Université de Liège
Département des Sciences et Gestion
de l'Environnement
Unite de Biologie du Comportement

Institut Royal des Sciences Naturelles
de Belgique
Operational Directorate Natural Environment
Conservation Biology Unit

Eco-ethology of a population of bonobos (*Pan paniscus*) living in the western forest-savannah mosaics of the Democratic Republic of Congo

Dissertation submitted for the degree of Doctor of Sciences

Adeline Serckx

April 2014

Collaborating institutions:

Max Planck Institute for Evolutionary Anthropology – Department of Primatology

Université de Kinshasa - Ecole Régionale post-universitaire d'Aménagement et de gestion Intégrés des Forêts et Territoires tropicaux

WWF - Congo

JURY COMPOSITION FOR THE THESIS DEFENSE

Emmanuel Serusiaux Université de Liège	President
Jan Bogaert Gembloux AgroBiotech. - Université de Liège	Reporter
Zjef Pereboom Royal Zoological Society of Antwerp, Center of Research and Conservation University of Utrecht, the Netherlands	Reporter
Barbara Fruth Royal Zoological Society of Antwerp, Center of Research and Conservation Ludwig-Maximilian University, Germany	Reporter
Hjalmar Kühl Max Planck Institute for Evolutionary Anthropology, Germany German Centre for Integrative Biodiversity Research, Germany	Reporter
Alain Hambuckers Université de Liège	Reporter
Roseline C. Beudels-Jamar Institut Royal des Sciences Naturelles de Belgique	Co-supervisor
Marie-Claude Huyen Université de Liège	Co-supervisor
Pascal Poncin Université de Liège	Supervisor

“A long time ago, Bonobo and the humans were living together in the villages. One day, the tax inspector visited the village and Bonobo had no money. For lack of two francs, Bonobo run away in the forest with his wife. Too shameful of its behaviour and while hairs were growing on his body, Bonobo did not dare to come back in the village and became the Human of the forest.”

“A long time ago, the oil palm and the raphia palm were fighting to know which one was the most powerful. The oil palm said “my fruits provide oil”, the raphia palm retorted “with my branches, clothes are weaved”. While they could not find a common ground, they asked Bonobo to stop the quarrel. Bonobo agreed that oil palm was right. The raphia palm was angry and responded “since you gave right to the oil palm, I take back my branches with which your clothes are weaved”. He took back the clothes and Bonobo was naked. Shameful, Bonobo ran away in the forest and never came back in the village.”

Teke tales

ACKNOWLEDGEMENTS / REMERCIEMENTS

When I started my PhD thesis, I never imagined how much this project would become a wonderful adventure. I learnt so much about sciences, I met so many interesting people. I also had the opportunity to experience the life in Congo. I never expected I should have to fight against ants to protect my house, to spend 36 hours on a plastic seat in a boat to reach the field or to attach my phone on a stake to be able to make phone calls! But it was so wonderful to be immersed in the Teke culture, I only keep good memories of all these months spent in the field. I must confess that I do not consider this thesis as my work but rather as a wonderful project that I had the chance to conduct. So many people help me by giving time, energy, advices and I really would like to thank you all for your contributions in my thesis!

Let's go back a few years ago to remember thanks to whom this project has been possible.

November 2008

Roseline, I remember when I entered for the first time in your office. I did not have any idea of what I could do in my life but I was sure that I wanted to work in conservation biology. You asked me "if you had the choice, what would you really like to do?". I was dreaming about bonobos and this wonderful adventure started. Thanks you so much for having opened the doors of my deepest dreams, thanks you for all your advices, for sharing your experience, for all the time you spent to correct my work even when you were travelling across the world. You really support me since the beginning and nothing would have been possible without you!

December 2008

One month later, I arrived at the University of Liege with an outline of this PhD project. I really thank Pascal Poncin for welcoming me in his team, for having supported my project and for giving me the opportunity to work in the Primatology Research Group.

The second person who gave me the opportunity to accomplish this project is without any doubt Marie-Claude. You gave me judicious advices, constant support, so many times for reading, correcting and commenting my writings. You always find the solution to overcome each obstacle in this PhD and I cannot thank you enough for what you have done.

September 2009

My thesis really started after months of preparation and thanks to the funding of the FRIA (Fonds pour la Formation a la Recherche dans l'Industrie et l'Agriculture) and of the F.R.S-F.N.R.S (Fonds National pour la Recherche Scientifique). Other funding also helped me later, that I should already thank: the University of Liege, the Leopold III foundation and the ERAIFT (Ecole Régionale post-universitaire d'Aménagement et de gestion Intégrés des Forêts et Territoires tropicaux).

Since this period, I am also benefiting from the help and the advices of Alain Hambuckers and Regine Vercauteren. Thanks you so much for having participated to the development of this work! I also would like to thank Jan Bogaert and Jean-Louis Doucet, who were always present to answer my questions.

I warmly thank all my colleagues from the University and the Museum for those funny lunch time and for the nice atmosphere in our offices. A special thanks to Barbara, Fany and Chab for the great times at the congresses.

March 2010

When I arrived for the first time in the field, I met Pupa (Valentin Mbenzo). You gave yourself the mission to make me meet everybody in the villages, to teach me everything about the place, the local culture, the bonobos and your work. I am really convinced this is thanks to you that all my work on the field was possible, even when you were not there anymore. Thanks you for continuing to take care of me and I really hope that we could have new opportunities to work together.

I am grateful to Menard Mbende for all his help and his advices in the field, for his wonderful capability to resolve each problem, for all his stories about Congo and for his humour in each situation.

Je dois aussi remercier Daniel Malalu, qui m'a conduit un peu partout sur le terrain, à répétitions de « *sois calme* » à chaque pente où j'avais peur que les freins de la voiture lâchent et en me mettant en tête ce refrain qui ne m'a toujours pas quitté (« *Mon père avait raison, ma mère avait raison,…* »).

I also thank Jean Mobuli and Petra Lahaan, even if they arrived later in the field. Jean, tu as vraiment transformé cette base WWF en un endroit agréable à vivre et tu fais un travail formidable. Don't give up ! Nous revenons bientôt avec un disque dur pleins de films pour occuper tes longues soirées d'hiver. Petra, thanks you so much for our collaboration, I really hope we will have new opportunities to meet each other.

Je remercie également toutes les autres personnes du WWF-Congo pour leur aide dans la préparation de chaque mission de terrain, et tout particulièrement Raymond Luebuenamo qui m'a ouvert les portes de Malebo. And besides all the support of WWF-Congo, I warmly thank people from WWF-Belgique, who helped me numerous time!

Je remercie également Mbou-Mon-Tour de m'avoir accueilli dans leur ferme, Paulin pour ton aide quotidienne, Jean-Christophe pour le travail formidable que vous accomplissez.

Je dois aussi dire un tout grand merci aux chefs de terre de Nkala et Mpelu, merci de m'avoir accueilli dans vos villages, de m'avoir permis de travailler dans vos forêts, de m'avoir fait partager avec vous et avec les autres villageois de si bons moments, de si bonnes fêtes du 30 juin. Nazali kobosana bino te, nakozonga mpembeni !

September 2010

Mais l'ensemble de ce travail n'aurait vraiment pas été possible sans l'aide de tous mes assistants de terrain, Yaya Cicé, Petit Mowa, Mpesse, Mafa, Bula, Pala, Papa Fido, et tous ceux qui nous ont aidé à couper les transects chaque année.

Cicéron, tu as vraiment accompli un travail formidable et je t'en suis énormément reconnaissante. Sans toi, cette thèse n'aurait pas été possible. Tu as su gérer nos équipes en mon absence, apprendre à chacun le travail avec une patience et un savoir-faire impressionnant. Travailler avec toi était une expérience magnifique, tu t'es investi, tu t'es intéressé à ce que nous faisions et tu m'as appris tellement de choses. J'espère que tu garderas cette curiosité et cette soif d'apprendre et qu'elles te permettront d'accomplir cette nouvelle aventure qu'est l'université. Je te souhaite énormément de courage, je suis toujours là si tu as besoin de moi et j'attends avec impatience de retravailler avec toi.

Mowa, j'ai passé des moments formidables avec toi en forêt, merci pour ton dévouement dans notre travail. Je te souhaite pleins de succès à l'école et j'espère que nous pourrons retravailler ensemble bientôt.

Je remercie également les pisteurs bonobos, qui m'ont aidé à localiser les sites de nids, à collecter les fèces, et qui ont partagé avec moi leurs connaissances des bonobos de la région.

Wivine, merci pour tous ces bons petits plats que tu m'as cuisiné pendant toutes ces soirées, merci d'avoir partagé avec moi ton expérience aux champs, à la pêche. Tu étais notre rayon de soleil chaque soir quand tu arrivais avec tes enfants à la ferme. Ces moments sont gravés en moi.

April 2011

During my third field mission, I had the wonderful opportunity to meet Gay Reinartz and Patrick Guislain. Thanks you so much for the time you took to discuss about my project, helping me to adjust methodologies, sharing with me your knowledge about forests and your experience in Congo.

I also have to thank Fiona Maisels, who gave me precious advices to prepare the transect designs.

Céline Devos, you became a friend, you helped me so much in the field, reading my abstract on the terrace, advising me for my work. And Fredo for those wonderful evenings! You taught me how to cook unexpected meals with cans and you make me discovered how to prepare bread in the oven (yes bread in the middle of Congo, and it is just so delicious!).

I thank the Master students who came in 2011 and 2012, Sophie Hannay, Marie Vimond and Emilien Raynaud, helping me to collect more and more data.

And I could not forget Franck, we spent so many wonderful time together, laughing at "*Il est pas là Pala, et Bokula il est pas beaucoup là*" and reinventing whirlwind.

January 2013

This project took a new scope thanks to the wonderful help from the people of the Max Planck Institute. Christophe, thanks you so much for welcoming me in the department!

Hjalmar, you taught me so many things. I do not know how I can thank you for all this time and this energy you gave me. You taught me how to approach my research questions, how to respond to them. You really brought me a new way of thinking and gave new facets to this research that I would never imagine when I started. You gave me all the keys to succeed and I can only hope I will have the opportunity to continue to work with you, I still have so many things to learn from you!

`Roger <- Thanks (you).` You taught me so many things in R and about statistics. Your courses are just fascinating and I am so grateful I had the opportunity to follow them. You also spent so many times to answer all my questions. Statistics was a dark science for me and you succeed to transform it as a wonderful tool to approach my research questions.

Barbara, Gottfried, I warmly thank you for all your help, you always opened your doors when I had questions and I am impatient to have the opportunity to work with you.

Cleve, thanks you for reading all my manuscripts, I know it was sometimes a hard job! Alexandra, merci pour ces bons moments à arpenter les villes autour de Leipzig avec toi!

A long time ago

Je ne pourrais pas terminer ces remerciements sans m'attarder sur mes amis et ma famille.

Mes tendres amis qui sont présents depuis si longtemps, vous êtes si importants dans ma vie. Céline, tu m'accompagnes depuis mes premiers pas, présente à chaque étape, me soutenant dans chaque épreuve. *Les filles*, vous savez à quel point nos soirées sont essentielles pour moi, vous apportez tant de gaieté et de joie dans ma vie. Justine, merci de m'avoir ouvert la voie de chaque étape administrative en les réalisant une année avant moi ! Fany, merci d'avoir pris soin de moi pendant ces dernières semaines de rédaction.

Maman, Grany, Marraine, merci pour votre soutien quotidien, vous n'imaginez pas combien vous me manquez pendant tous ces voyages. Maman, ma tendre maman, ton soutien est tellement indispensable dans ma vie, tu as fait de moi ce que je suis, tu m'as donné toutes les clefs pour atteindre mes rêves, tu es présente à chaque seconde. Que ferais-je sans toi ?

Mes petits « *bro* », ces incroyables lascars, vous apportez tant de douceurs et de piquants dans ma vie.

Jief, mon compagnon de vie, de rire (et de travail). Tu me soutiens à chaque étape. Merci pour ton écoute, ton aide et tes conseils avisés à n'importe quelle heure de la journée et de la nuit. Tu es « *my boy lollipop* » qui égaie chaque seconde de vie. Je ne pourrais en dire plus ici, tu sais à quel point tu contribues à mon équilibre et mon bonheur.

Et je devrais peut-être aussi remercier mes chats, qui se sont fait un devoir de me réveiller chaque matin, me rappeler l'heure des repas et le moment de s'arrêter pour aller dormir …

Today

I warmly thank Barbara Fruth, Hjalmar Kühl, Emmanuel Serusiaux, Zjef Pereboom, Jan Bogart and Alain Hambuckers for having accepted to evaluate this work. I am looking forward to your comments and remarks, I am confident it will lead to interesting discussions.

I will finish with a warm thank to you, the people who will open this manuscript. I hope you will find the answers you are looking for and I am impatient to discuss with you about this research.

Et merci à tous ceux qui m'ont gentiment prêté leurs photos pour mettre quelques couleurs dans ce document !

Une page de ma vie se tourne aujourd'hui mais l'aventure n'est pas finie. C'est en grande partie grâce à vous tous, Merci !

SUMMARY

The bonobo is the last Great Ape that has been discovered (1929) and represents, with the Chimpanzee, our closest relative. Bonobos are endemic to the Democratic Republic of Congo, and people thought that the species was only inhabiting the dense tropical forests of the Central Cuvette until, in the 1990s, Thompson identified a population living in a transitional ecotone of moist forests and savannahs, at the southern extremity of the bonobo distribution range. Her findings changed our perception of the ecological limit of the species range but, until now, bonobos remain mainly studied in the dense forests. In 2005, another population living in forest-savannah mosaics, this time in the western extremity of the distribution range, has been documented by an extensive survey conducted by the World Wide Fund for Nature (WWF). This new discovery pointed out again the peculiarity of this environment and the necessity to understand how bonobos were evolving within this habitat.

The forest-savannah mosaics are characterized by a high diversity of micro-habitats and more pronounced seasons. Both factors inducing larger spatio-temporal variations of food availability than in the dense rainforests, bonobos probably require more flexibility and plasticity to adapt to this type of environment. The study of populations inhabiting forest-savannah mosaics is thus essential to adequately describe the full adaptation spectrum of the species. Understanding how bonobos could adapt and subsist in fragmented habitat is also particularly important in the current context of global landscape modification, since the forests of the Congo Basin are being cleared or degraded at a rapidly increasing rate. Furthermore, the study of forest-savannah mosaics populations could also shed light on the different socio-ecological evolution of bonobos and chimpanzees. Scientists generally suggest that this divergence in social patterns between the two species reflects differences in environment quality prevailing when the two species separated but it remains unclear if current environmental variation could influence their present socio-ecological traits. The study of bonobo populations within their entire distribution range is indispensable to address this type of question.

The main objective of my study was to shed light on the etho-ecological requirements of the bonobo population living in the forest-savannah mosaics of western DRC, by covering topics helping to adequately formulate conservation measures that could further be applied in the region.

In the first chapter of the study, we investigate how bonobos use the forests and which environmental variables explain their home range use. By using an adequate scale search in species distribution modelling, we link their environment requirements with behavioural characteristics operating at different scale ranges. We highlight that forest structure explains nesting site location at large scale, above 750 m of radius around nest occurrence (and preferentially at least above 1200 m), which reflects bonobo ranging strategies. On the other hand, food availability acts at smaller scales: terrestrial herbaceous vegetation is influential under 300 m and fruit availability under 600 m, indicating sleeping site selection and feeding behaviour around nesting sites, respectively. Additionally, our results suggest that environmental constraints have locked the bonobos into particular areas which are intensively co-used by humans. This study provides, for the first time, precise information on the ecological requirements of bonobos in forest-savannah mosaics and offers a new approach for modelling scale search that could be widely applied when researchers endeavour to highlight the influential scale range of spatial or temporal variables in diverse research topics.

In the second chapter, we estimate population density over the study site and investigate population dynamics over years. Our results highlight significant variation of yearly density in one of the two study communities, suggesting that this community has significant variability in use of its home range. This finding highlights the importance of forest connectivity, a likely prerequisite for the ability of bonobos to adapt their ranging patterns to fruit availability changes. We further test whether the high seasonality of fruit availability influences bonobo cohesiveness at night. We found no influence of overall fruit availability on nest grouping patterns. Only fruit availability at the nesting sites showed a positive influence, indicating that bonobos favour food ‘hot spots’ as sleeping sites. This characteristic being similar in the populations living in the dense forests, it suggests that bonobos stay highly cohesive, despite the period of food scarcity, and thus, that this species trait is probably conservative as it does not reflect current environmental variations.

In the third chapter, we describe bonobo diet in the study site by investigating the seasonality patterns of food consumption and the nutritional drivers of food species selection. We show that bonobo diet is restricted to a few fruit species, which are selected for their high carbohydrate contents. An in-depth investigation of the most consumed species revealed three major groups of plant species association in daily food consumption. Although the preferential combination of species is related to seasonal fruitage, we also demonstrate that the peculiar association of these species enables to maintain constant nutrient balance over time. Finally, as the dominant species are characteristics of various habitat types, it suggests that bonobos have to travel large daily distances in order to maintain the nutritional balance.

In conclusion, our results emphasize that bonobos have adapted their diet and their foraging strategy to the forest-savannah mosaics by maximizing access to large forest patches or varying home range size according to fruit availability. Sleeping behaviour and cohesiveness, on the other hand, seem to be a species conservative trait. Our research demonstrates, in a conservation perspective, that bonobos are probably already highly constrained by their ecological requirements and that conservation actions should rapidly be taken to assure their subsistence in those fragmented forests.

RÉSUMÉ

Le bonobo est le dernier grand singe à avoir été découvert (1929) et représente, avec le chimpanzé, notre plus proche cousin. Les bonobos sont endémiques à la République Démocratique du Congo, et les scientifiques pensaient que l'espèce vivait uniquement dans les forêts tropicales denses de la Cuvette Centrale jusqu'à ce que, dans les années '90, Thompson identifie une population vivant dans un écotone de transition de forêts humides et de savanes, dans l'extrémité sud de l'aire de distribution de l'espèce. Sa découverte a changé la perception des limites écologiques de l'espèce mais, jusqu'à ce jour, le bonobo reste principalement étudié en forêts denses. En 2005, une autre population vivant en mosaïques de forêts-savanes, cette fois à l'extrémité ouest de l'aire de distribution, a été documentée lors d'un vaste inventaire forestier mené par le « World Wide Fund for Nature » (WWF). La découverte de cette nouvelle population redirigea l'attention sur cet environnement particulier et la nécessité de comprendre comment les bonobos évoluent au sein de cet habitat.

En effet, les mosaïques de forêts-savanes sont caractérisées par une grande diversité de micro-habitats et des saisons plus prononcées qu'en forêts denses. Ces deux facteurs induisant de fortes variations spatio-temporelles de la disponibilité alimentaire, les bonobos doivent probablement montrer plus de flexibilité et de plasticité pour se maintenir dans cet environnement. L'étude de ces populations vivant en mosaïques de forêts-savanes est donc essentielle pour couvrir de manière adéquate le spectre d'adaptation de l'espèce. Ces informations sont particulièrement importantes dans le contexte actuel de modification globale des paysages. En effet, les forêts du Bassin du Congo sont sujettes à une déforestation et une dégradation des habitats dans les taux sont en pleine croissance, et nous n'avons, à ce jour, aucune idée des capacités d'adaptation et de subsistance du bonobo dans un habitat fragmenté. Par ailleurs, l'étude de ces populations vivant dans un environnement avec des variations écologiques plus élevées qu'en forêts denses pourraient nous permettre de mieux comprendre les différentes évolutions socio-écologiques du bonobo et du chimpanzé. Les scientifiques suggèrent généralement que la divergence des patterns sociaux des deux espèces reflète des qualités d'environnement différentes lors de la séparation des deux espèces. Cependant, nos connaissances actuelles ne nous permettent pas de déterminer si les variations environnementales actuelles continuent d'influencer les traits socio-écologiques observés. L'étude de populations de bonobos sur l'ensemble de l'aire de distribution de l'espèce est donc indispensable pour examiner ce type de question.

L’objectif de ma recherche était d’identifier les besoins étho-écologiques d’une population de bonobos vivant dans les mosaïques de forêts-savanes de l’ouest de la République Démocratique du Congo et ce, en m’intéressant particulièrement aux thématiques permettant ensuite de formuler des mesures adéquates de conservation à appliquer dans la région.

Dans le premier chapitre de cette étude, nous analysons comment les bonobos utilisent les forêts et les variables environnementales expliquant l’utilisation du domaine vital. En appliquant une recherche d’échelle spatiale adéquate dans un modèle de distribution d’espèce, nous faisons le lien entre les besoins environnementaux de l’espèce et les caractéristiques comportementales opérant dans les différents domaines d’échelle. Nos résultats démontrent que la structure spatiale de la forêt explique la localisation des sites de nids à large échelle, soit dans un rayon au-delà de 750 m autour des nids observés (et préférentiellement au-delà de 1200 m), ce qui reflète les stratégies de déplacements du bonobo dans son domaine vital. Par contre, la disponibilité alimentaire ne joue un rôle qu’à plus petites échelles puisque les plantes herbacées terrestres et la disponibilité en fruits influencent la présence de nids dans un rayon inférieur à 300 m et à 600 m, respectivement, révélant les critères régissant la sélection des sites de nids et la stratégie alimentaire autour de ceux-ci. Nos résultats suggèrent également que les contraintes environnementales sont probablement tellement puissantes qu’elles obligent les bonobos à utiliser des zones où l’activité humaine est importante. Notre étude fournit les premières informations précises des besoins écologiques des populations de bonobos en mosaïques de forêts-savanes. Elle offre également une nouvelle approche pour la recherche d’échelle spatiale en modélisation, approche qui pourra être appliquée dans de nombreux domaines de recherche dans lesquels l’identification des domaines d’échelles est nécessaire, tant pour des variables spatiales que temporelles.

Dans le second chapitre, nous réalisons une estimation des densités de population dans le site d’étude et investiguons la dynamique de population sur plusieurs années. Nos résultats mettent en évidence une variation annuelle significative de la densité de population pour l’une des deux communautés de bonobos étudiées, suggérant que cette communauté utilise son domaine vital de manière très variable. Ce résultat met en lumière l’importance de la connectivité entre les forêts, afin de permettre aux bonobos d’adapter leurs patterns de déplacement en fonction de la disponibilité alimentaire. Nous avons ensuite testé si la forte saisonnalité de la disponibilité en fruits influence les patterns de groupements des bonobos aux sites de nids. Nos résultats suggèrent une forte cohésion aux sites de nids, mais ce, indépendamment de la disponibilité globale en fruits de la forêt. Par contre, la disponibilité en fruits au sein du site de nids semble favoriser la cohésion nocturne des bonobos, indiquant que ceux-ci choisissent des lieux de ‘hot-spot’ alimentaires pour placer leurs sites de nids. Ces traits comportementaux sont similaires à ceux des populations de bonobos vivant en forêts denses et suggèrent que la cohésion des bonobos est un trait conservatif partagé par l’ensemble de l’espèce et non le reflet des variations environnementales actuelles.

Dans le troisième chapitre, nous décrivons le régime alimentaire des bonobos dans le site d’étude. Nous étudions en particulier les patterns saisonniers de consommation des ressources alimentaires et les facteurs nutritionnels conduisant à la sélection de ressources. Nos résultats indiquent que le régime alimentaire du bonobo repose sur très peu d’espèces de plantes, sélectionnées pour leur contenu riche en carbohydrates. Nos analyses plus détaillées des espèces les plus consommées ont mis en évidence trois groupes majeurs d’association d’espèces dans le régime alimentaire. Bien que cette combinaison préférentielle d’espèces soit liée aux patterns saisonniers de fructification, nous démontrons également que l’association spécifique de ces espèces permet de maintenir un équilibre d’apport en nutriments constant dans le temps. Finalement, ces espèces les plus consommées sont également caractéristiques de différents types d’habitat, ce qui suggère que les bonobos doivent probablement réaliser, quotidiennement, de longs déplacements afin de maintenir cet équilibre nutritionnel.

Pour conclure, nos résultats mettent en évidence que les bonobos adaptent leur régime alimentaire et leurs stratégies de recherche alimentaire aux mosaïques de forêts-savanes en maximisant l’accès à de grands patchs forestiers et en variant la taille de leur domaine vital en fonction de la disponibilité alimentaire. Le comportement et la cohésion sociale au site de nids, par contre, semblent être des traits conservatifs de l’espèce. Dans une perspective de conservation, notre recherche démontre que les bonobos sont probablement déjà hautement contraints par leurs besoins écologiques et que les actions de conservation devraient rapidement être mises en place pour assurer la subsistance de cette population dans ces fragments forestiers.

TABLE OF CONTENTS

Chapter 1:

Chapter 2:

Chapter 3:

LIST OF ACRONYMS

DRC	Democratic Republic of Congo
IUCN	International Union for Conservation of Nature
MMT	Mbou-Mon-Tour
MYA	Millions of year
REDD+	Reducing Emissions from Deforestation and forest Degradation + Conservation and Sustainable Development
WWF	World Wide Fund For Nature

INTRODUCTION

© Adeline Serckx

I GENERAL CONTEXT, PROBLEMATIC AND OBJECTIVES

© Zanna Clay

I.1 The value of a bonobo population in forest-savannah mosaics

I.1.1 GLOBAL CONTEXT OF HABITAT CHANGES ACROSS TROPICAL FORESTS

Humans have used, encroached and cut forests down for the last ten thousand years since agriculture was discovered and wild animals domesticated and turned into livestock. But rapid human population growth, and human infrastructure development, particularly since the last century, completely modified the planet. Human population almost tripled during the last 65 years (Table 0-1 – Page 5; United States Census Bureau), which induced a huge need for agriculture land. Urbanization grew rapidly, leading to the development of urban markets through conversion of all lands surrounding the cities for agricultural or industrial production. Food consumption patterns often shifted toward more consumption of livestock products, requiring additional land to produce the same amount of food (Gerbens-Leenes and Nonhebel 2002). By connecting almost all places of the world and by giving access to regions where forests were still extensive, globalization completely modified the relationship and scales of exchanges between man and Nature. A large extent of relatively intact tropical forests became more accessible and exploitation accelerated. At the beginning of the 1990s, the effects of global changes became more tangible and scientists developed new methods to quantify and map deforestation (Table 0-2 – Page 5) (Riitters et al. 2000, Pan et al. 2011), to identify the key drivers of these changes (Lambin et al. 2003, Turner et al. 2007, Riitters et al. 2012) and to predict their consequences (Fischer and Lindenmayer 2007, Lambin et al. 2013). Deforestation and forest degradation are now considered important causes of climate change, responsible for 6 to 17 percent of global warming pollution, as well as key drivers to biodiversity loss and major threats to the livelihoods of forest people (Pan et al. 2011).

The rate of deforestation and forest degradation varies considerably across the tropical world. Land use practices are different from country to country (i.a. cattle ranching and soy plantations in Latin America vs. palm oil plantations and timber industry in South Asia) and did not induce the same levels of deforestation. But every country in the world is now faced with the major consequences of biodiversity erosion, e.g. the dramatic decline in Sumatra of tigers (Linkie et al. 2008), elephants (Choudhury et al. 2008) and orang-utans (Ancrenaz et al. 2008) or the massive effects of habitat fragmentation in Amazonia (Laurance et al. 2002). In contrast to this, Africa is often said to have been spared, probably because deforestation is still occurring at smaller scales, to supply nearby cities in charcoal production or cultivated products (de Wasseige et al. 2009). However, pressure is growing, and the situation could change rapidly and the coming years will be critical for forest resources of the Congo Basin.

I.1.2 THE CONGO BASIN

In contrast to most regions of the world, human population growth is still extremely high in Central Africa and population could double in the next 35 years (Table 0-1 – Page 5; United States Census Bureau). The recurrent political instability of some regions, and the resulting civil wars regularly induce vast human population migrations, leading to high level of poverty and internal land use conflicts (Devers and Vande Weghe 2006). Rural communities are still heavily dependent upon readily-available resources, living from slash-and-burn agriculture and subsistence hunting. A decrease in soil fertility and tree regeneration has already been observed, and the limited access to agricultural technologies should rapidly increase the needs of new agricultural land surfaces. New lands for fuelwood will also be required as charcoal represents more than 80 % of the domestic energy consumption (de Wasseige et al. 2012). In the same time, urbanisation is already bringing about large degraded areas around big cities and major transport networks (IUCN and ICCN 2012).

Besides the land requirements of local populations, the Congo Basin is also rich of several resources mondially coveted. One third of world mineral ressources is found in Africa and the subsurface strata of the Congo Basin offers very important oil deposits and mineral resources, such as iron, copper, manganese, uranium or even diamonds and gold. Until now, much of these resources have been exploited in small scale operations but mining represents nevertheless already a significant threat to forest ecosystems. Large scale monoculture of palm oil plantations and logging concessions are developing in almost all Congo Basin countries. In addition to deforestation, pollution and natural resources degradation, the exploitation of resources also accelerate the development of infrastructure and of transport networks, significantly increasing the access to new parts of the forests (de Wasseige et al. 2012).

The Congo Basin is also home to a large number of endemic species, with subregions considered as biodiversity hotspots (Devers and Vande Weghe 2006). Especially, three species of Great Apes are inhabiting these forests: the chimpanzees, with three of the four subspecies, *Pan troglodytes troglodytes*, *P. t. ellioti* and *P. t. schweinfurthii*; three subspecies of gorillas, *Gorilla gorilla gorilla*, *G. beringei beringei* and *G. b. graueri*; and the bonobos, *Pan paniscus* (Figure 0-1 – Page 6). These populations are under a lot of pressure, they are already highly threatened by human activities through habitat destruction and/or poaching (Junker et al. 2012) and their potential adaptation capabilities to fragmented habitats are still poorly understood.

Table 0-1: Population estimation and their annual growth rate across the world (United States Census Bureau)

	1950	**1975**	**2000**	**2015**	**2025**	**2050**
World	2558 (NA)	4089 (NA)	6090 (1.2)	7253 (1.1)	7,987 (0.9)	9,376 (0.5)
Europe	547 (NA)	679 (NA)	731 (0.0)	744 (0.1)	745 (-0.1)	708 (-0.4)
North. America	166 (NA)	239 (NA)	313 (0.1)	357 (0.8)	384 (0.7)	441 (0.5)
Latin America	165 (NA)	321 (NA)	518 (1.3)	617 (1.0)	673 (0.7)	747 (0.1)
Oceania	12 (NA)	21 (NA)	30 (1.3)	37 (1.2)	41 (0.9)	48 (0.4)
Asia	1438 (NA)	2413 (NA)	3695 (1.3)	4348 (0.9)	4713 (0.7)	5190 (0.1)
Africa	229 (NA)	416 (NA)	804 (2.3)	1150 (2.3)	1430 (2.1)	2242 (1.5)
Middle Africa	28 (NA)	42.2 (2.1)	97.7 (2.9)	147.2 (2.4)	185.1 (2.1)	288.6 (1.5)

Population estimates are presented in million, with the growth rate expressed as percentage in brackets. Middle Africa includes Angola, Cameroon, Central African Republic, Chad, Democratic Republic of Congo, Equatorial Guinea, Gabon, Republic of Congo, Sao Tome and Principe.

Table 0-2: Area of forests and land-use change by biome, or region (inspired from Pan et al. 2011)

Biome and region	**Total forest area (Mha)**			**Net change (Mha yr^{-1})**	
	1990	***2000***	***2007***	***1990-1999***	***2000-2007***
Boreal	1102.7	1110.6	1135.2	0.791 (↑ 0.07%)	3.059 (↑ 0.3%)
Temperate	733.6	746.1	766.1	5.346 (↑ 0.7%)	5.285 (↑ 0.7%)
Tropic	2123.0	2009.2	1949.4	-11.380 (↓ 0.5%)	-8.546 (↓ 0.4%)
South Asia	325.4	301.1	297.3	-2.430 (↓ 0.75%)	-0.543 (↓ 0.19%)
Africa	749.2	708.6	684.7	-4.060 (↓ 0.54%)	-3.420 (↓ 0.48%)
America	1048.4	999.5	967.4	-4.890 (↓ 0.47%)	4.583 (↓ 0.46%)

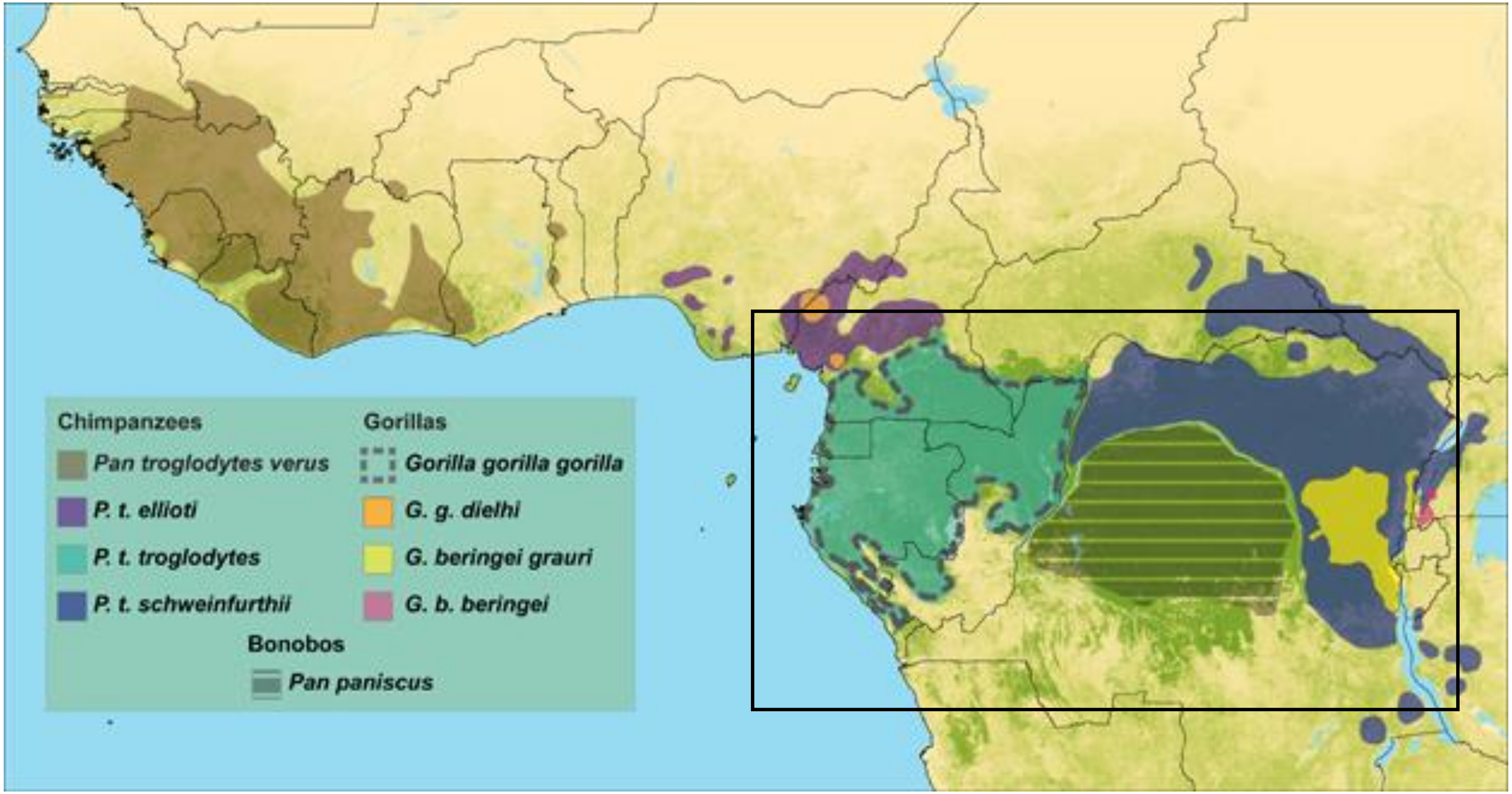


Figure 0-1: Distribution range of Great Apes in Africa (picture taken from Mitchell and Gonder 2013)

The Congo Basin is highlighted by the black rectangle. Within the Congo Basin, three of the four subspecies are living: *Pan troglodytes troglodytes* (in Republic of Congo and Central African Republic), *Pan troglodytes ellioti* (in Cameroon), *Pan troglodytes schweinfurthii* (in DRC). The two subspecies of Gorilla are found too, *Gorilla gorilla* (in Republic of Congo, Central African Republic and Cameroon), *Gorilla beringei* (in DRC) and the Bonobo, *Pan paniscus*, endemic to DRC.

I.1.3 PRIMATES LIVING AT THE EDGE

Besides habitat loss, deforestation and forest degradation cause diverse indirect threats to Great Apes. The proximity of villages and transport networks have already been identified as a major driver of ape density decline (Reinartz et al. 2006, Kuehl et al. 2009, Wich et al. 2012, Junker et al. 2012, Hickey et al. 2013, Imong et al. 2014) and can even explain gorilla patchy distribution within suitable forest habitats (Sawyer and Brashares 2013). Road opening have harmful consequences for animal species, such as edge and barrier effects, road-related mortality or human access to new forest parts (Laurance et al. 2008, 2009). Human proximity commonly leads to increased hunting and poaching for bushmeat trade of large mammals (de Wasseige et al. 2012). Furthermore, the increased human-ape proximity could conduct to higher risk of disease transmission (Gillespie et al. 2005, Goldsmith et al. 2006) or to ape crop raiding which generates human-ape conflits and often, ape hunting (Reynolds et al. 2003, Goldsmith et al. 2006).

While indirect consequences of deforestation and forest degradation have already been widely demonstrated, we still do not know what Great Apes could afford in term of habitat loss or fragmentation and their adaptation capabilities. Primates in forest fragments have mainly been studied in Latin America (Marsh 2003). Species will react differently, even in same fragments, depending on their flexibility in feeding ecology, their tolerance towards secondary forests or their dispersal capacity between forest patches (Chapman et al. 2003, Gilbert 2003, Umapathy and Kumar 2003) and, negative effects seem to be higher for frugivorous species (Chiarello 2003, Gilbert 2003). As a consequence, primate population will show demographic changes such as lower fertility and birth rates or modification of age/sex composition (Chapman et al. 2003, Umapathy and Kumar 2003), which will ultimately lead to smaller populations, loss in genetic variability and ultimately to inbreeding depression (Goncalves et al. 2003, Li et al. 2003).

Facing those potential devastating effects for primate persistence, it becomes more and more important to integrate factors of landscape ecology in primate studies, first to understand the habitat characteristics influencing their occurrence but also to set up appropriate conservation actions. Studies on animal distribution modelling have already demonstrated that patch size (Arroyo-Rodríguez and Dias 2010), shape (Nams 2012), isolation and connectivity (Prugh 2009) as well as within-patch (Thornton et al. 2010, Ye et al. 2013) and landscape matrix quality (Watling et al. 2011) will influence animal occurrence. For primates, those predictors are still poorly used despite their obvious interest. For example, studies on howler monkey showed that patch size is the main factor constraining populations in fragmented habitats while patch isolation did not seem to be a strong predictor, probably because of the ability of howlers to move among forest patches (Arroyo-Rodríguez and Dias 2010). In chimpanzees or bonobos, predictors expressing forest cover appear to be essential to explain population density (Torres et al. 2010, Hickey et al. 2013). But forest cover remains an imprecise variable which will not help to extrapolate how Great Apes would survive in fragmented forests. Questions such as "*Would they be more affected by forest patch quality or by patch isolation?*" or "*What would be their ability to adapt their feeding ecology to more disturbed conditions?*" remains open. The opportunity to study a population which has adapted to fragmented forests in a long-term evolutionary process appears to be a formidable opportunity to address such questions.

I.2 **New perspectives for our understanding of the species**

The bonobo is a forest dwelling species. Endemic to the southern part of the Congo River, people thought for a long time that the species was exclusively linked to the dense tropical forests until, in the 1990s, Thompson identified a bonobo population in the southern extremity of the species distribution range, a drier environment characterized by a transition between moist forests and savannahs (Thompson 1997, 2001). Her finding changed our perception of the ecological limit of the species, but until now, bonobos remain mainly studied in the dense forests of the Central Cuvette.

However, this transitional ecotone of the southern part of the range, similar to the forest-savannah mosaics of western Democratic Republic of Congo (DRC), can show large differences in comparison to the dense forests. Micro-habitats within the forests are diversified and can change over only a few meters, seasons are generally more pronounced and savannah can bring additional food supply (Thompson 1997, 2003). Food availability will thus show more spatio-temporal variations, probably requiring more flexibility and plasticity from the bonobos to adapt to this type of environment. But until now, with the exception of the consumption of some fruit species (Thompson 2003, Inogwabini and Matungila 2009), the precise role of savannahs for bonobos remains unknown. In addition, we still lack comparisons of ranging patterns, home range use, daily mean travelling distance or even diet between the two types of habitats. And yet, such information would be essential to adequately cover the adaptation spectrum of the species and to understand how bonobos could adapt and survive through changes in their habitats due to deforestation or forest degradation within the dense forests.

A recent genetic study underlined the fact that the geographical patterns of bonobo genetic diversity seem to be shaped by paleoenvironmental changes during the Pleistocene (Kawamoto et al. 2013). The western population has been isolated since those geographical events from the other populations, and could show interesting cultural differences to study in addition to their conservation value in terms of the global gene pool diversity.

The different socio-ecological evolutions of bonobos and chimpanzees have stirred considerable fascination among scientists. The sister species are showing differences in social organization and cohesiveness (Furuichi 2009), which probably reflect different evolutionary responses to their environments since the end of the Pleistocene. But so far, it remains unclear if current environmental variation could influence the socio-ecological traits of both species.

The study of bonobo populations in their entire distribution range is indispensable to help address these questions. In addition, the forest-savannah mosaic habitat is particularly interesting for our understanding of the evolution of the early hominoids since it is considered to be the closest habitat to the archaic environment where the common ape/human ancestor has evolved (Thompson 1997).

