (*G.g. graueri*), which is that SEC increases with increasing distance from roads. *G.g. graueri* showed only a moderate positive gradient towards roads, similarly the effect for *G.g. diehli* was weak. One explanation for this might be that their ranges are the most fragmented of all taxa considered, making road-SEC relationships highly stochastic.

The forest variables are of particular interest, as they confirm an important issue. Relationships between occurrence of some taxa (*G.g. gorilla, P. paniscus*) and forest cover are only moderate for central Africa. This is because several large forest blocks host almost no apes anymore, like the Minkebe forest block or other regions in Gabon (Walsh *et al.*, 2003). Similarly, bonobo distribution does not match completely with forest cover in DRC (Hickey *et al.,* in prep).

Parameter values for human impact were negative for all eight taxa. However, weights differed considerably between species and regions. Weights were lowest for *G.g. diehli* and *P.t. schweinfurtii*, confirming the close spatial association between humans, on the one hand, and Cross River gorillas and Eastern chimpanzees on the other, in many places. Nevertheless, the negative estimates for all taxa strongly confirm SEC loss in proximity to humans.

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ANNEX 2: Appendix S1

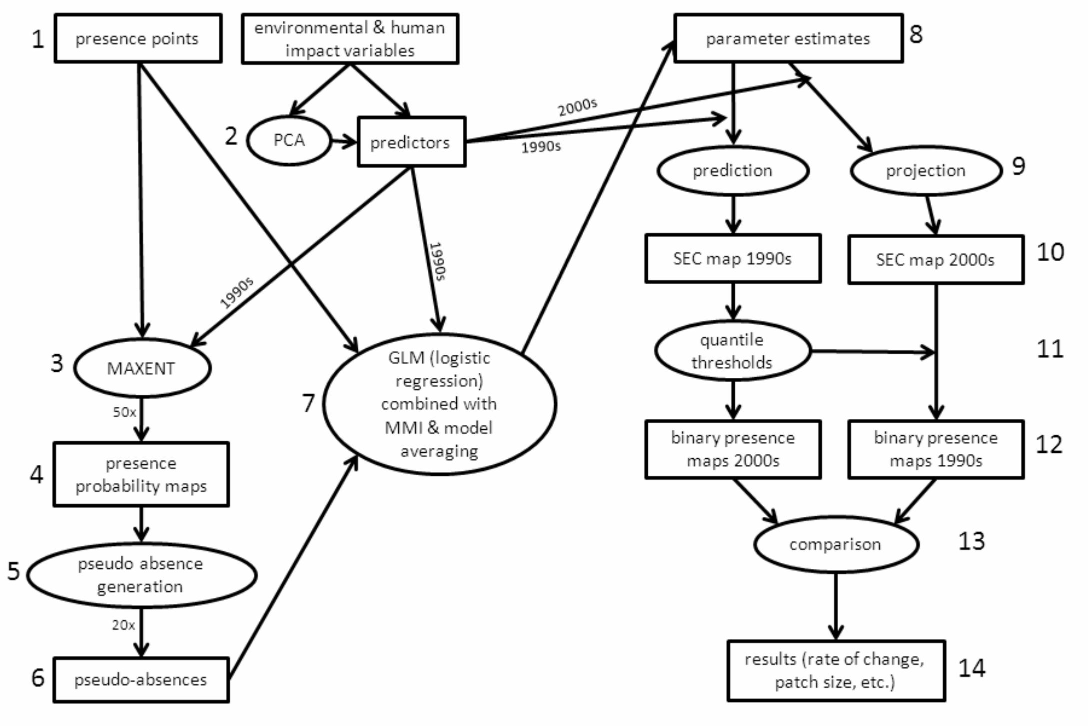

Fig. S1-1: Flowchart depicting the process of the analysis and the flow of data. Rectangles denote data (in- and output of analytical steps) and ellipsoids denote analytical steps and processes. Arrows pointing at arrows denote that data were combined. Note that the entire process was conducted separately for each taxon. Note that some of the environmental variables entered the process directly others as Principal Component Factor scores combining several of them. Note also that the entire model was derived from environmental and human impact variables as they were in the 1990s, and that human impact variables from the 2000s were only used to project the model to this period. Numbers refer to text passages in the main text. Abbreviations: GLM, Generalized linear model; MMI, Multi model inference, PCA, Principal component analysis.

Ape presence localities

Presence localities of eight African great ape taxa were included in the model (Fig. S1-1).

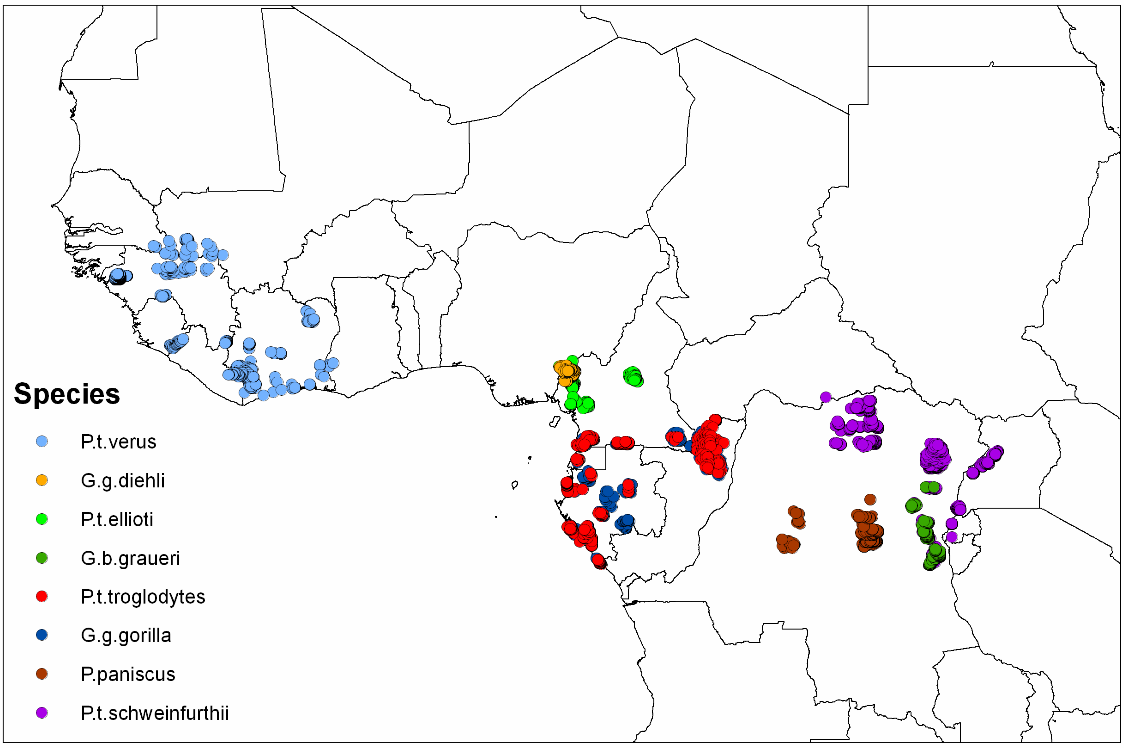

Fig. S1-2: Great ape presence localities available at the time of the study extracted from the A.P.E.S. database (http//:apes.eva.mpg.de) and used as input for the ape habitat model.

Predictor variables

For vegetation, we used two measures of forest cover: percentage of forest cover at each sampling location, and the proportion of forest cover within an 8-km radius. Originally, we planned to include these measures separately for both time periods, the 1990s and 2000s. However, a random probe test showed that the two available layers were incompatible due to different classification methods (see below), which did not allow us to reliably estimate change in vegetation cover. Therefore we averaged the available percentages of forest layers of the periods 1992/1993 and 2000 and included them as a single predictor into our model (Table 1).

We characterized human impact using five proxy variables for human populations, socio-economics and infrastructure (Table 1). We included human density as the number of individuals per km². The human influence index (HII), we calculated for each 5x5 km pixel as the inverse distance weighted average of human density in all pixels (Fotheringham, 1981). Poverty index was calculated as human population density divided by a measure of intensity of night time light, which has been proposed as a proxy for socio-economic status (Elvidge *et al.*, 1997).

Roads have been shown to have a detrimental effect on wildlife in Africa (*e.g.*, Lahm *et al*., 1998; Laurance *et al*., 2006, Yackulic *et al*., 2011), because uncontrolled roads provide access for poaching and forest encroachment. Therefore we included distance to roads as an additional predictor. Lastly, we included distance to rivers. Navigable rivers are widely used as transportation routes, particularly in regions with low road density; thus they can have similar detrimental effects as roads.

To reduce the redundancy inherent in our sets of predictor variables, we ran two separate Principal Component Analyses (PCA; see below).

We extracted or derived all predictor variables from a grid of approximately 5x5 km resolution. GIS layers for all variables were prepared in R v. 2.10.1 (R Development Core Team 2009-2011) or ESRI® ArcMap™ v. 9.2, respectively.