I.3 **Conservation challenges**

While this western population of bonobo could be of major interest for science, and recent inventories suggested that the region might house significant numbers of bonobos (Inogwabini et al. 2007), it remains true that western DRC could also be the theater of acute challenges. The DRC is the largest country within the Congo Basin but also one of the most unpredictable. Still recovering and rebuilding itself from the successive civil wars of the 1990s and early 2000, the ongoing instability in the eastern region continues to weaken the country. Moreover, DRC is showing the highest population growth of the Congo Basin (2.5% estimated for 2015, United States Census Bureau), leading to a continuous demand in terms of food supply, employement, education and health, demands that are increasingly difficult to meet by governmental development projects. As a consequence, development actions are mainly developed in and around the largest cities where one third of the country's population is now living, while rural communities do not benefit from any help and thus still rely on slash-and-burn agriculture and subsistence hunting (Devers and Vande Weghe 2006). Government or affiliate authorities are generally under-represented in rural regions which leads to a weak respect of laws, e.g. illegal logging concessions are established without difficulty, the restrictive periods for hunting or fishing are mostly not applied, protected species are hunted throughout the country, etc.

The global state of the country leads now to a devastating loss of biodiversity, for which the main factor is poaching for the bushmeat trade (Amman 2001, Wilkie 2001, Devers and Vande Weghe 2006, de Wasseige et al. 2009, de Wasseige et al. 2012, IUCN and ICCN 2012). The rise in illegal poaching/hunting is exacerbated by rapid social change, an increase in demand for meat, and eroding traditional taboos. The economic dynamics of the bushmeat trade are often complex. Research has shown that there is a strong cultural attachment to bushmeat, inducing the fact that a high proportion of urban citizens will consume it and would even like to increase their consumption despite the availability of domestic meat and despite their possible higher price than domestic meat (IUCN and ICCN 2012). As a result, forests next to cities and transport networks are completely depleted.

The western population of bonobo is located less than 400 km of Kinshasa and only 25 km of the Congo River and could rapidly become a target for bushmeat traders. Until now, bonobos are not hunted in the region thanks to the local ancestral taboos of the Teke ethnic group but this "*natural*" protection could rapidly change with regards of the financial attraction that bushmeat trade could bring to the population. Some cases of bonobo poaching have already been reported (local population, pers. comm.) to WWF-DRC (World Wide Fund for Nature), which started its conservation program in 2007. The region has only raised poor interest from commercial companies as no mineral or oil ressources have been found in the soil strata, but logging concessions are now increasingly developed. Consequently, immigrant populations which do not share bonobo taboos with the Teke people might settle in the area and the risk of the development of a bushmeat trade network could rapidly arise, as already observed in some logging concessions of the country (Amman 2001). The current status of the bonobo population could then rapidly change: conservation actions are urgently needed in the region.

But rural communities of western DRC, and particularly the Teke ethnic group, are still completely dependent on readily-available resources of their forests and on slash-and-burn agriculture. Their protein consumption entirely relies on subsistence hunting and fishing. Their agriculture, almost only composed of manioc fields, is developed on forest soils. This, and the current human population pressure, make the designation of a protected area in the region unthinkable and unrealistic. However, under the impulse of the president of the local NGO Mbou-Mon-Tour, Jean-Christophe Bokika, and the ongoing conservation actions lead by WWF-DRC, the communities of different villages have accepted to dedicate some part of their communal forests for bonobo conservation through the setting up of “community natural reserve”. These reserves could only be a success if alternatives means of subsistence are developed for the population and if integrative forest management measures are developed. Consequently, we first need to understand bonobo etho-ecological requirements as well as human forest-use practices in order to identify appropriate land use patterns. Only by doing this shall we ensure long term persistence of the bonobo population while allowing human development to happen. If managed carefully, those reserves could become an example of possible human-ape coexistence in a fragmented environment.

I.4 Objectives of the study

The main objective of my study was to shed light on the etho-ecological requirements of the bonobo population living in the forest-savannah mosaics of western DRC. As the population had never been studied in depht before, I wanted to cover general topics such as population density estimation, home range use or diet which are essential to adequately formulate conservation measures that could be applied in the region.

In the **first chapter** of my thesis, I investigated how bonobos were using the forests and which environmental variables were explaining their home range use. By improving current methodology of scale search in species distribution modelling, I then linked their environment requirements with behavioural characteristics operating at different scale ranges: ranging, feeding and sleeping behaviours. Our study provides, for the first time, precise information on the ecological constraints of bonobos in forest-savannah mosaics but also offers a methodology that could be widely applied when researchers endeavour to highlight the influential scale range of spatial or temporal variables in diverse research topics.

In the **second chapter**, I estimated population density over the study site and investigated the possible explanation of the yearly variation in one of the bonobo communities studied. I looked into bonobo night cohesiveness in relation to fruit availability. The evolution to higher cohesiveness within bonobos communities than within chimpanzees' communities is often related to the larger food availability within bonobos' habitats. But such hypothesis were made based on bonobo populations living in the dense tropical forests of central DRC. I wanted to investigate if bonobos communities stay highly cohesive in an environment with more spatio-temporal variations in terms of habitats, and if current variation in fruit availability could still influence bonobo grouping patterns. This chapter should contribute to shed further lights on bonobo social traits in comparison to those of the chimpanzee.

In the **third chapter**, I described bonobo diet in the study site. I investigated seasonal variations and nutritional drivers of food species selection. I further discussed the relative importance of the most consumed species and the potential implications for bonobo foraging strategy. With this chapter, I come up with preliminary answers on how bonobos have adapted their diet to the forest-savannah mosaics.

I.5 **Thesis outline**

In the first part of the manuscript, I briefly introduce general information on the species “bonobo”: the recent discovery, the taxomony, the geological and geographical events explaining its speciation with chimpanzee, the habitats in its current geographical distribution range. I summarize current state of art of feeding ecology and social organization by making comparison with chimpanzees, and continue with the current major threats to their survival. I present the region and the study site in more details (location of the region, habitat, fauna, local community) in order to highlight the general context of the research in term of conservation perpectives. I finally describe the methodology used in order to give a general overview of the different types of data collection. The three following chapters present the study results and follow the typical format of journal articles (Introduction – Methods – Results – Discussion – References). With the general discussion and conclusion, I tried to link the different chapters together by summarizing the typical ecological and behavioural traits I highlighted for this bonobo population and its peculiar environment. I underline the interesting analytical methodology I use to address the different questions of my research and briefly contextualize the possible applications of my results in conservation programs. The bibliography section gathers all the references cited in the different chapters and in the introduction. Finally, the appendices provide my report to WWF-Congo on the forest surveys for animal and human monitoring conducted in 2011, 2012 and 2013, the publication of forest elephant decline in which I collaborated by sharing data on the animal forest survey, the complete questionnaire I used to gather socio-economic data and the list of preferred tree species for nesting in the study site.

II THE SPECIES *PAN PANISCUS*

© Fabrice Dentressangle

II.1 **Taxonomy, species discovery and evolutionary history**

Bonobo, *Pan paniscus*, is the last Great Ape that was described (1929) and is, with the chimpanzee, our closest relative. It forms, with the other Great Apes and *Homo sapiens*, the Hominidae family; it is classified in the genus *Pan* with the chimpanzee.

At the beginning of the 20th century, different scientists pointed out unexpected differences between "chimpanzee specimens" to be part of the same species but we had to wait for the complete anatomical description of a cranium by Ernst Schwarz in 1929 in the Tervueren museum so that the existence of two sister species was concluded. First called "*pygmee chimpanzee*" in contrast to the "*common chimpanzee*", the confusion between both species seems to come from the relative smaller size of the observed bonobo individuals that scientists considered to be juvenile chimpanzees. The terminology "*bonobo*" appeared later and its origin remains confused; the widespread hypothesis being an erroneous transcription of the DRC city, Bolobo, on a box transporting individuals. But scientists rapidly adopted this new name to support the existence of two separate species. In the 1930s, Eduard Tratz and Heinz Heck realized the first comparison between bonobos and chimpanzees. They pointed out differences in vocalization, sensitive and nervous behaviours in bonobos, while chimpanzees were considered as irritable and violent, and a bonobo copulation *more hominum* in constrast to a *more canum* copulation of chimpanzees (De Waal and Lanting 1997). Those characterizations probably lead to the still current bonobo reputation of being a "*peaceful and love making*" species.

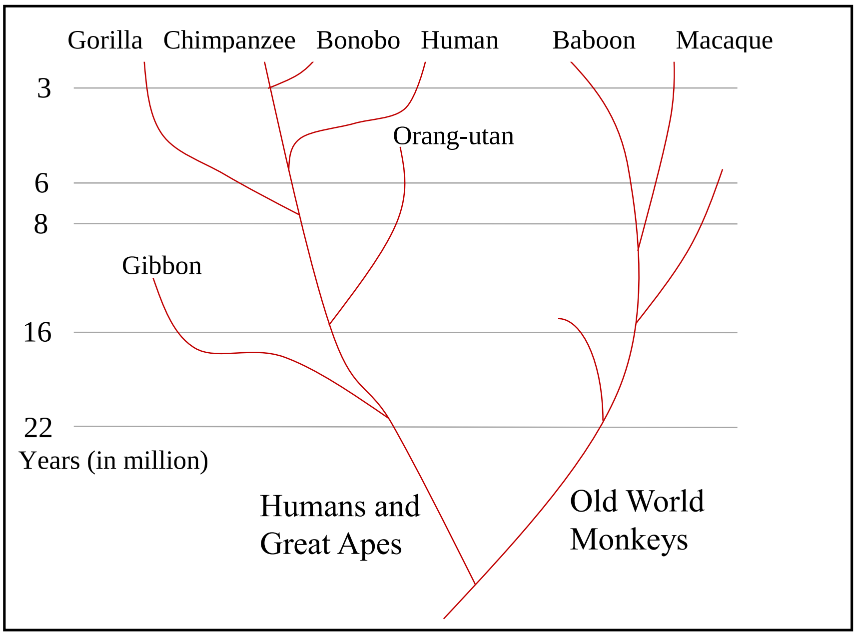


Figure 0-2: Evolutionary history of Great Apes (inspired from De Waal and Lanting 1997)

Bonobo holds a unique place in the range of Great Apes as it is the only species living in the southern part of the Congo River[1]. The geological events, which separated ancestral ape populations and gave rise to different ape lineages, coincide with the timing of the emergence of early Hominids east of the Great Rift, during Miocene through Pliocene epoch (10 – 2 millions of years). Around 12 MYA, African climates were becoming dryer and more seasonal in character. In parallel, landscape itself changed: rifting and uplift produced the highlands of East Africa.

Between 12 and 8 MYA, the African continent experienced tectonic activity inducing large changes in the reliefs with the apparition of the Great Rift Valley and elevation of the rift wall. The western side of the rift, today known as the Congo Basin, received substantially heavier rainfalls. During this period, many ape types became extinct, but the *Proto-pan* persisted.

Around 5 MYA, climatic differences between the east and the west parts of the Great Rift increased, and the Great Lakes System was established. Eastern landscape became dryer which promoted the development of the great upland savannas of East Africa. The earliest primitive hominid emerged in the eastern region of the rift, taking advantages of the new environmental opportunities by exploiting the transition from forest to the drier and new open habitats. In parallel, between 6 and 4 MYA, large changes in climatic phases occurred, with severe droughts followed by humid climates, forcing ape populations to follow appropriate habitats in order to survive.

Around 4 MYA, further hydrological changes took place, with the extension of coastal estuaries from the Atlantic Ocean in the inland of the Congo Basin. A semi-transcontinental water barrier slowly developed which reproductively separated populations of the ancestral *Pan* stock, approximately 3.5 MYA. Rainfall and lake-water levels, previously restrained in the center of the continent by topography, continued to flow but modified into the form of a river system, today known as the Congo River (Thompson 2003).

---

[1] The following description is largely inspired from Thompson 2003.

II.2 **Habitat and geographic distribution**

Bonobos inhabit mainly the dense tropical forests of Central DRC (Figure 0-3), described as the most suitable conditions for their survival (Hickey et al. 2013). They inhabit primary and secondary forests, as well as seasonally inundated swamp forests (Fruth et al. 2008). They are known to prefer mixed mature and old secondary forests with herbaceaous (Marantaceae) or woody understory (Reinartz et al. 2006) but recent studies suggest that we should reconsider the importance of swamp forests when describing their habitat preferences (Furuichi et al. 2012). In the beginning of the 1990s, Thompson described a bonobo population living in the southern extremity of their distribution range, a rather drier area characterized by a transition between moist forests and savannahs (Thompson 1997, 2001). Her finding challenged the established view that bonobos are strictly arboreal apes, specialists of lowland forest environments. In 2007, bonobo populations were also described from the eastern part of the distribution range, in the Thuapa-Lomami-Lualaba landscape (Hart 2007). All those recent findings suggest that the species distribution range and its habitat requirements are maybe still not well known. Moreover, so far, long-term studies have only occurred in dense forests (Lomako Reserve, Wamba-Luo Reserve, and Lui Kotale in Salonga National Park Figure 0-3), limiting our knowledge on the species adaptation capabilities.

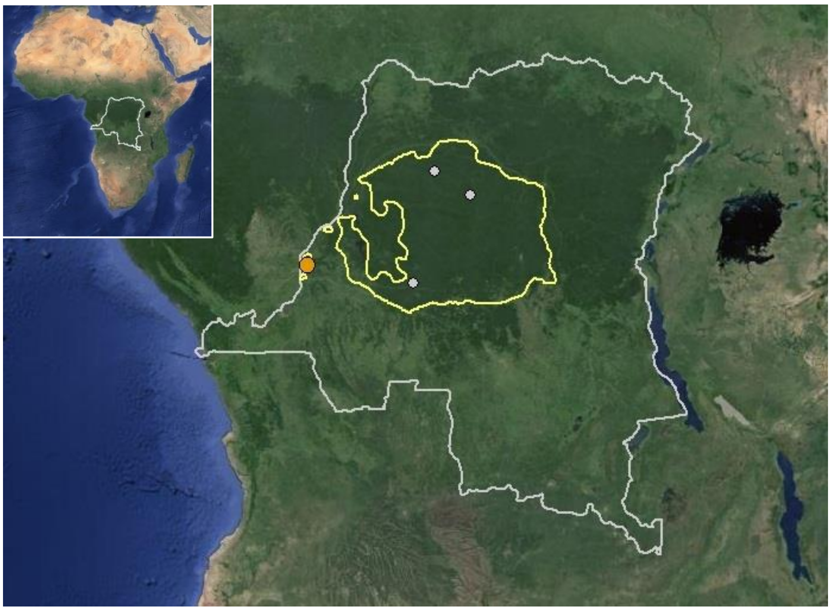


Figure 0-3: Bonobo distribution range

The delimitation of DRC are indicated in grey while the official distribution range of bonobos (UICN, 2014) is presented in yellow. Grey points located the three study sites where bonobos have been studied for many years (From North to South: Lomako Reserve, Wamba-Luo Reserve, and Lui Kotale in Salonga National Park). The orange point highlights our study site.

II.3 **Feeding ecology**

Bonobo is considered to be a frugivorous species, eating preferentially ripe fruits (Conklin-Brittain et al. 2001). They also consume large quantities of terrestrial herbaceous vegetation in comparison to chimpanzees, probably because of the higher nutritional quality of the herb species present in bonobo distribution range (Malenky and Stiles 1991, Malenky and Wrangham 1994). Invertebrate consumption is quite low and is restricted to few species as compared to chimpanzees (McGrew et al. 2007). Until now, bonobos have never been observed to use tools to dig for insects in the wild. For a long time, the species was considered to rarely consume vertebrates, with few observations of squirrel and small duiker hunting (Conklin-Brittain et al. 2001). But recent studies highlighted that Lui Kotale bonobos consume more meat than other bonobo populations and have greater variation in the mammalian species exploited than previously thought, since they also eat small monkeys (Hohmann and Fruth 2008, Surbeck and Hohmann 2008, Surbeck et al. 2009). Their findings suggest that the assumption that bonobos consume less meat than chimpanzees could be more an artefact of the limited numbers of observations and of the peculiarities of bonobo populations studied (Surbeck et al. 2009).

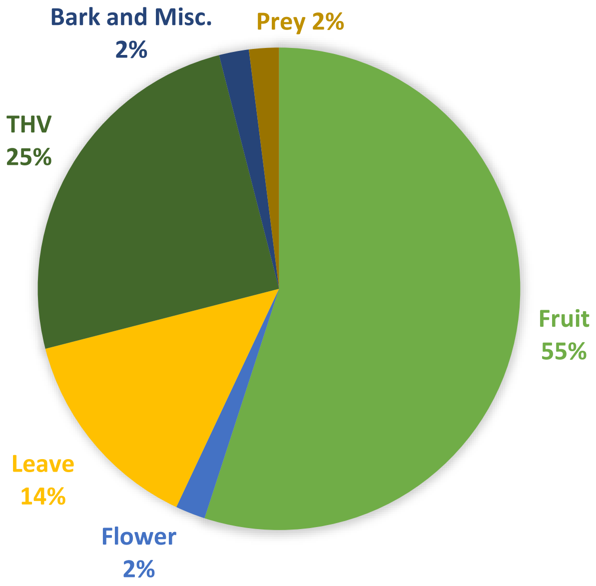


Figure 0-4: Bonobo diet (inspired from Conklin-Brittain et al. 2001, data summarizing 6 studies representing two sites)

Feeding ecology has always been a topic of major interest in animal behaviour and ecology since food resources are an essential part of species survival. Resource density and food selection can affect ranging patterns and habitat use (Furuichi et al. 2001a, 2008) and, in the case of chimpanzees and bonobos, it could also play a major role in social organisation. Both species are highly frugivorous and their evolution in fission-fusion dynamic systems was likely to maintain their frugivorous habits in periods of fruit scarcity (Newton-fisher et al. 2000, Hashimoto et al. 2003, Basabose 2004, Mulavwa et al. 2008). Large variations have been highlighted between chimpanzee study populations in terms of food selection and food processing (Hohmann et al. 2010). But the fact that there are only few bonobo study populations, together with the fact they are all located in similar habitats, explain why there is little feeding variation highlighted for the species, although Thompson already described savannah fruit consumption in period in forest fruit scarcity (Thompson 2003).

Food availability has also been investigated for its possible role in the different evolution of social structure between bonobos and chimpanzees, suggesting that larger resource density and food patch size have enabled more cohesiveness in bonobo communities (Furuichi 2009). However, a recent study on nutritional ecology through nutritional analyses of fruit and leaves consumed by chimpanzees and bonobos showed that dietary quality reflects food selectivity rather than habitat ecology (Hohmann et al. 2010). Variation between habitat quality and nutritional ecology exist, but the availability of high quality fruit was not higher for bonobos than for chimpanzees (Hohmann et al. 2010). Such findings reopen the question of the role of feeding ecology in the evolutionary differences of sociality between the sister species and further attempts to explain current differences in behavioural ecology of *Pan* species among sites should be made. Research on bonobo feeding ecology in a poorly studied environment such as the forest-savannah mosaics would also be a useful tool to improve our understanding on chimpanzee-bonobo differences.

II.4 **Social organization**

Bonobos live in cohesive communities of relatively large party size (i.e., the percentage of the total community size) (Chapman et al. 1994, Hohmann and Fruth 2002, Furuichi et al. 2008). Even if evolving in a fission-fusion dynamic system, current studies show that bonobo parties usually range in the same general area (Figure 0-5) and tend to aggregate towards the evening (Furuichi 2009).

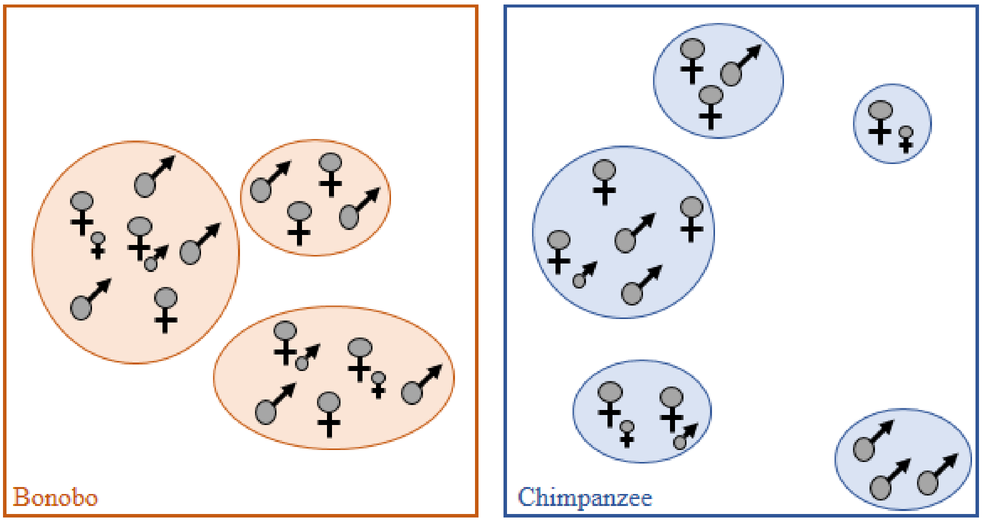


Figure 0-5: Simplified representation of the differences in social organization between bonobos and chimpanzees

In this figure, we try to show how bonobos live in more cohesive communities with a larger relative party size. The composition of chimpanzee parties changes more frequently than that of bonobos. Individual chimpanzees, usually adult females with infants, or small parties, as male patrols, more often travel at a distance from the main parties. In opposition, bonobo parties usually range in the same general area and females occupy central positions within parties.

Bonobo social structure is particularly interesting in an perspective of evolutionary adaptation for fitness maximization: while young females leave their native group at maturity to cohabit with unrelated individuals, they will then form close associations with other females, enabling them to reach high social position within their group (Furuichi 2009). Females occupy central position in the parties, with higher social status for older individuals which often initiate party travelling (Furuichi 1997). Resident females bonds are generally observed by recurrent spatial proximities. Those associations regularly change while mixed-sex dyads, involving both close kin or unrelated individuals, seem to be more stable along time (Hohmann et al. 1999). High-ranking males also usually stay in central position of mixed parties, increasing their chance of access to oestrous females. Male dominance rank among males is influenced by mother status among females and change in dominance between high-ranking males seems to be linked with a corresponding change in dominance between their mothers (Furuichi 1997). Social tension within the group is regulated by social play, grooming or sexual contacts and females often use genital contacts to favour reconciliation (Hohmann and Fruth 2000, Palagi et al. 2006).

In contrast, composition of chimpanzee parties changes more frequently than that of bonobos (Figure 0-5 – Page 21). Females do not have central positions in parties and do not form close within-sex associations. Individual chimpanzees, usually adult females with infants, often travel at a distance from the main parties (Boesch 1996, Furuichi 2009). Chimpanzees are more territorial and often make male patrol parties to inspect and protect the home range (Lehmann and Boesch 2003). In opposition, bonobos often permit inter-groups encounters with few aggressive interactions (Idani 1990).

Factors explaining how bonobos have evolved to their current social structure and higher cohesiveness are still unknown but numerous studies have investigated the possible explanations and differences with chimpanzees (Furuichi 2009). Several sociological factors have been pointed out: the prolonged oestrus of bonobo females which implies a constant attractiveness for males (Furuichi and Hashimoto 2002), the close association between mothers and their adult sons (Furuichi 1997), the strong social bonds between females (Wrangham 1993) and the high female social status (Furuichi 1997, White and Wood 2007). Different ecological factors have also been suggested to play a role such as larger food patch size (White and Wrangham 1988, Hohmann et al. 2006), higher availability of terrestrial herbaceous vegetation (Malenky and Wrangham 1994) and the feed-as-you-go foraging strategy (i.e., foraging during travel between fruit patches) (Wrangham 2000). Authors conclude a probable different nature of the fission-fusion social structure in the two species (Furuichi 2009), suggesting that the grouping patterns of chimpanzees and bonobos have evolved through a process of long-term ecological and behavioural adaptations rather than merely reflecting a flexible response to current environmental differences. However, Boesch pointed out that chimpanzee grouping patterns in Taï (Ivory Coast) were similar to those of bonobos inhabiting similar rainforest study sites (Boesch 1996). This finding supports the fact that we need social and ecological data for much of the bonobos' habitat, including the forest-savannah environment, which will allow a socio-ecological comparison of both species across their ranges (Furuichi 2009).

II.5 Conservation status and major threats

Bonobos are classified as “endangered” by the International Union for Conservation of Nature (IUCN) since 1996. The species has experienced a significant decrease of population size in the past 20 to 30 years and current estimations show that this reduction will continue over the next 50 years, potentially leading to a decrease larger than 50 % in 75 years (Fruth et al. 2008).

The most important threat for bonobo survival is commercial poaching for bushmeat, pets or medicinal purpose (Fruth et al. 2008, IUCN and ICCN 2012). Despite being fully protected by law in DRC as well as in international treaties, bonobos are still killed, traded and consumed in many parts of their range. The very long interbirth interval (4.5 to 8 years according to the study) hampers recovery. Bonobo poaching is often linked to broad-scale commercial poaching to supply urban bushmeat markets, one of the principal threats to wildlife throughout central Africa (IUCN and ICCN 2012). In few areas, bonobos are still protected by ancestral beliefs, but those local taboos are rapidly changing due to years of civil wars, immigrant movements and the breakdown of law and order in DRC (Fruth et al. 2008).

Figure 0-6: Picture of slash-and-burn subsistence agriculture at the study site (© Adeline Serckx)

Habitat destruction in the bonobo’s range results from slash-and-burn subsistence agriculture, with more intense effects close to human settlements with high population density, and along transport and communication network (rivers and roads). However, the post-wars rehabilitation of infrastructure has rapidly worsened habitat degradation, by facilitating industrial logging and agriculture, mining and oil extraction, as well as opening the forests for bushmeat trade. Even if current annual forest loss is still comparatively low in DRC compared to other tropical forest regions, deforestation rate will rapidly increase with the current human population growth and infrastructure development (IUCN and ICCN 2012). A recent study already estimated that bonobos have suffered a 29 % reduction of suitable conditions within their distribution range since the 1990s (Junker et al. 2012).

Associated with the increasing contact rates between bonobos and humans, the risk of epidemics spreading among wild bonobos is also a cause of serious concern, particularly when we remember the massive declines in chimpanzee and gorilla populations due to the Ebola virus recent outbreaks (IUCN and ICCN 2012).

Beside these major threats, the participants to the 2012 workshop for the development of the "*bonobo conservation strategy for 2012-2022*" also highlighted many different indirect factors which contribute to the persistence of the direct threats. Among them were listed the high demand for bushmeat, the widespread availability of firearms, weak law enforcement, weak stakeholder commitment (administrative authorities and local communities), logging (with distinction among artisanal, legal industrial logging and illegal industrial logging), mining and oil extraction, infrastructure development, insufficient subsistence alternatives, human population growth and commercial agriculture (IUCN and ICCN 2012).

Figure 0-7: Pictures of the illegal logging which occured close to the study site (left side: abandoned trunks along the road, © Remy-Bernard Beya, WWF; right side: log wood ready to be transported, © Greenpeace press release)

Five main intervention strategies have been suggested to reduce bonobo major threats, that should be applied in the next 10 years: strengthening institutional capacity, consultation and collaboration with local actors living close to the bonobos, public awareness and lobbying to decrease ignorance and non-respect of the law, research and conservation monitoring activities and sustainable funding such as payment for ecosystem services (IUCN and ICCN 2012). If truly applied effectively, their positive effects should be seen in the years to come.

III THE STUDY SITE

© Celine Devos

III.1 **Location and Status**

The study site is located in the South of the Lake Tumba Landscape, in western Democratic Republic of Congo. The Lake Tumba Landscape is part of a larger transborder conservation landscape, the Lake Télé-Lake Tumba Landscape. It extends over 126.000 km² within the Republic of Congo (42.000 km²) and within the Democratic Republic of Congo (84.000 km²). The landscape has been first delimited in order to cover the largest expand of swamp forests worldwide (de Wasseige et al. 2009), and is classified as one of the 12 priority eco-systems for conservation by the Central African Regional Program for the Environment CARPE (Inogwabini et al. 2007). Following the discovery of several bonobo populations outside the southern part of the landscape, the lanscape has been extended in order to cover to the North of the Bateke Plateaux where those bonobo populations were living.

The first biological inventories conducted in the landscape have highlighted a high botanical and zoological richness: more than 23 mammals and birds species listed on the IUCN Red List, a diversified herpetofauna and ichtyofauna with several endemic species and two lakes considered themselves as two aquatic eco-regions housing endemic species (Devers and Vande Weghe 2006). The landscape has also an important potential for Great Apes conservation as it includes three Ape species, i.e., the western lowland gorilla (*Gorilla gorilla gorilla*), the chimpanzee (*Pan troglodytes*) and the bonobo (*Pan paniscus*) (Figure 0-8 – Page 28), for which forest surveys conducted by WCS (the Wildlife Conservation Society) have highlighted large population densities for gorillas and chimpanzees - De Wasseige et al. 2008 -, and by the WWF, for bonobos - Inogwabini et al. 2007). Furthermore, this region plays an important role in the hydrological regulation of the Congo Basin, as well as an important role in climate regulation in Central Africa (Devers and Vande Weghe 2006). Despite this ecological importance, only two protected areas have been designated in the DRC part of the landscape: the Tumba-Lediima Natural Reserve, created in 2007, but overlaps with several logging concessions have made conservation actions until now almost impossible, and the Ngiri National Reserve, created in 2011 (Figure 0-9 – Page 29).

I conducted my research in the South of the Lake Tumba Landscape, in the northern part of the Bateke Plateaux, close to the WWF Malebo research station (16.41-16.56°E, 2.45-2.66°S, Figure 0-9 – Page 29 and Figure 0-10 – Page 30), in the contiguous forests of Nkala and Mpelu villages. This region is characterized by a forest-savannah mosaic and includes cattle ranching and logging concessions. Some illegal logging concessions were also active at times in the area. Since 2007, WWF, in collaboration with the local NGO Mbou-Mon-Tour, started a large conservation program in villages surrounding the study site, comprising forest elephant monitoring, bonobo monitoring, habituation of two bonobo groups for eco-tourism activities development, and water quality monitoring. WWF combined these activities with the setting up of local “community committees” in order to help with natural resources management, agriculture improvement and development of alternative activities. After the climate conference in Cancun, in November 2010, the site was also designated as “REDD pilot site of DRC”, and a pilot REDD+ program (Reducing Emissions from Deforestation and forest Degradation + Conservation and Sustainable Development) was initiated by WWF in the entire Landscape. Since 2013, WWF and Mbou-Mon-Tour are working on the elaboration of a “community natural reserve” status for the forests where bonobos occur.

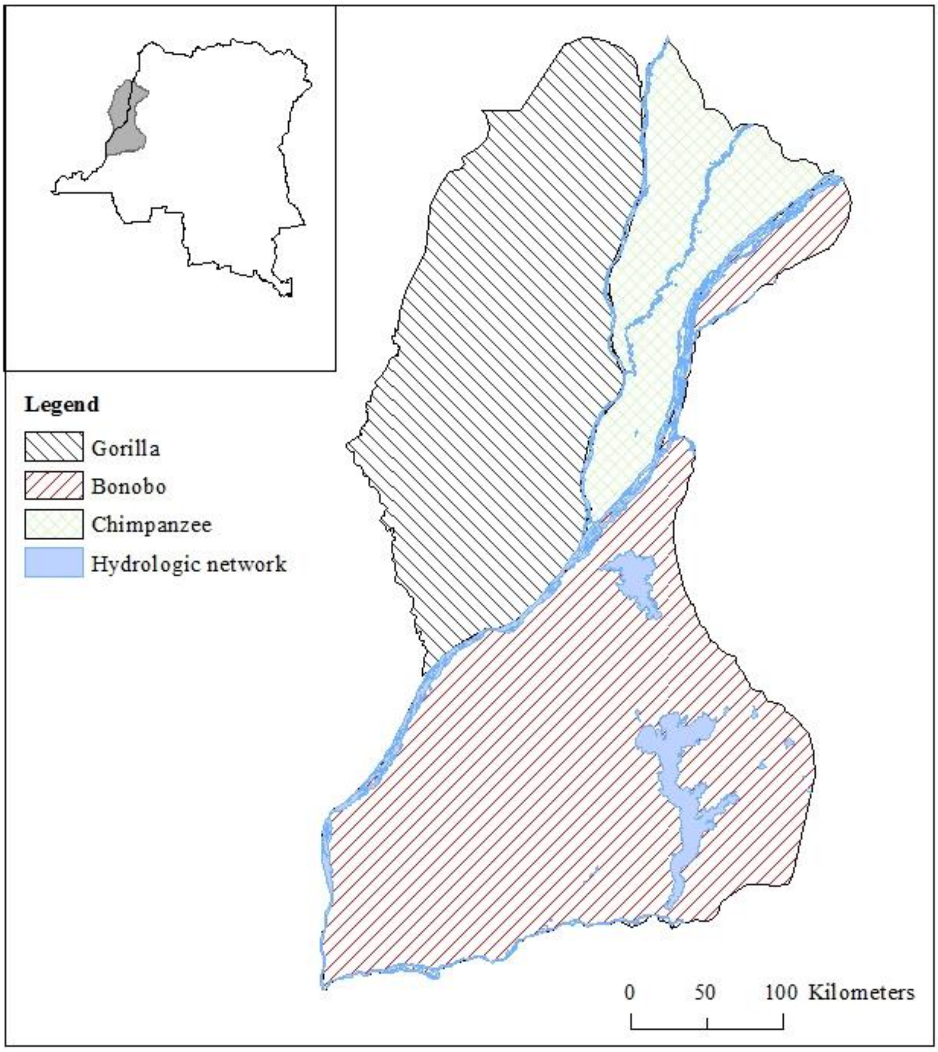


Figure 0-8: Lake Tele-Lake Tumba Landscape with Great Apes distribution areas

The Lake Tele-Lake Tumba Landscape extends over 126.000 km² within the Republic of Congo (42.000 km²) and within the Democratic Republic of Congo (84.000 km²) and includes three Great Ape species (Devers and Vande Weghe 2006). The western lowland gorilla range within the landscape (*Gorilla gorilla gorilla*) is indicated in black lines, the chimpanzee (*Pan troglodytes*) in green lines and the bonobo (*Pan paniscus*) in red lines.

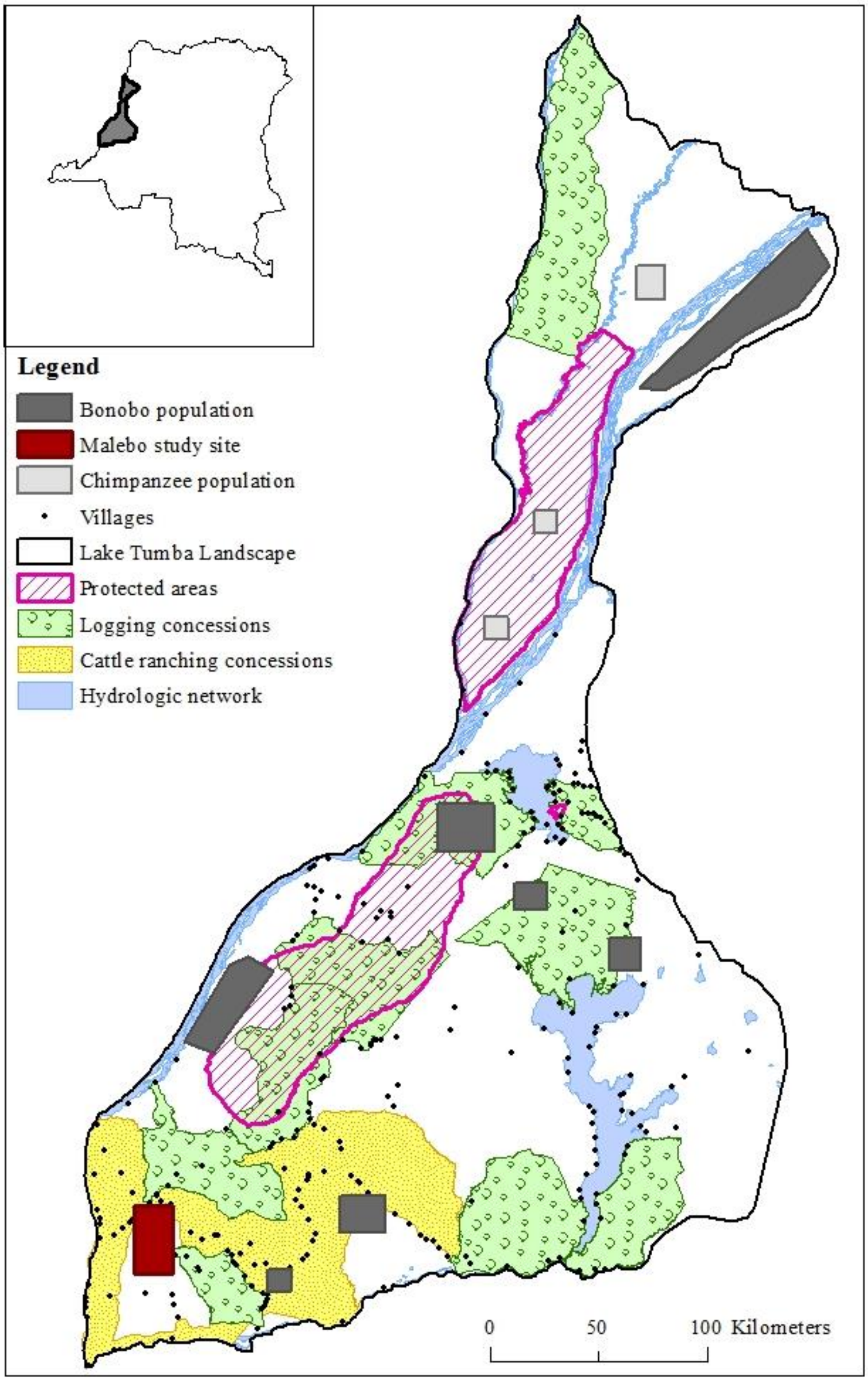


Figure 0-9: Lake Tumba Landscape

On this map, we present in pink dashed lines the protected areas (the Ngiri National Reserve between the Congo River and the Oubangui River, the Tumba-Lediima National Reserve on the South bank of Congo River) and the logging concessions in green, underlying their delimitation conflict. The cattle ranching concession are indicated in yellow and the hydrological network in blue. Black points show the villages. The bonobo populations already identified in the landscape are depicted in dark grey polygons while chimpanzee populations are in light grey. The Malebo research study site is in red.

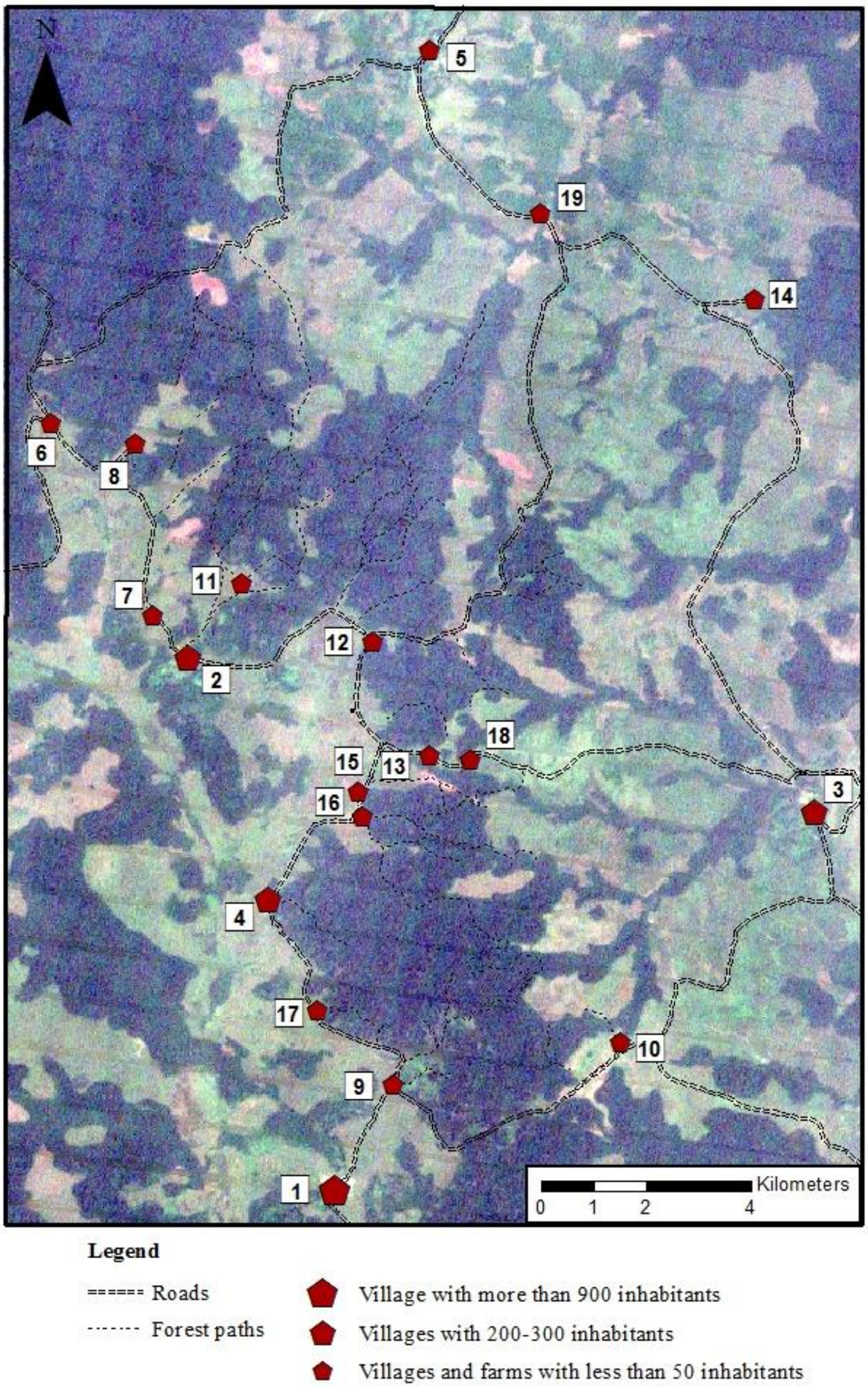


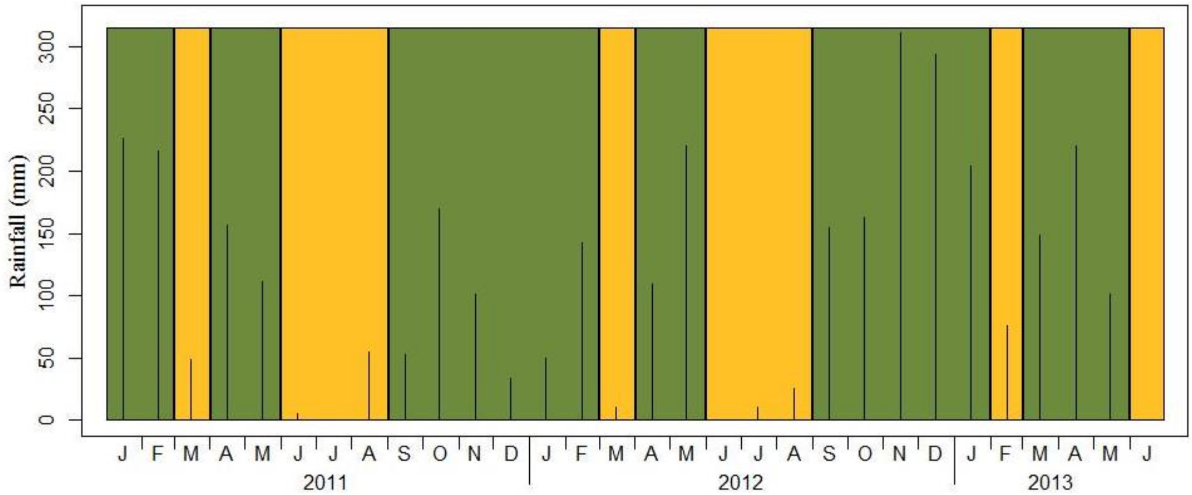
Figure 0-10: Map of the study site (Landsat7 – 2007- in true colours, 16.41-16.56°E, 2.45-2.66°S, West DRC)

Dark colours indicate forest patches while light colours depict savannahs. Parallel dashed lines indicate the roads surrounding the study site, whereas dotted lines indicate the main forest paths. Villages are depicted as red pentagons. Numbers correspond to the village names (1: Nkoo, 2: Mpelu, 3: Lebomo, 4: Nkala, 5: Malebo, 6: Mavula, 7: Bosatore, 8: Mokoabuo, 9: Clinic of Nkoo, 10: Lensiana, 11: Biomengele, 12: Ngandjele, 13: Motsuemontore, 14: Ezano, 15: Mayi Monene, 16: Mbou-Mon-Tour, 17: Moza, 18: Bosieli and 19: WWF-base)

III.2 **Climate**

Annual rainfall oscillates around 1500-1600 mm (Inogwabini et al. 2008) but the rainfall amounts I recorded at the site were slightly less abundant: 1180 mm in 2011, 1470 mm in 2012 and 750 mm for mid 2013 (Figure 0-11). The climate is generally characterised by two dry seasons: a small dry season in February or March and a longer dry season from June to August (Inogwabini et al. 2008). The mean daily temperature fluctuates around 25°C (Vancutsem et al. 2006) and the mean relative humidity reaches 87% (Inogwabini et al. 2008).