Comparison of vegetation layers

We extracted twenty-five values of percentage forest cover from both forest layers (GLCF AVHRR Continuous Fields Tree Cover Project; MODIS Vegetation Continuous Fields) for areas that did not change in percentage forest cover from the 1990s to the 2000s. We used satellite images from the 1990s and the 2000s (https://zulu.ssc.nasa.gov/mrsid/) to identify areas for which percentage forest did not change noticeably. We extracted values approximately evenly distributed across the range in values of percentage forest cover. We then compared values from the 1993 AVHRR and the 2000 MODIS layer (Fig. S1-2) and concluded that values extracted from the two forest cover layers varied considerably and, thus, should not be included in our analysis as separate layers for the two time periods, but rather as an average representing both time periods.

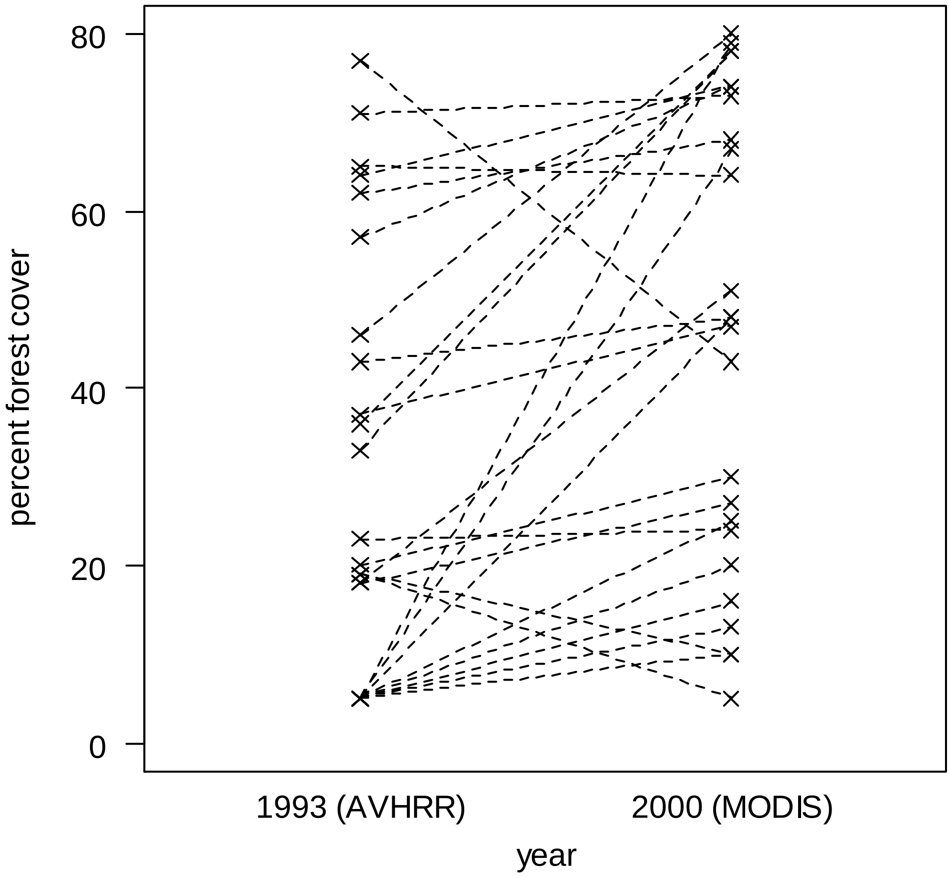

Fig. S1-3: Percent forest cover for twenty-five sites where forest cover did not change between 1993 and 2000 (assessed from satellite images) extracted from two different vegetation layers, namely GLCF AVHRR Continuous Fields Tree Cover Project and MODIS Vegetation Continuous Fields. Due to high variance between the two layers, we included the averaged percent forest cover, rather than using both layers as separate predictors for both time periods in our model.

Protected area

Our initial analysis also included each area's protection status (IUCN categories one and two only) as one of the predictor variables for ape occurrence, because we expected higher ape occurrence probabilities inside than outside protected areas (*c.f.* Hall *et al.*, 1998). However, since the majority of presence localities included in our model was collected inside protected areas, we decided to exclude this variable after visual inspection of our probability maps, as it biased the model results and considerably under-estimated ape occurrence probability outside protected areas.

Ebola

Although disease - specifically Ebola - is an important predictor of ape occurrence probability (Walsh *et al.*, 2003; Bermejo *et al.*, 2006), we excluded this factor from our analysis. Accurate and detailed spatial information on Ebola outbreak sites for the 1990s is very limited (although more information is available for the 2000s) meaning that we could not use Ebola outbreak sites as predictor variables to fit our models using Ebola outbreak sites for the 1990s as predictor variables. Consequently, results of SEC for *G. g. gorilla* and *P. t. troglodytes* do not include the devastating effects Ebola, so our estimates of SEC decline are conservative.

Spatial resolution

In ArcMap, we standardized each variable's grid extent and cell size and, where necessary, adjusted grid resolution by re-sampling from the original finer resolution. All maps with covariate values thus finally had a pixel size of ca. 25 km^2, yielding a 1392*923 grid with 1,284,816 pixels.

Principal Components Analysis

To reduce redundancy inherent in the set of predictor variables we ran two separate Principal Component Analyses (PCA): PCA 1 included all variables that had different values for the two time periods (Human population density, Human Influence Index, poverty); PCA 2 included all variables for which we did not have separate datasets for the two time periods (six climatic variables, distance to roads and distance to rivers). Prior to this, we visually ensured that all predictor variables had approximately symmetric distributions and transformed variables if necessary (Table S1-1). We used Varimax rotation to rotate factors such that each variable loaded strongly on one Principal Component (PC) and weakly on the others (Quinn & Keough, 2002; Field, 2005).

Table S1-1: Transformations used to reveal approximately symmetric distributions of all predictor variables.

Variable name	**Transformation**
Human population density	$x^{1/8}$
Human influence index	$x^{1/3}$
Poverty	$x^{1/6}$
Distance to rivers	$x^{1/3}$
Distance to roads	$x^{1/4}$
Precipitation driest	$x^{1/4}$
Seasonality temperature	$x^{1/2}$
Mean annual precipitation	$x^{1/2}$
Mean annual temperature	x^{4}

Percentage forest cover, forest in neighbourhood and distance to roads correlated only weakly with any other variable and also did not load strongly on the same PC as any other variable, so we excluded these from the PCA and included them as separate predictor variables in our model. Last, we also excluded the variable distance to rivers, as we expected an interaction between this variable and distance to roads and factor 1 (human impact), which would be difficult to specify, if distance to rivers loads strongly with other variables on the same PC.

PCA 1 revealed one PC with an Eigenvalue > 1, explaining 87% of the total variance. After Varimax rotation, all three human impact variables (human population density, human influence index and poverty) loaded strongly on this PC (Table S1-2).

Table S1-2: Loadings for the variables included in PCA 1 on the single Principal Component revealed.

Variable name	**PC1**
Human population density	0.95
Human influence index	0.82
Poverty	0.93
Eigenvalue	1.62
% variance explained	87.0

PCA 2 revealed two PCs with an Eigenvalue ≥ 1, together explaining 89 % of the total variance. After Varimax rotation, all climatic variables loaded most strongly on the first PC and mean annual temperature loaded most strongly on the second PC (Table S1-3).

Table S1-3: Loadings of the variables included in PCA 2 on the two Principal Components. Figures in bold indicate the largest absolute loading of a variable.

Variable name	**PC2**	**PC3**
Precipitation driest	**0.72**	-0.40
Seasonality precipitation	**-0.66**	0.49
Seasonality temperature	**-0.88**	0.40
Mean annual precipitation	**0.87**	-0.34
Minimum temperature	**0.92**	0.22
Mean annual temperature	-0.12	**0.99**
Eigenvalue	2.05	1.06
% variance explained	69.8	18.9

MAXENT analysis

We repeated the MAXENT analysis fifty times per taxon, and for each run we made random partitions of the occurrence locality grid cells. Each partition was created by randomly selecting 75% of the occurrence locality grid cells as training data, with the remaining 25% reserved for testing the resulting models. We used recommended default values (Phillips *et al*., 2006) for the convergence threshold (10^{-5}), maximum number of iterations (500) and regularization value (10^{-4}) and let the program automatically select ‘features’ (environmental variables or functions thereof), following default rules according to the number of presence records (Phillips *et al*., 2006). Overall model performance was evaluated by means of the ‘Area under the Curve’ (AUC) determined by the Receiver Operating Characteristic Curves (ROC) analysis (Phillips *et al*., 2006).

MAXENT model fitting procedures for eight great ape taxa yielded models with a good fit, with the ROC plots for both the training and the test datasets revealing mean AUC values between 0.857 and 0.966 and 0.790 and 0.932, respectively (Table S1-4).

As the probability of pseudo-absences being selected near actual presences was higher for taxa with a small geographical range, maximum occurrence probabilities were higher for models of taxa with larger ranges than for taxa with relatively small ranges.

Table S1-4: Training and test AUC values (mean and range) and from fifty MAXENT models for eight great ape taxa.

Species name	**training**	**test**
G. gorilla diehli	0.857 (0.837-0.878)	0.790 (0.742-0.848)
G. beringei graueri	0.931 (0.917-0.950)	0.914 (0.832-0.963)
G. gorilla gorilla	0.916 (0.902-0.929)	0.885 (0.847-0.920)
P. paniscus	0.966 (0.952-0.977)	0.929 (0.860-0.974)
P. t. schweinfurthii	0.945 (0.938-0.951)	0.929 (0.912-0.944)
P. t. troglodytes	0.947 (0.938-0.960)	0.922 (0.875-0.958)
P. t. verus	0.898 (0.863-0.924)	0.858 (0.806-0.894)
P. t. ellioti	0.966 (0.960-0.970)	0.932 (0.894-0.964)

Details of the model of suitable environmental conditions (i.e., logistic regression)

The response variable was the confirmed presence localities of the particular taxon combined with a set of pseudo-absences. The Number of pseudo-absences selected from within the different taxa's geographical limits ranged between 1,163 and 9,169. The model included the seven predictors described above (with distance to rivers and distance to roads transformed as shown in Table S1-1) as they were derived from the 1990 dataset. In addition to these predictors, we included the two-way interactions between distance to rivers and human impact on the one hand (Table 2), and distance to roads, on the other hand, assuming that the effect of distance to rivers might be stronger with smaller human impact and larger distances to roads. We also included the two climatic factors as squared terms since we assumed that for those factors an optimum value for ape habitat suitability might exist. Prior to fitting the models and deriving squared terms and interactions, we z-transformed all seven main effects to a mean of zero and standard deviation of one.

To avoid depending on a single (and potentially unduly complex) model, and to avoid overfitting and bias, we used multimodel inference (Burnham & Anderson, 2002). Specifically, we evaluated all of the possible models that could be built out of the set of main effects, non-linear terms and interactions. Models were constructed such that whenever a squared term was included, the corresponding linear term was included as well and that whenever an interaction was included, the two main effects involved were included, too. Hence, the total number of models was 468 (including the null model with no predictors). In each of the models we further included an autocorrelation term to account for potential spatial non-independence in the residuals (see below).

To derive predictions for a particular data set, we first determined Akaike weights (Burnham & Anderson, 2002) for each of the 468 models, and then averaged their predicted occurrence probabilities per cell with the contribution of the individual models being weighted by their Akaike weights. After this was completed for all 1,000 datasets, we averaged the predicted occurrence probabilities per cell across all 1,000 predictions.

Projections to the 2000s were made using the parameter estimates from the 1990s model, and environmental and human impact layers for the 2000s. These projections were made for each of the 1,000 sets of coefficients derived from the 1,000 data sets and then averaged. Per data set, we averaged the coefficients revealed from the 468 models with the contribution of the individual models being weighted by their Akaike weights. Predictions were made per cell.

Drawing inference based on summed Akaike weights

To make inferences about the importance of each of the terms in the models (main effects, interactions and non-linear terms) we determined for each of the terms the sum of the Akaike weights of the models in which they were comprised. However, due to interactions and squared terms being in the full model, the number of models per term varied considerably (i.e., terms were presented in 23–69% of the models with the intercept being in all models), and hence summed Akaike weights were no more comparable between different terms. Nevertheless to make them comparable, we first divided summed Akaike weights per term by the respective expected value, which we assumed to be the proportion of models the respective term was included in. Furthermore, to come up with an estimate of what could be regarded as a 'considerable' deviation from this expected value, we took the following approach. First, we ran a simulation with models based on pure random data. This revealed that the distribution of Akaike weights per model very closely followed a log-normal distribution. Based on this, we ran 10,000 simulations, each of which first generated 468 (i.e., the number of models in our set) log-normally distributed values summing to a total of one. We then summed these generated weights as we did for the original results, and hence came up with a distribution of summed Akaike weights, as expected given no impact of a particular term on the response. Finally, we determined the upper 2.5 percentile of the resulting distribution per term and considered a term as having considerable impact on the response when its actual summed Akaike weight was above this threshold.

Spatial autocorrelation

Presences and pseudo-absences modelled were likely to show spatial autocorrelation unexplained by the predictors included in the models, leading to non-independent residuals, which is an essential assumption of the analysis we conducted. We hence explicitly included autocorrelation in the model. We did this by first running the full model (i.e., the one with all main effects, squared terms and interactions included) and then deriving the residuals from it. We then determined, separately for each cell, the weighted average of the residuals of all other cells whereby the weight equalled

$w_{ik} = \frac{e^{(\frac{d_{ik}}{\sigma})^2}}{\sigma\sqrt{2\pi}}$ (*i.e.*, a Gaussian distribution), with d_{ik} being the distance between the two cells i and k, and σ being set to 10 km. We then included the resulting values as an ‘autocorrelation term’ in all models for the respective taxon.

Model comparison and evaluation

Since we could not evaluate the SEC models with independent data (except for Liberia, see below) we here provide a list of references and other studies in preparation and compare them with our model predictions.

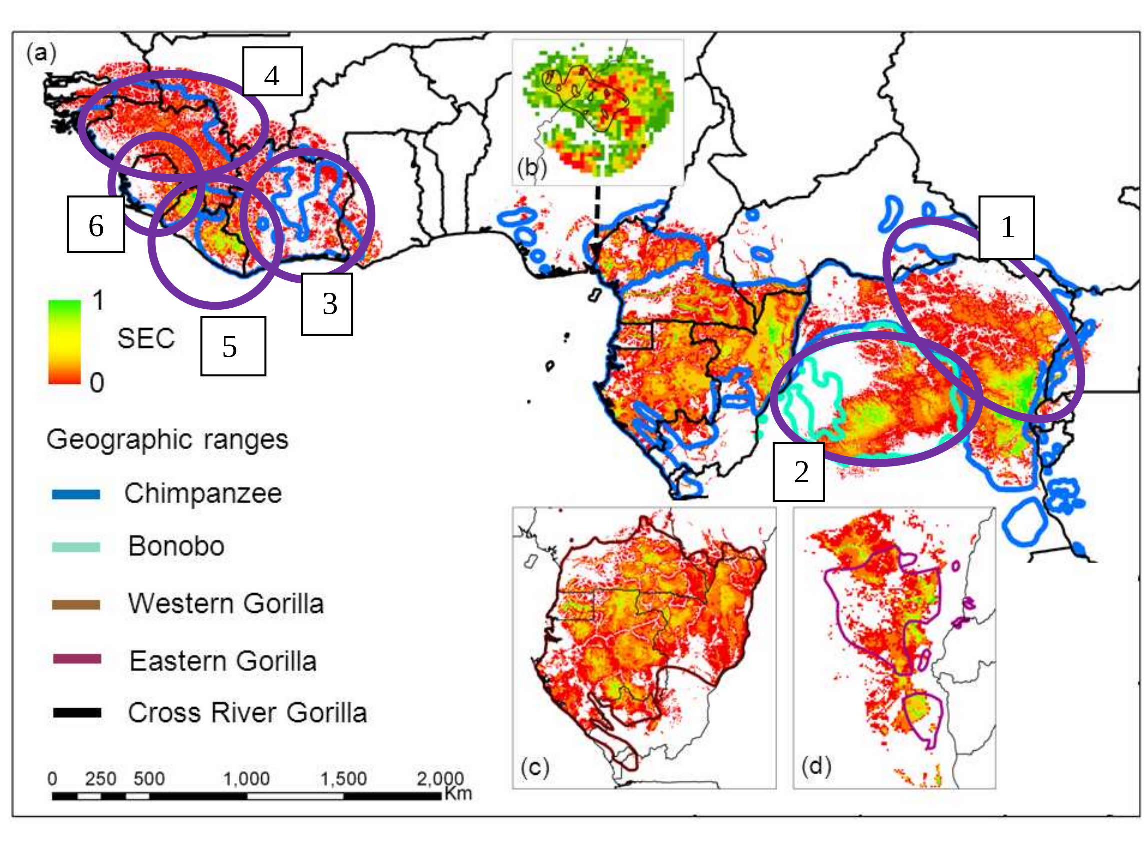

Figure S1-4: SEC map with regions highlighted (purple line) for which a quantitative or qualitative comparison with results with another study was possible.

3. Eastern chimpanzees

To examine model accuracy, we visually compared predictions of current suitable ape habitat distribution with those published by Plumptre *et al.* (2010). For eastern chimpanzees, models generally agreed, except for an area at the southern tip of their distribution in the DRC and Tanzania (Fig. S1-5). Here, our model predicted low suitability, whereas Plumptre *et al.* (2010) considered this area as one of the most suitable for eastern chimpanzees. Second, our model predicted suitable habitat for eastern chimpanzees east of the Congo River in the DRC along the border to Uganda, Burundi and Rwanda. However, Plumptre *et al.* (2010) predicted only low to intermediate suitability values for this area. These inconsistencies may be due to differences in presence localities, spatial resolution, environmental predictor variables and methodology. Our model results concurred with those of Plumptre *et al.* (2010) in that rainfall and temperature variables seemed to be important predictors of habitat suitability in this species (Table 3).