Figure 0-11: Rainfall at the study site



The figure indicates rainfall recorded at Mbou-Mon-Tour farm each month. Colours depict common dry and humid seasons, in yellow and green respectively.

III.3 **Habitat**

The region can be characterized as a forest-savannah mosaic, with an altitude range from 300 to 700 m. The ecotone exhibits an interesting savannah re-colonization dynamic wherein *Uapaca* species pioneer the process. However, the savannahs have been exploited for cattle ranching since the late 1950s, with fire as a management tool. Until recently, the management of the cattle ranching society, ORGAMAN, were burning three times a year to ensure that palatable herbs were always available (Inogwabini et al. 2008) but current management has decreased burning frequency to once a year, during the dry season. Local communities are also starting fires in savannahs but without any management planning. Those activities mainly prevent the natural expansion of forests and have maintained the current savannah-forest mosaic system in the region.

At the time of our research, the study site encompassed 170 km², made up of 102 km² of forest patches of various shapes and sizes which are connected by many corridors (Figure 0-10 – Page 30). Forests mostly represent *terra firma* soil conditions and encompass various habitat types, i.e., re-colonizing *Uapaca sp.*, old secondary, mixed mature, old growth mono-dominant, riverine gallery and Marantaceae forests (Inogwabini et al. 2008), with large variations taking place over a few meters only. Tree species dominance also presents large variations depending on the forests, e.g. *Klaneidoxa gabonensis* is one of the most abundant species in Nkala forest while, at Mpelu, the species is quite rare. In opposition, *Dialium sp.*, *Santiria trimera* or *Coelocaryon preussii* are more represented within Mpelu forest. In both forests, species as *Plagiostyles africana*, *Polyalthia suaveolens*, *Strombosia pustulata*, *Staudtia kamerunensis*, *Sorindeia africana*, *Duvigneaudia inopinata*, *Pancovia laurentii*, *Pentaclethra eetveldeana*, *Chaetocarpus africanus* or *Uapaca sp.* were largely present (J-F Bastin PhD thesis). Surrounding savannahs are mainly herbaceous and partially used for cattle ranching.

III.4 **Fauna**

Six species of primates are generally considered to be present in the study site (Conservation plan of WWF 2010-2011 & discussions with the local community) but, beside the Red-tailed Monkey (*Cercopithecus ascanius*), they are difficult to observe and I did not manage to confirm their presence: the black mangabey (*Lophocebus atterrimus*), the wolf's mona monkey (*Cercopithecus mona wolfi*), the brazza's monkey (*Cercopithecus neglectus*), the thollon's red colobus (*Procolobus tholloni*) and the angolensis colobus (*Colobus angolensis*). Several species of duikers are also present, with the blue duiker (*Cephalophus monticola*) and the bay duiker (*Cephalophus dorsalis*) being probably the most abundant species remaining in the area. Tracks and scats of red river hog (*Potamochoerus porcus*), porcupine (*Atherurus africanus*) and forest buffalo (*Syncerus caffer nanus*) are also regularly observed while traces of giant pangolin (*Smutsia gigantea*) and leopard (*Panthera pardus*) are rare. The region might be of high interest for birds and reptiles; inventories are still missing but a herpetologist observed that many reptile species typic of savannahs or forests were cohabiting together (Eli Greenbaum, pers.comm.). In the northern part of the study site (North-East of WWF Malebo Research Station), forest elephant (*Loxodonta africana*) traces are regularly observed. Until 2010, small groups of lions (*Panthera leo*) were seasonally recorded in the region but the species does not seem to be present any longer. The complete list of animal present in the study site is provided in Table 0-3 (Page 34).

Figure 0-12: Picture taken in 2012 with a camera trap in the forests at the North of Malebo research station (© Franck Trolliet)

Table 0-3: Animal species present in the study site

Common name	**Scientific name**	**Lingala name**	**Kiteke name**
Primates			
Bonobo	Pan paniscus	Mokomboso	Ebubu
Red-tailed Monkey	Cercopithecus ascanius	Keskes	Tsheke
Black Mangabey	Lophocebus aterrimus		Nzila
Wolf’s Mona Monkey	Cercopithecus wolfi		Ngi
Thollon's Red Colobus	Piliocolobus tholloni		Nkaana
Angolensis Colobus	Colobus angolensis		Vuu
Brazza’s Monkey	Cercopithecus neglectus		Mosila
Artiodactyla			
Forest Buffalo	Syncerus caffer	Mpakasa	Mpeeyo
Bay Duiker	Cephalophus dorsalis	Nkulupa	Nfini
Blue Duiker	Cephalophus monticola	Mboloko	Nseyi
Bushbuck	Tragelaphus scriptus	Nkayi	Nkaa
Bongo	Tragelaphus eurycerus		Ngonzu
Black Duiker	Cephalophus niger	Mbende	Mbimi
Sitatunga	Tragelaphus spekei	Mbuli	Mvuli
Peter’s Duiker	Cephalophus callipygus		Ntswa
-	Cephalophus sp.	Intsa	Nsa
-	*Non identified*	Mbengele	Mbokeli
Red River Hog	Potamochoerus porcus	Nsombo	Ngwuyian
Proboscidea			
Forest Elephant	Loxodonta africana	Zoku	Nzoo
Carnivora			
Leopard	Panthera pardus	Nkoyi	Ngoo
Lion	Panthero leo	Ntambo	Nkweyi
Serval	Felis serval		Lebwalengo
African Civet	Civettictis civetta	Libobi/Dzobo	Ngaatsiu
Slender mongoose	Herpestes sanguinea		Mfuu
Spotted Hyena	Crocuta crocuta	Ngombolo	Ngombul
Servaline Genet	Genetta servalina		Mbala
Pholidota			
Small Pangolin	Uromanis tetradactyla Phataginus tricuspis		Nzanium
Geant Pangolin	Smutsia gigantea		Nkau
Tubulidentata			
Aardvark	Orycteropus afer		Mbeno
Rodentia			
Rat	Thryonomys sp.	Simbiliki	Nsili
Gambia Pouched Rat	Cricetomys gambianus	Montomba	Nkuli
Porcupine	Atherurus africanus	Yiko	Nkeyon
Squirrel		Poo/Esende	Nsini

Reptiles			
Tortoise		Koba	Mfulu
Crocodile	Crocodylus suchus	Lokese	Nkulu
Varan	Varanus ornatus	Mbambi	Mbaami
Varan	Varanus niloticus	Lebamu	
Crocodile	Crocodylus niloticus	Ngando	

Species have been identified by discussions with the local assistants and with reference to the book "*The Kingdon field guide to African mammals*" (Kingdon and Pagel 1997). The mammal list has been confirmed by Menard Mbende, WWF scientist (inventory leader and chief of Malebo WWF Station). Reptiles have been identified by showing a collection of pictures of Eli Greenbaum to my main local assistant.

III.5 **Local community**

Human activities and settlements are concentrated on the west side of the study area. Six villages and twelve farms are directly adjacent to the forests studied and the local communities belong mainly to the Teke ethnic group. The majority of the people live from subsitence agriculture, subsistence hunting and fishing. Their field crops are located inside the forests and they generally do not go far away from their village for hunting or fishing (5 km of distance maximum). Almost all animal species are hunted with the exception of forest elephants and buffalos because of legal prohibition, and with the additional notable exception of bonobos (which are poached elsewhere despite being protected by law) because of local taboos: the most common ancestral story implies that bonobos are human ancestors who decided to go in the forest to hide from tax inspectors and never came back to the villages. Hunting is generally performed with guns, nets or with the use of traps. Fishing habits differ for women and men, but they use all rivers whatever their sizes. Periods for hunting and fishing are fixed by law but not respected in the area. The collection of non-timber forest products is quite limited: leave and stems of Marantaceae, some species of mushrooms, raphia and small wood for house building (summary of interview results, see IV.7 Socio-economic data – Page 55). On the other hand, inhabitants of villages situated within cattle ranching concessions (villages n° 3, 5, 14 and 18 in Figure 0-10 – Page 30) come from various regions of DRC and have different forest use habits compare to those of the Teke people (e.g., larger distance of travelling for hunting, larger plantations).

III.6 **Bonobos**

A bonobo population, probably made up of two communities, inhabits Nkala and Mpelu forests, and, since 2007, has been the subject of a habituation and conservation program by WWF (Inogwabini et al. 2008). Other bonobo communities have been identified in forests surrounding the study site. However, factors explaining bonobo presence in forest patches are not yet sufficiently known to allow us to predict other possible bonobo community presence in the region.

IV GENERAL METHODS

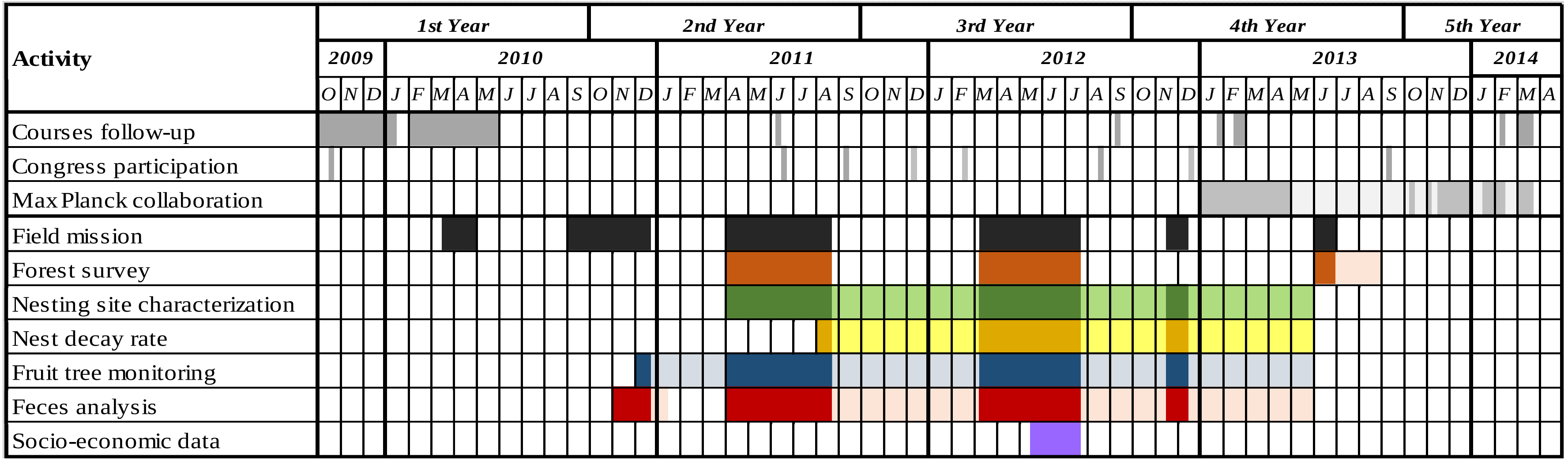
© Adeline Serckx

IV.1 **Field work and data collection**

I realised six field missions during my PhD (a total of 16 ½ months spent in the field). The first mission was dedicated to field familiarization, encounters with local people and WWF workers. Whenever possible, I went into the forest with WWF habituation trackers in order to state if direct observations could be possible for further data collection. I decided indirect observations would be more appropriate as bonobo habituation was still in its first stage (distance of observation of 25-30 m, many days where bonobos were lost and where we did not succeed to find them). The focus of the second field mission was on selecting field assistants, training them for data collection (use of compass and GPS for transect cutting and plot delimitation, plant species identification, tree diameter measures, seed recognition, feces analysis, nest characterization). We set up permanent transects and plots for fruit tree monitoring and familiarized ourselves with feces analysis. We started fruit tree monitoring at the end of the mission. We conducted the first forest survey for bonobo data collection during the third field mission. In parallel, we started feces analysis and nesting site characterization (with the help of two master thesis students). I also began nest decay rate monitoring. These three lines of data were continuously collected by my field assistants until the end of May 2013. During the fourth mission, we conducted a second bonobo forest survey during which a complete forest characterization exercise was also realised. I collected socio-economic data by doing a population census and interviewing local people in all villages surrounding the study site. A master thesis student also helped in nesting site data collection. The fifth mission main objective was to ensure the continued effectiveness of data gathering by the field assistants, and to complete the herbarium started by J-F Bastin in the area (474 samples of 178 tree species belonging to 44 families are now registered in the herbarium and botanical library of the Université Libre de Bruxelles ("BRLU"), with reference IDs Bastin-Serckx#1-474). During the sixth mission, I set up a third forest survey in collaboration with WWF and closed the other research fields.

For my personal training, I followed different courses during my PhD: primatology, teledetection, geo-referenced information systems, Distance software, R software and statistical analyses (introduction to statistics, generalized linear models, non-parametric tests). I took part to several international meetings to present the first results on my PhD thesis (see details in Table 0-4 – Page 39). At the beginning of 2013, I started to collaborate with the Max Planck Institute for Evolutionary Anthropology specifically for data analyses and modelling.

Table 0-4: Calendar of the PhD thesis



Activity	1st Year												2nd Year												3rd Year												4th Year												5th Year						
	2009			2010												2011												2012												2013												2014			
	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A
Courses follow-up	■	■	■	■	■	■	■	■													■																■				■	■												■	■	
Congress participation	■																				■			■			■		■						■				■									■							
Max Planck collaboration																																								■	■	■	■	▒	▒	▒	▒	▒	▒	■	■	■	■	■	
Field mission						■	■					■	■	■	■				■	■	■	■	■							■	■	■	■	■				■	■						■										
Forest survey																			■	■	■	■	■							■	■	■	■	■											■	▒	▒								
Nesting site characterization																			■	■	■	■	■	▒	▒	▒	▒	▒	▒	■	■	■	■	■	▒	▒	▒	■	■	▒	▒	▒	▒	▒											
Nest decay rate																							■	▒	▒	▒	▒	▒	▒	■	■	■	■	■	▒	▒	▒	■	■	▒	▒	▒	▒	▒											
Fruit tree monitoring															■	▒	▒	▒	■	■	■	■	■	▒	▒	▒	▒	▒	▒	■	■	■	■	■	▒	▒	▒	■	■	▒	▒	▒	▒	▒											
Feces analysis														■	■	▒			■	■	■	■	■	▒	▒	▒	▒	▒	▒	■	■	■	■	■	▒	▒	▒	■	■	▒	▒	▒	▒	▒											
Socio-economic data																																■	■	■																					

The courses I followed are: teledetection and primatology in 2009, geo-referenced information systems in the beginning of 2010, Distance software in June 2011, R software in September 2012, introduction to statistics in January 2013, generalized linear models in February 2013, non-parametric tests in February 2014 and up-dates on generalized linear models in March 2014. I participated to the following international meetings (in chronological order): the Francophone Society of Primatology (2009), the Association for Tropical Biology and Conservation, the American Society of Primatology, the Belgian Group for Primatology (2011), the Society for Tropical Ecology, the International Primatological Society, the Belgian Groups for Primatology (2012), the European Federation of Primatology (2013). Max Planck collaboration started in 2013 (medium grey indicates my stay in the institute while light grey is periods during which we collaborated at distance). Field missions are highlighted in dark grey. The lines of research are presented in different colours: the dark colours underline data collection during field missions and their equivalence in light colours shows periods where data have been collected by field assistants.

IV.2 **Forest survey**

I delimited the size and shape of our study site based on WWF staff knowledge of bonobo home ranges in the Mpelu and Nkala forests and added connecting corridors. In April 2011, I conducted a pilot study during which we recorded all bonobo nests on reconnaissance walks (recces) to define the total sampling effort needed to perform a precise density estimation (Buckland et al. 2001, Kuehl et al. 2008). Based on the results of the pilot study, I created a survey design with 114 transects running from west to east, spaced 500 m apart and of variable lengths, adding to a total of 179.1 km surveyed through the forest (Figure 0-14 – Page 45). We sampled transects in May to July 2011, mid-March to mid-July 2012 and June to August 2013. Due to external constraints, we were not able to visit some transects each year (see Table 0-5 – Page 43 for the exact annual total efforts). The three observers were trained together and used a consistent methodology.

Figure 0-13: Pictures of data collection during forest survey (© Adeline Serckx)

Bonobo data collection

We systematically collected information on bonobo nests (Figure 0-15 – Page 46) and recorded their perpendicular distances from the transects using a tape measure, following the methodology recommended by the IUCN guidelines (Kuehl et al. 2008) and Buckland et al. (Buckland et al. 2001). Other indices of bonobo presence were also collected (direct observation or vocal indices, food remains, foot print) and, whenever possible, their perpendicular distance from the transects were recorded too. When observing food remains, we identified the species, counted them and noted the part of the plant which was eaten.

Forest characterization

We described forest habitat types according to the dominant understory, the tree species dominance in the canopy, the canopy openness and the soil conditions. In order to depict dominant understories, we noted, for each 25m-segment, one or two of the following categories (based on the classification in Reinartz et al., 2006): open, liana, woody, Marantaceae or other terrestrial herbaceous vegetation (THV) (with specification of the species for Marantaceae and THV). In order to identify tree species dominance in the canopy, we measured all trees with a DBH (diameter at breast height, defined as 130 cm) larger than 50 cm within a 10 m strip on both sides of the transects. For trees covered by lianas, we were not able to measure their DBH and we assigned to them the median DBH value of the survey (67 cm) for further data analyses. For trees with several stems at 130 cm, we summed their stem DBH measures. We took the lower threshold of 50 cm to measure DBH because those trees usually include the majority of fruiting trees in a tropical forest (Doucet 2003, Madron and Daumerie 2004, Bourland et al. 2012, Menga et al. 2012) and we wanted to further use this information to estimate an index of fruit tree availability. In other to estimate canopy openness, we recorded every 6.25 m of transect if the canopy was between *(i)* 2 and 10 m, *(ii)* 10 and 20 m and *(iii)* above 20 m (presence-absence data, recorded as 1 or 0). We added up the three values of each observation point and further calculated their mean within each 25m-segment of transects in order to get an index from 0 to 3 of canopy openness. In order to define soil conditions, we recorded the dominant soil type within each 25m-segment by distinguishing *terra firma*, seasonally inundated and inundated soils.

Traces of human presence

Each year, all human indices have been recorded by distinguishing 10 categories (see details in Table 0-6 – Page 43). Their encounter rates are presented in Table 0-7 (Page 43) and are briefly discussed in the Appendix I (Report to WWF – November 2013 – Page 225).

Animal traces

All animal traces have also been recording during the forest surveys (see species and types of observation in Table 0-8 – Page 44). Their encounter rates are presented in Table 0-9 (Page 44) and are briefly discussed in the Appendix I (Report to WWF – November 2013 – Page 225). Note that, in 2013, a first team opened the transects and a second team travelled on along them 7 to 15 days later to record information (the second team was able to be more silent to favour animal observation). The encounter rates of 2013 are then not comparable with those obtained in 2011 and 2012.

Data valorization

Forest survey data have been used to estimate bonobo density in the study site and to study their yearly variation (Chapter 2, Serckx et al. 2014). This information in combination with the encounter rates of human and animal signs of presence have later been reported to WWF (Appendix I: Report to WWF – November 2013 – Page 225). Forest characterization and nest data of 2011 and 2012 have been analysed in the paper on scale search in species distribution modelling (Chapter 1, Serckx et al. in prep). Finally, the “non-observation” of signs of the presence of elephants in the study site (survey data of 2011) have been integrated by Fiona Maisels who realised a meta-analysis on forest elephant decline in Central Africa (Maisels et al. 2013) (provided in Appendix II – Page 239).

Table 0-5: Area and total effort of forest survey per year

	Area (km²)	Total effort 2011 (km)	Total effort 2012 (km)	Total effort 2013 (km)
Global	93.84	130.1	179.1	175.5
Nkala	32.45	49.9	61.9	61.9
Mpelu	54.26	72.7	109.7	106.1
Lokoso&Mankere	7.13	7.5	7.5	7.5

The 3 different areas are located in Figure 0-14 (Page 45) and were used to estimate bonobo density for Nkala and Mpelu bonobo communities.

Table 0-6: Description of the different human indices observed on the transects

Indices of human presence
Encounter of people on travel paths
Marantaceae cutting : stems for mat fabrication or leaves for cooking (with specification of the species), Liana cutting
Cut of small trees (for house building)
Former presence of people for fishing (with identification of the type of fishing when possible)
Traps (with indication of the material used: cable, nylon thread or wood and the target species)
Cartridges
Former presence for net hunting
Forest travel paths (with specification of travel path type : for villagers or for WWF habituation trackers)
Fire remains
Indice of machete cuts

Table 0-7: Encounter rate of human indices

	2011	**2012**	**2013**
Encounter of people	0.02	0.02	0.02
Marantaceae cutting	0.08	0.11	0.12
Cut of small trees	0.01	0	0.01
Fishing indices	0.02	0.04	0.12
Traps in cable	0.02	0.05	0.13 (+0.03)[1]
Traps in nylon	0.04	0.13	0.07 (+0.02)[1]
Other traps (wood or non-defined)	0.05	0.03	0.02 (+0.01)[1]
Cartridges	0.05	0.03	0.11
Net hunting	0	0.11	0.01
Other signs of hunting	0	0.03[2]	0.01
Fire remain	0	0.01	0.03
Machete cut	0	0.08	0.05

[1] Number in brackets are the encounter rate of former trap (non-used anymore).[2] indicates 6 signs in which 3 were indices of forest hunting camp.

Table 0-8: Animal species observed on transects

Animal species	**Type of observation**
Large duiker (with species identification in vernacular name when possible)	Trail, print, feces or direct observation
Small duiker	Trail, print or direct observation
Buffalo	Trail or print
Hornbill	Vocal or direct observation (and number of individuals when possible)
Small rodent	Print
Pangolin	Print
Partridge	Print
Porcupine	Trail or print
River hog	Trail, print, food remain, noise
Small monkeys (with species identification in vernacular name when possible)	Vocal or direct observation (and number of individuals when possible)

Note: the perpendicular distance have been recorded in 2013

Table 0-9: Encounter rate of animal species

	2011	**2012**	**2013**
Large duiker	0.02	0.38	0.37
Small duiker	0	0	0.06
Buffalo	0.03	0.08	0.14
Hornbill	NA	NA	0.11
Small rodents	0	0.02	0.03
Pangolin	0	0.01	0.01
Partridge	NA	NA	0.02
Porcupine	0	0.31	0.39
River Hog	0.35	0.79	1.50
Small monkeys	0	0.02	0.17

NA indicates that we did not look for these species in 2011 and 2012.

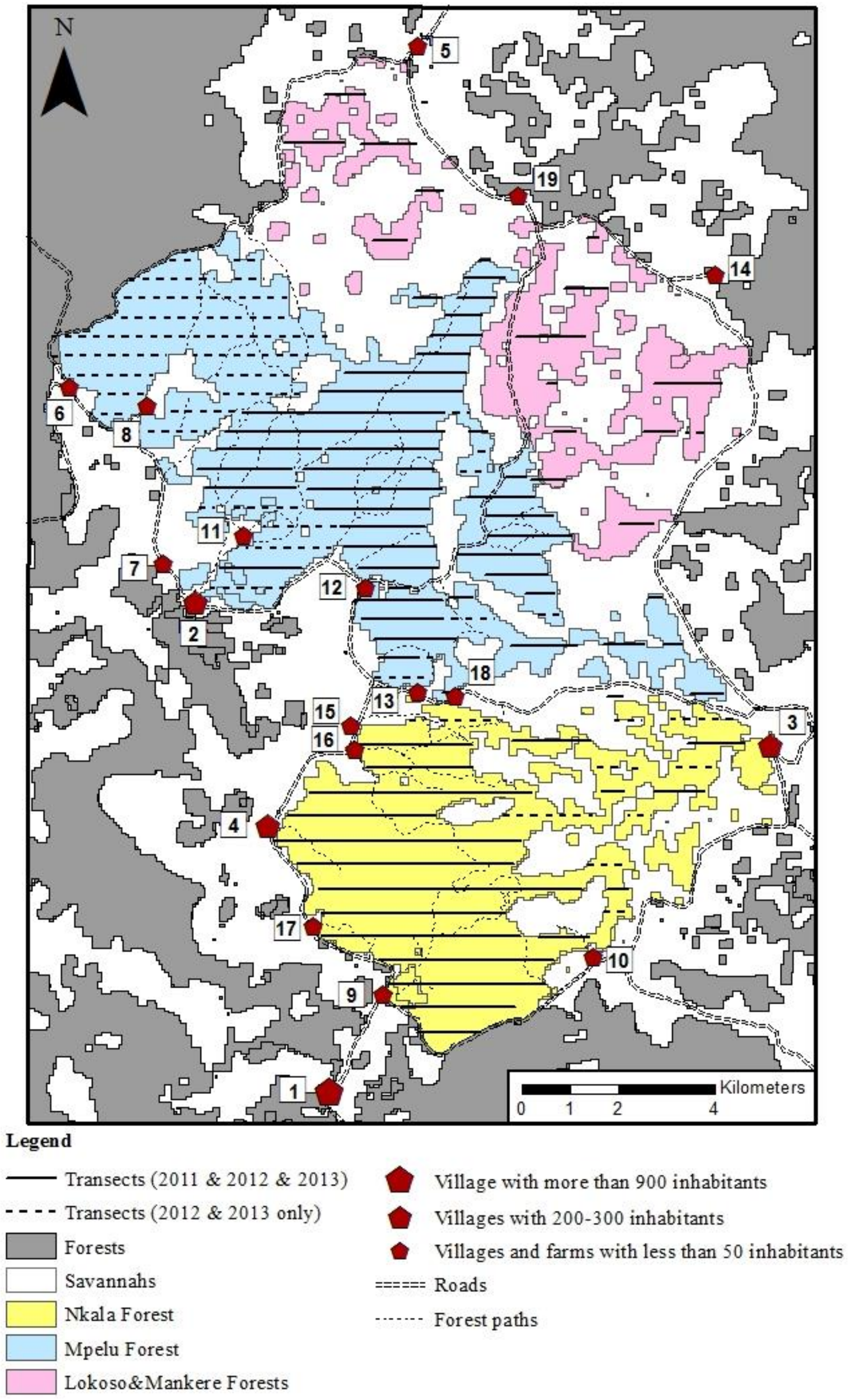


Figure 0-14: Map of the study site (16.41-16.56°E, 2.45-2.66°S, West DRC) with transects

Forest cover is indicated in grey and savannah in white [the map is based on the non-supervised classification – RED and IR on a Landsat7 (2007)]. Colours in forests represent the delimitation we used to estimate bonobo density per community (Lokose&Mankere being corridors where bonobos were never observed). Parallel dashed lines indicate the roads surrounding the study site, whereas dotted lines indicate the main forest paths. Horizontal solid lines depict the line transects travelled each year while the horizontal dashed lines indicate transects travelled only in 2012 & 2013. Villages are depicted as red pentagons. Numbers correspond to the village names in Table 0-10 (Page 56) and Number 19 represents the WWF-base.

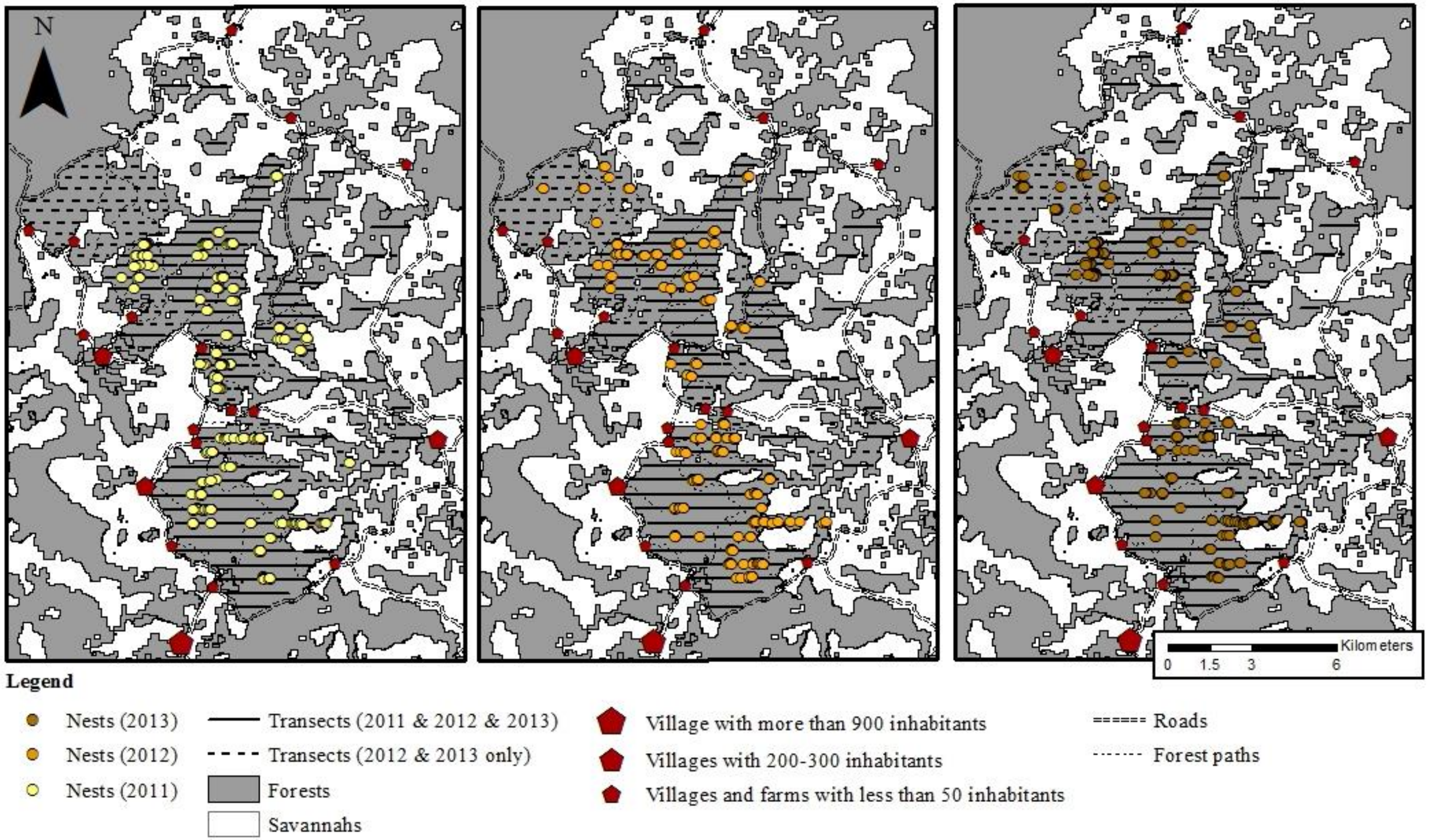


Figure 0-15: Map of the study site (16.41-16.56°E, 2.45-2.66°S, West DRC) with nest observed each year on transects

Forest cover is indicated in grey and savannah in white [the map is based on the non-supervised classification – RED and IR on a Landsat7 (2007)]. Parallel dashed lines indicate the roads surrounding the study site, whereas dotted lines indicate the main forest paths. Horizontal solid lines depict the line transects travelled each year while the horizontal dashed lines indicate transects travelled only in 2012 & 2013. Nests are indicated with different colours for each year. Villages are depicted as red pentagons.

IV.3 **Nesting site characterization**

Between May 2011 and May 2013, we gathered data on bonobo nesting sites (n=104, Figure 0-18 – Page 49) randomly selected from nesting sites found by the trackers who followed bonobos daily for the WWF habituation program. At each nesting site, we first explored the surrounding area to ensure that we had found all of the nests. We considered nests as being part of the same nesting site when the maximal distance between two nests did not exceed 30 m (Fruth 1995, Mulavwa et al. 2010). We counted only fresh nests, i.e., nests built the previous night, with green leaves and traces of feces or urine (Furuichi et al. 2001b). Presence of old nests was nonetheless recorded in order to get information on nesting site re-use. The type of understory, soil conditions and canopy openness (following the same categories used in the forest surveys) were noted under each nest in order to get a general characterization of habitat type. Tree species dominance in the canopy was obtained by idenfying all trees of the nesting site with a DBH above 70 cm.

Figure 0-16: Picture of a bonobo in its nest (© Fabrice Dentressangle)

Nesting tree

For each tree containing a nest, we identified the species (n=1872), and recorded its DBH and height (estimated by eyes). The location of each nesting tree was geo-referenced. We measured the distance and the angle between nesting trees to further draw the configuration of the nesting site. In order to get information on possible strategy on predator avoidance, we recorded the number of trees which could enable an access to the nesting tree and the presence-absence of lianas on the nesting tree.

Control tree

In order to further investigate nesting site characteristics, we randomly chose, in a subset of 97 nesting sites, a maximum of 30 control trees, which we identified to species level and recorded the DBH. These trees were distributed between the nesting trees, and we collected data on a total of 2259 control trees.

Nest

For each nest, we recorded their size (small – medium – large) and we estimated their height by eyes. In order to investigate possible strategy to favour confort, we noted the nest position within the tree with the categories suggested by Fruth (Fruth and Hohmann 1993, Fruth 1995): on the side of a branch (S), on the top of the tree (T), on the top of two trees (T-T), mixing the top of a tree and the side of a branch from another tree (S-T) and on the side of the branches of two trees (S-S) (Figure 0-17). For a nest on a branch, we also noted if the nest was leaning against the trunk. In order to investigate the potential confort strategy, we used the nesting tree species to gather information about leaf size used to build the nest. As Fruth and Hohmann (1993) demonstrated, bonobos tend to chose small leaf size to build their nest.

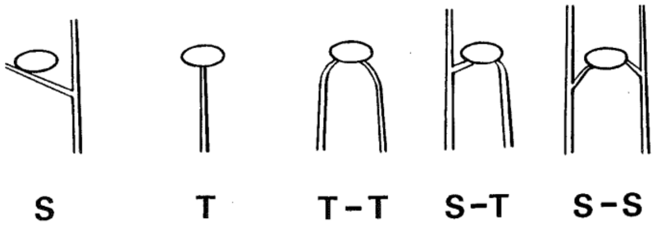


Figure 0-17: Pictures of the different positions of a nest within a tree (picture taken from Fruth and Hohmann 1993). The different positions are detailed in the text.

Data valorization

Species information of the nesting and control trees have been used in the paper on bonobo cohesiveness at night in order to determine a predictor of the density of suitable trees in which to build nests within each nesting site (Chapter 2, Serckx et al. 2014). Data collected by Marie Vimond (2011) and Emilien Raynaud (2012) have also been valorized in their respective Master Theses.

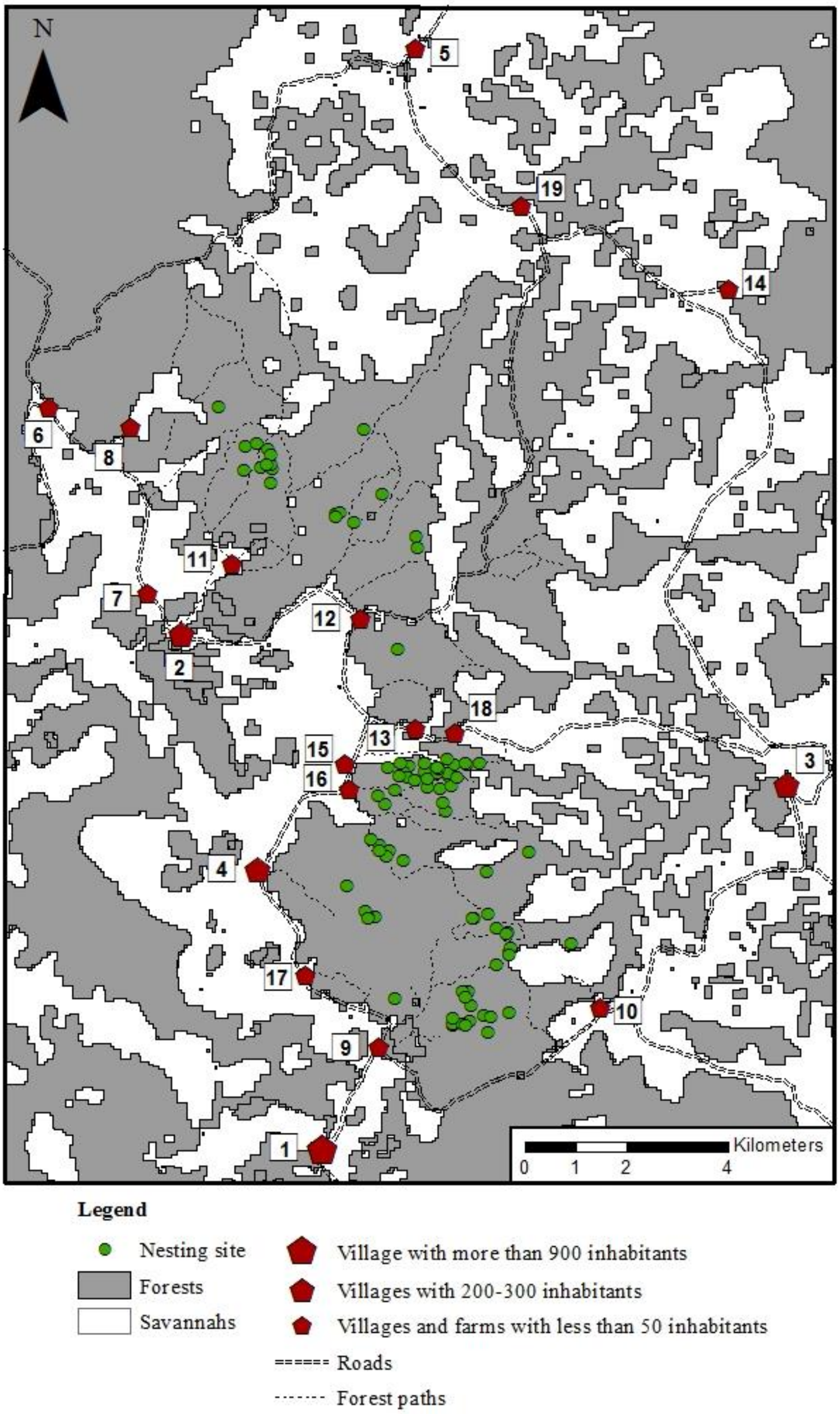


Figure 0-18: Map of the study site (16.41-16.56°E, 2.45-2.66°S, West DRC) with nesting sites

Forest cover is indicated in grey and savannah in white [the map is based on the non-supervised classification – RED and IR on a Landsat7 (2007)]. Parallel dashed lines indicate the roads surrounding the study site, whereas dotted lines indicate the main forest paths. Green points indicate nesting sites which have been characterized. Villages are depicted as red pentagons. Numbers correspond to the village names in Table 0-10 (Page 56) and Number 19 represents the WWF-base.

IV.4 **Nest decay rate**

We conducted a nest decay rate study between August 2011 and May 2013, following previously validated methodology (Plumptre and Reynolds 1996, Laing et al. 2003, Kuehl et al. 2008, Mathewson et al. 2008, Devos and Laguardia 2011). We made repeated visits to all nests identified as fresh during our nesting site study and assessed their conditions. For months where we characterized numerous nesting sites, we randomly selected three sites to be monitored for the nest decay study. We made weekly visits to a total of 42 nesting sites containing 610 nests until the nests had completely disappeared (Devos and Laguardia 2011) (Figure 0-20 – Page 51). At each visit we noted the degree of nest degradation according to the following categories: *(i)* new: only green leaves; *(ii)* recent: a mixture of green and brown leaves; *(iii)* old: only brown leaves; *(iv)* very old: brown leaves and the nest is losing its structure (Furuichi et al. 2001b); and finally, *(v)* disappeared: nest no longer recognizable (Kouakou et al. 2009). We estimated mean nest decay time by using the method proposed by Laing et al. 2003. More specifically, we used the logistic regression model with left truncation. We bootstrapped the nest data (n=1000) to estimate confidence intervals at 2.5%.