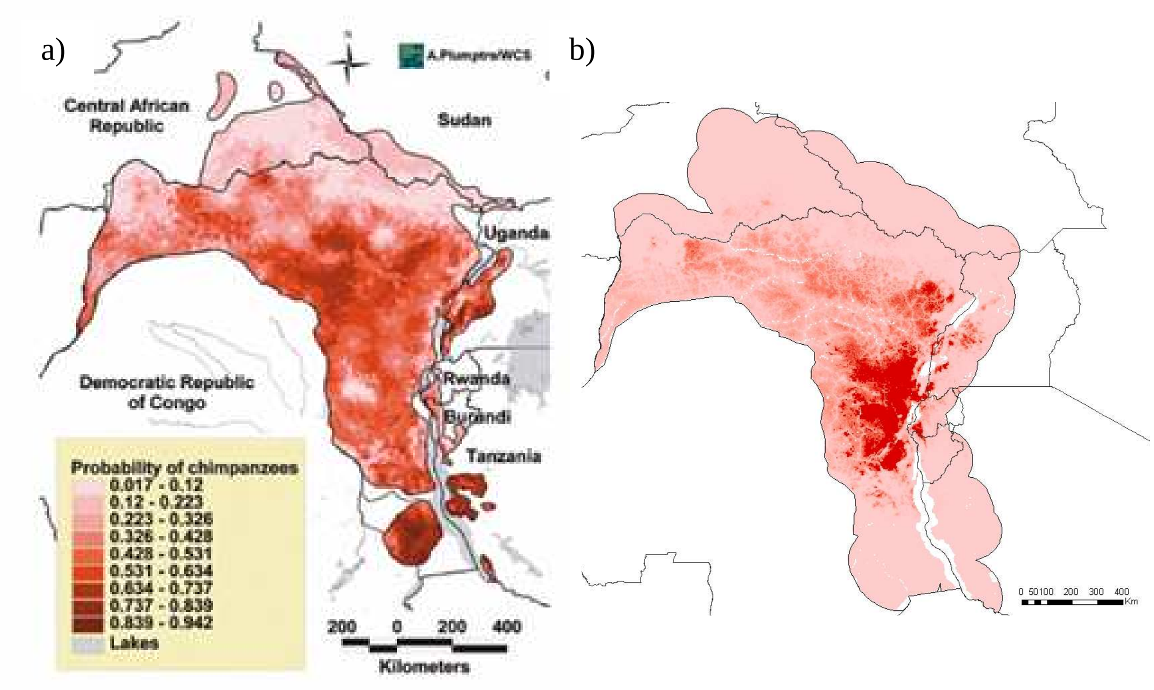

Fig. S1-5: Predicted distribution of suitable chimpanzee habitat in DRC, Central African Republic and Sudan by (a) Plumptre *et al.* (2010) and (b) this study. Chimpanzee habitat suitability ranges from light- to dark red, indicating low to high suitability, respectively.

4. Bonobo

A study in preparation by Hickey *et al.* (in prep.) suggests very similar regions with high and low occurrence probabilities of bonobos as predicted by our SEC model. Bonobos seem to be largely confined to the Salonga region, the Tshuapa-Lomami region, the Maringa-Lopori region and the Lac Tumba Lac/ Mai-Ndombe region. Areas in-between have low probability values. This coincides very much with our SEC model predictions.

3. Ivory Coast

The West African chimpanzee SEC model predicts very low probability values for Ivory Coast, in particular in the central regions. Only in the Tai region, the North-West, North-East and South-West of the country small SEC patches remain. This overlaps very much with recent surveys that have been conducted in the country (Comoe region: Campbell *et al.*, 2008, WCF 2009; Cavally: WCF 2009; Goin-Débé: 2009)

4. Guinea

An on-going field survey in the Fouta-Djallon regions indicates a widespread distribution of chimpanzees (Regnaut pers. comm.). The West African chimpanzee SEC model predicts intermediate to low SEC values for this region, but also suggest a widespread distribution of chimpanzees.

5. Liberia

During a recent nationwide survey in Liberia 118 sampling locations were visited where line transect nest counts were conducted. This survey was based on a completely systematic design using a grid with a cell size of 9x9km. Groups of two transects were placed in every third grid cell (27km spacing). This survey dataset we used to evaluate the Liberian part of the SEC model for *Pan troglodytes verus*. First, we extracted for each transect the SEC value of the 5x5km pixel, in which the transect was located. We then used SEC as the sole predictor of the transect nest observations in a Generalized Linear Model (GLM). We ran two GLMs, one with the raw nest counts on each transect, a negative binomial error term and an offset term to account for differing transect length, and one with a binary response (nests present or absent). Both models showed a good correlation between transect nest counts and the SEC model.

Table S1-5: GLM results from comparison of transect nest survey in Liberia with SEC model prediction for West African chimpanzees. The values given are the parameter estimates (p-values).

Model	intercept	SEC
Binomial	-1.7796 (7.96e-09)	2.9704 (0.0254)
Negative Binomial model	-0.8775 (0.0193)	3.9659 (0.0258)

6. Sierra Leone

In Sierra Leone, signs of chimpanzees encountered by Brncic *et al*. (2010) generally matched with areas predicted suitable for chimpanzees by our model, with the exception of an area in the east, near the border to Liberia, for which our model appears to have over-estimated habitat suitability, as well as in western and central Sierra Leone, for which our model predicted only low to intermediate habitat suitability, but in which survey teams found signs of chimpanzee presence (Fig. S1-6). These discrepancies may be due to the fact that our model only included presence localities from Gola Forest, a forest block located in the southeast of the country on the border to Liberia. However, survey results reported by Brncic *et al*. (2010) showed that chimpanzees in Sierra Leone survived in areas inhabited by relatively high human densities and impacted by subsistence farming – habitat previously thought of as unsuitable for chimpanzees and for which we had no presence data at the time of our study. This may explain the relatively low suitability values predicted by our model and emphasizes the need for more survey data from different areas over the whole range of environmental conditions to improve model accuracy.

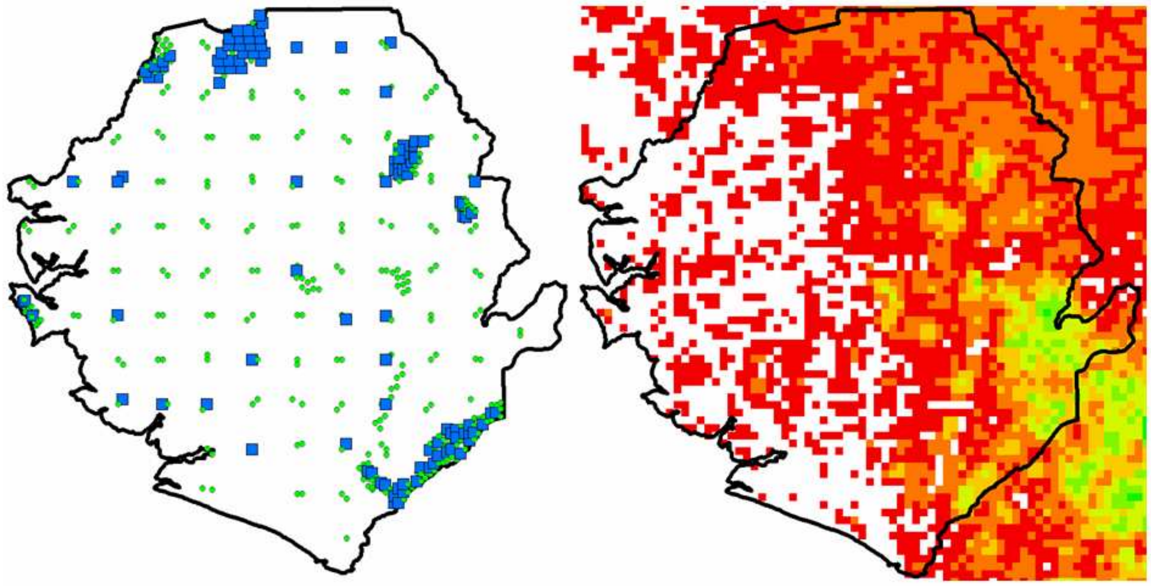

Fig. S1-6: (a) Distribution of signs of chimpanzee presence (blue squares) along transects, transect without signs of chimpanzee presence in green, data were recorded during a nationwide survey in 2008/2009 (Brncic, unpublished data), (b) chimpanzee habitat suitability in Sierra Leone predicted by our model (colours range from red over yellow to green, indicating low, intermediate and high SEC, respectively). White indicates unsuitable habitat.

Discussion of modelling results (table 3 main document)

Variables used in the models differ considerably across species in their estimated coefficients and overall importance. For instance parameter estimates for 'distance to rivers', which may indicate different suitability due to either a natural gradient of riverine vegetation or routes of transportation and access for hunters, were negative for six of the eight taxa (*G.g.gorilla, G.g.graueri*, *P.t.troglodytes*, *P.t. schweinfurtii*, *P.t. verus*, *P. panicus*). This suggests that hunting pressure potentially emanating from rivers may be less elevated for these taxa, than for *G.g. diehli and P.t.ellioti*. Rather, habitat conditions *(i.e.* vegetation) may be particularly suitable along watercourses. However, for *P. panicus* and *P.t. schweinfurthii* variable weights are only moderate suggesting a much weaker effect than for the other species.

As shown in many previous studies (e.g., Lahm *et al.*, 1996, Laurance *et al.*, 2006) roads often have a detrimental effect on wildlife, as they provide easy access to hunters. This is also what we find for all, but one taxon (*G.g. graueri*), which is that SEC increases with increasing distance from roads. *G.g. graueri* showed only a moderate positive gradient towards roads, similarly the effect for *G.g. diehli* was weak. One explanation for this might be that their ranges are the most fragmented of all taxa considered, making road-SEC relationships highly stochastic.

The forest variables are of particular interest, as they confirm an important issue. Relationships between occurrence of some taxa (*G.g. gorilla, P. paniscus*) and forest cover are only moderate for central Africa. This is because several large forest blocks host almost no apes anymore, like the Minkebe forest block or other regions in Gabon (Walsh *et al.*, 2003). Similarly, bonobo distribution does not match completely with forest cover in DRC (Hickey *et al.*, in prep).

Parameter values for human impact were negative for all eight taxa. However, weights differed considerably between species and regions. Weights were lowest for *G.g. diehli* and *P.t. schweinfurtii*, confirming the close spatial association between humans, on the one hand, and Cross River gorillas and Eastern chimpanzees on the other, in many places. Nevertheless, the negative estimates for all taxa strongly confirm SEC loss in proximity to humans.

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ANNEX 3: List of ligneous species identified in the Ivorian Nimba, with scientific and Yakuba names

Scientific name	Family	Yakuba name
Acacia ataxacantha	Leguminosae-Mim.	Danh
Acacia kamerunensis	Leguminosae-Mim.	Danh
Acacia pennata	Leguminosae-Mim.	Danhgblo
Acioa barteri	Chrysobalanaceae	
Adenia rumicifolia	Passifloraceae	Kponzébieu
Aframomum excapum	Zingiberaceae	Sein
Aframomum latifolium	Zingiberaceae	Sein
Aframomum longiscapum	Zingiberaceae	Sein
Aframomum melegueta	Zingiberaceae	Sein
Aframomum sceptrum	Zingiberaceae	Sein
Aframomum strobilaceum	Zingiberaceae	Sein
Aframomum subsericeum	Zingiberaceae	Sein
Aframomum sulcatum	Zingiberaceae	Sein
Aganope leucobotrya	Leguminosae-Pap	Lümonka bhieumonka
Aidia genipiflora	Rubiaceae	Luogalü
Albizia adianthifolia	Leguminosae-Mim.	Zâeulianzé
Albizia ferruginea	Leguminosae-Mim.	Gbéansâa
Albizia zygia	Leguminosae-Mim.	Zâeutii
Alchornea cordifolia	Euphorbiaceae	Fon
Allophylus africanus	Sapindaceae	
Allophylus talbotii	Sapindaceae	
Alstonia boonei	Apocynaceae	Yon
Amanoa bracteosa	Euphorbiaceae	Blîdow
Amphimas pterocarpoides	Leguminosae-Pap.	Gbeugodôlü
Annickia polycarpa	Annonaceae	Gblein
Anopyxis klaineana	Rhizophoraceae	
Anthocleista djalonensis	Gentianaceae	Gölügueïnzé
Anthocleista nobilis	Gentianaceae	Gölü
Anthocleista vogelii	Gentianaceae	Gölügon
Anthonotha fragrans	Leguminosae-Caes.	Gbeugon
Anthonotha macrophylla	Leguminosae-Caes.	Gbeu
Antiaris toxicaria	Moraceae	Kpo(u)
Antidesma laciniatum	Euphorbiaceae	
Antidesma venosum	Euphorbiaceae	Bômâlé
Antrocaryon micraster	Anacardiaceae	Gblôo
Apodiscus chevalieri	Euphorbiaceae	
Artabotrys jollyanus	Annonaceae	Méétiibhieugblo
Atractogyne bracteata	Rubiaceae	Déïgon
Aubrevillea platycarpa	Leguminosae-Mim.	Bîeuhtii
Aulacocalyx divergens	Rubiaceae	
Aulacocalyx jasminiflora	Rubiaceae	
Baphia nitida	Leguminosae-Pap.	
Beilschmiedia mannii	Lauraceae	Slanlü

Scientific name	**Family**	**Yakuba name**
Bertiera racemosa	Rubiaceae	
Blighia unijugata	Sapindaceae	Gointii
Blighia welwitschii	Sapindaceae	Goin
Bombax buonopozense	Malvaceae (Bombacaceae)	Gouégbéné
Bridelia grandis	Euphorbiaceae	Gouéan
Bridelia micrantha	Euphorbiaceae	Goan
Bussea occidentalis	Leguminosae-Caes.	Kpaklo
Caesalpinia benthamiana	Leguminosae-Caes.	Kpotroh
Caloncoba brevipes	Achariaceae	
Caloncoba echinata	Achariaceae	
Calpocalyx brevibracteatus	Leguminosae-Mim.	Kpouheu
Calycobolus africanus	Convolvulaceae	Déebhieu
Calycobolus heudelotii	Convolvulaceae	Vâapou
Campylospermum reticulatum	Ochnaceae	
Campylospermum squamosum	Ochnaceae	
Canarium schweinfurthii	Burseraceae	Bîn
Carapa procera	Meliaceae	Gbon
Carpolobia alba	Polygalaceae	
Carpolobia lutea	Polygalaceae	
Cassia aubrevillei	Leguminosae-Caes.	
Cassia fikifiki	Leguminosae-Caes.	
Cassipourea gummiflua	Rhizophoraceae	
Ceiba pentandra	Malvaceae (Bombacaceae)	Goué
Celtis adolfi-friderici	Ulmaceae	Kossingon
Celtis brownii	Ulmaceae	Kossin
Celtis mildbraedii	Ulmaceae	Tiriko
Cercestis afzelii	Araceae	Gbao
Chidlowia sanguinea	Leguminosae-Caes.	Bâa
Chrysophyllum africanum	Sapotaceae	Boodèin
Chrysophyllum taïense	Sapotaceae	
Chrysophyllum giganteum	Sapotaceae	Boodèingon
Chrysophyllum perpulchrum	Sapotaceae	Boodèintii
Chrysophyllum pruniforme	Sapotaceae	Nyonyilü
Chrysophyllum subnudum	Sapotaceae	Boodèingon
Cleistopholis patens	Annonaceae	Seupoâ
Coelocaryon sphaerocarpum	Myristicaceae	
Cola boxiana	Malvaceae (=Sterculiaceae)	
Cola caricifolia	Malvaceae (=Sterculiaceae)	Gbéangö
Cola gigantea	Malvaceae (=Sterculiaceae)	Gbéangögon
Cola heterophylla	Malvaceae (=Sterculiaceae)	
Cola lateritia	Malvaceae (=Sterculiaceae)	Gbéangögon
Cola nitida	Malvaceae (=Sterculiaceae)	Gô
Cola reticulata	Malvaceae (=Sterculiaceae)	
Combretum grandiflorum	Combretaceae	
Combretum mildbraedii	Combretaceae	
Combretum paniculatum	Combretaceae	Kiékpo
Copaifera salikounda	Leguminosae-Caes.	