Data valorization

The nest decay rate estimated during my PhD has been used to convert nest density into bonobo density in different analyses (Chapter 1, Serckx et al. In prep.; Chapter 2: Serckx et al. 2014).

Figure 0-19: Pictures of a fresh nest (on the left, © Adeline Serckx) vs. an old nest (on the right, © Sophie Hannay)

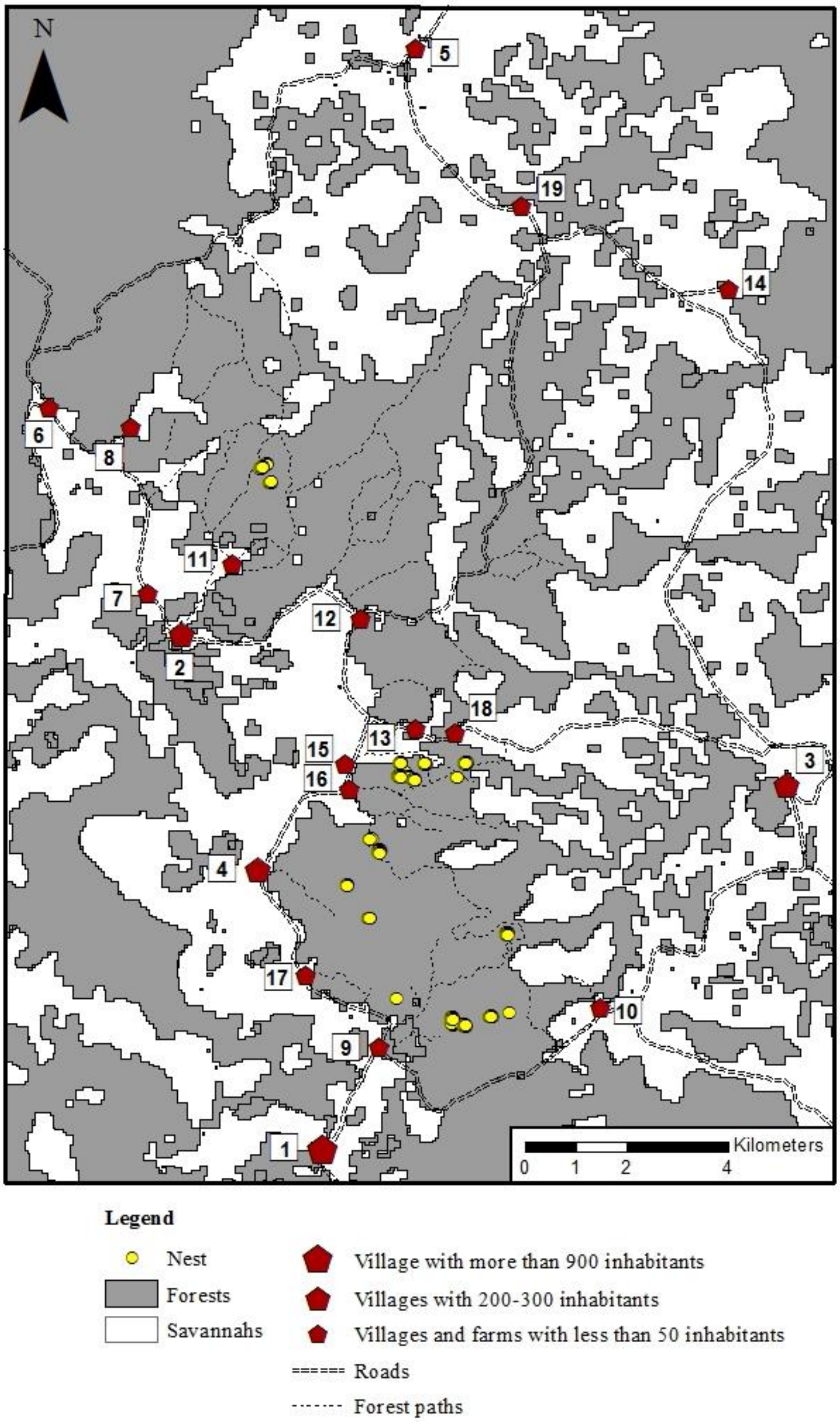


Figure 0-20: Map of the study site (16.41-16.56°E, 2.45-2.66°S, West DRC) with nest followed nest decay rate

Forest cover is indicated in grey and savannah in white [the map is based on the non-supervised classification – RED and IR on a Landsat7 (2007)]. Parallel dashed lines indicate the roads surrounding the study site, whereas dotted lines indicate the main forest paths. Yellow points indicate nests which have been followed until they disappeared. Villages are depicted as red pentagons. Numbers correspond to the village names in Table 0-10 (Page 56) and Number 19 represents the WWF-base.

IV.5 **Fruit monitoring**

We recorded data on fruiting trees within 14 plots of 0.04 ha each, for a total of 0.56 ha in Nkala forest between May 2011 and June 2013 (Figure 0-21 – Page 53). We randomly chose plot locations placed along the transects in order to facilitate our access to them. In November and December 2011, all trees with a DBH larger than 10 cm were marked, identified to the species level and their DBH was measured (n=346). In May 2012, in order to improve our representation of fruiting trees, we added 8 additional plots: 5.75 ha in total, five 1 ha plots and three 0.25 ha plots, in which trees (n=2239) had been previously identified during a tree abundance survey (PhD thesis of J-F Bastin). Every two weeks, we visited each of the plots and recorded which trees were fruiting by inspecting their crowns and counting fruits on the ground. We calculated an index of 'fleshy fruit availability'. Fruit species considered for this index were derived by selecting tree species *(i)* eaten by bonobos in the region (information from the feces analysis) and at different study sites (Kano and Mulavwa 1992, Beaune et al. 2013) or *(ii)* producing fleshy fruits (Tailfer 1989, Wilks and Issembe 2000, Djoufack et al. 2007). We used the basal area to estimate their canopy volume (Strier, 1989 cited in Basabose, 2002) and calculated an fleshy fruit availability index as: $F_m = \sum p_{ki} * ba_k$ where p is the proportion of trees of the *k* species bearing fruits during the plot visit *i* and and *ba* is the basal area (in square meters per hectare) of species *k* in the forest. We estimated a daily index by assigning for each date the index of the closest recorded plot visit.

Data valorization

The information on trees being in fruits have been used to study bonobo cohesiveness at night in relation to fruit availability (Chapter 2, Serckx et al. 2014) and to relate bonobo diet with fruit availability in the forests (Chapter 3, Serckx et al. in prep).

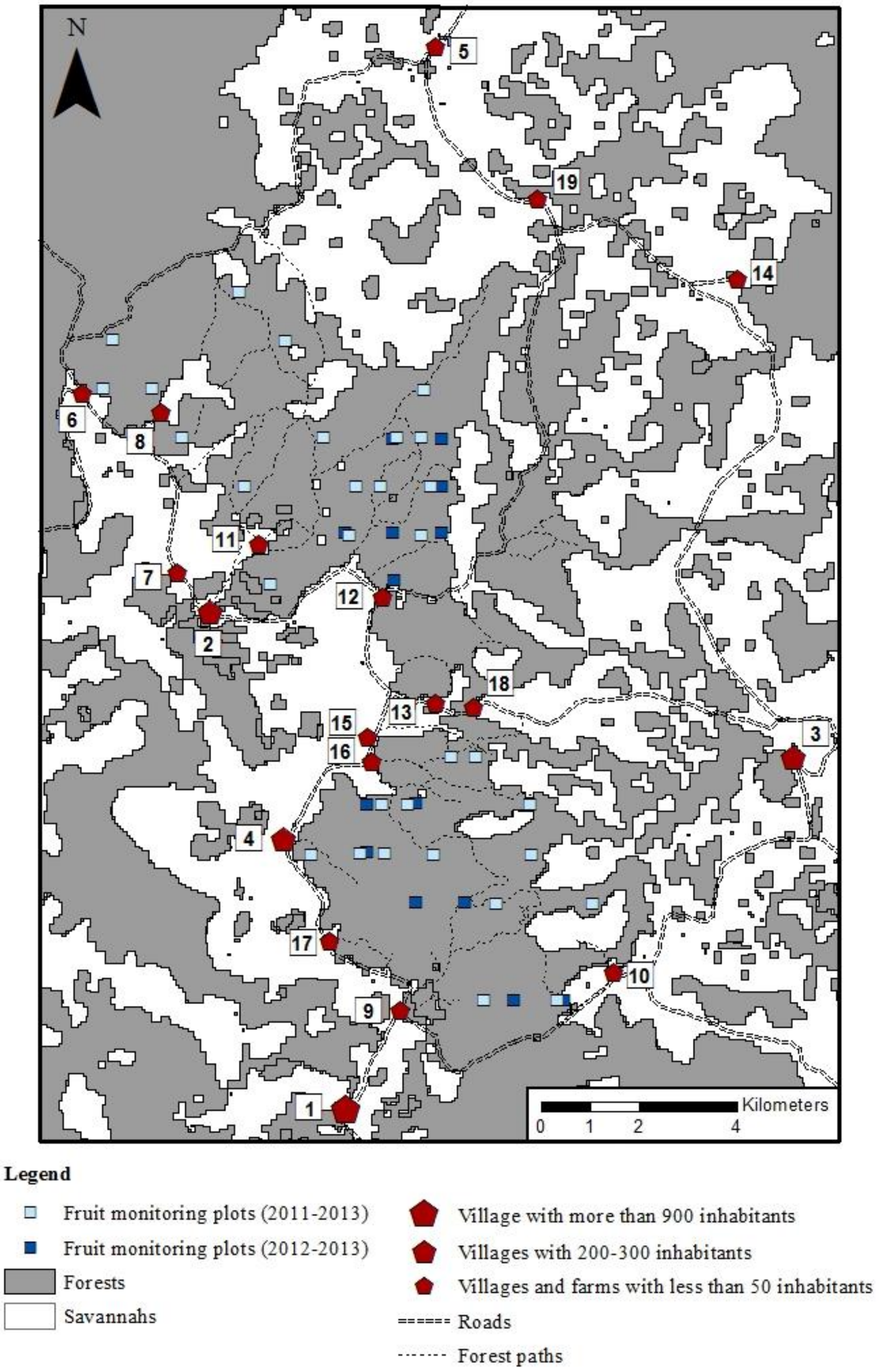


Figure 0-21: Map of the study site (16.41-16.56°E, 2.45-2.66°S, West DRC) with plots for fruit monitoring

Forest cover is indicated in grey and savannah in white [the map is based on the non-supervised classification – RED and IR on a Landsat7 (2007)]. Parallel dashed lines indicate the roads surrounding the study site, whereas dotted lines indicate the main forest paths. Light blue squares indicate plots monitored from 2011 to 2013 while dark blue squares indicate plots added in May 2012. Villages are depicted as red pentagons. Numbers correspond to the village names in Table 0-10 (Page 56) and Number 19 represents the WWF-base.

IV.6 Feces analysis

Feces analysis was performed for the bonobo community of Nkala forests. Between May 2011 and June 2013, trackers, who followed bonobos daily for the WWF habituation program, collected feces at nesting site (one fecal sample from below each fresh nest, n=2272, in 270 days), stored them in plastic bags and brought them back to Mbou-Mon-Tour farm where we realized all *in situ* analyses within the forty eight hours after collection. Each sample was weighted to the nearest gram (Moscovice et al. 2007). Samples were washed in 1-mm mesh sieves. The contents of each sample were divided into *(i)* fruits with large seeds, i.e. species for which we could count the number of seeds (including seeds, skin and pulp remains), *(ii)* fruits with small seeds, i.e. uncountable seeds (seeds, skin and pulp remains), *(iii)* foliage (fiber, digested fragments of leaves and flower), *(iv)* fragments of insects or other animal matter and *(v)* other items. The volume percentage of each of these contents was estimated by 5% interval (Basabose 2002). We further identified clean fruit seeds to the species level and we counted them. The total number of seeds of a given fruit species in each fecal sample was divided by the wet weight of the fecal sample and multiplied by 100 to obtain a standardized measure of the relative amount of seeds consumed per fruit species per fecal sample (Moscovice et al. 2007). Non-fruit plant foods were identified and described as precisely as possible from macroscopic observations.

Data valorization

Information on the species eaten by bonobos in the region have been used in different models in order to get a predictor of species potentially eaten present on the transects (Chapter 1, Serckx et al. In prep.) and in nesting sites (Chapter 2, Serckx et al. 2014). Bonobo diet was more precisely characterized in chapter 3 (Serckx et al. In prep.).

Figure 0-22: Pictures of feces analysis (© Adeline Serckx)

IV.7 **Socio-economic data**

In May and June 2012, we collected socio-economic data in the six villages and the twelve farms surrounding the study site. We developed a questionnaire based on the "Poverty and Environment Network (PEN) prototype questionnaire" ("PEN Prototype Questionnaire" 2008). A minimum of 30% of adults in all villages and farms were chosen by random sampling (Shibia 2000, Kideghesho et al. 2006, Nyariki 2009). A total of 201 adults were interviewed (Table 0-10 – Page 56) with, as a first objective, to collect information on their hunting, fishing and Non-Timber Products Crops (NTPC) uses of the forests. We also asked questions on family composition, agriculture, livestock breeding, wood collection for cooking, food habits, well-being, general feeling about conservation and knowledges about bonobos (an overview of the questions is given in Table 0-11 – Page 57 and the complete questionnaire is available in Appendix III – Page 253).

With the help of local assistants, we created a forest map with forest names used by local population (Figure 0-24 – Page 59). As local forest names are actually derived from small rivers flowing in the forest, we first geo-referenced thes rivers. In order to draw forest boundaries, we assumed forest boundaries are located at equal distance of the neighbouring rivers and we drew them manually using ArcGIS 10.1.

Data valorization

Information on human forest use have been used in different models in order to get a predictor of human pressure in the different parts of the forests (Chapter 1, Serckx et al. In prep. and Chapter 2, Serckx et al. 2014).

Figure 0-23: Picture of an interview (© Alexandra Ley)

Table 0-10: ***Socio-economic data***

		Population					Interviewed people			Interviewed people per activity				
		Nb household	Nb men	Nb women	Nb children	Total	Total	Men	Women	Hunters (M)	Fishermen (W)	Fishermen (M)	NTPC (W)	NTPC (M)
1	Nkoo	168	169	202	540	911	50	35	15	16	13	20	7	9
2	Mpelu	43	50	58	153	261	50	30	20	19	20	23	20	19
3	Lebomo	37	37	34	141	212	26	14	12	7	9	8	3	2
4	Nkala	34	36	49	110	195	39	21	18	7	18	14	16	10
5	Malebo	10	9	11	38	58	6	3	3	1	3	2	3	2
6	Mavula	10	10	12	25	47	6	3	3	3	3	2	3	1
7	Bosatore	7	5	7	22	34	2	1	1	1	1	1	1	1
8	Mokoabuo	6	5	8	17	30	4	2	2	1	2	1	2	1
9	Dispensaire de Nkoo	4	4	4	19	27	2	1	1	0	0	0	0	0
10	Lensiana	4	4	3	18	25	0	0	0	0	0	0	0	0
11	Biomengele	3	3	3	13	19	3	2	1	2	1	1	1	1
12	Ngandjele	3	3	6	7	16	2	1	1	0	1	0	1	0
13	Motsuemontore	2	2	4	9	15	2	1	1	1	1	0	0	0
14	Ezano	3	2	2	8	12	1	1	0	1	0	1	0	1
15	Mayi Monene	2	2	3	5	10	2	1	1	0	1	1	0	0
16	Mbou-Mon-Tour	4	4	4	2	10	2	1	1	0	1	0	0	0
17	Moza	1	1	1	6	8	2	1	1	0	1	0	1	0
18	Bosieli	1	1	1	5	7	2	1	1	1	1	1	1	0
	TOTAL	**342**	**347**	**412**	**1138**	**1897**	**201**	**119**	**82**	**60**	**76**	**75**	**59**	**47**

The numbers beside the village names were used to locate them on the study site maps (Figure 0-24 – Page 59). In the ‘Population’ part of the table, we present results of the village population census realized in 2012. The ‘Interviewed people’ part of the table indicates first the sampling effort for the socio-economic data collection (total per village and per gender). Finally, the ‘Interviewed people per activity’ part of the table gives the number of interviewed individuals (per village and per gender) who indicated that they regularly enter the forest for hunting, fishing or collecting non-timber products (‘NTPC’ = non-timber products collect) and thus answered those parts of the questionnaire.

Table 0-11: Overview of the questionnaire

Overall subject	**Type of questions**
Basic data	Family composition Education level of the interviewed person Main occupations (classified by importance) Possessions ownership (bike, motorbike, furniture in the house, etc.)
Agriculture	Number of fields and their size Field location in the forest Species cultivated (classified by importance)
Livestock Breeding	Species Number of animals Types of health care, food support and enclosure Objective of the animal breeding (sell or consumption) Satisfaction on the current way to do animal breeding
Wood collection for cooking	Frequency Number of persons of the family People feeling about decrease/increase in wood availability in the forest and how they react to that
Tree plantation	Species Location (forest vs. village) Use targeted (consumption, sell, parcel separation, etc.)
Collection of non-timber products	Species Weekly frequency Location of the areas where they collect each type of item
Food habits	Bush meat and fishes consumptions *Separately for bush meat and fishes*: Weekly frequency Species consumed and preferred (classified by importance for bush meat) Origin of food (purchase, personal hunting or fishing, location of purchase) Change in consumption during the 5 last years and why Tolerance to stop eating them and required alternatives

Hunting	Weekly frequency Type of hunting Main species hunted Distance travelled to go hunting Objective of the activity (eating or selling, location of selling) Tolerance to stop hunting and required alternatives *For each forest region* Type of hunting Main hunted species (asked for ‘today’ and ‘before conservation programs’)
Fishing	Weekly frequency Type of fishing Distance travelled to go fishing Objective of the activity (eating or selling, location of selling) Tolerance to stop fishing and required alternatives *For each forest region* Type of fishing Main species (asked for ‘today’ and ‘before conservation programs’)
Well-being	How they feel according to the others Differences ‘today’ and ‘before conservation programs’ and identified reasons of the changes
Feeling about conservation	Current feeling Expectations towards conservation
Bonobo	Knowledge about the species Traditional story

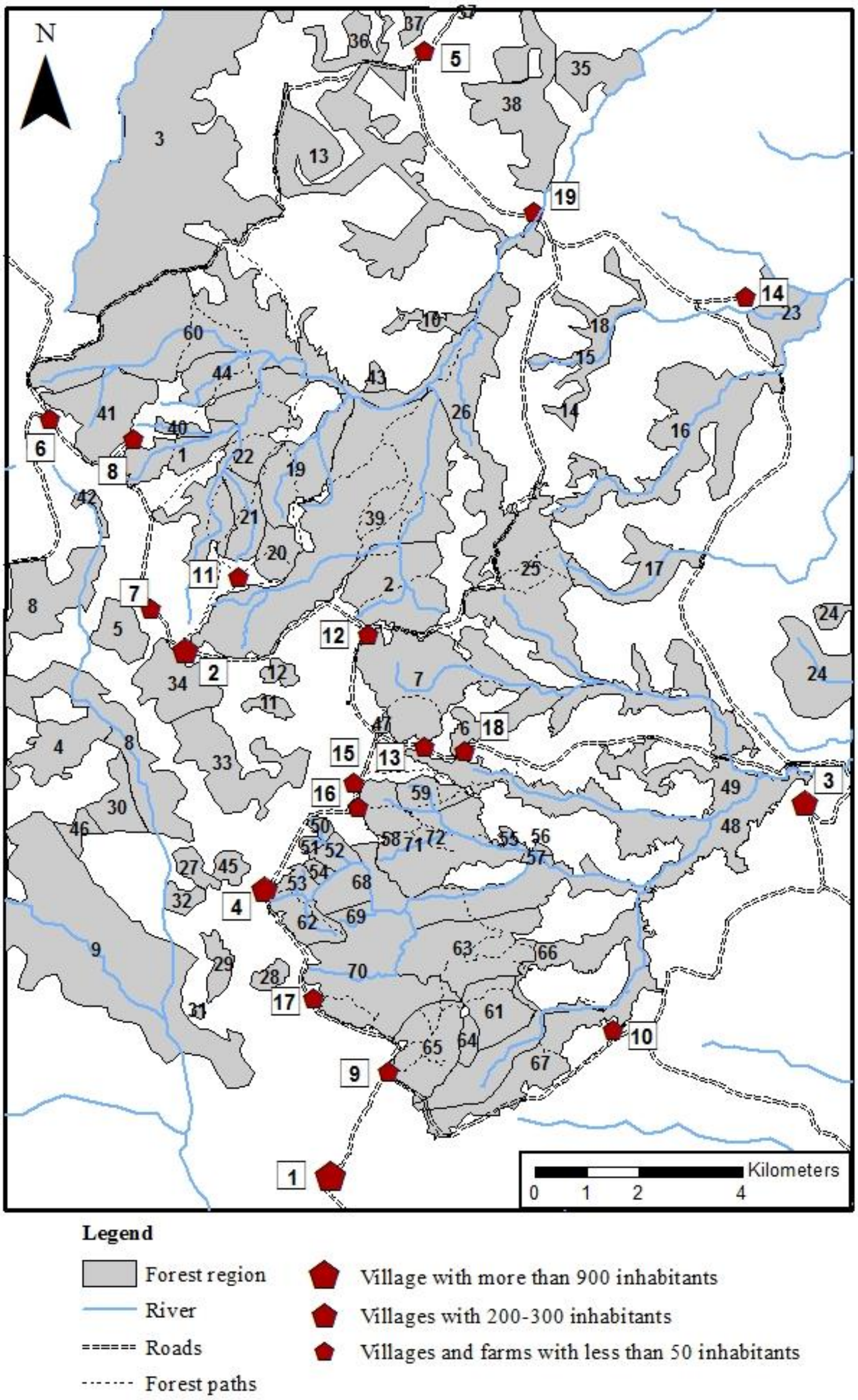


Figure 0-24: Map of the study site (16.41-16.56°E, 2.45-2.66°S, West DRC) with forest names used by local population

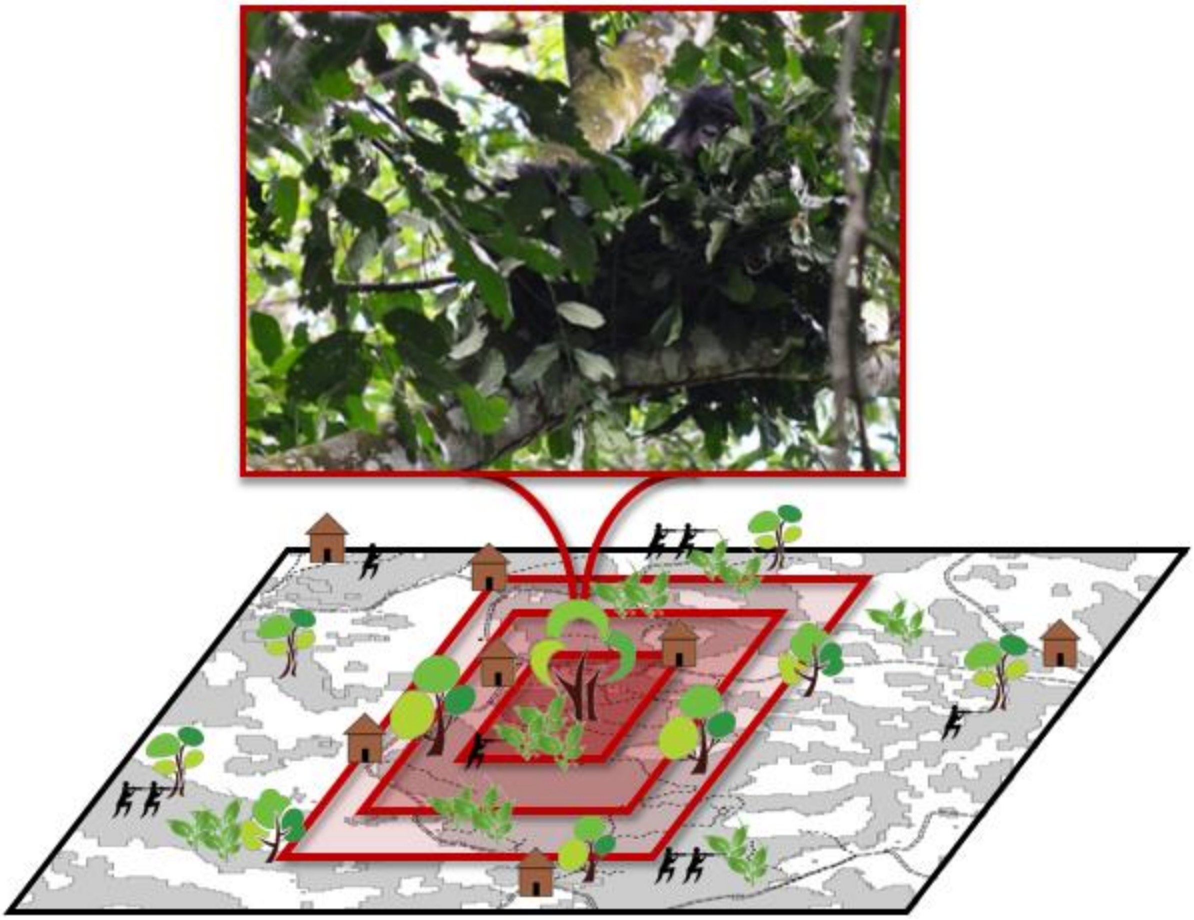
The forest region are shown in grey with a number related to its name (Table 0-12 – Page 60). Parallel dashed lines indicate the roads surrounding the study site, whereas dotted lines indicate the main forest paths. Blue ligns represent the small rivers in the forests. Villages are depicted as red pentagons. Numbers correspond to the village names in Table 0-10 (Page 56) and Number 19 represents the WWF-base.

Table 0-12: Forest names used by local population

ID	**Name**	**ID**	**Name**	**ID**	**Name**
1	Mbelbel	25	Minkalu	49	Mambubi
2	Matshuka	26	Mesuli Meko	50	Tshibou
3	Moba	27	Ngamolanu	51	Buabu
4	Lesani	28	Ngonui	52	Mosulbola
5	Nianzali	29	Ekelenswa	53	Mayele-Mpibe
6	Montsuomontore	30	Mbudza	54	Mofuma
7	Lekwa	31	Masue	55	Nkulbankeon
8	Mbali	32	Ngalwa	56	Nkulansua
9	Lebfiri	33	Nkomo	57	Mayilansei
10	Bantsua	34	Manzien	58	Mvubu
11	Mosulmanfu	35	Bebal Bebal	59	Mosulmonayi/Bebala
12	Mosulmanfu	36	Epale	60	Bambu
13	Lokoso	37	Mbako	61	Mokabu
14	Mampina	38	Malbain	62	Mekwe-Mekwe
15	Elokompamba	39	Leyabi	63	Besia-sia
16	Mankere	40	Mokoabuo	64	Malbere
17	Mankere	41	Bempibi	65	Bolobo
18	Mankere	42	Mabana	66	Lensiana
19	Mangwe	43	Nkulende	67	Mbala
20	Manzalmuele	44	Mabamziame	68	Lebomo
21	Manzo	45	Eluelyira	69	Ebarbambore
22	Nkubekabe	46	Mankee	70	Bekero
23	Obalakuma	47	Nkulubatu	71	Nkulbebubu
24	Lenga	48	Nzuma	72	Nsei

CHAPTER 1:

OPTIMIZING SCALE SEARCH FOR PREDICTOR INFLUENCE IN SPECIES DISTRIBUTION MODELS



Serckx A, Huynen M-C, Beudels-Jamar R C, Vimond M, Bogaert J, Mundry R, Kühl H S. Optimizing scale search for predictor influence in species distribution models. *In prep*.

I RÉSUMÉ

Le rôle de l'échelle spatiale dans la formation des patterns écologiques tels que la distribution d'espèces est un thème de recherche majeur depuis plusieurs décennies. De nombreux progrès ont été accomplis quant à la manière d'identifier l'influence des échelles spatiales. Généralement, l'effet d'un prédicteur sur une réponse est évalué selon des échelles spatiales multiples et discrètes afin d'identifier l'échelle optimale d'influence. Cependant, cette approche peut être problématique. Si l'influence d'un prédicteur à multiples échelles n'est pas testée à l'aide d'une approche systématique de la variation spatiale de l'influence de ce prédicteur, le risque d'erreur de type I est largement augmenté. De plus, le concept visant à identifier une unique échelle d'influence pour un prédicteur n'a probablement pas de sens. L'influence de l'échelle d'un prédicteur sur une réponse suit généralement une forme sigmoïdale, le domaine d'influence optimale étant indiqué par un large plateau et non par un pic de corrélation. Ceci favorise clairement une approche multi-modèles, plutôt que l'inférence à partir d'un modèle unique pour les études de distribution d'espèces. Par conséquent, nous avons besoin d'approches efficaces d'un point de vue computationnel et ce, particulièrement si plusieurs prédicteurs sont évalués. Dans cette étude, nous utilisons des données de bonobos (*Pan paniscus*) pour construire des modèles de distribution d'espèces qui évaluent simultanément l'influence de plusieurs échelles, de prédicteurs et de terme d'autocorrélation, et qui modélisent l'effet décroissant des prédicteurs à distance croissante du point d'observation. Nous commençons avec une résolution d'échelle grossière afin d'établir rapidement la forme approximative de la variation de l'influence d'un prédicteur sur la densité de bonobos. Cette recherche d'échelle est ensuite raffinée en augmentant la résolution sur une gamme d'échelle afin d'évaluer, par exemple, la limite inférieure et supérieure d'influence d'un prédicteur ou le domaine d'échelles auquel les changements d'influence d'un prédicteur sont les plus grands. Plus précisément, nous avons utilisé des variables prédictrices de la structure de la forêt, de la disponibilité en plantes herbacées terrestres ou en fruits afin de refléter les contraintes environnementales sur les comportements de déplacement, d'alimentation et de nidification du bonobo. Un grand nombre de modèles prédisait nos données de manière équivalente. Ces modèles ont révélé des courbes sigmoïdales de forme opposée pour la structure de la forêt par rapport à la disponibilité en plantes herbacées terrestres et en fruits, indiquant des échelles optimales d'influence supérieure à 750 m ou inférieures à 300 et 600 m, respectivement. L'inférence de ces modèles multi-échelles a également fourni des estimations

de paramètres robustes. L’approche proposée est très flexible et peut être appliquée pour de nombreuses espèces, diverses échelles spatiales et différents paramètres écologiques.

II ABSTRACT

The role of spatial scale in ecological pattern formation such as species distribution is a major theme in research since decades. Much progress has been made on how to identify most influential spatial scales. Commonly, the effect of a predictor on a response is evaluated over multiple and discrete spatial scales to identify an optimal scale of influence. However, this approach can be problematic. If testing of predictor influence at multiple discrete scales is disconnected from the systematic assessment of spatial variation in predictor influence it can result in greatly inflated type I error rates. Furthermore, the concept of identifying a single and most influential scale of predictors is likely to be misleading. The influence of predictor scale on a response is usually rather sigmoid than humped-shaped, which results in largely flat likelihood surfaces. This strongly favours multi-model rather than single model inference on species distribution and computationally effective approaches are needed, in particular if multiple predictors are evaluated. Here, we use data on bonobos (*Pan paniscus*) to build distribution models which simultaneously evaluate the influence of multiple scales, predictors and autocorrelation, and also account for spatial decay effects. We start with a very coarse resolution of scales to establish the approximate shape of variation in predictor influence on bonobo density in a resource efficient manner. This coarse scale search is then subsequently refined by increasing scale resolution for selected ranges to assess for instance lower or upper scales of predictor influence or scales at which changes in predictor influence are greatest. More specifically we used forest structure, herb and fruit tree availability as predictors to reflect environmental constraints on bonobo ranging, feeding and nesting behaviour. A large number of models fitted the data equally well. They revealed opposing sigmoidal, functional shapes for forest structure, herb and fruit tree availability with importance at scales above 750 m, and below 300 or 600 m, respectively. Subsequent multi-scale, multi model inference provided robust estimation of parameters. The proposed approach is very flexible and can be applied to a wide range of species, spatial scales and ecological settings.

Keywords: multi-model inference, scale range, scale search, species distribution models, weighting functions, computational efficiency, bonobo

III INTRODUCTION

The role of spatial scale is a major research theme in ecology since decades due to its significance in understanding biological patterns and processes (Wiens 1989, Levin 1992, Marceau 1999, Wheatley and Johnson 2009). The current context of global landscape modification and habitat fragmentation makes this topic even more relevant (Riitters et al. 2000). The effect of spatial scales in species-environment dependencies give crucial insight into underlying processes, such as ranging (Johnson et al. 2004a, Rhodes et al. 2005, Forester et al. 2009), foraging (Johnson et al. 2004b, Henry et al. 2012), feeding (Boyce 2006, Mayor et al. 2007), sleeping or resting behaviours (Fischer and Lindenmayer 2006, Meyer and Thuiller 2006). It is needed for understanding effects of habitat changes (Fischer and Lindenmayer 2006) and for suggesting valuable areas and management practices for conservation (Vaughan and Ormerod 2003, Johnson et al. 2004c, Nams et al. 2006, Seo et al. 2009). Much conceptual and methodological progress has been made on how to identify appropriate spatial scales in species-environment relationships (Urban 2004, Mayor et al. 2009, Wheatley 2010). However, scale search becomes quickly intractable when evaluating multiple predictors (Aue et al. 2012). Hence resource efficient scale search techniques are needed to predict pattern and processes across scales (Wheatley and Johnson 2009).

The structure of typical ecological information, including field (Anderson et al. 2005, Mayor et al. 2007, Rhodes et al. 2009) and remotely sensed data (Woodcock and Strahler 1987, Marceau and Hay 1999) give the opportunity to work at discrete scales including different grain ("size of individual units of observation") and extent ("the overall area encompassed by a study") (Wiens 1989). Various studies have used this to better understand foraging behaviour, home range use, the influence of the spatial distribution of food resources, the selection of sleeping and resting sites or the geographical distribution of populations. For instance, in elks predator avoidance defines occurrence at larger spatial scales than suitability of habitat (Anderson et al. 2005, Fortin et al. 2005). In Cross River Gorillas human impact explains patchy distribution inside suitable habitat, whereas food availability is acting only at smaller spatial scales (Imong et al. 2014, Sawyer and Brashares 2013).

However, the precise scale of influence is usually unknown. This often leads to an arbitrary choice of grain and extent when evaluating species-environment relationships (for a review see Wheatley and Johnson 2009). To overcome this problem, some authors have suggested to incorporate information on animal movement (Forester et al. 2009), such as home range behaviour (Rhodes et al. 2005), or niche partitioning between sympatric species (Pita et al. 2011) to approximate suitable scales. The drawback is that this often requires radio-telemetry data or other highly detailed information on how animals use their environment. This limits the common use when evaluating species-environment relationships.

Another proposed solution is to gather scale information from existing literature. However, the influence of scale is not static, but will vary according to environmental and demographic context. Home range sizes were shown to differ even within a population (Mule deer: Nicholson et al. 1997, Kie et al. 2002; Moose: van Beest et al. 2011), core areas can vary over time (Grey-cheeked mangabey: Janmaat et al. 2009) and foraging behaviour can vary spatio-temporally (e.g. primates: Boyer et al. 2006, Bowyer and Kie 2006). To overcome these issues several authors have therefore suggested to work with a scale continuum instead of assuming one fixed and discrete scale in order to identify scale dependencies in the given context (Johnson et al. 2004b, Nams et al. 2006, Mayor et al. 2009, Wheatley 2010).

The evaluation of a range of scales for identifying those that best explain observed patterns require a careful selection procedure to not violate fundamental statistical principles. First, testing multiple predictors across a large number of scales increases the probability of erroneous significance. This is equivalent to a stepwise model selection procedure in which several variables are added and removed according to their significance to finally reach the best model. This approach leads to the problem of greatly inflated Type I error rates (i.e., the probability of erroneously rejecting a true null hypothesis, Whittingham et al. 2006, Mundry and Nunn 2009, Forstmeier and Schielzeth 2011). Second, conventional regression models do not take into account the decreasing influence of a predictor as a function of distance through space or time. Commonly, a metric on a predictor is calculated for a discrete buffer around the location of observation. Values are treated equally no matter how far apart they are in time or space from the location of observation. When representing the pattern of species-environment relationships over a scale continuum, such approach often results in a hump-shaped correlation with a peak at one discrete scale. The conclusion that this maximum correlation between species occurrence and a predictor indicates the most meaningful scale of influence is, in fact, a misinterpretation (Aue et al. 2012). Such correlation patterns actually reflect underlying opposing trends in the increasing area to consider and the decreasing predictor influence with increasing distance from the point of observation.

Aue et al. (2012) showed that working with realistic distance weighting functions in a regression can solve this problem. It will naturally introduce the decreasing influence of environmental predictors with distance and will give sigmoid correlation curves across scales (Figure 1-1 – Page 68). Those curves depict scale ranges of predictor influence with minima and maxima. This is in strong contrast to the idea of one optimal or most influential scale. It also suggests that the common selection of one “best scale model” is likely not to be appropriate in species distribution models, but should rather be based on multi-scale and –model inference. At the same time, Henry et al. (2012) highlight that an autocorrelation term based on distance weighted observations at neighbouring locations can be incorporated and can reflect movement patterns of foraging animals. These approaches are all very promising, however Aue et al. (2012) concluded that a widespread use of distance weighted effects could be compromised by computational constraints.

In summary, optimizing scale search in species distribution models thus requires to carefully consider multiple testing issues, to incorporate distance weighted functions to appropriately reflect predictor influences, to make inferences from a large number of equally well fitting models rather than single best fitting models and to use computationally efficient approaches.

In this study we build distribution models to simultaneously evaluate the influence of multiple scales and predictors, including autocorrelation and distance weighting functions. We use this approach to characterize the influence of small to large scale environmental predictors for resting, feeding and ranging behaviour in a bonobo population in western Democratic Republic of Congo.

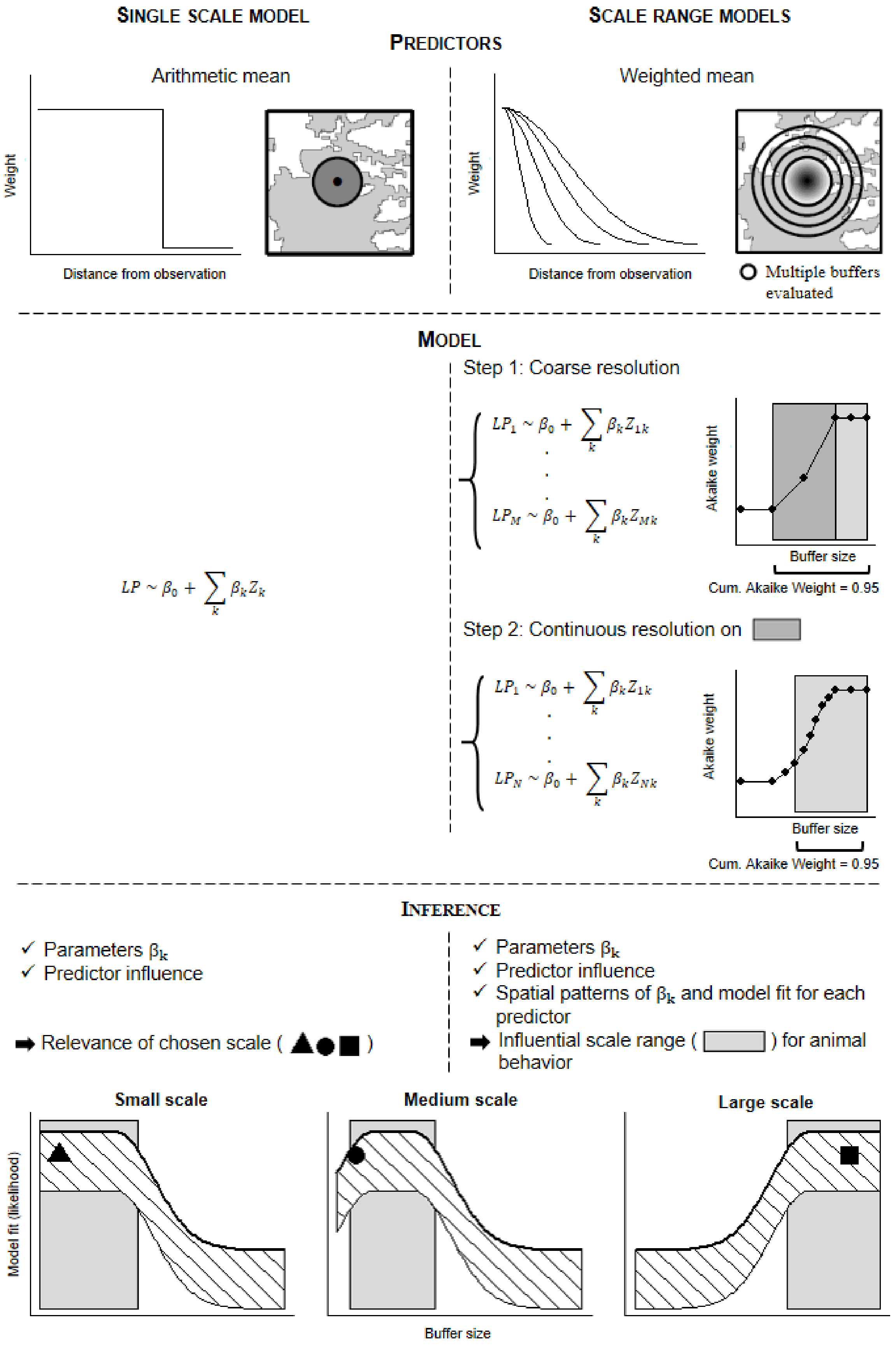


Figure 1-1: ***Principles of single scale versus scale range species distribution models*** *(legend on next page)*

Figure 1-1: Concepts of single and scale range models differ with regard to predictor extraction, model building and inference. The evaluation of a ‘single scale model’ with mean predictor values provides information on the scale defined by expert opinion. In contrast a set of ‘scale range models’ that contain distance weighting functions for predictors will provide a systematic assessment of predictor scale- response relationships. To improve computational efficiency, ‘scale range models’ are implemented with a two steps procedure: a scale search at coarse resolution is first tested. Based on its outcome, a second search is implemented with finer resolution on the scale range of greatest changes.