Scientific name	Family	Yakuba name
Cordia africana	Boraginaceae	
Cordia platythyrsa	Boraginaceae	
Corynanthe pachyceras	Rubiaceae	Gbanlü
Costus afer	Zingiberaceae	
Costus deistelli	Zingiberaceae	
Costus dubius	Zingiberaceae	
Coula edulis	Olacaceae	Sâa (Schlâa)
Craterispermum candatum	Rubiaceae	Yèitagbèkèlü
Crossostemma laurifolium	Passifloraceae	Gbésségblo
Croton macrostachyus	Euphorbiaceae	
Croton sylvaticus	Euphorbiaceae	
Crudia gabonensis	Leguminosae-Caes.	
Cryptosepalum tetraphyllum	Leguminosae-Caes.	
Cuviera acutiflora	Rubiaceae	
Cuviera macroura	Rubiaceae	Blîcafé
Dacryodes klaineana	Burseraceae	Zion
Dactyladenia barteri	Chrysobalanaceae	
Dactyladenia scabrifolia	Chrysobalanaceae	
Dactyladenia whytei	Chrysobalanaceae	
Dalbergia afzeliana	Leguminosae-Pap.	Tunula
Dalbergia saxatilis	Leguminosae-Pap.	Tunula
Daniellia thurifera	Leguminosae-Caes.	Blèin
Dasylepis brevipedicellata	Achariaceae	
Deinbollia pinnata	Sapindaceae	
Detarium senegalense	Leguminosae-Caes.	
Dialium aubrevillei	Leguminosae-Caes.	
Dialium dinklagei	Leguminosae-Caes.	
Dialium guineense	Leguminosae-Caes.	
Dichapetalum martineaui	Chailletaceae (=Dichapetaleae)	
Dichapetalum sp.	Chailletaceae (=Dichapetaleae)	
Diospyros cooperi	Ebenaceae	Dûeuh
Diospyros heudelotii	Ebenaceae	Dûeuh
Diospyros mannii	Ebenaceae	Dûeuhgon
Discoglypremna caloneura	Euphorbiaceae	Plou
Distemonanthus benthamianus	Leguminosae-Caes.	Wowkozoalü
Dracaena arborea	Dracaenaceae	Zjlü
Drypetes aubrevillei	Euphorbiaceae	Schleulü
Drypetes afzelii	Euphorbiaceae	
Drypetes aylmeri	Euphorbiaceae	
Drypetes chevalieri	Euphorbiaceae	Sanpou
Drypetes inaequalis	Euphorbiaceae	Sanpou
Drypetes ivorensis	Euphorbiaceae	
Drypetes leonensis	Euphorbiaceae	
Drypetes pellegrinii	Euphorbiaceae	Kpoun
Drypetes principum	Euphorbiaceae	
Duboscia viridiflora	Malvaceae (Tiliaceae)	
Elaeis guineensis	Palmae (=Arecaceae)	Seuh

Scientific name	Family	Yakuba name
Entada pursaetha	Leguminosae-Mim.	Dunh(bhieu)
Entandrophragma angolense	Meliaceae	Biélülianzé
Entandrophragma candollei	Meliaceae	Bièlü
Entandrophragma cylindricum	Meliaceae	Bièlügon
Entandrophragma utile	Meliaceae	Bièlüpou
Eriocoelum pungens	Sapindaceae	
Eriocoelum racemosum	Sapindaceae	
Erythrina mildbraedii	Leguminosae-Pap.	
Erythrina vogelii	Leguminosae-Pap.	Seugueïnzé
Erythrophleum ivorense	Leguminosae-Caes.	Glü
Erythrophleum suaveolens	Leguminosae-Caes.	Kpuèh
Erythroxylum mannii	Erythroxylaceae	Leuin
Eugenia pobeguinii	Myrtaceae	
Ficus anomani	Moraceae	Kloh
Ficus barteri	Moraceae	Kloh
Ficus eriobotryoides	Moraceae	
Ficus exasperata	Moraceae	Niè
Ficus kamerunensis	Moraceae	Kloh
Ficus macrosperma	Moraceae	Kloh
Ficus mucuso	Moraceae	Flôbloh
Ficus ovata	Moraceae	
Ficus praticola	Moraceae	Kloh
Ficus sur	Moraceae	Bloh
Ficus umbellata	Moraceae	Kloh
Ficus thoningii	Moraceae	
Ficus variifolia	Moraceae	Kloh
Friesodielsia enghiana	Annonaceae	
Funtumia africana	Apocynaceae	Naabèin
Funtumia elastica	Apocynaceae	Naabèin
Garcinia afzelii	Guttiferae	Mangbeulü
Garcinia epunctata	Guttiferae	Petit colagon
Garcinia gnetoides	Guttiferae	
Garcinia kola	Guttiferae	Petit cola
Garcinia ovalifolia	Guttiferae	Petit colagon
Garcinia smeathmannii	Guttiferae	
Gilbertiodendron limba	Leguminosae-Caes.	Sadélü
Gilbertiodendron preussii	Leguminosae-Caes.	Sadélü
Glenniea adamii	Sapindaceae	Zin
Gouania longipetala	Rhamnaceae	
Greenwayodendron oliveri	Annonaceae	Gbalü
Grewia hookerana	Malvaceae (Tiliaceae)	
Grewia malacocarpa	Malvaceae (Tiliaceae)	Gbalügouïn
Guarea cedratra	Meliaceae	Wâagon
Guarea thompsonii	Meliaceae	
Guibourtia copallifera	Leguminosae-Caes.	
Guibourtia ehie	Leguminosae-Caes.	
Guibourtia leonensis	Leguminosae-Caes.	

Scientific name	Family	Yakuba name
Hallea ledermannii	Rubiaceae	
Halopegia azurea	Marantaceae	
Hannoa klaineana	Simaroubaceae	Tonpiéyèüh
Harungana madagascarensis	Guttiferae	Loo
Heritiera utilis	Malvaceae (Sterculiaceae)	Dân(lü)
Hippocratea africana	Celastraceae	Kpeunalianzé
Hippocratea clematoides	Celastraceae	Kpeuna
Holarrhena floribunda	Apocynaceae	
Holoptelea grandis	Ulmaceae	
Homalium africanum	Salicaceae	
Homalium smythei	Salicaceae	
Homalium stipulaceum	Salicaceae	
Hugonia rufipilis	Linaceae	Teklangblo
Hymenocardia lyrata	Euphorbiaceae	
Hypselodelphys violacea	Marantaceae	Gongo
Idertia morsonii	Ochnaceae	Sanlianzé
Ilex mitis	Aquifoliaceae	
Irvingia gabonensis	Irvingiaceae	Kpé
Khaya grandifoliola	Meliaceae	
Khaya ivorensis	Meliaceae	
Kigelia africana	Bignoniaceae	Glotinlü
Klainedoxa gabonensis	Irvingiaceae	Gôh
Laccosperma secundiflorum	Palmae (=Arecaceae)	
Landolphia dulcis	Apocynaceae	Bambouan
Landolphia heudelotii	Apocynaceae	Séan séan
Landolphia hirsuta	Apocynaceae	
Landolphia incerta	Apocynaceae	Déegblo
Landolphia owariensis	Apocynaceae	Kpèè
Lannea welwitschii	Anacardiaceae	Wowlogon
Lasiodiscus chevalieri	Rhamnaceae	
Lasiodiscus fasciculiflorus	Rhamnaceae	
Lasiodiscus mannii	Rhamnaceae	
Lecaniodiscus cupanioides	Sapindaceae	Kan
Leptaulus daphnoides	Icacinaceae	
Leptoderris brachyptera	Leguminosae-Pap.	Kpangon
Leptoderris fasciculata	Leguminosae-Pap.	Kpang
Lophira alata	Ochnaceae	Plo
Lovoa trichilioides	Meliaceae	Bièlütii
Macaranga barteri	Euphorbiaceae	Vongho
Macaranga heterophylla	Euphorbiaceae	Gbéangô
Macaranga heudelotii	Euphorbiaceae	Vonghotii
Macaranga hurifolia	Euphorbiaceae	Vonghopou
Maesobotrya barteri	Euphorbiaceae	Nyan
Mammea africana	Guttiferae	Mängpou
Manilkara obovata	Sapotaceae	
Manniophyton fulvum	Euphorbiaceae	
Maranthes aubrevillei	Chrysobalanaceae	

Scientific name	**Family**	**Yakuba name**
Maranthes glabra	Chrysobalanaceae	
Marantochloa congensis	Marantaceae	
Marantochloa cuspidata	Marantaceae	
Marantochloa filipes	Marantaceae	
Marantochloa flexuosa	Marantaceae	
Marantochloa leucantha	Marantaceae	
Marantochloa macrophylla	Marantaceae	Loh
Marantochloa purpurea	Marantaceae	
Mareya micrantha	Euphorbiaceae	Glakpeün
Margaritaria discoidea	Euphorbiaceae	Kînpou
Massularia acuminata	Rubiaceae	Nuombonyonkpoun
Megaphrynium macrostachyum	Marantaceae	
Memecylon aylmeri	Melastomataceae	
Memecylon lateriflorum	Melastomataceae	
Memecylon polyanthemos	Melastomataceae	
Microdesmis keayana	Pandaceae	Seün
Milicia excelsa	Moraceae	Gueû(pou)
Milicia regia	Moraceae	Gueû(tii)
Millettia dinklagei	Leguminosae-Pap.	Niouan léssein
Millettia lane-poolei	Leguminosae-Pap.	Niouan
Millettia zechiana	Leguminosae-Pap.	Kpeubibeulü
Momordica cabraei	Cucurbitaceae	
Momordica foetida	Cucurbitaceae	Guèingblo
Monodora brevipes	Annonaceae	
Monodora tenuifolia	Annonaceae	Kpanlü
Morus mesozygia	Moraceae	
Musanga cecropioides	Cecropiaceae	Lo
Mussaenda erythrophylla	Rubiaceae	Tobwanlé
Myrianthus arboreus	Cecropiaceae	Gbaoh
Myrianthus libericus	Cecropiaceae	Sogbaoh
Myrianthus serratus	Cecropiaceae	Sogbaoh
Napoleonaea vogelii	Lecythidaceae	Déï
Nauclea diderrichii	Rubiaceae	Leüh
Nauclea pobeguinii	Rubiaceae	Dâa
Neoboutonia diaguissensis	Euphorbiaceae	
Neostenanthera gabonensis	Annonaceae	Gbalügon
Nesogordonia papaverifera	Malvaceae (Sterculiaceae)	
Neuropeltis acuminata	Convolvulaceae	Yôo
Newtonia aubrevillei	Leguminosae-Mim.	Gonlélü
Newtonia duparquetiana	Leguminosae-Mim.	
Nuxia congesta	Stilbaceae	
Ochna membranacea	Ochnaceae	Gonbéyiri
Octoknema borealis	Olacaceae (Oktoknemataceae)	Lîlilü
Okoubaka aubrevillei	Santalaceae	
Omphalocarpum pachysteloides	Sapotaceae	Blîssé
Ongokea gore	Olacaceae	Kouli
Pachypodanthium staudii	Annonaceae	