IV METHODS

IV.1 Study site

The study site is located in the South of the Lake Tumba landscape (the North of Bateke Plateaux) in western Democratic Republic of Congo, close to the WWF Malebo research station (16.41-16.56°E, 2.45-2.66°S, Figure 1-2 – Page 72). This region can be characterized as a forest-savannah mosaic. The altitude ranges from 300 to 700 m (Inogwabini et al. 2008), and the mean daily temperature fluctuates around 25°C (Vancutsem et al. 2006). Annual rainfall oscillates around 1500-1600 mm, and is interrupted by two dry seasons in February and July-August (Inogwabini et al. 2008). Forests mostly represent *terra firma* soil conditions and encompass various habitat types, i.e. re-colonizing *Uapaca sp.*, old secondary, mixed mature, old growth mono-dominant, riverine gallery and Marantaceae forests (Inogwabini et al. 2008). The study site encompassed 170 km², made up of 102 km² of forest patches of various shapes and sizes which are connected by many corridors. Surrounding savannahs were mainly herbaceous and partially used for cattle ranching. Human activities and settlements were concentrated in the west side of the study area. Six villages and twelve farms were directly adjacent to the forest and agriculture was located inside the forest. Two bonobo communities inhabited the forests, and have since 2007 been the subject of habituation and conservation programs by WWF-DRC (Inogwabini et al. 2008).

IV.2 Data collection

From May to July 2011 and from Mid-March to Mid-July 2012, we collected data on bonobo density, human indices and habitat types in the forests of the study site using standard line transect methodology (Buckland et al. 2001, Kuehl et al. 2008). We sampled 114 transects running from west to east, spaced 500 m apart and of variable lengths, with a total length of 179.1 km (Figure 1-2 – Page 72).

We systematically collected information on bonobo nests and recorded their perpendicular distances from the transects using a tape measure. We recorded all types of human hunting signs, i.e., cartridges, trap types (wood, nylon thread, cable), net hunting signs. We described forest habitat types according to the dominant understory and tree species dominance in the canopy. In order to depict dominant understories, we noted within 25m-segments one or two of the following categories (based on the classification in Reinartz et al., 2006): open, liana, woody, Marantaceae or other terrestrial herbaceous vegetation (THV) (with specification of the species for Marantaceae and THV). In order to identify tree species dominance in the canopy, we measured all trees with a DBH larger than 50 cm within a 10 m strip on both sides of the transects (Appendix A – Page 96). Those trees usually include the majority of fruiting trees in a tropical forest (Doucet 2003, Madron and Daumerie 2004, Bourland et al. 2012, Menga et al. 2012) and were used to estimate an index of fruit tree availability.

In order to complete our information on human forest use, we geo-referenced roads and main forest travel paths and we collected socio-economic data in all villages and farms surrounding the study site. Between May and June 2012 we conducted a population census (Appendix B – Page 96). We interviewed 119 men on their possible hunting activities (women do not hunt in the area) with a total of 60 men who answered they regularly enter the forests for hunting. We asked about the frequency and location of hunting activity in the forest. The villagers indicated the location of their activity on a map using the local names for each location in the forest (later called 'forest region').

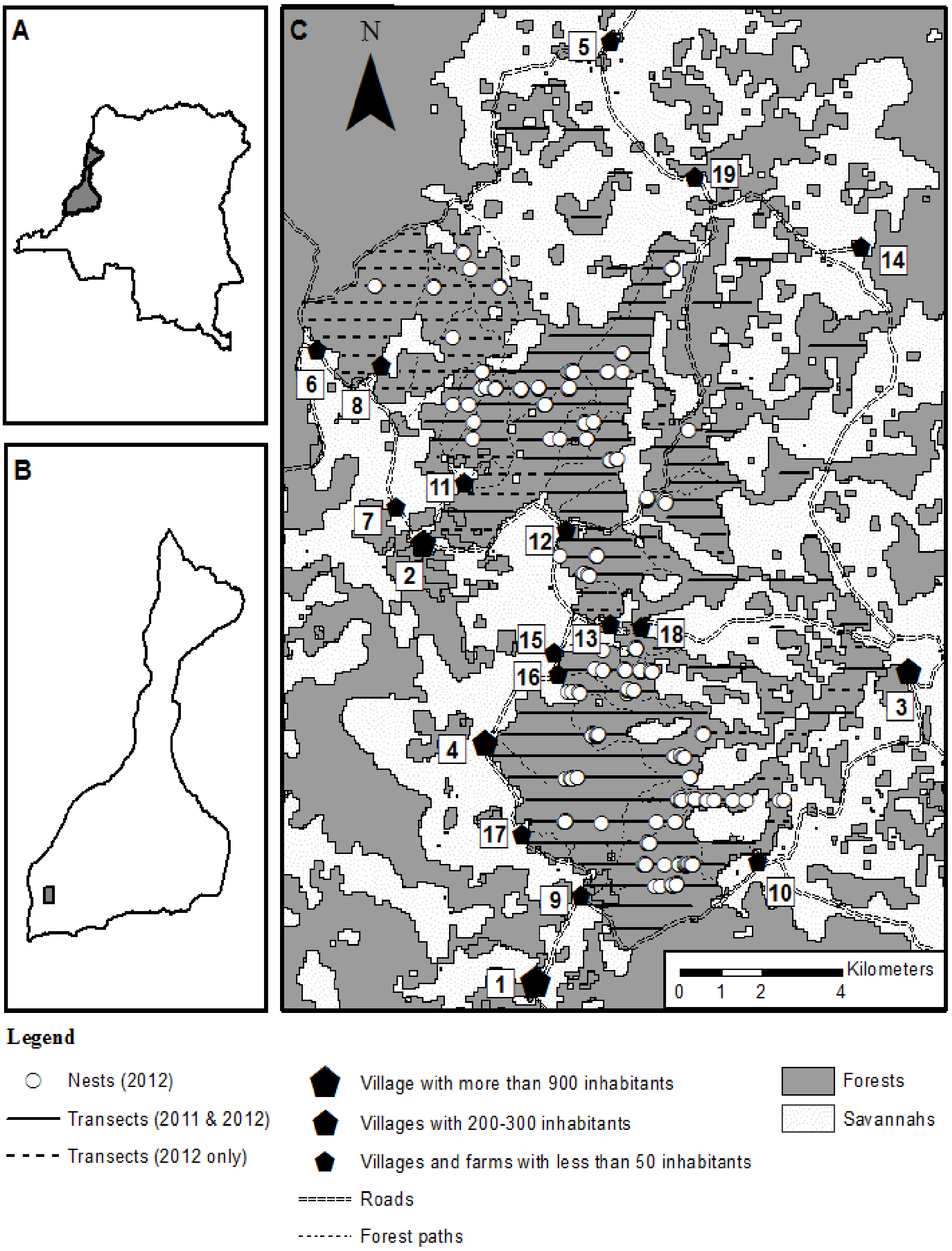


Figure 1-2: Map of the study site

A. Location of the Lake Tumba landscape in Democratic Republic of Congo. B. Location of the study site inside Lake Tumba landscape. C. Map of the study site. Horizontal solid lines depict the line transects travelled in 2011 and 2012 whereas the horizontal dashed lines indicate transects travelled only in 2012. Numbers next to villages correspond to the village names in the Table B1 of the Appendix B (Page 96) and Number 19 represents the WWF-base.

IV.3 **Analytical methods**

IV.3.1 GENERAL CONCEPT

The principal idea is to combine standard species distribution modelling based on generalized linear modelling (Guisan and Zimmermann 2000, Guisan and Edwards 2002, Hedley and Buckland 2004, Araújo and Guisan 2006, Wich et al. 2012, Murai et al. 2013) with weighting functions to account for the decreasing influence of predictors with increasing distance from points of observation (Henry et al. 2012, Aue et al. 2012). This approach first requires a careful selection of scale ranges to be evaluated and informed by expert opinion in order to consider only biologically meaningful scales. Second, the concept of selecting a "best model" (hereby referred to as '*single scale model*') is likely not to be appropriate, if predictor-response curves follow sigmoid rather than humped-shaped curves across spatial scales. A large number of models may equally well represent predictor influence within suitable scale ranges and it may therefore be more appropriate to use multi-model inference (hereby referred to as '*scale range models*'). Both approaches reduce the risk of model misspecification caused by the testing of arbitrary scales and thus greatly inflated type I error rates (Whittingham et al. 2006, Mundry and Nunn 2009, Forstmeier and Schielzeth 2011). To overcome computational constraints, model and scale evaluation is implemented first at a coarse resolution with few selected scales which span over the entire ranges to be evaluated and defined by expert opinion. Based on this outcome, a refined and more continuous scale search is implemented in a subsequent step and for a subset of the scale range to locate minima, maxima or greatest changes of predictor influences. Such incremental and resource efficient approach is in particular important, if applied to complex models with the simultaneous evaluation of multiple predictors, scales and autocorrelation.

IV.3.2 RESPONSE VARIABLE

Bonobos, like all Great Apes, are very elusive and direct observations in their tropical forest habitat are generally impossible. Therefore one usually relies on their sleeping nests for estimating abundance (Plumptre 2000, Kuehl et al. 2008). Apes build nests every night and, due to their long decay time, nests are abundant within their home ranges. For this reason, we used 'bonobo nest counts' as response variable. We summed all nest observations for transect segments of 500m length (n=411). We chose this segment length for several reasons. First, we wanted to use a large enough segment length to avoid an extremely skewed distribution of the response with a high proportion of segments without any observations and few segments with a large number of nest observations. On the other hand we wanted to use a segment length small enough to evaluate local scale effects on bonobo nest distribution. Segments located at transect extremity were sometimes shorter than 500 m.

IV.3.3 PREDICTOR VARIABLES

We defined seven predictor variables to characterize the ecological and anthropogenic environment of the study bonobo population (Table 1-1 – Page 76). We first defined the predictor ‘patch structure’ to characterize forest structure at the study site, a forest-savannah mosaic. Bonobos are a mainly forest dwelling species, which should be reflected in their ranging behaviour in this forest-savannah mosaic. We therefore expected this predictor to have an influence at larger scales; bonobo mean daily foraging travel distance was estimated as 2.6 km in dense forests (Furuichi et al. 2008). We first created a map of forests and savannahs in the study site, based on a non-supervised classification of a satellite image with 50 m resolution (Appendix C – Page 98). From this map, we calculated the ‘patch structure’ by using a sliding window of 3 by 3 pixels and by summing for the central pixel, the number of paired adjacent pixels classified as forest in each window (Riitters et al. 2000). We finally divided the number of paired adjacent pixels by the maximum number of paired adjacent pixels, i.e. 12.

In order to quantify food availability inside the forests, we defined two predictors representing the availability of *(i)* fruit trees and *(ii)* preferred terrestrial herbaceous vegetation (THV). Bonobos generally select food ‘hot-spot’ areas for sleeping (Serckx et al. In press.; Fruth, pers. comm.). We therefore expected both predictors to be relevant at small scale ranges. The mean radius of bonobo nesting sites is 100 m in the study site (Serckx unpublished data). For the index ‘preferred THV’, we calculated the proportion of two Marantaceae species, *Haumania liebrechtsiana* and *Marantochloa leucantha*, and one THV genus, *Aframomum sp*. for 25m-segments along transects. These are highly preferred by bonobos (Malenky and Stiles 1991, Reinartz et al. 2006, Serckx unpublished data). We then interpolated values across the study site with a resolution of 25 m by using the IDR function in ArcGIS 9.3 (with a power of 2 and a variable search radius). Second we calculated an index of ‘fleshy fruit availability’. Fruit species considered for this index were derived by selecting tree species *(i)* eaten by bonobos at different study sites (Kano and Mulavwa 1992, Beaune et al. 2013; Serckx et al. In prep.) or *(ii)* producing fleshy fruits (Tailfer 1989, Wilks and Issembe 2000, Djoufack et al. 2007). We used the basal area (in square meters per hectare) to estimate their canopy volume (Strier, 1989 cited in Basabose, 2002) and calculated an index for 25m-segments along the transects by summing the basal area of all selected species of the segment. We then interpolated a map with the same method as for ‘preferred THV’.

Next, as chimpanzees and other primates are known to show a high degree of site fidelity and often re-use nesting sites (Lehmann & Boesch, 2003; Murray et al., 2008; Janmaat et al., 2009; Stewart et al., 2011), we incorporated the number of nests observed in 2011 in the transect segment as a ‘nesting site fidelity’ predictor. This predictor should be important at a small scale as it could account for nesting site characteristics and preferences which were not represented by other variables. As not all transects were travelled in 2011, we excluded transect segments for which this predictor was not available (127 segments). We did not apply the distance weighting function and the scale search for this predictor as data did not cover the entire study site and an interpolation map would not be meaningful.

Finally, in order to control for human pressure, we used three variables representing different types of influence. First, we summed the ‘hunting signs’ observed on transects for each transect segment and expected it to influence bonobo density at small scales of less than 100 m (Reinartz et al. 2006) as bonobos could easily avoid them. Second, we derived ‘hunting pressure’ from our questionnaire data by estimating a daily mean number of adults who could potentially enter a specific forest area (Appendix C – Page 98). As this predictor was estimated from the mean value of different forest regions covering areas of several square kilometers (mean region area = 2.5 km²; range = 0.1 to 10 km²) and was representing the forest use of humans during the day, we considered that this predictor would depict human avoidance at intermediate scale (1 to 3 km) (Wich et al. 2012). Third, we used the ‘village influence’ predictor. It is a composite measure consisting of the influence of the population size of each village and the closest forest path or road, weighted by the distance to the transect segment (Appendix C – Page 98). As village size is known to influence ape density at large distance (Imong et al. 2014, Murai et al. 2013) we used all villages of the study site to estimate the value for each segment.

Table 1-1: Predictor variables, expected scale ranges and biological interpretation

Predictors	Unit	Formula	Expected scale range of influence	Biological meaning of the expected scale range	Main references
Patch structure	-	$\frac{pairs\ of\ forest\ pixels}{max\ of\ pairs\ of\ pixels,\ i.e.12}$	Large (~2.6km*)	Ranging behaviour – bonobo is a forest dwelling species, they need forest to find food and suitable places for sleeping	(Riitters et al. 2000, Furuichi et al. 2008)
Preferred THV	-	$prop.of\ suitable\ understory$	Small (~100m**)	Sleeping behaviour – bonobos favour food 'hot-spot' area for sleeping	(Malenky and Stiles 1991, Reinartz et al. 2006)
Fleshy fruit availability	m^2/ha	$\sum_{tree} basal\ area^{(1)}$	Small (~100m**)	Sleeping behaviour – bonobos favour food 'hot-spot' area for sleeping	(Kano and Mulavwa 1992, Beaune et al. 2013)
Hunting signs	-	$\sum hunting\ signs$	Small (less than 100m**)	Sleeping behaviour – The predictor represents discrete "objects" within the forest easy to avoid by bonobos	(Reinartz et al. 2006)
Hunting pressure	$nb\ events/day.km^2$	$\frac{\sum_{village}(prop\_quest\_hunters\ * nb\_men\_village}{forest\_region\_area}$	Intermediate (1 to 3 km)	Feeding or Ranging behaviour – The predictor is a proxy of human forest use	(Wich et al. 2012)
Village influence	$nb\ villagers/km$	$\sum_{village}\frac{nb\ villagers}{dist.village * \exp(dist.travel\ paths)^{(2)}}$	Large (up to 15km)	Ranging behaviour – The predictor indicates the forest area with potentially higher human pressure that bonobos should not use to avoid contacts with humans	(Kuehl et al. 2009, Junker et al. 2012, Hickey et al. 2013, Imong et al. 2014)
Nesting site fidelity	-	$\sum nests\ in\ 2011$	Small (~100m**)	Sleeping behaviour – The predictor represents nesting site characteristics and preferences which were not accounted by other variables	(Lehmann and Boesch 2003, Janmaat et al. 2009, Stewart et al. 2011)

(1) $Basal\ area = ((DBH/2)^2.\pi).10000/25.20$ where DBH is in meter and $10000/25.20$ is used to represent the basal area per hectare (25 m is the segment length of observation, 20m represent both sides of the transects where data were collected, and 10000m convert the value in hectare)

(2) We use an exponential to represent that human perturbation will mostly occur close to the travel paths, as people mainly used them to travel in the forest

* 2.6 km corresponds to the mean daily foraging travel distance in dense forests (Furuichi et al. 2008), ** 100m to the mean nesting site radius in the study site (Serckx, unpublished data)

IV.3.4 MODEL BUILDING

In order to build an appropriate bonobo distribution model, we needed to consider several issues. First, in order to account for the skewed distribution of the number of bonobo nests on the transect segments, we used generalized linear models with a negative binomial error function. Second, we wanted to convert our response, the ‘nest counts’ into bonobo density. We therefore included an offset term into our model. This term transforms nest counts into nest density by accounting for the variable length of the transect segments and for the effective strip width, which was estimated as 19m for this survey (see Serckx et al. In press., Buckland et al. 2001; Hedley and Buckland 2004). It further contained a nest construction rate of 1.37 per day (Mohneke and Fruth 2008), the proportion of nest-builders of 0.75 (infants sleep in their mother’s nest, Fruth 1995) and nest decay time (183 days, Serckx et al. In press.) to convert nest density into bonobo density. Third, we expected ‘preferred THV’ and ‘fleshy fruit availability’ to influence bonobo density non-independently. Locations with high proportions of ‘preferred THV’ and high values of ‘fleshy fruit availability’ are *Marantaceae* forests. This habitat type is often characterized by high food availability. It contains mainly trees with DBH above 50 cm but also has low density of suitable trees for nesting because bonobos prefer trees with relatively small DBH (Fruth 1995) (mean DBH of 22 cm in the study site, Serckx unpublished data). Thus, we added an interaction between the two predictors. Last, we needed to account for spatial autocorrelation. We used the average of the residuals of all other transect segments derived from the full model and weighted by distance as an additional predictor. The weight function had the shape of a Gaussian distribution with a mean of zero (maximal weight at distance equals zero) and a standard deviation chosen such that the likelihood of the full model with the derived variable ('autocorrelation term’) included was maximized (Fürtbauer et al. 2011). The general model formulation was

$$E(n_i) = exp\left[\ln(offset) + \beta_0 + \sum_k \beta_k Z_{ik} + \beta_{ac} ac_i + err.term\right]$$

where n_i is the number of nests on segment i, β are the parameters for each variable, Z_{ik} are the values of the k linear predictors on segment i, ac_i is the autocorrelation term in the segment i, *err.term* is the error function. In this study, the linear predictor became

$$hunting\ \ signs\ + hunting\ \ pressure + village\ \ influence +\ patch\ structure + \\ + nesting\ site\ fidelity +\ preferred\ THV +\ fleshy\ fruit\ availability + (preferred\ THV\ \times \\ fleshy\ fruit\ availability)$$

Prior to the analysis, we checked distributions of all predictors and transformed them if necessary to achieve more symmetrical distributions; ‘preferred THV’ and ‘fleshy fruit availability’ were square-root transformed, ‘hunting signs’, ‘hunting pressure’, ‘village influence’ and ‘nesting site fidelity’ were log-transformed, ‘patch structure’ was square-root transformed for the scale range models. We z-transformed all predictors to a mean of zero and a standard deviation of one to get comparable estimates and better interpretation of the model (Schielzeth 2010). For the single scale model, we visually examined correlations between predictors and calculated Spearman correlations. We checked model assumptions by running variance inflation factors, dfbetas and leverage (Quin and Keough 2002, Field 2005). All investigations of model assumptions did not reveal any problems (Appendix D – Page 99). For the scale range models, we presumed the model assumptions were still fulfilled as the environmental predictor values extracted at all discrete scales were highly correlated with those of the single scale model (Appendix D – Page 99). All analyses were conducted using R (R Development Core Team 2013) and the additional packages gtools (Warnes et al. 2013), car (Fox and Weisberg 2011), MASS (Venables and Ripley 2002).

IV.3.5 SINGLE SCALE MODEL

In order to compare results of the scale range models with those of a single scale model, we first ran the simplest version of a species distribution model, i.e. a single model with fixed predictor scales defined by expert opinion. This model was built by using all seven predictors. We extracted ‘patch structure’ for a circle area with a radius of 2.6 km around each transect segment, ‘preferred THV’ and ‘fleshy fruit availability’ for a strip with a width of 100m on each side of every transect segment. Values of the predictors were extracted as the arithmetic mean over the predefined buffer. In order to test the importance of the environmental predictors on bonobo density, we compared the fit of the full model to a null model that only comprised the three predictors of human pressure, the autocorrelation term and the offset term using a chi-square test (Forstmeier and Schielzeth 2011).

IV.3.6 SCALE RANGE MODELS

We applied scale search for three environmental predictors, ‘patch structure’, ‘fleshy fruit availability’ and ‘preferred THV’. For computational efficiency, we first defined few scales at coarse resolution to be included with an emphasis on large scale for ‘patch structure’ (buffer radiuses of 60, 210, 600, 1050, 1500, 1950, 2400 and 2700 m) and on small scale for ‘preferred THV’ and ‘fleshy fruit availability’ (60, 120, 210, 360, 600, 1500 and 2400 m). The threshold of 60 and 2700 m was based on the minimum resolution of data and bonobo home range size, respectively. We extracted predictor values for each scale using weighted means based on Gaussian weighting function as Aue et al. (2012) demonstrated this is the most realistic function to represent the decreasing influence of predictor values with increasing distance from points of observations. For computational efficiency, we fixed the standard deviation to a third of the buffer radius in order to account for 99.73% of the predictor values within the buffer of interest (Sokal and Rohlf 1996). For all other predictors, we used the same values like in the single scale model.

In order to assess the relative importance of each scale through the entire range and for each predictor, we calculated their cumulative Akaike weight by adding the Akaike weight of each model comprising the considered scale (Burnham and Anderson 2002). We defined a scale range of interest by accounting for the largest Akaike weights up to a total of 0.95. In order to define the scale range that should be investigated at finer resolution, we graphically represented the cumulative Akaike weight in function of the buffer sizes and selected the area of greatest changes, i.e. the decreasing curve (Figure 1-3 – Page 82). The upper plateau already indicated the influential scales and necessitated a less refined investigation.

We further implemented a new set of models at finest resolution based on the outcome on the first step. For ‘patch structure’, we improved resolution from 600 to 2700 m by adding buffers of 750, 900, 1200, 1800, 2100 m radiuses; for ‘fleshy fruit availability’, 30 to 600 m (additional buffers of 30, 300, 450 m radiuses); for ‘preferred THV’, 30 to 360 m (additional buffers of 30, 300 m radiuses). As previously, we calculated the cumulative Akaike weight of each scale and defined the final influential scale range of the predictors by accounting for scales with largest Akaike weights up to a total of 0.95. In order to get model inference, we selected the set of models comprising only the influential scale ranges of the three environmental predictors. We calculated the global mean estimates by weighting the parameter estimates of each model with its Akaike weight and calculated their respective weighted standard error. We visually investigated variation in predictor significance through the set of models.

For the purpose of comparison with findings of previous studies, we also implemented predictor scale search *(1)* for ‘non-distance weighted’ models where the three predictors were extracted based on the arithmetic mean and *(2)* for ‘mixed distance weighted’ models where only predictors acting at large scale were extracted with a weighted mean.

V RESULTS

V.1 Single scale model

The single scale full model containing all environmental predictors revealed overall significance (comparison between the full and the null model, χ^2= 53.05, df= 5, p<0.000). All three environmental predictors ‘patch structure’, ‘fleshy fruit availability’ and ‘preferred THV’ were significant, with the strongest effect by ‘patch structure’. None of the predictors controlling for human pressure did seem to influence bonobo density on the sampled transects (Table 1-2 – Page 81).

V.2 Scale range models

Overall, the effect of the predictor variables remained similar compared to the single scale model. ‘Patch structure’ was influencing bonobos above 750 m and with a plateau of largest influences between 1200 and 2700 m, while both predictors of food availability ‘fleshy fruit availability’ and ‘preferred THV’ were acting at smaller scales, from 30 to 600 m and from 30 to 360 m respectively (Figure 1-4 – Page 83). Human predictors remained non-significant. However, the strength of predictor influence changed slightly, showing a smaller effect of ‘patch structure’, ‘preferred THV’, the interaction between ‘fleshy fruit availability’ and ‘preferred THV’ and ‘nesting site fidelity’ in comparison with the single scale model (estimated β equals 0.97 vs. 1.07, 0.87 vs. 0.92, -0.88 vs. -0.91 and 0.51 vs. 0.57 respectively, Table 1-2 – Page 81). In contrast, the estimate of ‘fleshy fruit availability’ increased (β = 0.64 vs. 0.45). Interestingly, the effect of the autocorrelation term also increased (β = 0.49 vs. 0.27) and the variable became significant for almost all models.

Investigations in model inference revealed small variations of predictor effect through the influential scale ranges of the three environmental predictors (largest standard error of 0.005 for ‘patch structure’ and ‘fleshy fruit availability’, Table 1-2 – Page 81) and predictor significant remained stable with the exceptions of few models for which p-values of ‘patch structure’ and ‘fleshy fruit availability’ were between 0.05 and 0.11 (Figure 1-5 – Page 84).

The assessment of *(1)* non-distance weighted models *(2)* mixed distance weighted models revealed unrealistic spatial patterns (Figure 1-3 – Page 82) and showed that the variation of predictor influence was more widespread, with more changes in predictor significance (Table 1-2 – Page 81 and Appendix E – Page 102).

Table 1-2: Results of single scale model and scale range models

	Single scale model				***Scale range models*** All distance weighted	***Scale range models*** Non distance weighted	***Scale range models*** *Mixed distance weighted*
	Estimates	*Std. Error*	*z-value*	*p-value*	*Estimates*	*Estimates*	*Estimates*
Intercept	*-1.96*	*0.24*	*-8.09*	*0.000*	*-5.01 ± 0.002**	*-5.02 ± 0.004**	*-5.02 ± 0.002**
Patch structure	*1.07*	*0.29*	*3.71*	*0.000*	*0.97 ± 0.005***	*0.95 ± 0.008***	*0.97 ± 0.006***
Influential Scale range					*750 – 2700 m*	*360 – 2700 m*	*450 – 2700 m*
Fleshy fruit availability	*0.45*	*0.27*	*1.69*	*0.092*	*0.64 ± 0.005**	*0.66 ± 0.007**	*0.65 ± 0.006**
Influential Scale range					*30 – 600 m*	*30 – 450 m*	*30 – 450 m*
Preferred THV	*0.92*	*0.31*	*2.92*	*0.003*	*0.87 ± 0.003***	*0.89 ± 0.004***	*0.89 ± 0.003***
Influential Scale range					*30 – 300 m*	*30 – 210 m*	*30 – 210 m*
Interaction Fruit and THV	*-0.91*	*0.26*	*-3.47*	*0.001*	*-0.88 ± 0.003***	*-0.89 ± 0.005***	*-0.90 ± 0.004***
Hunting signs	*0.04*	*0.18*	*0.21*	*0.838*	*-0.01 ± 0.002*	*-0.01 ± 0.003*	*-0.01 ± 0.002*
Hunting pressure	*0.03*	*0.19*	*0.16*	*0.871*	*0.03 ± 0.003*	*0.06 ± 0.003*	*0.03 ± 0.004*
Village influence	*0.31*	*0.25*	*1.24*	*0.213*	*0.37 ± 0.001*	*0.39 ± 0.002*	*0.38 ± 0.002*
Nesting site fidelity	*0.57*	*0.17*	*3.27*	*0.001*	*0.51 ± 0.001**	*0.51 ± 0.003**	*0.51 ± 0.001**
Autocorrelation term	*0.27*	*0.20*	*1.38*	*0.166*	*0.50 ± 0.002**	*0.48 ± 0.008**	*0.50 ± 0.002**
Nb of parameters	***10***				***13***	***10***	***11***
AIC	***562.57***				***566 - 575.1***	***558.5 - 571.7***	***561.4 – 573.4***
Ln likelihood	***-271.29***				***-270 - -274.6***	***-269.3 - -275.8***	***-269.7 - -275.2***

Parameter estimates for scale range models are Akaike weighted estimates of all single models in the 95% confidence set; * indicate if the predictor was significant through all scale range models (** highlights predictors which were only significant upon within their influential scale ranges).

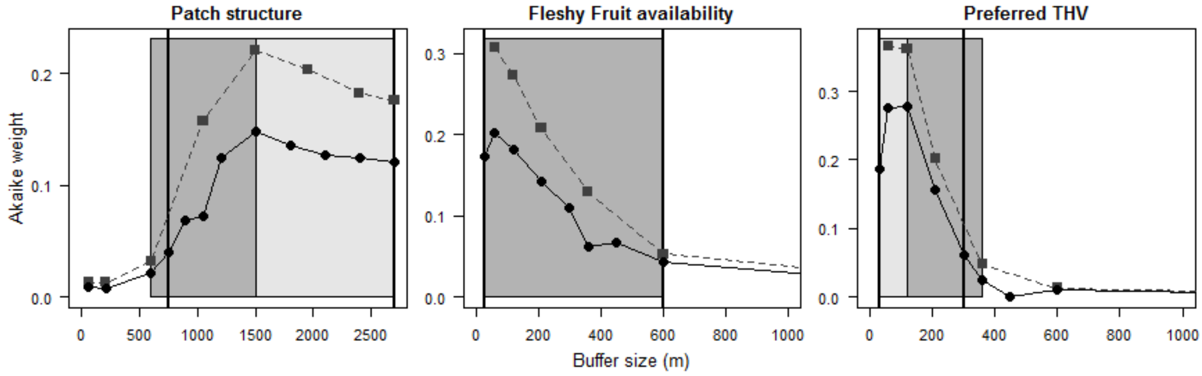


Figure 1-3: Stepwise procedure to assess influential scale ranges

Grey squares depict the Akaike weights of each discrete scale tested within the set of models at coarse resolution. Rectangles in light grey indicate the upper plateau of the curve, representing the discrete scales being part of the influential scale range, while rectangles in dark grey highlight the scale range of greatest changes needing to be more investigated in the subsequent step. The refined scale search is indicated by the black points connected by black solid lines and the final influential scale range is highlighted by the vertical black lines. The graphs of ‘Fleshy fruit availability’ and ‘preferred THV’ have been truncated at 1000 m to improve figure readability.

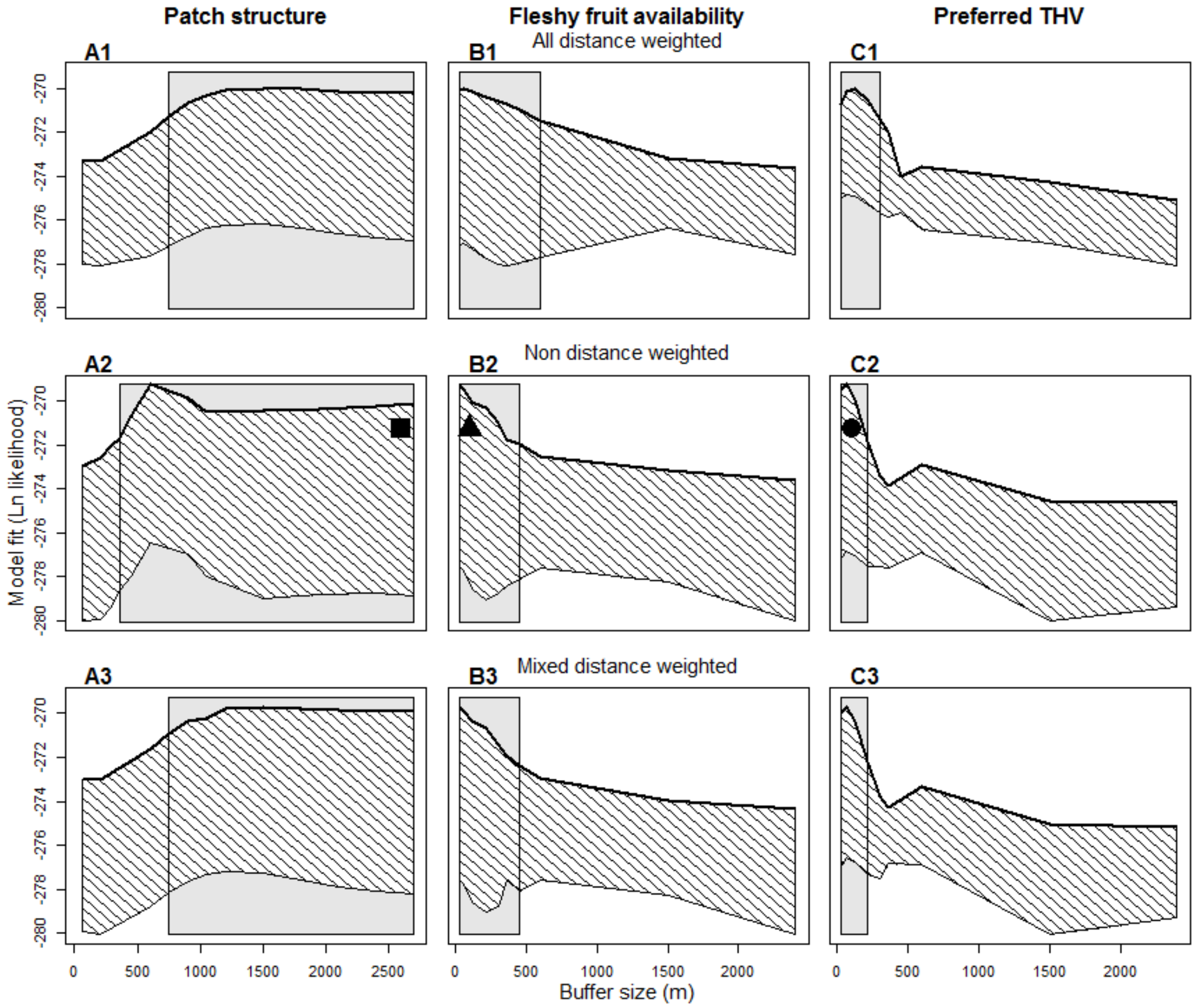


Figure 1-4: Spatial scale patterns for environmental predictors

The maximized model likelihood for scale ranges of the three predictor is represented by the solid curve for (1) distance weighted mean predictors, (2) arithmetic mean of predictors and (3) mixtures distance weighted and arithmetic mean predictors. The grey area shows the model likelihoods of all models evaluated. The large variation in model fit is due to the inclusion of less influential spatial scales. The three points (circle, square, triangle) indicate the model likelihoods of the ‘single scale models’ at the scale we predefined for each predictor.

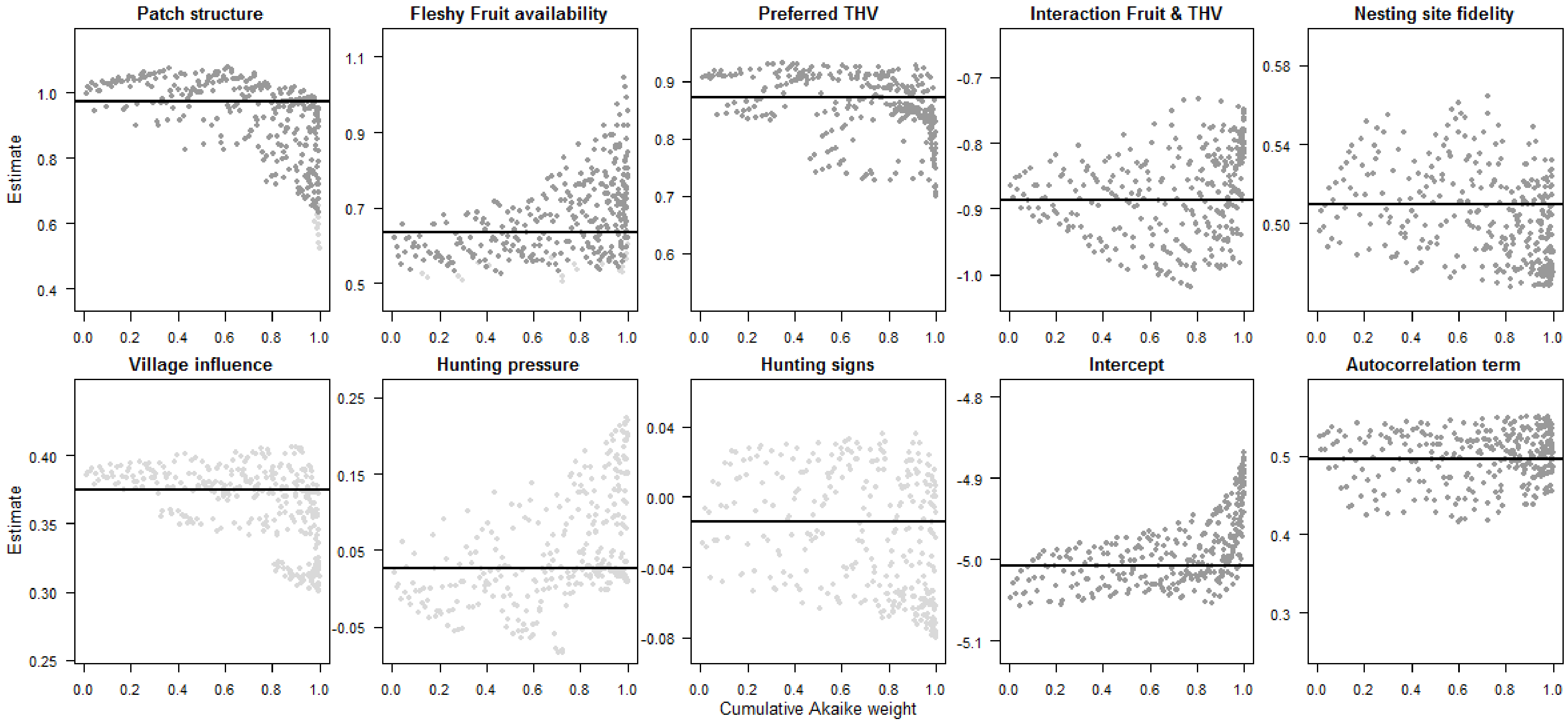


Figure 1-5: Variation in parameter influence

Parameter estimates are presented according to the cumulative Akaike weight of the models (X-axis) within the influential scale ranges of the three environmental predictors. The colour of the points indicates the significance of the parameters (dark grey points are significant parameters, p-value < 0.05; light grey points are non-significant ones). The horizontal lines indicate the global mean estimates of the parameters. Predictor significance remained stable through the entire scale ranges with the exceptions of few models where ‘patch structure’ and ‘fleshy fruit availability’ showed p-values between 0.05 and 0.11.

VI DISCUSSION

The simultaneous evaluation of multiple predictors and their influential scales, autocorrelation and spatial decay effects in species distribution models requires both computationally efficient approaches and suitable concepts for result interpretation. In this study we applied a resource efficient two-step procedure to evaluate most influential predictor scale ranges on bonobo density. Additionally, we applied multi-scale, multi-model inference to account for sigmoid predictor scale - response curves with a large number of equally well fitting models within suitable predictor scale ranges.

In the specific case of our bonobo study population this approach revealed forest structure (represented by the predictor ‘patch structure’) as most influential above 750 m, with largest influences between 1200 and 2700 m, whereas we observed reverse scale effects for the two food availability predictors, ‘fruit tree availability’ and ‘preferred THV’ being important below 600 and 300 m respectively. The identified scale ranges correspond well to scales of bonobo ranging, feeding and nesting behaviour.

VI.1 Interpreting scale information

As demonstrated by Aue et al. (2012), the use of distance weighting functions with sigmoid correlation curve between predictor scales and response facilitates more realistic representations of species-environment relationships across scales (Figure 1-3 – Page 82). For our predictor ‘patch structure’ that acted on the larger scale, found results underline that standard non-distance weighted predictor value extraction leads to a large error in influential scale range specification (‘patch structure’: correlation peak at 600 m for standard extraction *vs.* influential plateau between 1200 to 2700 m for weighted extraction, Figure 1-3 – Page 82).

However, in contrast to Aue et al. 2012, we also used small scale predictors with inverse environmental scale-response relationships. The shape of the correlation curve changed slightly when comparing distance and non-distance weighted predictor scales. A peak emerged at a small scale for ‘preferred THV’ and showed an immediate decrease in the correlation strength for ‘fleshy fruit availability’. In such cases, the accuracy of the observed spatial pattern will depend on the resolution of the data. In our study, we probably worked with a resolution too coarse for the small scale predictors (25x25m pixels). This has weakened our efforts to capture precisely the decreasing influence of the food availability predictors with increasing distance and it likely also explains why we did not improve model likelihood when using distance weighted function. Nevertheless, the use of weighting functions decreases variation and smoothes environment-response relationships and thus reduces the risk of over-interpreting effects of small peaks present in the curves (Figure 1-3 – Page 82; Appendix E – Page 102).

When interpreting results on scales in species distribution models, the concept of selecting one ‘best model’ or ‘single scale model’ is often not appropriate. A large number of models built for scales located in the asymptotic parts of sigmoid predictor scale-response relationships fit data equally well. This is because there are minimum or maximum requirements for certain ecological or environmental conditions, such as habitat area, size of feeding and roosting spots, amount of food resources. In our study for instance, bonobos require a minimum home range area covered by forest. On the other hand the density of herbaceous vegetation seems to be relevant for bonobo nesting behaviour only on the smaller scale.

We dealt with this model uncertainty by making inference on a set of models and not a single scale model alone. Such set of models is very useful in analysing consistency in model results. In our study, models including the influential scale ranges of the three environmental predictors showed only little variation in predictor influence (Figure 1-4 – Page 83). Outside those influential ranges, variation in predictor estimates was much larger (Appendix F – Page 105). In the case of ‘patch structure’ and ‘preferred THV’, predictors were not significant anymore. In contrast, ‘fleshy fruit availability’ remained significant independent of scale. This possibly suggests that this particular predictor represents alternative ecological conditions, with fruit availability being important on the small scale, but forest characteristics such as forest structure on the larger scale.

VI.2 **Coarse vs continuous scale model fitting**

In order to maximize computational efficiency we used a two-step approach starting with a coarse scale search that can be performed quickly and then refined it on a more continuous scale for selected ranges. The advantage of this approach is to rapidly establish the approximate shape of the predictor scale – response curve. This helps to decide for which range to refine the scale search, e.g. ranges of greatest change, minimum or maximum predictor influence.