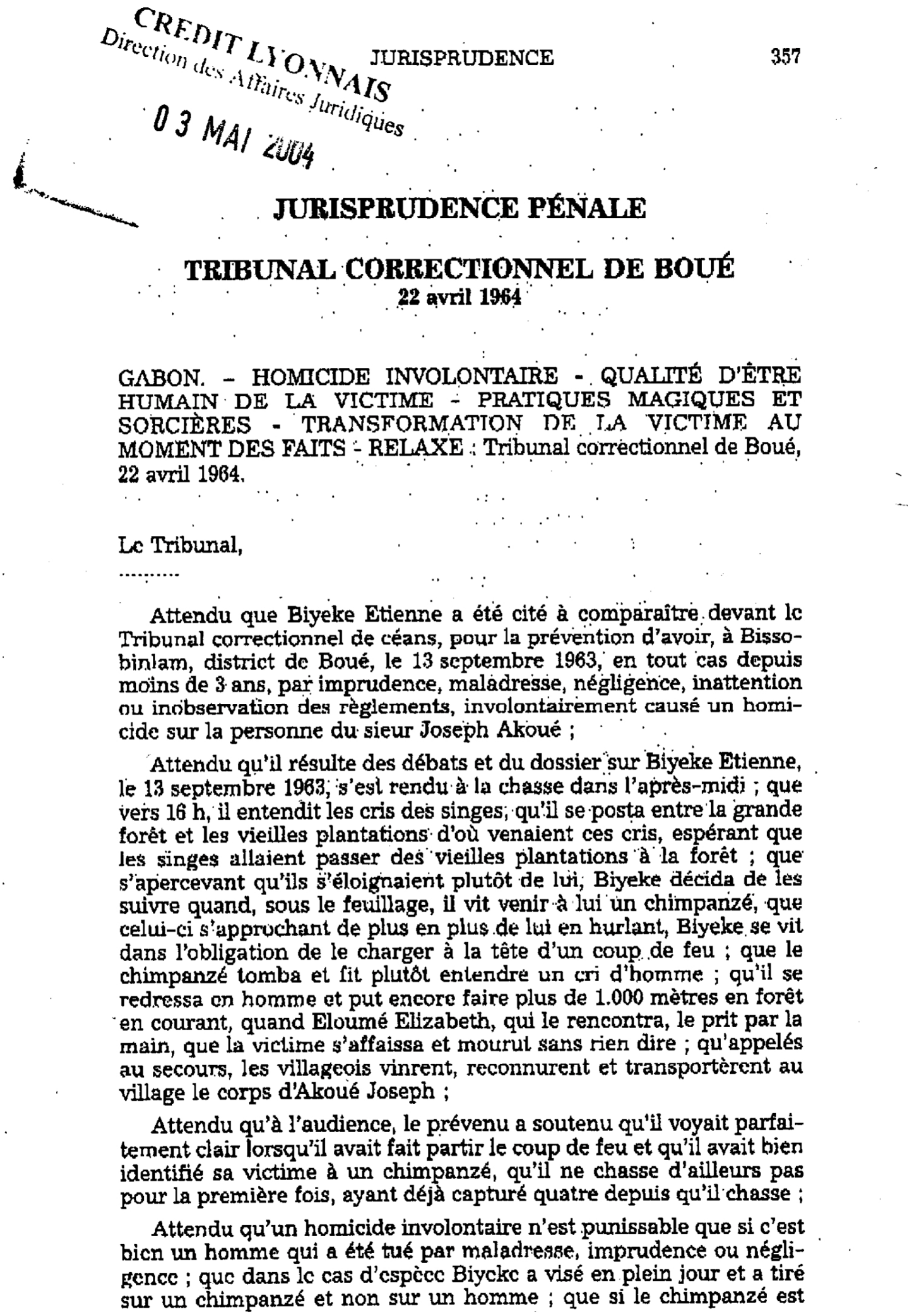
Scientific name	Family	Yakuba name
Panda oleosa	Pandaceae	Kpon
Parinari excelsa	Chrysobalanaceae	Kpôo
Parkia bicolor	Leguminosae-Mim.	Woolü
Pausinystalia lane-poolei	Rubiaceae	
Pavetta micheliana	Rubiaceae	
Pentaclethra macrophylla	Leguminosae-Mim.	Gbîeu
Pentadesma butyracea	Guttiferae	Mängtii
Petersianthus macrocarpus	Lecythidaceae	Pin
Phyllanthus discoideus	Euphorbiaceae	Lütiihè
Phyllanthus margariana	Euphorbiaceae	
Picralima nitida	Apocynaceae	Kouyéplein
Piper guineense	Piperaceae	Nlâa
Piper umbellatum	Piperaceae	Wenlé
Piptadeniastrum africanum	Leguminosae-Mim.	Bîeuh
Polycephalium capitatum	Icacinaceae	Bonlé
Pouteria altissima	Sapotaceae	Tonpiélah
Pouteria aningeri	Sapotaceae	Tonpiélah
Pouteria sp	Sapotaceae	
Protomegabaria stapfiana	Euphorbiaceae	Dôoh
Pseudospondias microcarpa	Anacardiaceae	
Psydrax manensis	Rubiaceae	
Psydrax parviflora	Rubiaceae	
Pteleopsis hylodendron	Combretaceae	
Pycnanthus angolensis	Myristicaceae	Diin
Raphia hookeri	Palmae (=Arecaceae)	Lüweu
Rhabdophyllum calophyllum	Ochnaceae	
Rhaphidophora africana	Araceae	Gbaogon
Rhaphiostylis ferruginea	Icacinaceae	
Ricinodendron heudelotii	Euphorbiaceae	Kô
Rinorea microdon	Violaceae	Boohtii
Rinorea oblongifolia	Violaceae	Booh
Rothmannia hispida	Rubiaceae	
Salacia lehmbachii	Celastraceae	Kpeunapou
Salacia owabiensis	Celastraceae	Kpeunatii
Salacia togoica	Celastraceae	Kpeunagon
Samanea dinklagei	Leguminosae-Mim.	Bîeusan
Samanea saman	Leguminosae-Mim.	Bîeusan
Santiria trimera	Burseraceae	Kpänkpän
Sarcophrynium brachystachyum	Marantaceae	
Sarcophrynium prionogonium	Marantaceae	
Scottellia klaineana	Achariaceae	
Smeathmannia laevigata	Passifloraceae	
Smeathmannia pubescens	Passifloraceae	
Solanum erianthum	Solanaceae	Nawangon
Solanum torvum	Solanaceae	Nawan(mou)
Soyauxia grandifolia	Medusandraceae	Boâwin
Spondianthus preussii	Euphorbiaceae	