Current methods in species distribution modelling either use predefined single scales to be evaluated (Anderson et al. 2005, Fortin et al. 2005, Sawyer and Brashares 2013), leading to the risk of not capturing scale effects if expert opinion was not accurate. Or a scale continuum (Johnson et al. 2004b, Nams et al. 2006, Mayor et al. 2009, Wheatley 2010) is evaluated, often at the risk of Type I error rate inflation, if ‘best model’ selection is performed. For instance in our study the different human impact predictors became occasionally significant, when particular environmental predictor scales were incorporated (Appendix F). It is unlikely that this was a true effect, as human impact predictors overall did not play a role in explaining bonobo density distribution. These issues can only be prevented by a systematic assessment and causal understanding of predictor scale influence.

VI.3 **Fields of applications**

The suggested approach may be very promising for fitting even very complex species distribution models and there is a wide range of potential applications, like in conservation or landscape management. However, the implementation of these models requires a certain level of technical and quantitative expertise which may limit accessibility and applicability by practitioners in these fields.

Nevertheless, predictor scale search is an essential tool in many fields of applications. It is needed in the context of global landscape modification to understand the impact of fragmentation on animal persistence (Santos-Filho et al. 2012), within-patch (Thornton et al. 2010) and landscape matrix quality (Watling et al. 2011), or the effect of patch sizes and isolation (Prugh et al. 2008). For example, the spatial pattern of patch structure in our study revealed that bonobos living in forest-savannah mosaics tends to discriminate forest patches below 4.5 km² (circular area of about 1.2 km). This value could be further investigated by accounting separately for forest patch shape and size or possible negative edge effects (Arroyo-Rodríguez and Dias 2010, Nams 2012, Hickey et al. 2013). Such type of information could further be very useful in landscape management for conservation purpose (Nams et al. 2006) or to assess the impact of logging on faunal biodiversity (e.g. the effect of road opening) (Laurance et al. 2008, 2009, Clark et al. 2009, Nasi et al. 2012).

The proposed approach is not limited to spatial scale, but can also be applied in the temporal domain. The use of weighting function is particularly interesting to study animal relationships over extensive periods, e.g. to better understand behaviours favouring individual affiliations such as grooming reciprocity in primates (Gomes and Boesch 2011, Adiseshan et al. 2011, Majolo et al. 2012). Similarly, scale search techniques can simultaneously be incorporated for space and time, such as in models on long-term spatial memory and foraging behaviour in primates (Janmaat et al. 2013b).

VI.4 **Conclusions**

Modellers of species distribution increasingly incorporate techniques to optimize predictor scale-response relationships. In particular if done for multiple predictors and their influential scales, this makes model fitting quickly very complex and results are difficult to interpret. Combining an initial coarse scale search with a more continuous one which is restricted to locations of greatest interest helps to understand spatial scale patterns and to estimate model parameters in a reasonable amount of time. Inferences based on single models and scales are often not appropriate and multi-scale, multi-model inference will provide more robust parameter estimates. Incorporating predictor scales into species distribution models is an open field for both research and application and will provide novel tools for gaining interesting insights into species-environment relationships.

VII ACKNOWLEDGMENTS

This project was funded by the National Fund for Scientific Research (FNRS, Belgium), the Fonds Leopold III from the Royal Belgian Institute of Natural Sciences (Belgium) and the Ecole Régionale post-universitaire d'Aménagement et de gestion Intégrés des Forêts et Territoires tropicaux (ERAIFT, Democratic Republic of Congo). We would like to thank WWF-DRC, and especially Petra Lahann, for their support in the field, as well as the Minister of Foreign Affairs and International Cooperation of The Democratic Republic of The Congo who permitted us to conduct our research. We are also grateful to Fiona Maisels and Celine Devos for their invaluable helps in the design of our study. This research would not have been possible without the help of our local field guides. Ciceron Mbuoli Mbenkira deserves a special thank you for his incredible work during the entire period of data collection. We also thank the Robert Bosch Foundation, the Max Planck Society, Barbara Fruth and Gottfried Hohmann from the Lui Kotal Project for data sharing and Cleve Hicks for their suggestions during the preparation of this paper. Finally, we thank our anonymous reviewers for their helpful comments.

VIII REFERENCES

Adiseshan, A., T. Adiseshan, and L. A. Isbell. 2011. Affiliative relationships and reciprocity among adult male bonnet macaques (*Macaca radiata*) at Arunachala Hill, India. American journal of primatology 73:1107–1113.

Anderson, P., M. G. Turner, J. D. Forester, J. Zhu, M. S. Boyce, H. Beyer, and L. Sotwell. 2005. Scale-dependent summer resource selection bu reintroduced elk in Wisconsin, USA. The journal of wildlife management 69:298–310.

Araújo, M. B., and A. Guisan. 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography 33:1677–1688.

Arroyo-Rodríguez, V., and P. A. D. Dias. 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. American journal of primatology 72:1–16.

Aue, B., K. Ekschmitt, S. Hotes, and V. Wolters. 2012. Distance weighting avoids erroneous scale effects in species-habitat models. Methods in Ecology and Evolution 3:102–111.

Basabose, A. K. 2002. Diet composition of Chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. American Journal of Primatology 58:1–21.

Beaune, D., F. Bretagnolle, L. Bollache, C. Bourson, G. Hohmann, and B. Fruth. 2013. Ecological services performed by the bonobo (*Pan paniscus*): seed dispersal effectiveness in tropical forest. Journal of Tropical Ecology 29:367–380.

Van Beest, F. M., I. M. Rivrud, L. E. Loe, J. M. Milner, and A. Mysterud. 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? The Journal of animal ecology 80:771–785.

Bourland, N., L. Koudia Yao, P. Lejeune, B. Sonké, J. Philippart, K. Daïnou, F. Fétéké, and J.-L. Doucet. 2012. Ecology of *Pericopsis elata* (Fabaceae), an endangered timber species in southeastern Cameroon. Biotropica 44:840–847.

Bowyer, R. T., and J. G. Kie. 2006. Effects of scale on interpreting life-history characteristics of ungulates and carnivores. Diversity and Distributions 12:244–257.

Boyce, M. S. 2006. Scale for resource selection functions. Diversity and Distributions 12:269–276.

Boyer, D., G. Ramos-Fernández, O. Miramontes, J. L. Mateos, G. Cocho, H. Larralde, H. Ramos, and F. Rojas. 2006. Scale-free foraging by primates emerges from their interaction with a complex environment. Proceedings of the Royal Society of Biological sciences 273:1743–1750.

Buckland, S. T. ., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Page 432. Oxford University Press, Oxford.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference a practical information-theoretic approach. Second edition. Page 488. Springer, New York.

Clark, C. J., J. R. Poulsen, R. Malonga, and P. W. Elkan. 2009. Logging concessions can extend the conservation estate for Central African tropical forests. Conservation biology : the journal of the Society for Conservation Biology 23:1281–93.

Djoufack, S. D., B. A. Nkongmeneck, J. Dupain, S. Bekah, K. K. Bombome, M. A. Epanda, L. Van Elsacker, and Editeurs. 2007. Manuel d'identification des fruits consommés par les gorilles et les Chimpanzés des basses terres de l'Ouest; Espèces de l'écosystème du Dja (Cameroun). Page 107 (M. A. Epanda and L. Van Elsacker, Eds.).

Doucet, J.-L. 2003. PhD Thesis. L'alliance délicate de la gestion forestière et de la biodiversité dans les forêts du centre du Gabon. University of Liege.

Field, A. 2005. Discovering Statistics using SPSS. Sage Publications, London.

Fischer, J., and D. B. Lindenmayer. 2006. Beyond fragmentation : the continuum model for fauna research and conservation in human-modified landscapes. Oikos 2:473–480.

Fischer, J., and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation : a synthesis. Global Ecology and Biogeography 16:265–280.

Forester, J. D., H. Kyung Im, and P. J. Rathouz. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology 90:3554–3565.

Forstmeier, W., and H. Schielzeth. 2011. Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. Behavioral ecology and sociobiology 65:47–55.

Fortin, D., H. Beyer, M. Boyce, and D. Smith. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Fox, J., and S. Weisberg. 2011. An R companion to applied regression. Page 472. Sage, Thousant Oaks CA.

Fruth, B. 1995. Nests and nest groups in wild bonobos: ecological and behavioural correlates. PhD Thesis. Ludwig-Maximilian University.

Fürtbauer, I., R. Mundry, M. Heistermann, O. Schülke, and J. Ostner. 2011. You mate, I mate: macaque females synchronize sex not cycles. PloS ONE 6:e26144.

Furuichi, T., M. Mulavwa, K. Yangozene, B. Motema-salo, G. Idani, and H. Ihobe. 2008. Relationships among fruit abundance, ranging rate, and party size and composition of Bonobos at Wamba. Pages 135–149 *in* T. Furuichi and J. Thompson, editors. The bonobos: Behavior, Ecology, and Conservation. Springer, New York.

Gomes, C. M., and C. Boesch. 2011. Reciprocity and trades in wild West African chimpanzees. Behavioral Ecology and Sociobiology 65:2183–2196.

Guisan, A., and T. C. Edwards. 2002. Generalized linear and generalized additive models in studies of species distributions : setting the scene. Ecological Modelling 157:89–100.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147–186.

Hedley, S. L., and S. T. Buckland. 2004. Spatial models for line transect sampling. Journal of Agricultural, Biological, and Environmental Statistics 9:181–199.

Henry, M., M. Fröchen, J. Maillet-Mezeray, E. Breyne, F. Allier, J.-F. Odoux, and A. Decourtye. 2012. Spatial autocorrelation in honeybee foraging activity reveals optimal focus scale for predicting agro-environmental scheme efficiency. Ecological Modelling 225:103–114.

Hickey, J. R., J. Nackoney, N. P. Nibbelink, S. Blake, A. Bonyenge, S. Coxe, J. Dupain, M. Emetshu, T. Furuichi, F. Grossmann, P. Guislain, J. Hart, C. Hashimoto, B. Ikembelo, O. Ilambu, B.-I. Inogwabini, I. Liengola, A. L. Lokasola, A. Lushimba, F. Maisels, J. Masselink, V. Mbenzo, N. M. Mulavwa, P. Naky, N. M. Ndunda, P. Nkumu, V. Omasombo, G. E. Reinartz, R. Rose, T. Sakamaki, S. Strindberg, H. Takemoto, A. Vosper, and H. S. Kühl. 2013. Human proximity and habitat fragmentation are key drivers of the rangewide bonobo distribution. Biodiversity and Conservation 22:3085–3104.

Imong, I., M. M. Robbins, R. Mundry, R. Bergl, and H. S. Kühl. (in review). Informing conservation management about structural vs. functional connectivity: a case study of Cross River gorillas.

Imong, I., M. M. Robbins, R. Mundry, R. Bergl, and H. S. Kühl. 2014. Distinguishing ecological constraints from human activity in species range fragmentation: the case of Cross River gorillas. Animal Conservation:1–9.

Inogwabini, B., M. Bewa, M. Longwango, M. Abokome, and M. Vuvu. 2008. The Bonobos of the Lake Tumba – Lake Maindombe Hinterland: threats and opportunities for population conservation. Pages 273–290 *in* T. Furuichi and J. Thompson, editors. The bonobos: Behavior, Ecology, and Conservation. Springer, New York.

Janmaat, K. R. L., S. D. Ban, and C. Boesch. 2013. Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons. Animal Behaviour 86:1183–1205.

Janmaat, K. R. L., W. Olupot, R. L. Chancellor, M. E. Arlet, and P. M. Waser. 2009. Long-term site fidelity and individual home range shifts in *Lophocebus albigena*. International Journal of Primatology 30:443–466.

Johnson, C., M. Boyce, R. Mulders, and A. Gunn. 2004a. Quantifying patch distribution at multiple spatial scales: applications to wildlife-habitat models. Landscape Ecology 29:869–882.

Johnson, C. J., K. L. Parker, D. C. Heard, M. P. Gillingham, S. E. Applications, and N. Dec. 2004b. A multiscale behavioral approach to understanding the movements of woodland Caribou. Ecological applications 12:1840–1860.

Johnson, C. J., D. R. Seip, and M. S. Boyce. 2004c. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. Journal of Applied Ecology 41:238–251.

Junker, J., S. Blake, C. Boesch, G. Campbell, L. Du Toit, C. Duvall, A. Ekobo, G. Etoga, A. Galat-Luong, J. Gamys, J. Ganas-Swaray, S. Gatti, A. Ghiurghi, N. Granier, J. Hart, J. Head, I. Herbinger, T. C. Hicks, B. Huijbregts, I. S. Imong, N. Kuempel, S. Lahm, J. Lindsell, F. Maisels, M. McLennan, L. Martinez, B. Morgan, D. Morgan, F. Mulindahabi, R. Mundry, K. P. N'Goran, E. Normand, A. Ntongho, D. T. Okon, C.-A. Petre, A. Plumptre, H. Rainey, S. Regnaut, C. Sanz, E. Stokes, A. Tondossama, S. Tranquilli, J. Sunderland-Groves, P. Walsh, Y. Warren, E. A. Williamson, and H. S. Kuehl. 2012. Recent decline in suitable environmental conditions for African great apes. Diversity and Distributions 18:1077–1091.

Kano, T., and M. Mulavwa. 1992. Appendix. Pages 225–232 *in* T. Kano, editor. The Last Ape: Pygmy Chimpanzee behavior and ecology. Stanford University Press, Stanford.

Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales : effects on spatial distribution of Mule Deer. Ecology 83:530–544.

Kuehl, H., F. Maisels, M. Ancrenaz, and E. . Williamson. 2008. Best Practice Guidelines for Surveys and Monitoring of Great Ape Populations. Page 32. Gland, Switserland.

Kuehl, H. S., C. Nzeingui, S. L. D. Yeno, B. Huijbregts, C. Boesch, and P. D. Walsh. 2009. Discriminating between village and commercial hunting of apes. Biological Conservation 142:1500–1506.

Laurance, W. F., B. M. Croes, N. Guissouegou, R. Buij, M. Dethier, and A. Alonso. 2008. Impacts of roads, hunting, and habitat alteration on nocturnal mammals in African rainforests. Conservation biology : the journal of the Society for Conservation Biology 22:721–732.

Laurance, W. F., M. Goosem, and S. G. W. Laurance. 2009. Impacts of roads and linear clearings on tropical forests. Trends in ecology & evolution 24:659–669.

Lehmann, J., and C. Boesch. 2003. Social influences on ranging patterns among chimpanzees (*Pan troglodytes verus*) in the Tai National Park, Cote d'Ivoire. Behavioral Ecology 14:642–649.

Levin, S. A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. Ecology 73:1943–1967.

Madron, L. D. De, and A. Daumerie. 2004. Diamètre de fructification de quelques essences en forêt naturelle centrafricaine. Bois et Forêts des Tropiques 281:87–95.

Majolo, B., G. Schino, and F. Aureli. 2012. The relative prevalence of direct, indirect and generalized reciprocity in macaque grooming exchanges. Animal Behaviour 83:763–771.

Malenky, R. K., and E. W. Stiles. 1991. Distribution of terrestrial herbaceous vegetation and its consumption by *Pan paniscus* in the Lomako Forest, Zaire. American journal of primatology 169:153–169.

Marceau, D. J. 1999. The scale issue in social and natural sciences. Canadian Journal of Remote Sensing 25:347–356.

Marceau, D. J., and G. J. Hay. 1999. Scaling and modelling in forestry: applications in remote sensing and GIS. Canadian Journal of Remote Sensing 25:342–346.

Mayor, A. S. J., J. A. Schaefer, D. C. Schneider, S. P. Mahoney, and S. J. Mayor. 2007. Spectrum of selection: new approaches to detecting the scale-dependent response to habitat. Ecology 88:1634–1640.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Ecoscience 16:238–247.

Menga, P., N. Bayol, R. Nasi, and A. Fayolle. 2012. Phenology and fructification diameter in wenge, *Millettia laurentii* de wild.: management implications. Bois et Forêts des Tropiques 66:31–42.

Meyer, C. B., and W. Thuiller. 2006. Accuracy of resource selection functions across spatial scales. Diversity and Distributions Distributions 12:288–297.

Mohneke, M., and B. Fruth. 2008. Bonobo (*Pan paniscus*) density estimation in the SW-Salonga National Park, Democratic Republic of Congo: common methodology revisited. Pages 151–166 *in* T. Furuichi and J. Thompson, editors. The bonobos: Behavior, Ecology, and Conservation. Springer, New York.

Mundry, R., and C. L. Nunn. 2009. Stepwise model fitting and statistical inference: turning noise into signal pollution. The American naturalist 173:119–123.

Murai, M., H. Ruffler, A. Berlemont, G. Campbell, F. Esono, A. Agbor, D. Mbomio, A. Ebana, A. Nze, and H. S. Kühl. 2013. Priority areas for large mammal conservation in Equatorial Guinea. PloS ONE 8:e75024.

Murray, C. M., I. C. Gilby, S. V Mane, and A. E. Pusey. 2008. Adult male chimpanzees inherit maternal ranging patterns. Current biology 18:20–24.

Nams, V. O. 2012. Shape of patch edges affects edge permeability for meadow voles. Ecological applications 22:1827–1837.

Nams, V. O., G. Mowat, and M. A. Panian. 2006. Determining the spatial scale for conservation purposes – an example with grizzly bears. Biological Conservation 128:109–119.

Nasi, R., A. Billand, and N. van Vliet. 2012. Managing for timber and biodiversity in the Congo Basin. Forest Ecology and Management 268:103–111.

Nicholson, M. C., R. T. Bowyer, J. G. Kie, S. Journal, and N. May. 1997. Habitat selection and survival of Mule Deer: tradeoffs associated with migration. Journal of Mammalogy 78:483–504.

Pita, R., A. Mira, and P. Beja. 2011. Assessing habitat differentiation between coexisting species: The role of spatial scale. Acta Oecologica 37:124–132.

Plumptre, A. J. 2000. Monitoring mammal populations with line transect techniques in African Forests. Journal of Applied Ecology 37:356–368.

Prugh, L. R., K. E. Hodges, A. R. E. Sinclair, and J. S. Brashares. 2008. Effect of habitat area and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences of the United States of America 105:20770–20775.

Quin, G. P., and M. J. Keough. 2002. Experimental designs and data analysis for biologists. Cambrige University Press, Cambrigde.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Reinartz, G. E., B. I. Inogwabini, M. Ngamankosi, and L. W. Wema. 2006. Effects of forest type and human presence on Bonobo (*Pan paniscus*) density in the Salonga National Park. International Journal of Primatology 27:1229–1231.

Rhodes, J., C. McAlpine, D. Lunney, and H. Possingham. 2005. A spatially explicit habitat selection model incorporating home range behavior. Ecology 86:1199–1205.

Rhodes, J. R., C. A. Mcalpine, A. F. Zuur, G. M. Smith, and E. N. Ieno. 2009. GLMM applied on the spatial distribution of Koalas in a fragmented landscape. Pages 469–492 *in* A. F. Zuur, E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith, editors. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.

Riitters, K., J. Wickham, R. O. Neill, B. Jones, and E. Smith. 2000. Global-scale patterns of forest fragmentation. Conservation Ecology 4:1–18.

Santos-Filho, M., C. A. Peres, D. J. Silva, and T. M. Sanaiotti. 2012. Habitat patch and matrix effects on small-mammal persistence in Amazonian forest fragments. Biodiversity and Conservation 21:1127–1147.

Sawyer, S. C., and J. S. Brashares. 2013. Applying resource selection functions at multiple scales to prioritize habitat use by the endangered Cross River gorilla. Diversity and Distributions 19:943–954.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103–113.

Searle, K. R., C. J. Stokes, and I. J. Gordon. 2008. When foraging and fear meet: using foraging hierarchies to inform assessments of landscapes of fear. Behavioral Ecology 19:475–482.

Seo, C., J. H. Thorne, L. Hannah, and W. Thuiller. 2009. Scale effects in species distribution models: implications for conservation planning under climate change. Biology letters 5:39–43.

Serckx, A., M.-C. Huynen, J.-F. Bastin, R. C. Beudels-Jamar, A. Hambuckers, M. Vimond, E. Raynaud, and H. Kühl. 2014. Nesting patterns of bonobos (*Pan paniscus*) in relation to fruit availability in a forest-savannah mosaic. PloS ONE:in press.

Sokal, R. S., and F. J. Rohlf. 1996. Introduction to Biostatistics. Page 363. W.H. Freeman and Company, New York.

Stewart, F. A., A. K. Piel, and W. C. McGrew. 2011. Living archaeology: artefacts of specific nest site fidelity in wild chimpanzees. Journal of human evolution 61:388–395.

Strier, K. 1989. Effets of patch size on feeding associations in muriquies (*Brachyteles brachnoides*). Folia primatologica 52:70–77.

Tailfer, Y. 1989. La foret dense d'Afrique centrale. Identification pratique des principaux arbres, Tome 1 et 2. C.T.A., Wageningen, Pays-Bas.

Thornton, D. H., L. C. Branch, and M. E. Sunquist. 2010. The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies. Landscape Ecology 26:7–18.

Urban, D. L. 2004. Modeling ecological processes across scales. Ecology 86:1996–2006.

Vancutsem, C., J. Pekel, J.-P. Kibamba, X. Blaes, C. de Wasseige, and P. Defourny. 2006. Carte de l'occupation du sol de la République Démocratique du Congo. (P. U. de Louvain, Ed.). Bruxelles.

Vaughan, I. P., and S. J. Ormerod. 2003. Improving the quality of distribution models for conservation by addressing shortcomings in the field collection of training data. Conservation Biology 17:1601–1611.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Page 495. Springer, New York.

Warnes, G. R., B. Bolker, and T. Lumley. 2013. gtools: Various R programming tools.

Watling, J. I., A. J. Nowakowski, M. a. Donnelly, and J. L. Orrock. 2011. Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. Global Ecology and Biogeography 20:209–217.

Wheatley, M. 2010. Domains of scale in forest-landscape metrics: implications for species-habitat modeling. Acta Oecologica 36:259–267.

Wheatley, M., and C. Johnson. 2009. Factors limiting our understanding of ecological scale. Ecological Complexity 6:150–159.

Whittingham, M. J., P. A Stephens, R. B. Bradbury, and R. P. Freckleton. 2006. Why do we still use stepwise modelling in ecology and behaviour? The Journal of animal ecology 75:1182–1189.

Wich, S. A., G. M. Fredriksson, G. Usher, H. H. Peters, D. Priatna, F. Basalamah, W. Susanto, and H. Kühl. 2012. Hunting of Sumatran orang-utans and its importance in determining distribution and density. Biological Conservation 146:163–169.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Wilks, C. M., and Y. A. Issembe. 2000. Les arbres de la Guinée Equatoriale: Guide pratique d'identification: région continentale. Projet CUREF, Bata, Guinée Equatoriale. Page 546. Prépresse Communications, France.

Woodcock, C. E., and A. H. Strahler. 1987. The Factor of scale in remote sensing. Remote Sensing of Environment 21:311–332.

IX APPENDIX A

Detailed description of tree species measures during field data collection

In order to identify tree species dominance in the canopy, we measured all trees with a DBH larger than 50 cm within a 10 m strip on both sides of the transects. For trees covered by lianas, we were not able to measure their DBH and we later assigned to them the median DBH value of the survey (67 cm). For trees with several stems at 130 cm, we summed their stem DBH measures. Finally we decided to also include in the analysis the trees with a DBH between 45 and 50 cm. Those trees were all noted during the survey but not measured and we assigned to them a DBH of 47.5 cm, as it only involved a maximum error of 0.0002 m^2/ha in the basal area calculation.

X APPENDIX B

Population census in villages surrounding the study sites in 2012 and sampling effort for the socio-economic data collection

We developed a questionnaire based on the "Poverty and Environment Network (PEN) prototype questionnaire" ("PEN Prototype Questionnaire" 2008). We randomly chose a minimum of 30% of adults in all local villages and farms (Shibia 2000, Kideghesho et al. 2006, Nyariki 2009) leading to a total of 119 men and 82 women interviewed.

References

Kideghesho, J. R., E. Røskaft, and B. P. Kaltenborn. 2006. Factors influencing conservation attitudes of local people in Western Serengeti, Tanzania. Biodiversity and Conservation 16:2213–2230.

Nyariki, D. M. 2009. Household Data Collection for Socio-Economic Research in Agriculture : Approaches and Challenges in Developing Countries. Journal of Social Sciences 19:91–99.

PEN Prototype Questionnaire. 2008. . http://www.cifor.org/fileadmin/fileupload/PEN/pubs/pdf_files/PEN_Prototype_Questionnaire_-_version_4-4_-_September_2008.pdf. Accessed 10 April 2013

Shibia, M. G. 2000. Determinants of Attitudes and Perceptions on Resource Use and Management of Marsabit National Reserve, Kenya. Journal of Human Ecology 30:55–62.

Table B1: Socio-economic data

		Population census					Interviewees			
		Nb	Nb men	Nb women	Nb children	Total	Total	Men	Women	Hunters (M)
1	Nkoo	168	169	202	540	911	50	35	15	16
2	Mpelu	43	50	58	153	261	50	30	20	19
3	Lebomo	37	37	34	141	212	26	14	12	7
4	Nkala	34	36	49	110	195	39	21	18	7
5	Malebo	10	9	11	38	58	6	3	3	1
6	Mavula	10	10	12	25	47	6	3	3	3
7	Bosatore	7	5	7	22	34	2	1	1	1
8	Mokoabuo	6	5	8	17	30	4	2	2	1
9	Clinic of Nkoo	4	4	4	19	27	2	1	1	0
10	Lensiana	4	4	3	18	25	0	0	0	0
11	Biomengele	3	3	3	13	19	3	2	1	2
12	Ngandjele	3	3	6	7	16	2	1	1	0
13	Motsuemontore	2	2	4	9	15	2	1	1	1
14	Ezano	3	2	2	8	12	1	1	0	1
15	Mayi Monene	2	2	3	5	10	2	1	1	0
16	MMT	4	4	4	2	10	2	1	1	0
17	Moza	1	1	1	6	8	2	1	1	0
18	Bosieli	1	1	1	5	7	2	1	1	1
	TOTAL	**342**	**347**	**412**	**1138**	**1897**	**201**	**119**	**82**	**60**

In the ‘Population census’ part of the table, we present results of the village population census realized in 2012. The ‘Interviewees’ part of the table indicates first the sampling effort for the socio-economic data collection (total per village and per gender) and the number of men who answered they regularly enter in the forests for hunting. The numbers in the first column indicate villages location in the map of the study site (Figure 1-2 in the paper – Page 72).

XI APPENDIX C

Complementary descriptions of predictor variables’ preparation

Forest-savannah classification map

We realized a non-supervised classification (Red and IR) on a subset of the Landsat7 (2007) satellite imagery (Landsat ID: L71181062_06220070102; used clip: 16.38-16.62°E, 2.42-2.67°S) with the software ENVI 5.0.2. We defined pixel resolution of 50 m and used a k-means algorithm with 15 classes and 30 iterations. We then aggregated classes as forest vs. savannah according to our transects knowledge and finally smoothed the results by the smoothed sieve (2-8 neighbours) and clump (3x3pixels) methods.

‘Human pressure’ index calculation

We derived ‘human pressure’ from our questionnaire data by calculating the daily number of adults who could potentially enter the region of the forest where the 25m-segment was located. For each village, we calculated the proportion of interviewed men going in a forest region (‘prop_quest_hunters’ in the formula). In order to obtain this index, we first estimated the probability of a man entering a particular forest region (i.e., the daily frequency of the hunting divided by the number of forest regions each person enters to engage in the activity) and then divided it by the number of interviewed men performing the activity. We estimated the proportion of men going to a forest region for each village and finally derived the overall index of human pressure for all villages:

$$Human\_pressure = \frac{\sum_{village}(prop\_quest\_hunters * nb\_men\_village)}{forest\_region\_area}$$

where nb_men_village is the number of men in a village and forest_region_area was the area of the forest region in square kilometers (used to account for differences in the sizes of the forest regions and to obtain values comparable between forest regions).

We finally calculated the mean value of the ‘hunting pressure’ for the transect segment.

'Village influence' calculation

In order to estimate the 'village influence', we first realized two maps in which each pixel (25m of resolution) consisted of the Euclidean distance either to the closest forest paths or to the closest road. We extracted for each transect segment the mean value of each parameter in a rectangle with a side of 19 m (corresponding to the effective strip width, Buckland et al. 2001) and kept, for each transect segment, the parameter for which the value was smaller. Finally, we summed, at the middle point of each transect segment, the population size of each village divided by the distance of the village and by the exponential distance of forest path / road. We used the exponential distance for the forest access as we considered human pressure will be high on the path / road but will decrease quickly as you move away from them.

XII APPENDIX D

Examination of the model assumptions

Singe scale model

Collinearity was not an issue since Spearman correlation coefficients were never higher than 0.52 (Table D1), and variance inflation was below 1.58 for all variables (Table D2). As our data showed some potentially influential cases of leverage, we ran again the model on a subset of our data (n=261 of the 284 transect segments). We checked model estimates and compared them with the estimates of the full model (Table D3). As there were only little variation, we kept the model with the all dataset. We then checked dfbeta to investigate if some transect segments particularly influenced the predictor estimates. Values for the 'hunting pressure' and 'hunting signs' predictors presented some issues (Table D4). For each predictor, we checked the transect segments which induce changes of more than 10 % of the estimate values (n=95 for 'hunting signs', n=43 for 'hunting pressure'). For 'hunting signs', almost all segments with hunting signs presence (34 on the 40 segments) presented dfbeta issues. We decided to run the model without this predictor to check if it has influenced the estimates of the other predictors. As the estimates were similar (Table D3), we kept the 'hunting sign' predictor. For 'hunting pressure', we ran the model with a subset of data excluding segments with dfbeta issues. Again, the estimates were similar in comparison with the first model (Table D3). We then decided to keep the entire dataset.

Scale range models

In order to check if model assumptions will be fulfilled for the scale range models, we looked at Pearson correlations between predictor values of the single scale model and their corresponding values extracted on each discrete buffer for the scale range models (Table D5). As Pearson correlations were mainly higher than 0.70 (with some values decreasing to 0.42 outside the optimal scale range), we assumed that the goodness of fit of the scale range models will be equivalent to the single scale model.

Table D1: Spearman correlations of the single scale model

	Nesting site fidelity	**Hunting signs**	**Hunting pressure**	**Village influence**	**Patch structure**	**Preferred THV**	**Fleshy fruit avail.**
Nesting site fidelity	1	0.0690	0.0082	0.1143	0.1047	0.3768	0.3414
Hunting signs		1	0.0450	-0.0778	-0.0020	0.0962	0.1025
Hunting pressure			1	0.3366	0.3207	0.0440	0.0475
Village influence				1	0.5105	0.0492	0.1302
Patch structure					1	0.1424	0.4040
Preferred THV						1	0.5206

Table D2: Variance Inflation Factors (VIF) of the single scale model

Predictors	**VIF**
Patch structure	1.37
Fleshy fruit availability	1.58
Preferred THV	1.49
Hunting signs	1.02
Hunting Pressure	1.23
Village influence	1.31
Nesting site fidelity	1.14

Table D3: Comparison between the estimates of the single scale model and estimates of different reduced models in order to investigate potential model assumptions issues *(see legend next page)*

	Estimates (single scale model) [1]	Estimates (subset after leverage) [2]	Estimates (w/o hunting signs) [3]	Estimates (subset after dfbeta issues) [4]
(Intercept)	-1.956***	-2.191***	-1.952***	-2.608***
Patch structure	1.073***	1.086**	1.056***	0.996***
Fleshy fruit availability	0.454	0.524	0.462	0.586
Preferred THV	0.915**	1.058**	0.916**	1.164**
Interaction Fleshy fruit availability & Preferred THV	-0.914***	-0.776*	-0.916**	-0.681**
Hunting signs	0.037	0.257	-	0.288
Hunting pressure	0.030	0.167	0.035	-0.247
Village influence	0.306	0.506	0.300	0.206
Nesting site fidelity	0.570**	0.442	0.570**	0.698***
Autocorrelation term	0.273	0.395	0.269	0.611***

Table D3: [1] Estimates of the single scale model. [2] Estimates for the model with a subset of data after having removed transect segments that induced large leverage. [3] Estimates for the model without the 'hunting signs' predictor (as all transect segments with presence of hunting signs underlines dfbetas issues). [4] Estimates for the model with a subset of data after removing transect segments that induced dfbetas issues for the 'hunting pressure' predictor. *** indicates predictors with a p-value below 0.0001, ** a p < 0.001, * a p-value < 0.05.

Table D4: Dfbeta (absolute maximum value) of predictor estimates

	Estimates	Dfbeta (maximum & absolute value)
(Intercept)	-1.956***	0.0459
Patch structure	1.075***	0.0533
Fleshy fruit availability	0.454	0.0774
Preferred THV	0.914**	0.0509
Interaction Fleshy fruit availability & Preferred THV	-0.914***	0.0623
Hunting signs	0.038	0.0644[1]
Hunting pressure	0.029	0.0606[1]
Village influence	0.306	0.0491
Nesting site fidelity	0.570**	0.0507
Autocorrelation term	0.274	0.0311

[1] This two values presented some issues. *** indicates predictors with a p-value below 0.0001, ** a p-value below 0.001, * a p-value below 0.05.

Table D5: Pearson correlations between predictor values of the single scale model and values extracted for each discrete buffer in the scale range models

	Extraction of the weighted mean value			**Extraction of the arithmetic mean value**		
Buffer radius	Patch structure	Fleshy fruit availability	Preferred THV	Patch structure	Fleshy fruit availability	Preferred THV
30 m	-	0.98	0.97	-	0.98	0.98
60 m	0.42	0.98	0.98	0.46	0.99	0.99
120 m	-	0.99	0.99	-	1.00	1.00
210 m	0.53	1.00	1.00	0.60	0.99	0.92
300 m	-	1.00	0.99	0.64	0.95	0.64
360 m	-	0.99	0.98	-	0.92	0.88
450 m	-	0.98	-	0.70	0.88	-
600 m	0.67	0.95	0.92	0.74	0.83	0.74
750 m	0.71	-	-	-	-	-
900 m	0.74	-	-	-	-	-
1050 m	0.77	-	-	0.87	-	-
1200 m	0.79	-	-	-	-	-
1500 m	0.84	0.81	0.70	0.94	0.70	0.52
1800 m	0.88	-	-	-	-	-
1950 m	0.90	-	-	0.98	-	-
2100 m	0.91	-	-	-	-	-
2400 m	0.94	0.74	0.59	1.00	0.65	0.46
2700 m	0.95	-	-	1.00	-	-

XIII APPENDIX E

Scale range models with non-distance weighted or mixed distance weighted predictor extraction

The first step at coarse resolution revealed slightly different scaling patterns in comparison with the distance weighted models (Figures E1 and E2). For this reason, the refined scale search of ‘patch structure’ changed in the case of the non-distance weighted models: we investigated from 210 to 2700 m by adding buffers of 300, 450, 900 m radiuses. In all other cases, the investigations remained identical as in the distance weighted models.

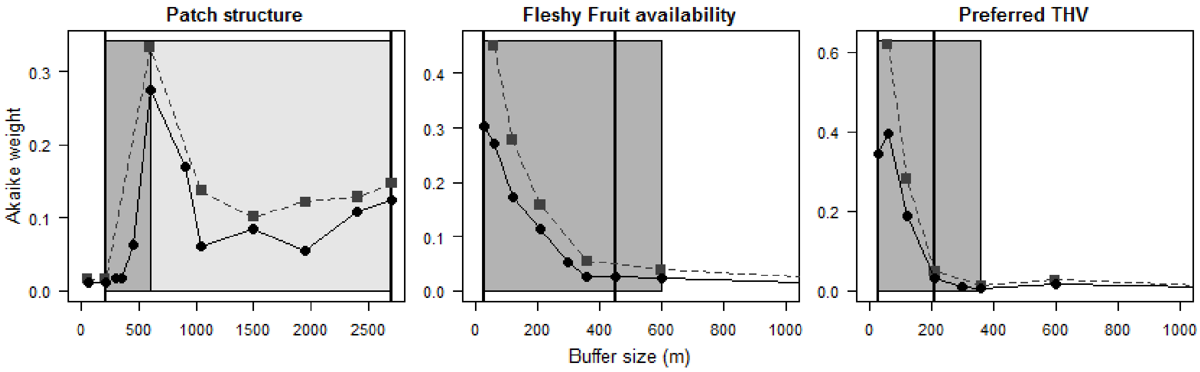


Figure E1: Stepwise procedure to assess influential scale ranges in non-distance weighted models

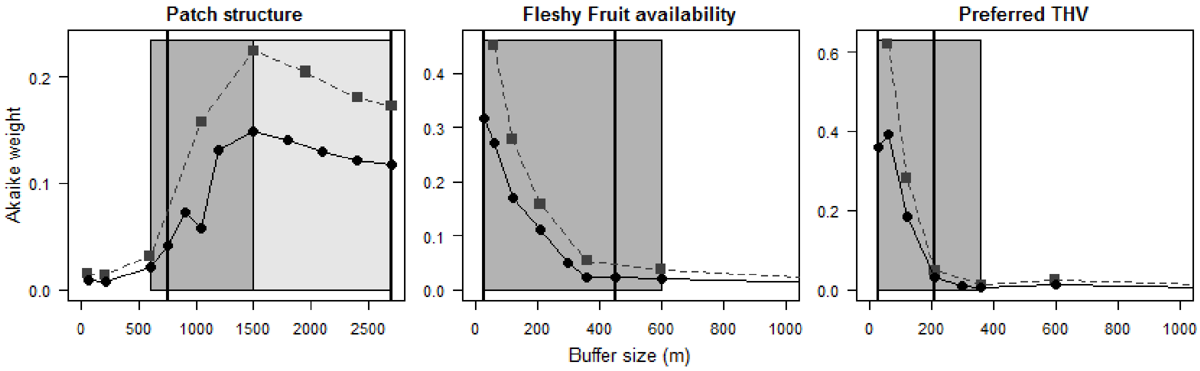


Figure E2: Stepwise procedure to assess influential scale ranges in mixed distance weighted models

Grey squares depict the Akaike weights of each discrete scale tested within the set of models at coarse resolution. Rectangles in light grey indicate the upper plateau of the curve, representing the discrete scales being part of the influential scale range, while rectangles in dark grey highlight the scale range of greatest changes needing to be more investigated in the subsequent step. The refined scale search is indicated by the black points connected by black solid lines and the final influential scale range is highlighted by the solid vertical black lines. The graphs of ‘Fleshy fruit availability’ and ‘preferred THV’ have been truncated at 1000 m to improve figure readability.

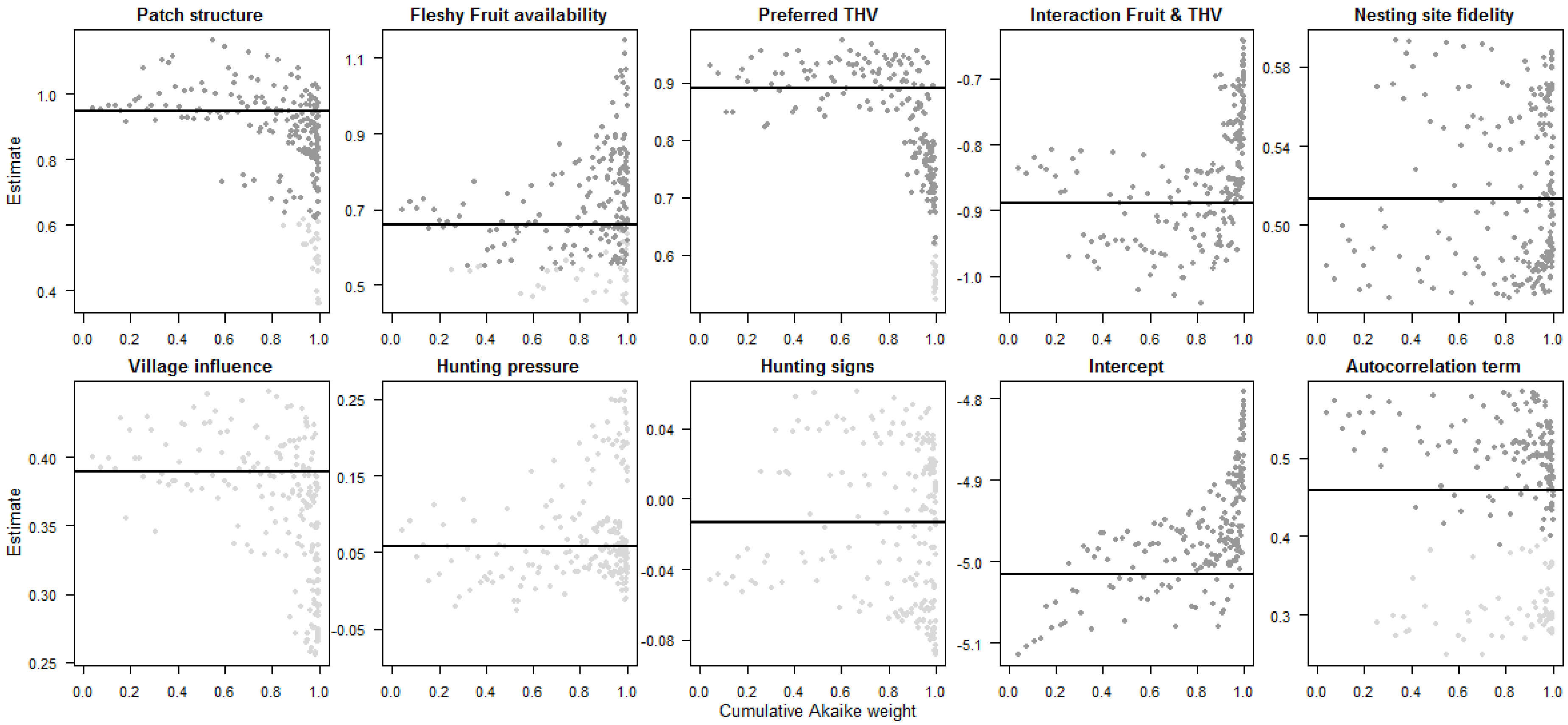


Figure E3: Variation in parameters' influence for the scale range models with predictors' non-distance weighted

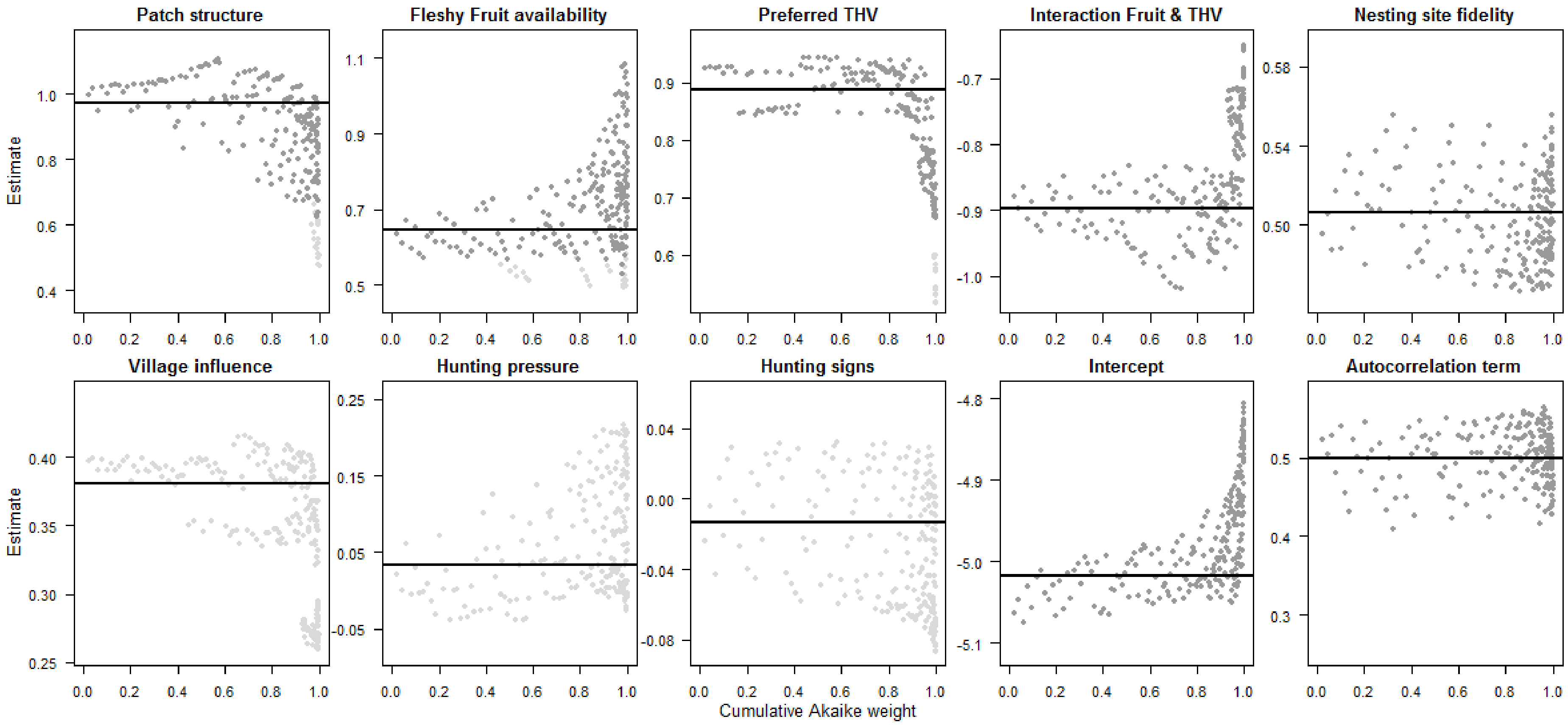


Figure E4: Variation in parameters' influence for the scale range models with predictors' mixed distance weighted

Parameter estimates are presented according to the cumulative Akaike weight of the models (X-axis) within the influential scale ranges of the three environmental predictors. The colour of the points indicates the significance of the parameters (black points are significant parameters, p-value < 0.05; grey points are non-significant ones). The horizontal lines indicate the global mean estimates of the parameters. Predictor significance was less stable than in distance weighted models as predictors became non-significant in some models ('preferred THV' and 'fleshy fruit availbility' had a p-value between 0.05 and 0.1 but 'patch structure' became clearly non-significant, p-value up to 0.27).

XIV APPENDIX F

Variation in parameter influence within all models implemented at the finest resolution

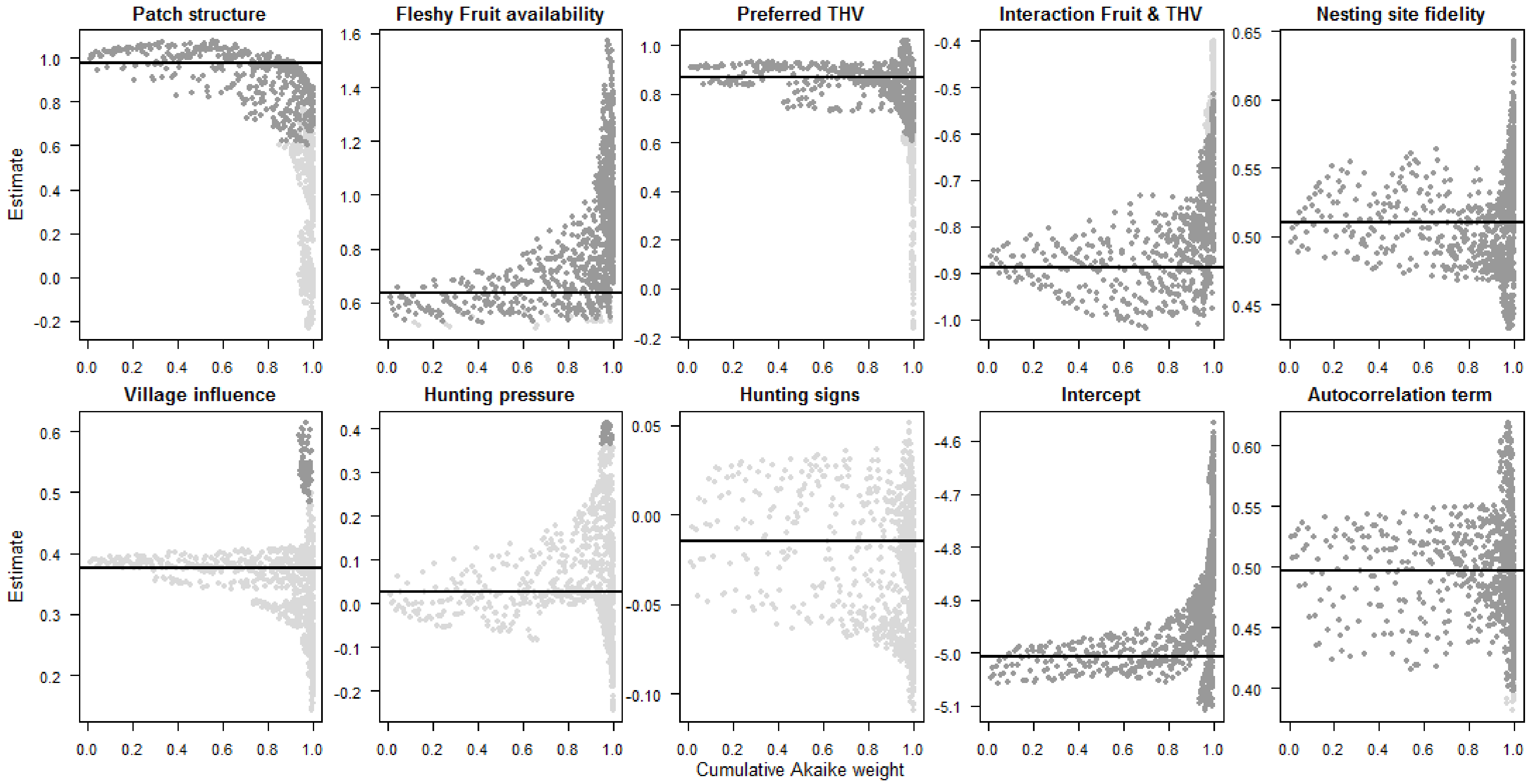


Figure F1: Variation in parameter influence within all models implemented at the finest resolution (see legend next page)

Figure F1: Parameter estimates are presented according to the cumulative Akaike weight of the models (X-axis) within the influential scale ranges of the three environmental predictors. The colour of the points indicates the significance of the parameters (black points are significant parameters, p-value < 0.05; grey points are non-significant ones). The horizontal lines indicate the global mean estimates of the parameters.

CHAPTER 2:

NEST GROUPING PATTERNS OF BONOBOS (*PAN PANISCUS*) IN RELATION TO FRUIT AVAILABILITY IN A FOREST-SAVANNAH MOSAIC

© Fabrice Dentressangle

Serckx A, Huynen M-C, Bastin J-F, Hambuckers A, Beudels-Jamar R C, Vimond M, Raynaud E, Kühl H S. 2014. Nest grouping patterns of bonobos (*Pan paniscus*) in relation to fruit availability in a forest-savannah mosaic. PloS ONE. *In press*.

I RÉSUMÉ

La comparaison des patterns de groupement du bonobo et du chimpanzé est un sujet de premier intérêt en socio-écologie. De nombreuses études ont mis en évidence que l'impact des facteurs sociaux et environnementaux a engendré une évolution différente de la cohésion sociale chez ces deux espèces sœurs. Cependant, nous manquons à l'heure actuelle d'informations sur les traits sociaux du bonobo au travers de l'ensemble de son aire de distribution, afin de réaliser des comparaisons inter-espèces précises. Dans cette étude, nous investiguons la cohésion sociale du bonobo aux sites de nids en fonction de la disponibilité en fruits. Notre site d'étude est situé dans les mosaïques de forêts-savanes de l'ouest de la République Démocratique du Congo (RDC), un habitat du bonobo qui a peu retenu l'attention des chercheurs jusqu'à présent, et qui est caractérisé par de larges variations interannuelles de la disponibilité en nourriture. Nous avons collecté les données au sein de deux communautés de bonobos. Nous utilisons le nombre de nids dans les sites dortoirs comme estimation du pattern de groupement nocturne et analysons ces données en regard à la disponibilité en fruits. Nous avons également modélisé la densité de populations des bonobos dans le site d'étude, afin d'investiguer d'éventuelles variations annuelles. Notre étude démontre que la densité d'une des communautés de bonobos a varié au cours des trois années d'inventaires, suggérant que cette communauté utilise son domaine vital de manière variable. Ce résultat met en évidence l'importance des connectivités entre patchs forestiers, une condition indispensable pour permettre aux bonobos d'adapter leurs patterns de déplacements en fonction des changements de disponibilité en fruits. Nous n'avons pas identifié d'influence de la disponibilité en fruits au sein de la forêt sur la cohésion des bonobos. Seule la disponibilité en fruits au sein des sites de nids influence la cohésion, indiquant que les bonobos favorisent des zones de 'hot-spot' alimentaire pour placer leur site de nids. Nos résultats confirment les observations observées dans les précédentes études réalisées dans les forêts tropicales denses de la RDC. Néanmoins, afin de clarifier l'impact de la variabilité environnementale sur la cohésion sociale du bonobo, des observations directes des bonobos en mosaïque de forêts-savanes sont nécessaires, ainsi que des comparaisons sur l'ensemble de l'aire de distribution du bonobo, réalisées à l'aide d'études utilisant une méthodologie systématique.

II ABSTRACT

A topic of major interest in socio-ecology is the comparison of chimpanzees and bonobos’ grouping patterns. Numerous studies have highlighted the impact of social and environmental factors on the different evolution in group cohesion seen in these sister species. We are still lacking, however, key information about bonobo social traits across their habitat range, in order to make accurate inter-species comparisons. In this study we investigated bonobo social cohesiveness at nesting sites depending on fruit availability in the forest-savannah mosaic of western Democratic Republic of Congo (DRC), a bonobo habitat which has received little attention from researchers and is characterized by high food resource variation within years. We collected data on two bonobo communities. Nest counts at nesting sites were used as a proxy for night grouping patterns and were analysed with regard to fruit availability. We also modelled bonobo population density at the site in order to investigate yearly variation. We found that one community density varied across the three years of surveys, suggesting that this bonobo community has significant variability in use of its home range. This finding highlights the importance of forest connectivity, a likely prerequisite for the ability of bonobos to adapt their ranging patterns to fruit availability changes. We found no influence of overall fruit availability on bonobo cohesiveness. Only fruit availability at the nesting sites showed a positive influence, indicating that bonobos favour food ‘hot spots’ as sleeping sites. Our findings have confirmed the results obtained from previous studies carried out in the dense tropical forests of DRC. Nevertheless, in order to clarify the impact of environmental variability on bonobo social cohesiveness, we will need to make direct observations of the apes in the forest-savannah mosaic as well as make comparisons across the entirety of the bonobos’ range using systematic methodology.

Keywords: bonobo; nest; grouping patterns; social cohesiveness; Ape population density

III INTRODUCTION

Nest-building is an important behavioural feature shared by all species of great apes and is considered to be a basal adaptation underlying the aptitude of great apes for manipulating objects in their environment. The deep ancestry of this trait has possible implications for our understanding of the cognitive evolution of early hominoids (Fruth and Hohmann 1996), as it permits higher-quality sleep by providing thermoregulation (Stewart 2011, Samson and Hunt 2012), reduced vulnerability to predators (Pruetz et al. 2008, Stewart 2011, Koops et al. 2012), more comfortable sleeping postures (Fruth 1995, Stewart et al. 2007, Koops et al. 2012), and protection against pathogens (Stewart 2011, Koops et al. 2012, Samson et al. 2013). The impact of environmental factors on the location of great ape nests has been the subject of a number of studies (Fruth 1995, Basabose and Yamagiwa 2002, Furuichi and Hashimoto 2004, Hernandez-aguilar 2006, Rothman et al. 2006, Russon et al. 2007, Grossmann et al. 2008, Stanford and O'Malley 2008, Mulavwa et al. 2010, Koops 2011, Hernandez-Aguilar et al. 2013), and nest counts are frequently used to estimate ape population density (Hashimoto 1995, Tutin et al. 1995, Plumptre and Reynolds 1997, Van Krunkelsven 2001, Brugiere and Sakom 2001, Ancrenaz et al. 2004, Reinartz et al. 2006, Devos et al. 2008, Sunderland-Groves et al. 2009, Kouakou et al. 2009, Hickey et al. 2013). However the functionality of great ape nesting sites in relation to the dynamics of their social organization has been much less well-documented (Fruth and Hohmann 1996). Bonobo nesting behaviour has not been as thoroughly investigated compared to that of chimpanzees (Kano 1992, Fruth 1995, Hohmann et al. 2006, Mulavwa et al. 2010). Nonetheless, several studies have already shown that nesting patterns could play an important role in their social behaviour. Fruth and Hohmann suggested that the aggregation of bonobos at nest sites at night could facilitate information transfer on the quality of food patches visited during the day (Fruth and Hohmann 1996), and that nests could serve as 'taboo zones' which can help bonobos avoid conflicts with group members (Fruth and Hohmann 1993). Variation in the size and location of nest groups could reflect differences in social organisation and could provide us with insight into the species-specific elements of bonobo social structure (Fruth and Hohmann 1996).

Comparisons between the social organization of bonobos and chimpanzees have been made using data from a number of habituated populations and show that bonobos live in more cohesive communities and with a larger relative party size (i.e., the percentage of the total community size) (Chapman et al. 1994, Boesch 1996, Hohmann and Fruth 2002, Furuichi et al. 2008). The composition of chimpanzee parties changes more frequently than that of bonobos.

Individual chimpanzees, usually adult females with infants, more often travel at a distance from the main parties, whereas bonobo parties usually range in the same general area and tend to aggregate towards the evening (Furuichi 2009). This trait is typical of all bonobo communities studied to date and thus appears to be characteristic of the species (for a review see Furuichi 2009), and numerous socio-ecological and environmental factors have been suggested to explain it: prolonged oestrus of bonobo females (Furuichi and Hashimoto 2002), close association between mothers and their adult sons (Furuichi 1997), strong social bonds between females (Wrangham 1993), high female social status (Furuichi 1997, White and Wood 2007), food patch size (White and Wrangham 1988, Hohmann et al. 2006), availability of terrestrial herbaceous vegetation (Malenky and Wrangham 1994), and a feed-as-you-go foraging strategy (i.e., foraging during travel between fruit patches) (Wrangham 2000). A number of authors have interpreted the evidence to imply a difference in the nature of the fission-fusion social structure in the two species (Furuichi 2009). This might suggest that the grouping patterns of chimpanzees and bonobos have evolved through a process of long-term ecological and behavioural adaptations rather than merely reflecting a flexible response to current environmental differences. However, Boesch pointed out that chimpanzee grouping patterns in Taï (Ivory Coast) were similar to those of bonobos inhabiting similar rainforest study sites (Boesch 1996). This finding supports the fact that we need social and ecological data for much of the bonobos' habitat, including the forest-savannah environment, which will render possible a socio-ecological comparison of both species across their ranges (Furuichi 2009).

Until now, socio-ecological data on bonobos has been available only from dense tropical forests. While chimpanzees have been known for decades to live in savannahs, bonobo distribution was thought to be limited to dense rainforests. This changed in the 1990s, when Thompson identified a bonobo population in the southern extremity of their distribution range, inhabiting a transitional ecotone between moist forests and savannahs (Thompson 1997, 2001). Her discovery changed our perception of the ecological limit of the species range, but bonobos within this habitat remained poorly studied. In 2005, a new population living in the forest-savannah mosaic of western Democratic Republic of Congo (DRC), this time in the western extremity of the distribution range, was documented by the local NGO Mbou-Mon-Tour and by an extensive survey conducted by the World Wide Fund for Nature (WWF) (Inogwabini et al. 2007, 2008). A study of bonobo genetic diversity across their entire distribution range has indicated that this population has probably been isolated from other populations since the Pleistocene (Kawamoto et al. 2013). This finding, combined with the fact that forest-savannah mosaics show large ecological variability compared to dense forests, suggests that this population could exhibit unique behavioural and ecological features. The region is characterized by high spatio-temporal variation in food availability. The home ranges of the local bonobos include forest patches of various shapes and sizes interspersed with numerous micro-habitats. In addition to this geographically patchy distribution of resources, periods of high scarcity in fleshy fruits were also documented. Studies in this region will provide us with an opportunity to better understand the full spectrum of bonobo adaptations. They also promise to clarify whether the grouping patterns of chimpanzees and bonobos reflect evolutionary adaptations or are reflections of current specific short-term environmental contexts.

Such research is also essential in the current context of the rapid human-engineered modification of the global landscape. The forests of the Congo Basin are being cleared or degraded at a rapidly increasing rate (de Wasseige et al. 2009), and climate change could modify the pattern of rain seasonality in the region. Both factors are likely to induce larger spatio-temporal variation in the availability of food for great apes and other wildlife species. While some studies have already pointed out the effects of habitat fragmentation and related human activities on declines in ape density (Junker et al. 2012, Hickey et al. 2013), we still have a poor understanding of how variation in food availability might impact the population densities and social organization of great apes. In order to address the questions, we must improve our knowledge on both the population dynamics and on social structures for each species across their distribution range. Given that unhabituated great apes are elusive and that direct observations of them in their forest habitats are generally impossible, this can be achieved only by developing a systematic methodology which can be applied to study unhabituated populations.

In this study we present the first precise estimate of bonobo densities for the Malebo region and investigate the population dynamics there over a period of years. We also provide the first analysis of bonobo grouping patterns in a forest-savannah mosaic by using a systematic methodology based on indirect observations using night nests. More precisely, we focus on the influence of environmental factors on nest group size, testing whether the high seasonality of fruit availability influences bonobo cohesiveness at night by using a predictor reflecting the availability of fleshy fruits at the time of the nest-building. We also include three predictors which are known to influence choice of nesting sites in dense forests in order to test their influence on nest grouping patterns in this new environment: the availability of fleshy fruits at nesting sites, density of preferred nesting trees and rainfall. Finally, we controlled for the influence of human activity. Our finding offers first insights into the socio-ecological traits characterizing bonobos living in a forest-savannah mosaic.

IV METHODS

IV.1 Ethics statement

This non-invasive research was conducted using only indirect signs of bonobo presence (nests) under the WWF-DRC research permit (RM441976, granted by the Minister of Foreign Affairs and International Cooperation of Democratic Republic of Congo). For the questionnaire survey, we used the Poverty and Environment Network (PEN) prototype questionnaire developed by CIFOR. The questionnaire was approved by the ethic committee of the Biology Department of the Unikin (University of Kinshasa) and was authorized to be performed through the WWF permit. We explained to each person to not answer to a question if they desired to do so. Before conducting each interview, the goal of the study was explained to the interviewees and we asked their verbal approval to the participation of the study before starting (written consent was not asked for as most of the people are illiterate).

IV.2 Study site

The study site is located in the South of the Lake Tumba landscape in western Democratic Republic of Congo, close to the WWF Malebo research station, in forests contiguous to Nkala and Mpelu villages (16.41-16.56°E, 2.45-2.66°S, Figure 2-1 – Page 115). This region can be characterized as a forest-savannah mosaic. The altitude ranges from 300 to 700m (Inogwabini et al. 2008), and the mean daily temperature fluctuates around 25°C (Vancutsem et al. 2006). Annual rainfall oscillates around 1500-1600mm, and is interrupted by two dry seasons in February and July-August (Inogwabini et al. 2008). Forests mostly represent *terra firma* soil conditions and encompass various habitat types, i.e., re-colonizing *Uapaca sp.*, old secondary, mixed mature, old growth mono-dominant, riverine gallery and *Marantaceae* forests (Inogwabini et al. 2008). At the time of our data collection, the study site encompassed 170km², made up of 102km² of forest patches of various shapes and sizes which are connected by many corridors. Surrounding savannahs were mainly herbaceous and partially used for cattle ranching. Human activities and settlements were concentrated in the west side of the study area. Six villages and twelve farms were directly adjacent to the forest and plantations were located inside the forest. A bonobo population, probably made up of two communities, inhabited Nkala and Mpelu Forests, and has since 2007 been the subject of habituation and conservation programs by the WWF-DRC (Inogwabini et al. 2008).

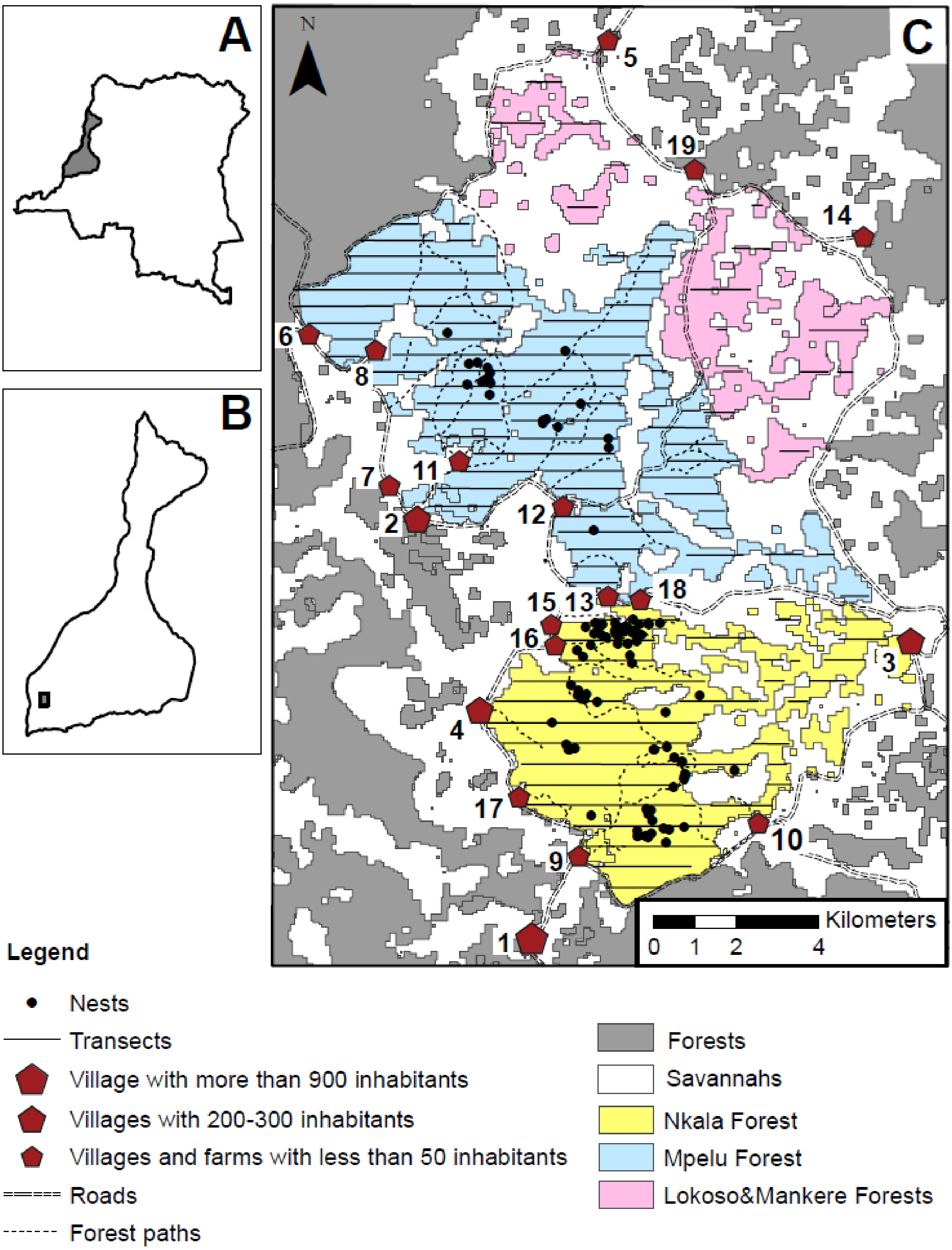


Figure 2-1: Map of the study site (16.41-16.56°E, 2.45-2.66°S, West DRC)

A. Location of the Lake Tumba landscape in Democratic Republic of Congo. B. Location of the study site inside Lake Tumba landscape. C. Map of the study site. Forests are indicated in grey and savannahs in white (the map is based on a non-supervised classification – RED and IR on a Landsat7 (2007)). To represent the further subdivisions we made of the area, we coloured in yellow and blue the two suspected home ranges of bonobo communities habituated by WWF-DRC. Pink indicates the forest patches of re-colonizing *Uapaca sp.* Villages are depicted as red pentagons. Number 19 represents the WWF-base. Parallel dashed lines indicate the roads surrounding the study site, whereas dotted lines indicate the main forest paths. Vertical solid lines depict the 114 line transects (179.1 km) travelled in 2011, 2012 and 2013, and the nesting sites visited for our nesting site study are depicted as filled-in black points.

IV.3 **Data collection**

We collected data between April 2011 and August 2013 with the help of local assistants and with the support of WWF-DRC. In order to estimate bonobo density, we conducted three forest surveys in which we counted nests along line transects. In addition, we carried out a study of nest decay rates, which was necessary in order to convert nest densities into densities of bonobos. We monitored fruiting trees in order to acquire data on the seasonality of fruit availability, and we collected data on nesting sites to provide information on nest grouping patterns. For our subsequent analysis focussing on bonobo cohesiveness at night, we combined (i) nesting site data (nest counts, fruit availability at nesting sites and density of suitable nesting trees out of total trees available at the study site), with information on (ii) fruit availability in the forest, (iii) monthly rainfall at the study site and (iv) human activities in the forest, the latter achieved by administering a questionnaire to local villagers (Table 2-1 – Page 120).

IV.3.1 RAINFALL

Between May 2011 and June 2013, rainfall was collected every twenty-four hours with a rain gauge at the Mbou-Mon-Tour farm (Figure 2-1 – Page 115, village number 16).

IV.3.2 TREE ABUNDANCE SURVEY

In order to acquire baseline data on tree species abundance in the study site, we carried out a plot survey between April and August 2011. Sampling design was fully randomized and systematic using a 1 km² grid. We made use of two plot sizes depending on their location in the forest: 0.25 ha for plots located less than 200 m from the forest edge (n=48) and 1 ha for plots in the interior of the forests (n=15). For each tree with a stem diameter at breast height (DBH, i.e., at 130 cm height) greater than 10cm, we recorded the tree species and DBH (9730 trees in 27 ha in total). Four hundred and seventy-four samples of 178 tree species belonging to 44 families were registered in the herbarium and botanical library of the Université Libre de Bruxelles ("BRLU"), with reference IDs Bastin-Serckx#1-474.

IV.3.3 SURVEY DATA

We delimited the size and shape of our study site based on WWF staff knowledge of bonobo home ranges in the Mpelu and Nkala forests and added connecting corridors. In April 2011, we conducted a pilot study during which we recorded all bonobo nests on reconnaissance walks (recces) to define the total sampling effort needed to perform a precise density estimation (Buckland et al. 2001, Kuehl et al. 2008). Based on the results of the pilot study, we created a survey design with 114 transects running from west to east, spaced 500 m and of variable lengths, adding to a total of 179.1 km surveyed through the forest (Figure 2-1 – Page 115). We sampled transects in May to July 2011, mid-March to mid-July 2012 and June to August 2013. Due to external constraints, we were not able to visit some transects each year (see Table 2-2 – Page 120, for the exact annual total efforts). We systematically collected information on bonobo nests and recorded their perpendicular distances from the transects using a tape measure, following the methodology recommended in the IUCN guidelines (Kuehl et al. 2008) and Buckland et al. (Buckland et al. 2001). The three observers were trained together and used a consistent methodology.

IV.3.4 SOCIO-ECONOMIC DATA

Between May and June 2012, we collected socio-economic data in the six villages and the twelve farms surrounding the study site (Figure 2-1 – Page 115). We developed a questionnaire based on the "Poverty and Environment Network (PEN) prototype questionnaire" ("PEN Prototype Questionnaire" 2008). We randomly chose a minimum of 30% of adults in all local villages and farms (Shibia 2000, Kideghesho et al. 2006, Nyariki 2009). We interviewed a total of 201 adults (Table 2-3 – Page 121) on their hunting and fishing activities as well as their collects of non-timber products. In addition, we asked about the frequency and location of each activity in the forest and the villager indicated the location of their activities on a forest map using the local names for each location in the forest.

IV.3.5 NESTING SITE DATA

Between May 2011 and May 2013, we gathered data on bonobo nesting sites (n=104). For each month, we randomly selected one nesting site out of all of the sites located by the WWF trackers who were conducting daily follows of the bonobos for the WWF habituation program. We selected only nesting sites at which the trackers had been present at the evening nest-construction time to insure that we used only night nests, and we always collected nesting site data within 48 hours of nest building. During the May-June 2011 and May-June 2012 periods, we intensified data collection by gathering information on all of the nesting sites found by the WWF trackers. At each nesting site, we first explored the surrounding area to ensure that we had found all of the nests. We considered nests as being part of the same nesting site when the maximal distance between two nests did not exceed 30 m (Fruth 1995, Mulavwa et al. 2010). We counted only fresh nests, i.e., nests built the previous night, with green leaves and traces of feces or urine (Furuichi et al. 2001b). For each tree containing a nest, from here on called a *nesting tree*, we recorded the species of tree (n=1872). In order to further investigate nesting site characteristics, we randomly chose, in a subset of 97 nesting sites, a maximum of 30 control trees, which we identified to species level. These trees were distributed between the nesting trees, for a total of 2259 control trees.

IV.3.6 NEST DECAY TIME

We conducted a nest decay rate study between August 2011 and May 2013, following previously validated methodology (Plumptre and Reynolds 1996, Laing et al. 2003, Kuehl et al. 2008, Mathewson et al. 2008, Devos and Laguardia 2011). We made repeated revisits to all nests identified as fresh during our nesting site study and assessed their conditions. For months where we characterized numerous nesting sites, we used only three randomly selected sites for the nest decay study. We made weekly visits to a total of 42 nesting sites containing 610 nests until the nests had disappeared (Devos and Laguardia 2011). At each visit we noted the degree of nest degradation according to the following categories: (i) new: only green leaves; (ii) recent: a mixture of green and brown leaves; (iii) old: only brown leaves; (iv) very old: brown leaves and the nest is losing its structure (Furuichi et al. 2001b); and finally, (v) disappeared: nest no longer recognizable (Kouakou et al. 2009). We estimated mean nest decay time by using the method proposed by Laing *et al.* 2003 (Laing et al. 2003). More specifically, we used the logistic regression model with left truncation. We bootstrapped the nest data (n=1000) to estimate confidence intervals at 2.5%.

IV.3.7 FRUITING TREE DATA

Between May 2011 and May 2013, we recorded data on fruiting trees within 31 plots of 0.04 ha each, for a total of 1.24 ha (14 plots in the Nkala Forest and 17 plots in the Mpelu Forest). We randomly chose plot locations placed along the transects in order to facilitate our access to them. In November and December 2011, all trees with a DBH larger than 10 cm were marked, identified to the species level and their DBH was measured (n=672). In May 2012, in order to improve our representation of fruiting trees, we added 14 additional plots (8.75 ha in total, from the tree abundance survey; Nkala Forest: five 1 ha plots and three 0.25 ha plots; Mpelu Forest: two 1 ha plots and four 0.25 ha plots). Every two weeks, we visited each of the plots and recorded which trees were fruiting by inspecting their crowns and counting fruits on the ground.

Table 2-1: Summary of data collection

Type of data	**Period of data collection**	**Sample size of the dataset**
Rainfall	May 2011 to June 2013	791 days
Tree abundance data	April to July 2011	8730 trees in 27ha of plots (15 plots of 1 ha, 48 plots of 0.25 ha)
Survey data	April to July 2011, Mid-March to Mid-July 2012, July to August 2013	114 line transects (total effort : 179.1 km)
Socio-economic data	Mid-May to mid-July 2012	201 people interviewed (see details in Table 2-3)
Nesting site data	May 2011 to May 2013	1872 nest trees at 104 nesting sites and 2259 control trees at 97 nesting sites
Nest decay time	May 2011 to May 2013	42 nesting sites (610 nests, part of the nesting site data)
Fruiting tree data	May 2011 to June 2013	672 trees between May 2011 and May2012, 4533 trees between May 2012 and May 2013

Table 2-2: Area and total effort per year used for to estimate bonobo population density

	Area (km²)	Total effort 2011 (km)	Total effort 2012 (km)	Total effort 2013 (km)
Global	93.84	130.1	179.1	175.5
Nkala	32.45	49.9	61.9	61.9
Mpelu	54.26	72.7	109.7	106.1
Lokoso&Mankere	7.13	7.5	7.5	7.5

Table 2-3: Socio-economic data

		Population					Interviewed people			Interviewed people per activity				
		Nb household	Nb men	Nb women	Nb children	Total	Total	Men	Women	Hunters (M)	Fishermen (W)	Fishermen (M)	NTPC (W)	NTPC (M)
1	Nkoo	168	169	202	540	911	50	35	15	16	13	20	7	9
2	Mpelu	43	50	58	153	261	50	30	20	19	20	23	20	19
3	Lebomo	37	37	34	141	212	26	14	12	7	9	8	3	2
4	Nkala	34	36	49	110	195	39	21	18	7	18	14	16	10
5	Malebo	10	9	11	38	58	6	3	3	1	3	2	3	2
6	Mavula	10	10	12	25	47	6	3	3	3	3	2	3	1
7	Bosatore	7	5	7	22	34	2	1	1	1	1	1	1	1
8	Mokoabuo	6	5	8	17	30	4	2	2	1	2	1	2	1
9	Dispensaire de Nkoo	4	4	4	19	27	2	1	1	0	0	0	0	0
10	Lensiana	4	4	3	18	25	0	0	0	0	0	0	0	0
11	Biomengele	3	3	3	13	19	3	2	1	2	1	1	1	1
12	Ngandjele	3	3	6	7	16	2	1	1	0	1	0	1	0
13	Motsuemontore	2	2	4	9	15	2	1	1	1	1	0	0	0
14	Ezano	3	2	2	8	12	1	1	0	1	0	1	0	1
15	Mayi Monene	2	2	3	5	10	2	1	1	0	1	1	0	0
16	Mbou-Mon-Tour	4	4	4	2	10	2	1	1	0	1	0	0	0
17	Moza	1	1	1	6	8	2	1	1	0	1	0	1	0
18	Bosieli	1	1	1	5	7	2	1	1	1	1	1	1	0
	TOTAL	**342**	**347**	**412**	**1138**	**1897**	**201**	**119**	**82**	**60**	**76**	**75**	**59**	**47**

The numbers beside the village names were used to locate them on the study site in Figure 2-1 ─ Page 115. In the 'Population' part of the table, we present results of the village population census realized in 2012. The 'Interviewed people' part of the table indicates first the sampling effort for the socio-economic data collection (total per village and per gender). Finally, the 'Interviewed people per activity' part of the table gives the number of interviewed individuals (per village and per gender) who indicated that they regularly enter the forest for hunting, fishing or collecting non-timber products ('NTPC' = non-timber products collect) and thus answered those parts of the questionnaire.

IV.4 **Analytical methods**

Prior to beginning our analysis of the social cohesion of bonobos at their nesting sites, we needed to estimate the density of bonobos in our study area, which was then modelled to understand their population dynamics over the years. Beside this, we modelled variation in fruit availability to investigate possible seasonal patterns. Finally, we modelled nest group size (i.e., the number of nests per site) according to fruit availability (across the entire home range and at the nesting site), 'density of suitable nesting trees', 'rainfall' and two control variables relating to human activities: 'village influence' and 'human forest use'.

IV.4.1 BONOBO POPULATION DENSITY ESTIMATE

We estimated the population density of bonobos in our study area from transect data. We walked 114 transects for 179.1 km of total effort, once per year in 2011, 2012 and 2013 (n=1411 nests). Density was estimated using Distance 6.0 Release 2 (Buckland et al. 2001, Thomas et al. 2010). We divided the study site into three parts for the analysis to estimate the population density in the two presumed home ranges of the bonobo population living in the area, as documented from WWF data (the Nkala and Mpelu Forests), and the *Uapaca sp.* forest patches (Lokoso&Mankere) located at the north-east boundary of the study site (Figure 2-1 – Page 115). These young forest patches were surveyed during the three year period as we did not know if bonobos from the Mpelu community might have encompassed it within their home range. As we found no evidence of bonobo use of the area, in the end we did not consider it in the analysis to avoid underestimation of bonobo density. We post-stratified the dataset by year and by the three parts of the study site, then fitted a global detection function in order to obtain an estimation of numbers of individuals for each community. We derived a global estimation of the bonobo community size by weighting the data considering the size of the three parts of the study site. We truncated the data, keeping only nests for which the probability of detection from the transect was above 0.15. We tested different functions to model the data and chose the function that minimized the Akaike's Information Criterion (AIC, Burnham and Anderson 2002). To convert bonobo nest density into density and number of bonobo individuals, we divided the nest density by the nest construction rate, the proportion of nest-builders and the nest decay time (Buckland et al. 2001). We used a nest construction rate of 1.37 per day (Mohneke and Fruth 2008) and considered the proportion of nest-builders in the population to be 0.75 (Fruth 1995). The construction rate and proportion of nest-builders were taken from the literature, as these can only be estimated by following habituated individuals.

IV.4.2 VARIATION IN BONOBO POPULATION DENSITY BETWEEN YEARS

In order to get a better understanding of variation in bonobo density between years, we analysed the transect dataset from each forest region surveyed in 2011, 2012 and 2013, and this independently for each presumed home range of the bonobo population (Nkala Forest: 31 transects, 61.9 km of total effort; Mpelu Forest: 72 transects, 111 km of total effort). The Lokoso&Mankere Forests were not taken into account for this analysis as we never observed nests in those forest patches during the surveys. We used a zero inflated generalized linear model with a negative binomial error structure and log link function (Zeileis et al. 2007), which enabled us to take into account the fact that the number of nests on transects was frequently zero but on some transects we occasionally found rather large numbers of nests. This type of model provides us with an option to independently model an excessive number of zeros together with count distribution, indicating which factors affected nest absence / presence on transects and which factors affected the number of nests encountered on transects. We used the specific year of the survey as a categorical predictor and we included its effect into the count and the zero inflation part of the model. We added an offset term to control for differences in transect length (for the zero inflated part this was 1/transect length; in both parts of the model we included the logarithm of the respective offset term). To account for spatial autocorrelation, we used the average of the residuals of all other transects derived from the full model and weighted by distance as an additional predictor. The weight function had the shape of a Gaussian distribution with a mean of zero (maximal weight at distance equals zero) and a standard deviation chosen such that the likelihood of the full model with the derived variable ('autocorrelation term') included was maximized. The autocorrelation was only included into the count part of the model.

As an overall test of the effect of year, we compared the fit of the full model including year, the offset and the autocorrelation term with a null model comprising only the offset and the autocorrelation term. When the overall effect of year was significant, we tested which part of the model was significant by comparing the full model with two reduced models lacking year, either in the zero inflated part of the model or in the count part of the model. For these model comparisons we used likelihood ratio tests (Dobson 2002). Finally, the effect of year was assessed by looking at estimates and p-values in the significant part of the full model. As year was a factor, we releveled it to obtain comparisons between the years 2012 and 2013. All analyses were conducted using R (R Development Core Team 2013) and the additional package pscl (Jackman 2012). We investigated model robustness by excluding data points one by one, rerunning the model and determining model coefficients and the significance of model comparisons. This did not reveal any obvious influential cases.

IV.4.3 VARIATION IN FRUIT AVAILABILITY BETWEEN YEARS

To test whether fruit availability exhibited seasonality and varied between forests, we used a generalized linear model. We used the 'availability of fleshy fruit' index calculated per forest every two weeks as response (n=106). Fruit species considered for this index were derived by selecting tree species *(i)* eaten by bonobos at different study sites (Kano and Mulavwa 1992, Beaune et al. 2013) (Serckx unpublished data) or *(ii)* producing fleshy fruits (Tailfer 1989, Wilks and Issembe 2000, Djoufack et al. 2007). For each fleshy fruit-bearing species, we calculated the fruit index as the proportion of fruiting trees and we multiplied this value by the basal area (in square meters per hectare) of the species for the forest in which the plot was located (total plot samples equals 11.25 ha for the Nkala Forest and 14.25 ha for the Mpelu Forest, from data acquired in the tree abundance survey). Fruit indices of all fleshy fruit species were summed to obtain the fruit availability index used as response in the model. As our response did not follow a normal distribution, we used a function (powerTransform from the R package 'car'(Fox and Weisberg 2011)) to estimate a normalizing transformation of the residuals. This function reveals a parameter that makes the residuals from the regression of the transformed response (here the fruit availability) on the predictors as close to normally distributed as possible. We used as predictor the 'date' at which fruit availability was calculated. 'Date' was converted to a circular variable and its sine and cosine were included into the model to estimate seasonal patterns. We used 'forest' as a categorical predictor to check for differences in fruit availability between the two forests. To test whether the effect of season differed between the two forests we also included the interaction between these two predictors into the model. To account for temporal autocorrelation, we used the average of residuals of all other values of fruit availability derived from the full model and weighted (with the same function as for the previous model) by temporal distance as an additional predictor. After running the model, we checked various model diagnostics (Cook's distance, dfbetas, dffits, leverage and Variance Inflation Factors) and none of these indicated obvious influential cases or outliers or collinearity problems. Inspection of a qq-plot of the residuals and residuals plotted against fitted values indicated no obvious violations of the assumptions of normally distributed and homogeneous residuals.