Scientific name	Family	Yakuba name
Spondias cytherea	Anacardiaceae	Tôn
Spondias mombin	Anacardiaceae	
Stachyanthus occidentalis	Icacinaceae	
Sterculia oblonga	Malvaceae (Sterculiaceae)	
Sterculia tragacantha	Malvaceae (Sterculiaceae)	Tou
Stereospermum acuminatissimum	Bignoniaceae	
Strephonema pseudocola	Combretaceae	
Strombosia pustulata	Olacaceae	Lütii
Strophanthus sarmentosus	Apocynaceae	
Strophantus gratus	Apocynaceae	
Strychnos afzelii	Loganiaceae	
Synsepalum afzelii	Sapotaceae	Lah(lü)
Synsepalum brevipes	Sapotaceae	Lah(lü)
Synsepalum cerasiferum	Sapotaceae	Lah(lü)
Syzygium guineense	Myrtaceae	
Syzygium rowlandii	Myrtaceae	
Tabernaemontana africana	Apocynaceae	Toakléïgon
Terminalia ivorensis	Combretaceae	Béïi
Terminalia superba	Combretaceae	Goueîn
Tetracera alnifolia	Dilleniaceae	Noogblo
Tetracera potatoria	Dilleniaceae	Gâa(gondé)
Tetrapleura tetraptera	Leguminosae-Mim.	Zan
Tetrorchidium didymostemon	Euphorbiaceae	Tomlo
Thaumatococus danielli	Marantaceae	
Theobroma cacao	Sterculiaceae	Cacao
Tieghemella heckelii	Sapotaceae	Pôo
Tiliacora leonensis	Menispermaceae	
Treculia africana	Moraceae	Lüu
Trema guineensis	Ulmaceae	Wowlo
Tricalysia bracteata	Rubiaceae	Yéïlayiri
Tricalysia faranahensis	Rubiaceae	
Trichilia martineaui	Meliaceae	
Trichilia megalantha	Meliaceae	Wâa
Trichilia monodelpha	Meliaceae	
Trichilia ornithothera	Meliaceae	
Trichilia prieureana	Meliaceae	
Trichilia tessmannii	Meliaceae	
Trichoscypha arborea	Anacardiaceae	Gbonlianzé
Trichoscypha barbata	Anacardiaceae	Gbontii
Trichoscypha lucens	Anacardiaceae	Gbongon
Trilepisium madagascariense	Moraceae	Pâa
Triplochiton scleroxylon	Malvaceae (Sterculiaceae)	Looh
Turraeanthus africanus	Meliaceae	Yèüh
Uapaca chevalieri	Euphorbiaceae	Tonpiésouan
Uapaca esculenta	Euphorbiaceae	Souan
Uapaca guineensis	Euphorbiaceae	Souan(tii)
Uapaca heudelotii	Euphorbiaceae	

Scientific name	Family	Yakuba name
Uncaria africana	Rubiaceae	Chlüsso
Undetermined 1	Sapotaceae	
Undetermined 2	Santalaceae	
Undetermined 3	Rubiaceae	Yenliélü
Undetermined 4	Meliaceae	
Undetermined 5	Papilionaceae	
Uvaria afzelii	Annonaceae	
Uvaria baumannii	Annonaceae	
Uvaria chamae	Annonaceae	
Uvariopsis guineensis	Annonaceae	Touabeulü
Vangueriella campylacantha	Rubiaceae	Toofonguénégon
Vangueriella vanguerioides	Rubiaceae	
Ventilago africana	Rhamnaceae	
Vernonia conferta	Asteraceae (=Compositae)	Loupou
Vernonia titanophylla	Asteraceae (=Compositae)	Loupoulé
Vismia guineensis	Guttiferae	Lôhbîeu
Vitex doniana	Verbenaceae	
Vitex grandifolia	Verbenaceae	
Vitex micrantha	Verbenaceae	Zenkodoalü
Vitex rivularis	Verbenaceae	Zenkodoalü
Warneckea cinnamomoides	Melastomataceae	
Warneckea membranifolia	Melastomataceae	
Xylia evansii	Leguminosae-Mim.	Wélü
Xylopia aethiopica	Annonaceae	Souo
Xylopia parviflora	Annonaceae	Kpâmapou
Xylopia quintasii	Annonaceae	Kpâmatii
Xylopia rubescens	Annonaceae	
Xylopia staudtii	Annonaceae	
Xylopia villosa	Annonaceae	Kpâma
Zanthoxylum gilletii	Rutaceae	Séehgueïnzé
Zanthoxylum rubescens	Rutaceae	Sénégueïnzé
		Blîbooh
		Bouboudé
		Bouzion
		Flô
		Foubhieu
		Gâagon
		Glakpeün
		Gôhté
		Goualélü
		Gouéa
		Kanteubieu
		Kbékélü
		Kîn
		Kinssin
		Kinssinbôa
		Kinssingon

Scientific name	Family	Yakuba name
		Klotinlü
		Kpanékpô
		Kpanglianzé
		Kpèï
		Kpongon
		Lueuhlügon
		Lütiipou
		Mangbeulügon
		Mangzébhieu
		Manyalü
		Manyalügon
		Séga
		Sièlü
		Souogon
		Tobwanlégon
		Tonpiéwâa
		Toronkinyiri
		Tozoaguein
		Tozoagueingon
		Wouan
		Zantin
		Zè
		Zenghé
		Zôbhieugblo Zanghabeulü

ANNEX 4: On metamorphis ability of animist people. Case law of Boué criminal court.



CREDIT LYONNAIS
Direction des Affaires Juridiques
03 MAI 2004

JURISPRUDENCE PÉNALE

TRIBUNAL CORRECTIONNEL DE BOUÉ

22 avril 1964

GABON. – HOMICIDE INVOLONTAIRE – QUALITÉ D'ÊTRE HUMAIN DE LA VICTIME – PRATIQUES MAGIQUES ET SORCIÈRES – TRANSFORMATION DE LA VICTIME AU MOMENT DES FAITS – RELAXE : Tribunal correctionnel de Boué, 22 avril 1964.

Le Tribunal,

……….

Attendu que Biyeke Etienne a été cité à comparaître devant le Tribunal correctionnel de céans, pour la prévention d'avoir, à Bissobinlam, district de Boué, le 13 septembre 1963, en tout cas depuis moins de 3 ans, par imprudence, maladresse, négligence, inattention ou inobservation des règlements, involontairement causé un homicide sur la personne du sieur Joseph Akoué ;

Attendu qu'il résulte des débats et du dossier sur Biyeke Etienne, le 13 septembre 1963, s'est rendu à la chasse dans l'après-midi ; que vers 16 h, il entendit les cris des singes, qu'il se posta entre la grande forêt et les vieilles plantations d'où venaient ces cris, espérant que les singes allaient passer des vieilles plantations à la forêt ; que s'apercevant qu'ils s'éloignaient plutôt de lui, Biyeke décida de les suivre quand, sous le feuillage, il vit venir à lui un chimpanzé, que celui-ci s'approchant de plus en plus de lui en hurlant, Biyeke se vit dans l'obligation de le charger à la tête d'un coup de feu ; que le chimpanzé tomba et fit plutôt entendre un cri d'homme ; qu'il se redressa en homme et put encore faire plus de 1.000 mètres en forêt en courant, quand Eloumé Elizabeth, qui le rencontra, le prit par la main, que la victime s'affaissa et mourut sans rien dire ; qu'appelés au secours, les villageois vinrent, reconnurent et transportèrent au village le corps d'Akoué Joseph ;

Attendu qu'à l'audience, le prévenu a soutenu qu'il voyait parfaitement clair lorsqu'il avait fait partir le coup de feu et qu'il avait bien identifié sa victime à un chimpanzé, qu'il ne chasse d'ailleurs pas pour la première fois, ayant déjà capturé quatre depuis qu'il chasse ;

Attendu qu'un homicide involontaire n'est punissable que si c'est bien un homme qui a été tué par maladresse, imprudence ou négligence ; que dans le cas d'espèce Biyeke a visé en plein jour et a tiré sur un chimpanzé et non sur un homme ; que si le chimpanzé est devenu homme après le coup de feu, Biyeke ne peut plus être retenu dans la prévention d'homicide involontaire ;

Attendu qu'il est de notoriété publique au Gabon que les hommes se changent soit en panthère, soit en gorille, soit en éléphant, etc., pour accomplir des exploits, éliminer les ennemis ou attirer sur eux de lourdes responsabilités, défendre leurs plantations et ravager celles des voisins et des amis ; que ce sont des faits qui sont inconnus du droit occidental et dont le juge gabonais doit tenir compte, qu'il est en effet inconcevable à l'esprit européen qu'un homme puisse faire plus de 400 km en 27 heures à pied, alors qu'un Bakoto de Makokou et Boué l'accomplissait ;

Attendu qu'il n'est pas aussi de la commune mesure qu'un individu ayant reçu une charge de plomb dans la tête, et après être tombé, se relève et arrive encore à faire plus de 1.000 mètres en forêt en courant ; que tel a été le cas d'Akoué Joseph ;

Attendu qu'il faut encore faire savoir que les transformations des hommes en animaux féroces sont encore en vue de ne pas effrayer le gibier, pour s'en saisir plus facilement ;

Attendu qu'Akoué Joseph, qui est parti en chasse sans armes, n'en avait donc pas besoin puisqu'il pouvait prendre du gibier autrement qu'avec une arme ;

Attendu que s'il faut punir les homicides involontaires de chasse, il y a lieu toutefois de considérer les cas et de sévir contre ces pratiques magiques et sorcières qui peuplent le Gabon, surtout en matière des opérations en forêt, et qui retardent énormément l'évolution de notre peuple ;

Attendu que le Tribunal a l'entière conviction qu'Akoué Joseph s'est transformé en chimpanzé en forêt où il aurait été en chasse sans arme et à l'insu de personne, et que Biyeke, notable, ancien combattant, largement décoré, plusieurs fois vainqueur des chimpanzés, ne pouvait pas tirer en plein jour sur un homme contre lequel il n'avait aucun antécédent défavorable ;

Par ces motifs, déclare Biyeke Etienne non coupable des faits qui lui sont reprochés.