As an overall test of the effect of seasonality we compared the fit of the full model including sine and cosine of the date, forest, their interaction and the autocorrelation term with a null model comprising only the forest and the autocorrelation term. To determine whether the effect of seasonality was the same in both forests, we compared the full model with a reduced model lacking the interaction. As the interaction was not significant, we removed it from the model and then tested the effect of seasonality by comparing this new model with a null model lacking date. Both comparisons were performed with an F-test. Finally, the effect of forest was obtained from estimates and p-values in the model lacking the interaction with season. All analyses were conducted using R (R Development Core Team 2013) and the additional package car (Fox and Weisberg 2011).

IV.4.4 EFFECT OF FRUIT AVAILABILITY ON BONOBO SOCIAL COHESIVENESS

To test which factors affected nest group size, we ran two models, one assuming we had one bonobo community (Model 1), and the other assuming two bonobo communities (Model 2). The same predictors were used in both models, and community size (log transformed) was incorporated as an offset term. We used generalized linear models with negative binomial error structure and log link function. We excluded data from the beginning of May 2011 as some predictors were not yet available for this period. The dataset included 90 nesting sites (1439 nests) and we used nest count per nesting site as response.

We included three predictors to estimate the effects of environmental variables. We first incorporated the 'density of suitable nesting trees'. This predictor gives the density of tree species preferred by bonobos for nest-building. To calculate this, we compared the distributions of individual nesting trees (n=1872) with their abundance in the forest (n=9730). Species for which identification to species level had not been achieved during the tree abundance survey were combined at the genus level in nesting tree abundance (5 species) and species not represented in the tree abundance survey were removed from nesting tree abundance (13 species). We first used a chi-squared test to check whether bonobos significantly preferred some tree species to build their nests (with the p-value determined based on permutation and not the chi square distribution, $p<0.001$). Binomial tests conducted separately for each species highlighted the preferred species (we use as significance threshold of $p<0.05$, n=24 tree species). Finally, we calculated the density of those preferred species at each nesting site. The second predictor we used represents the 'availability of fleshy fruits in the forest' at the time when the nesting site was built. We selected the same fruit species we used in our model on fruit availability variation. According to the model, the predictor was determined for the entire study area (Model1) or separately for the two forests in which each community was presumed to live (Model2). We estimated a daily mean proportion of fruiting trees from the fruiting tree study by assigning for each date the value of the closest recorded proportion of fruiting trees. The fruit index was calculated as the mean proportion of trees bearing fruit during the 14 days before the nests were built multiplied by their basal area in either the study area (Model1, n=9730) or in the forest (Model2, n=4548 in the Nkala Forest and n=5182 in the Mpelu Forest). Fruit indices of all fleshy fruit species were added to derive the fruit availability index. We then estimated 'availability of fleshy fruits at the nesting site'. In this case, we used the same fruit species selected before, but we only took into account the fruit availability in the area around the nesting site, and, for each nesting site, we calculated the fruit index as the proportion of fruiting trees multiplied by their basal area at the nesting site and summed this for all fleshy fruit species.

We used the measure of 'rainfall' for the 30 days before nest building to control for seasonal variation in climate. To control for the possible influence of human activity on bonobo nesting sites, we first used the predictor 'village influence'. To estimate this predictor, we summed for each nesting site the population size of each village divided by its distance to the nesting site. Secondly, we derived 'human forest use' from our questionnaire data by calculating the daily number of adults who could potentially enter the region of the forest where each nesting site was located in order to hunt, fish or collect non-timber products. Those activities were analysed by gender of the performer (e.g., hunting is only engaged in by men and 'fish-scooping' only by women). For each activity and for each village, we calculated the proportion of interviewed adults going in a forest region ('prop_quest_adult' in the formula). In order to obtain this index, we first estimated the probability of an adult entering a particular forest region (i.e., the daily frequency of the activity divided by the number of forest regions each person enters to engage in the activity) and then divided it by the number of interviewed adults performing the activity. We estimated the proportion of adults going to a forest region for each activity and each village and finally derived the overall index of human forest use for all villages and all activities:

$$Human\_forest\_use = \frac{\sum_{activity}\sum_{village}(prop\_quest\_adult * nb\_adults\_village)}{forest\_part\_area}$$

where nb_adults_village is the number of adults in a village (women or men according to the activity) and forest_part_area was the area of the forest region in square kilometers (used to account for differences in the sizes of the forest regions and to obtain values comparable between forest regions).

We further included an offset term to control for bonobo community size. Here, in contrast to the population density estimate, we used the number of nest-building individuals (log-transformed), which was also estimated using Distance 6.0 for each survey year. We used a nest-building individuals' estimate as we know that young bonobos do not make nest, instead sleeping in their mothers' nests. Here, we did not divide nest-density by the proportion of nest-builders (0.75 (Fruth 1995)) to obtain the number of nest-building individuals per forest region. For nesting site data collected between the periods of surveys, we did not have a bonobo community size estimate. To overcome this problem, we used community size estimated during the surveys before and after the nesting site was built and calculated a mean weighted by the time separating each survey and the build of the nest. We added an autocorrelation term, simultaneously taking into account temporal and spatial autocorrelation. For this, we used the average of residuals at all other nesting sites derived from the full model, weighted (with the same function as for the previous models) by spatial and temporal distances. This time we used two standard deviations, one for spatial and one for temporal autocorrelation, which were determined simultaneously.

All analyses were conducted using R (R Development Core Team 2013) and the additional packages gtools (Warnes et al. 2013), car (Fox and Weisberg 2011), and MASS (Venables and Ripley 2002). Prior to running each model, we checked that correlations between predictors were not an issue with a Spearman test and that all predictors had a symmetrical distribution. 'Human forest use' was log-transformed. All quantitative predictors were z-transformed to a mean of zero and a standard deviation of one to achieve more easily interpretable coefficients (Schielzeth 2010). We inspected two model diagnostics: Variance Inflation Factors (which was not an issue) and leverage. As our data showed some potentially influential cases, we used a subset of our data for the analysis (n=86 for both models). As the autocorrelation term was not significant, it was removed from the model for final results. After running the models, we corrected the AIC for small sample size. In order to test for the overall effect of the environmental variables ('availability of fleshy fruits in the forest', 'availability of fleshy fruits at the nesting site', 'density of suitable nesting trees' and 'rainfall'), we compared the fit of the full model including all predictors, the autocorrelation term and the offset term with a null model comprising only the intercept, the two variables controlling for human activity, the autocorrelation term and the offset term (chi-square test).

V RESULTS

V.1 Bonobo density estimation

Logistic regression revealed a mean nest decay time of 183 days (range: 179-188 days). In order to estimate bonobo density, we truncated our transect data at 35 m perpendicular distance, which led to a decrease in the number of nests from 1411 to 1341. We modelled the data with a half normal cosine function. The effective strip width ('ESW') was 19.1 m with a mean probability of detection of 0.55 (Table 2-4 – Page 129). For 2011, 2012 and 2013, respectively, we estimated bonobo density to be 0.63, 0.51 and 0.55 individuals per square kilometer in the Nkala Forest and 0.56, 0.21 and 0.32 individuals per square kilometer in the Mpelu Forest (Figure 2-2 – Page 130). As results showed large differences between years, especially for Mpelu community, we carried out further analyses to better understand the reason for these variations (Figure 2-3 – Page 131).

In the Mpelu Forest, we found an overall effect of year on nest density (model including year vs. null model, likelihood ratio test, chi square=9.59, df=4, p<0.05). More precisely, our results did not show an influence of year on the distribution of nests on the transects (model with year vs. reduced model lacking year only in the zero inflated part of the model, likelihood ratio test, chi square=3.71, df=2, p=0.16), but highlighted as a trend the influence of year on the number of nests on transects (model with year vs. reduced model lacking year in the count part of the model, likelihood ratio test, chi square=5.03, df=2, p=0.08). We further conducted pairwise comparisons between years, looking at the nest count portion of the model. Results indicated a trend showing a decrease in nest density between 2011 and 2012 (Table 2-5 – Page 129, p=0.050), a significant increase between 2012 and 2013 (Table 2-5, p=0.043) and no significant difference between 2011 and 2013 (Table 2-5, p=0.913). On the other hand, we did not find any effect of year on nest density in the Nkala Forest (model including year vs. null model, likelihood ratio test, chi square=3.27, df=4, p=0.51).

Table 2-4: Bonobo population density and number of adult individuals in 2011, 2012, 2013, respectively, as estimated with Distance 6.0

	% CV	D	D LCL	D UCL	N	N LCL	N UCL
Global estimation[1]	14.38	0.41	0.32	0.56	39	30	53
Mpelu 2011	36.5	0.56	0.27	1.13	31	15	61
Mpelu 2012	27.08	0.21	0.12	0.35	11	7	19
Mpelu 2013	26.24	0.32	0.19	0.53	17	11	28
Nkala 2011	27.85	0.63	0.36	1.12	20	12	36
Nkala 2012	22.65	0.51	0.32	0.79	16	11	25
Nkala 2013	33.54	0.55	0.28	1.07	17	9	35
Lokoso&Mankere 2011	0	0	0	0	0	0	0
Lokoso&Mankere 2012	0	0	0	0	0	0	0
Lokoso&Mankere 2013	0	0	0	0	0	0	0

We modelled data with a half normal cosine function and used a truncation distance of 35 m. We obtained an effective strip width (‘ESW’) of 19.1 m and a mean probability of detection of 0.55. %CV= Coefficient of Variation for the density estimate. D=density estimate. D LCL= Lower confidence limit (95%) of the density estimate. D UCL= Upper confidence limit (95%) of the density estimate. N= community size estimate (number of adults). N LCL= Lower confidence limit (95%) of the community size estimate. N UCL= Upper confidence limit (95%) of the community size estimate ([1]the global estimate was derived by weighting data with the area of the three parts of the study site).

Table 2-5: Variation in the density estimate between years (results of the zero inflated Generalized Linear Model with a negative binomial error structure and log link function)

Count model (with 2011 in the intercept)				
	Estimate	**Std. Error**	**z value**	**P value**
Intercept	1.172	0.311	3.763	**<0.001**
Year 2012	-0.685	0.349	-1.958	**0.050**
Year 2013	0.038	0.354	0.109	0.913
Ac.term	0.467	0.146	3.181	**0.001**
Count model (with 2012 in the intercept)				
	Estimate	**Std. Error**	**z value**	**P value**
Intercept	0.487	0.337	1.445	0.148
Year 2011	0.685	0.349	1.958	**0.050**
Year 2013	0.723	0.358	2.022	**0.043**
Ac.term	0.467	0.146	3.181	**0.001**

‘Year’ was dummy coded. The intercept represents 2011 in the first table and 2012 in the second table.

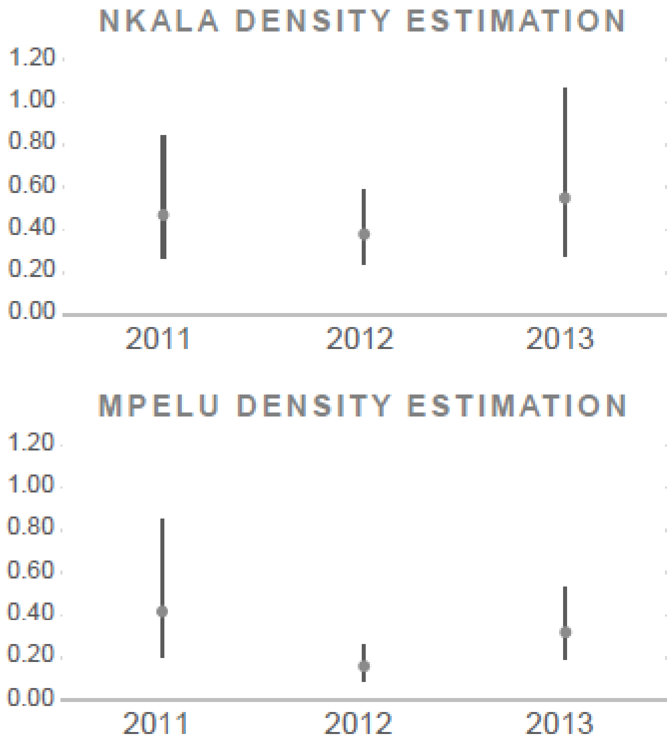


Figure 2-2: Bonobo population density over the three year period (2011, 2012 and 2013)

Points represent the population density estimation, with lines added showing the lower and upper boundary of the 95% confidence interval.

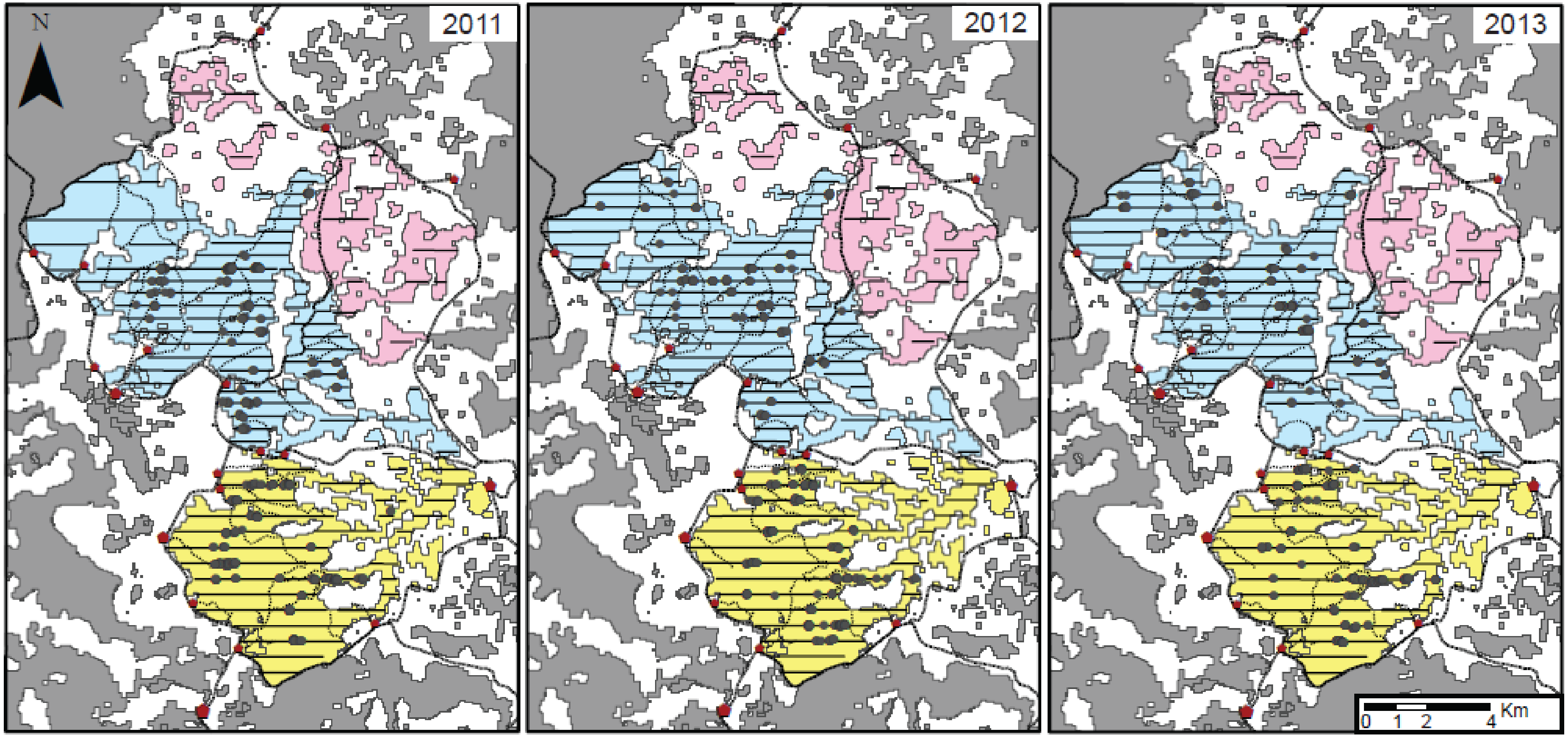


Figure 2-3: Map of the nests found on the transects during each survey (2011, 2012 and 2013)

We here indicate nests as grey points. The different forest colours represent the area subdivisions used for our population density estimation. The transect lines have been added as well (see Table 2-2 – Page 120 for the exact total effort of each year). Villages, roads and main forest paths are represented as in Figure 2-1 – Page 115.

V.2 Variation in fruit availability between years

Fruit availability showed high variation between the two years of data collection (Figure 2-4), with large differences between plots as well (Figure 2-5 – Page 133). Analysis revealed that the overall effect of seasonality was significant (model including date, forests and their interaction vs. model including only forest, $F_{2,106}=3.14$, $p<0.05$). The pattern of seasonality was similar in both forests (model including the interaction vs. model without it, $F_{2,106}=1.90$, $p=0.15$) and was significant in both forests (model with date and forest vs. model lacking date, $F_{2,106}=3.51$, $p<0.05$). We also found that fruit availability was significantly higher in the Nkala Forest (Table 2-6, $p<0.001$). A representation of fruit availability with the fitted model is presented in Figure 2-6 – Page 134.

Table 2-6: Variation in fruit availability between years (result of the Generalized Linear Model with a Gaussian error structure)

	Estimate	**Std. Error**	**t value**	**P value**
Intercept	5.668	0.074	76.285	**<0.001**
Nkala Forest	0.868	0.105	8.268	**<0.001**
sin (date)	0.197	0.074	2.649	**0.009**
cos (date)	-0.003	0.074	-0.039	0.969
Ac.term	0.251	0.053	4.753	**<0.001**

Here we show the results of the model, with sine and cosine of date representing seasonal patterns, and forest and an autocorrelation term (Ac.term) as predictors. Results indicate that forest had a significant effect on fruit availability (Mpelu Forest is included in the intercept as it is a categorical predictor). A significant effect of the seasonal pattern was obtained by comparing this model with a null model lacking date ($F_{2,106}=3.51$, $p<0.05$).

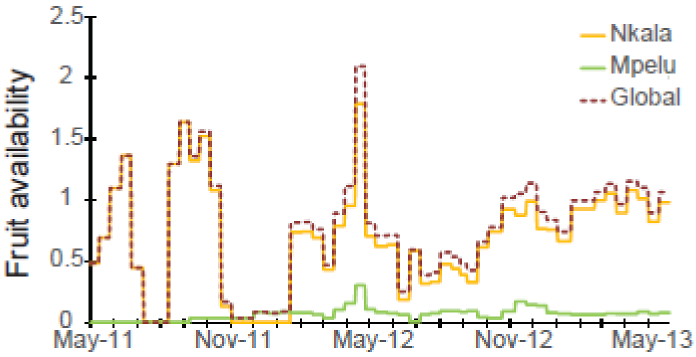


Figure 2-4: Global fleshy fruit availability and distribution per year

This figure represents the daily fleshy fruit availability of the forest used for the cohesiveness model in the Nkala and Mpelu Forests (used in Model2), as well as the sum for both forests together ('Global', used in Model1).

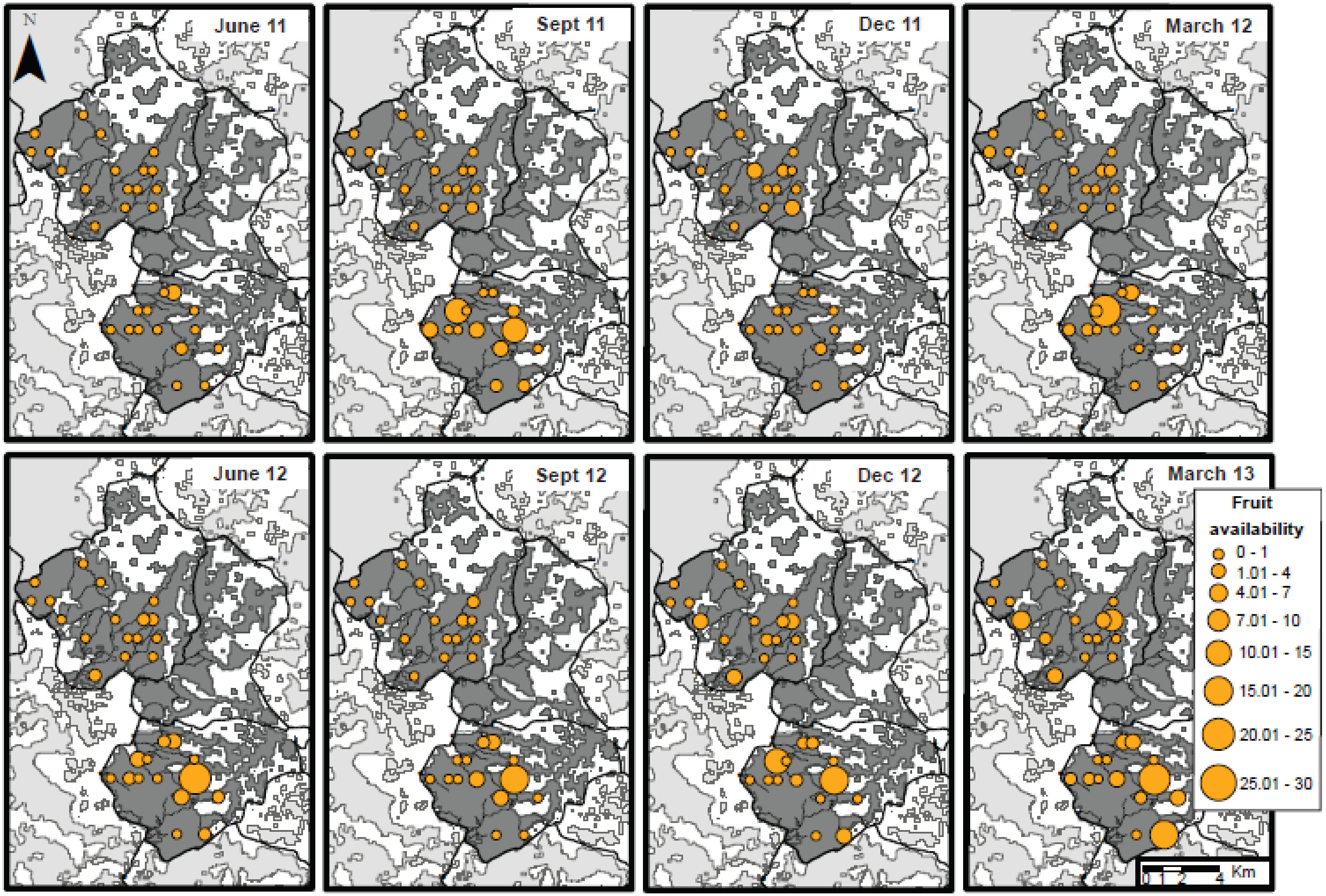


Figure 2-5: Maps of fleshy fruit availability and changes over time for each fruit tree plot *(see legend next page)*

Figure 2-5: The availability of fleshy fruit was calculated as the sum of the basal areas of the fruit-bearing observed in the plot, which was then divided by the plot area to reveal an index per hectare, similar to the fleshy fruit availability calculated for the nesting sites and the forest. Here we show a representation of the three-month mean. Circle sizes are proportional to the availability of fleshy fruits in the plots. Villages, roads and main forest paths are represented as in Figure 2-1 - Page 115.

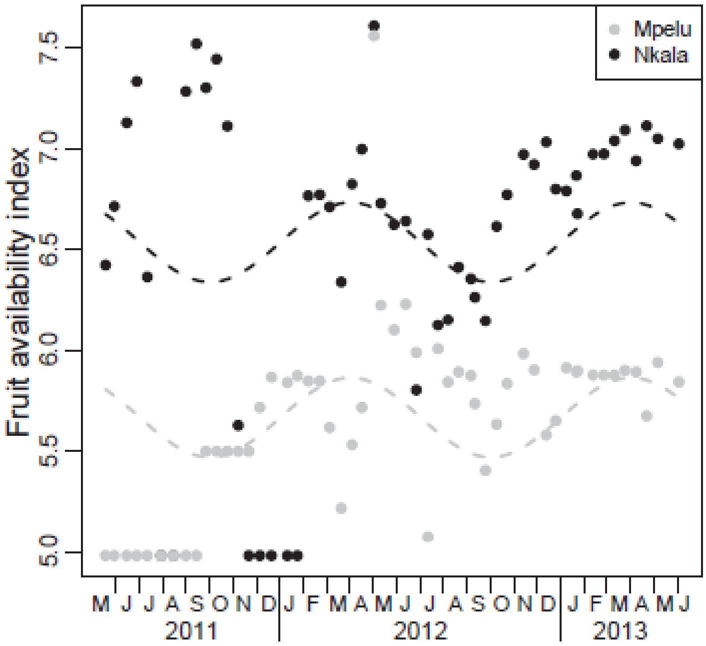


Figure 2-6: Temporal variation of fleshy fruit availability in ‘Nkala’ and ‘Mpelu’ forest

The results from the Nkala Forest are indicated in black and Mpelu in grey. Points represent fleshy fruit availability index every two weeks. Dashed lines indicate the fitted model. The dotted lines have the same amplitude as the model and revealed no significant interaction between seasonality and forest ($F_{2,106}$=1.90, p=0.15). The effect of seasonality was significant ($F_{2,106}$=3.51, p<0.05), and fruit availability clearly differed between the two forests (estimate=0.868, SE=0.105, t-value:8.268, p<0.001).

V.3 **Effect of fruit availability on bonobo social cohesiveness**

Because bonobo density varied between years in the Mpelu Forest, we hypothesized that, rather than having two communities within the study site, we might actually have one single large community, which regularly subdivides into smaller subgroups. Moreover, nest counts in some nesting sites were larger than the independently-derived estimation of the numbers of nest-building individuals in the two purported separate communities, suggesting that the two subgroups (if indeed they are separate subgroups) might sometimes aggregate (Figure 2-7 – Page 136, 80% of nesting site observations present a ratio of the nest count divided by the estimation of nest-building individuals equals or above 1). For this reason, when we analysed the effects of environmental factors on bonobo cohesiveness at nesting sites, we first compared two models representing either a single community hypothesis or a two community one. We compared the AICs of the two models to derive the most likely community composition of the area. Results clearly indicated that the ‘two community’ hypothesis better explains the number of nests in the nesting sites (comparisons of the AIC of the two models, Model1: one community, AIC=572 vs. Model2: two communities: AIC=539). The overall effect of the environmental variables was significant in the two communities model (χ^2= 11.42, df= 4, $p<0.05$), and the model revealed that ‘fruit availability at the nesting site’ significantly influenced the number of nests in nesting sites (Table 2-7 – Page 136, $p<0.05$, Figure 2-8 – Page 137) along with a trend for a positive influence of ‘density of suitable nesting trees’ (Table 2-7, p=0.050), but no influence of the ‘fruit availability in the forest’ (Table 2-7, p=0.249). ’Rainfall’ and the two predictors of human activity did not reveal any influence on the nest grouping patterns at the study site (Table 2-7).

Table 2-7: Effect of the environmental factors on nest community size (Generalized Linear Model Models with negative binomial error structure and log link function)

Two community hypothesis				
	Estimate	**Std.Error**	**z value**	**P value**
Intercept	0.287	0.035	8.304	**<0.001**
Density suitable nesting trees	0.070	0.036	1.960	**0.050**
Fruit availability forest	0.049	0.043	1.152	0.249
Fruit availability nesting site	0.109	0.046	2.381	**0.017**
Village influence	0.011	0.065	0.177	0.860
Human forest use	0.045	0.040	1.117	0.264
Rainfall	-0.016	0.041	-0.388	0.698

This table shows the result of the 'two community' hypothesis and the result of 'One community' hypothesis are not shown. P-values of the predictors revealed a significant influence of 'fruit availability at the nesting site' and a trend for a positive influence of 'density of suitable nesting trees' on the number of nests at a nesting site. The autocorrelation term was removed from the model as it was non-significant (p=0.42).

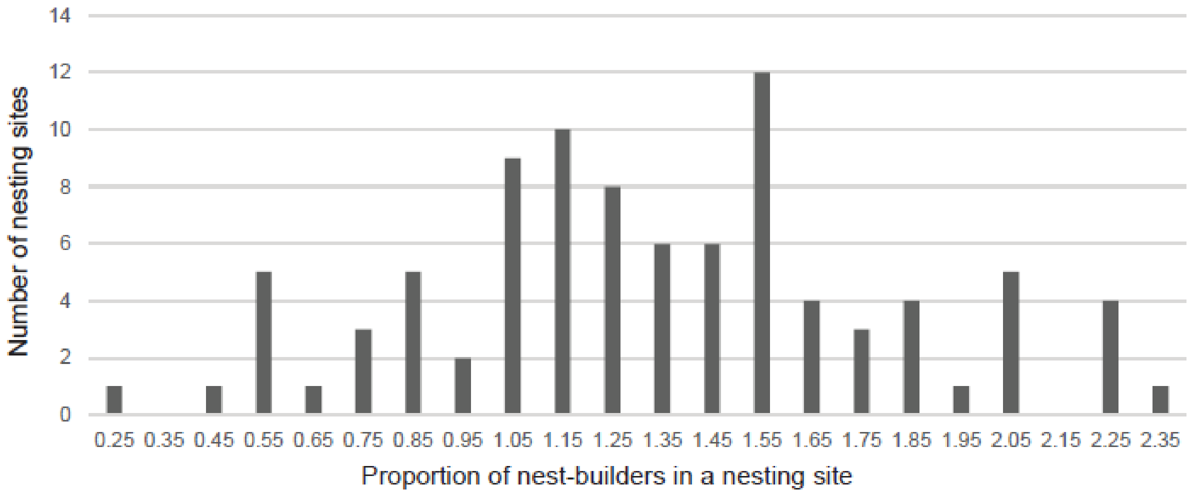


Figure 2-7: Frequency of the proportion of nest-building bonobos present at each nesting site

We calculated the proportion of nest-building bonobos as the number of nests divided by the estimated number of nest-builders in the community.

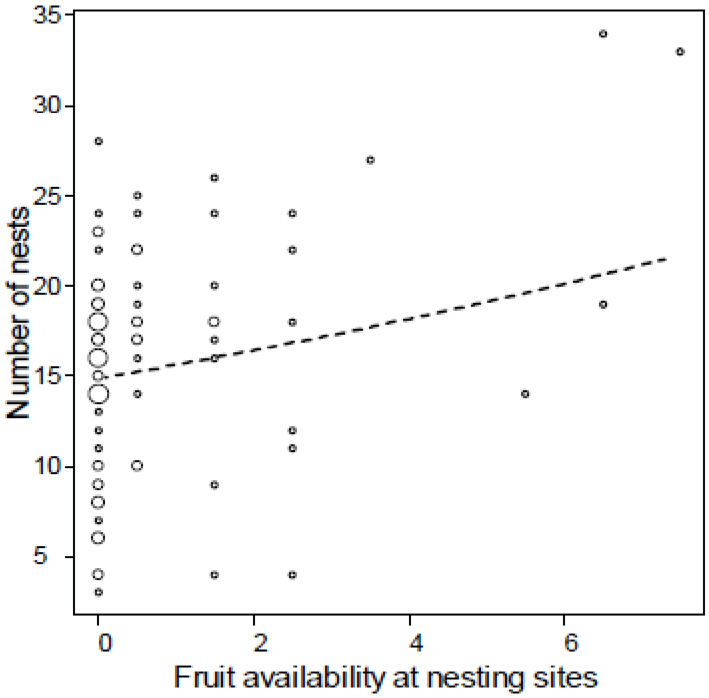


Figure 2-8: Number of nests at a nesting site as a function of fruit availability

The area of the circles indicate the number of nesting sites per fruit availability and number of nests. The dashed line represents the fitted model.

VI DISCUSSION

The primary aim of this study was to investigate the effects of fruit availability on bonobo cohesiveness at nesting sites in the forest-savannah mosaic of western DRC. This is a particularly interesting environment in which to study this phenomenon given its large spatio-temporal variation of resource availability. As expected, results indicated that fruit availability followed a seasonal pattern but also differed significantly in the various sampled forests (Figure 2-6 – Page 134). This latter finding was not surprising given that forest patches are composed of numerous micro-habitats in which the dominance of certain tree species varies. It also suggests that bonobos should be obligated to adapt their foraging strategies (daily travelled distance, party size, etc.) to the specific characteristics of their home range forests. Global fruit availability, however, did not seem to influence night grouping patterns, as only the availability of fruits at nesting sites was related to bonobo community cohesiveness (Table 2-7 – Page 136). Finally, our study of bonobo population density provided the quite unexpected result that community size varied between years in one of the studied forests (Mpelu). Additional long term studies including direct observations of bonobos would help determine whether or not this pattern is unique to our study region or is a common one for bonobos across their range.

Several competing hypotheses can be proposed to explain this surprising temporal variation in bonobo density. First we could argue that the variation is merely the result of sampling artefacts (nests) instead of the bonobos themselves. This is unlikely, however, as the transect effort was similar for each year of the study (81.4km, 111km and 108.9km for respectively 2011, 2012 and 2013), and the models of bonobo density variation gave accurate results. Those models indicated that the bonobos tended to use the same areas for nesting year after year (the effect of year was non-significant in the zero inflated part of the model, $p=0.15$), even when their average community size varied. This clumped distribution of nests on some of the transects suggests that bonobos maximize their access to feeding 'hot-spots'. This interpretation is supported by the results of another study which was carried out in the area, which found that variation along transects in bonobo nest density was explained by the availability of fleshy fruits and edible terrestrial herbaceous vegetation, as well as by previous evidence of nests (i.e., the nest density of a previous survey; Serckx *et al.* in prep). A second hypothesis that might explain the variation in bonobo density is the impact of poaching or disease events, two major threats to bonobo survival across their range (IUCN and ICCN 2012). Although this might explain the apparent population decrease between 2011 and 2012, but such events are nearly impossible to observe in the field (Hohmann pers. comm.) and were not observed by WWF trackers or the local community. Nevertheless the apparent high increase in bonobo density between 2012 and 2013 (from 0.21 to 0.32 ind / km², corresponding to 6 individuals being added to the community; Table 2-4 – Page 129) and the non-significant difference in bonobo density between 2011 and 2013 (Table 2-5 – Page 129) suggest that the poaching / disease hypothesis is insufficient to explain the variation in community size at our site. Finally, the density variation might have a very simple explanation: perhaps the study site did not encompass the entire home range of both communities. Previous studies have shown seasonal and yearly variations in home range size (Kano and Mulawva 1984), with overlaps between community home ranges of the same bonobo population (Idani 1990, Lacambra et al. 2005). Also fruit availability in the Mpelu Forest was significantly lower than in the Nkala Forest ($p<0.001$, Table 2-6 – Page 132) during the entire study, suggesting that the Mpelu community might have to adapt their foraging strategies to relative food scarcity. This hypothesis is reinforced by our observation of bonobo signs in 2013, at the north-west boundary of the study site, suggesting they also use the western forest patches which we did not survey. The home ranges of the bonobos which were estimated at the beginning of the WWF habituation program may then need to be readjusted to take into account the new picture painted by cumulative years of density estimation and direct observations as habituation progresses.

Our results show that the overall food had no clear influence on night time grouping patterns, as we found only a significant influence of local fruit availability on nest numbers, but no influence of the overall fruit availability of the forest (Table 2-7 – Page 136). This finding is consistent with the results of previous studies in the dense forests of central DRC, in which bonobos were found to aggregate at night close to food 'hot-spots' (Fruth pers. comm.) and in which fruit availability did not explain party size (Hohmann et al. 2006, Mulavwa et al. 2010). Our model indicated a trend for the density of nesting-tree species having a positive influence on bonobo grouping patterns. Bonobos are known to have preferences for certain tree species with the right leaf sizes and branch resistance in which to build their nests (Fruth 1995, Mulavwa et al. 2010, Fruth pers. comm.). The high abundance of these nesting-tree species in the Nkala and Mpelu forests probably explains why this factor had only a weak influence on bonobo social cohesiveness. In addition, the absence of a significant impact of human activities on the bonobos nesting patterns should be interpreted with caution and may be restricted to our study site, where the local ethnic group does not hunt bonobos due to ancestral taboos (Inogwabini et al. 2008).

Our results, however, include the unexpected discrepancy that the nest counts at nesting sites were often higher than the nest-building community size estimated in the home range of the respective bonobo community (Figure 2-7 – Page 136). Studies of bonobos and chimpanzees have generally shown opposite results, reflecting the fact that all community members, in both species, commonly do not sleep together at one nesting site (Mulavwa et al. 2010). This particular result may be due to an underestimation of the number of nest-building individuals at our study site. First, when we estimated bonobo density, we used a nest production rate obtained at another study site. Second, as we have already highlighted when explaining the yearly variation in the population density of the Mpelu community, we probably failed to account for the entire home range of the two communities. Since we calculated the number of individuals per community by multiplying the population density of each community by the respective home range area, our underestimation of the home range sizes likely led to a subsequent underestimation in the community size. This explanation is supported by the direct observations of bonobos by WWF trackers who made regular counts and produced slightly higher population estimates than our study (WWF estimates in 2013: 21 individuals in Nkala and 40 individuals in Mpelu although Mpelu community can be divided in two sub-groups – Lahann pers. comm. – vs. 17 individuals in each community in our study, Table 2-4 – Page 129). It is possible, however, that the bonobos may have on occasions built more than one nest prior to sleeping, or they may have reused nesting sites over successive nights. Previous studies carried out in dense forests have also shown that separate bonobo sub-communities sometimes join together into one larger community (Idani 1990, Kano 1992). This might explain large variation in nesting site size, but the results of modelling clearly favour the hypothesis that two separate communities are present in our study region. On the other hand, in our study we probably over-represented larger nest groups as we used only nesting sites previously located by the WWF trackers, who, when they had to make a choice, preferentially followed the largest bonobo parties for the purpose of habituation. Caution is therefore required when extrapolating average nest group size from our results, and we do not do it here. Overall, however, our findings still suggest that bonobos tend to aggregate as the evening approaches (Figure 2-7 – Page 136), as bonobos from dense forests do (Hohmann et al. 2006, Mulavwa et al. 2010, Fruth pers. comm.), and despite the fact that they have to deal with high variation in fruit availability in the forest-savannah mosaic. This supports the hypothesis that chimpanzee and bonobo grouping patterns have been formed by a long process of ecological and behavioural adaptations rather than reflecting current environmental variation (Furuichi 2009).

This study provides the first data on bonobo social cohesiveness in a forest-savannah mosaic, and also suggests interesting new approaches for conservation programs. First, the importance of food 'hot-spots' indicates that well-defined areas should be selected and made the focus of the integrated management of conservation programs in reserves or logging concessions. Secondly, our results indicating the importance of yearly variation in home range size underlines the importance of establishing connections between forests. This is important not only for the home range adaptations of bonobos to changing fruit availability, but for female migration between communities at maturity, both of which are crucial for the long term survival of the species.

Our overall conclusions will need to be confirmed by direct observations, but strongly indicate that bonobos remain highly socially cohesive in the forest-savannah mosaic of western DRC. That this is the case in a region where fruit availability shows high variability in over time and across space, suggests that the grouping patterns of the species are not driven by current environmental conditions. However, further studies using systematic methodology are required in order to compare the influence of fruit availability on bonobo and chimpanzee social cohesiveness across all their habitat ranges. This should allow us to determine whether the differences in grouping patterns between bonobos and chimpanzees are intrinsic to the species. Do they result from specific evolutionary events in the context of past environmental contexts or do they mainly reflect current variation in food availability in the ranges of chimpanzee and bonobos? Further research should also be conducted over larger spatial scales and in human-modified habitats, such as in logging concessions, in order to shed light on the plasticity of social structure in both species, in particular in regard to the potential impacts of human global landscape modification, e.g. resource-extraction, the opening of forests, forest fragmentation and / or increased human agricultural activity. In addition to those results, we have also presented here the first precise density estimation of bonobos for this unique habitat-type, which has until now been one of the least well-investigated ecotones within the bonobo range. Our estimation of the bonobo population density in this area falls within the range of population densities found across Congo Basin Cuvette (IUCN 2013), suggesting that the Lake Tumba Landscape harbours a significant population of bonobos and urgently requires further surveys in order to allow us to more accurately estimate the global bonobo population size (IUCN and ICCN 2012). Furthermore, our results suggest that bonobos living in forest-savannah mosaics may be obligated to adapt their foraging strategies to the availability of fruit by significantly altering their home ranges. This finding should be investigated further with regards to its consequences for the conservation of this species within fragmented habitats. Finally, we would like to suggest that, whenever possible, researchers make use of data covering a period of several years when modelling great ape densities, as this should enable to better interpret changes in communities densities which are of vital importance when making species or site comparisons.

VII PUBLIC ACCESS TO DATA

All raw data from the survey on apes are archived into the IUCN/SSC A.P.E.S. database (http://apes.eva.mpg.de/) (Kühl et al. 2007).

VIII ACKNOWLEDGMENTS

We would like to thank WWF-DRC, and especially Petra Lahann, for their support in the field, as well as the Minister of Foreign Affairs and International Cooperation of The Democratic Republic of The Congo who permitted us to conduct our research. We are also grateful to Fiona Maisels and Celine Devos for their invaluable helps in the design of our study. This research would not have been possible without the help of our local field guides. Ciceron Mbuoli Mbenkira deserves a special thank you for his incredible work during the entire period of data collection. We also thank the Max Planck Society, Roger Mundry for providing us with R scripts and statistical support, and Barbara Fruth, Fany Brotcorne and Cleve Hicks for their suggestions during the preparation of this paper. Finally, we thank Takeshi Furuichi and an anonymous reviewer for their helpful comments.

IX REFERENCES

Ancrenaz, M., R. Calaque, and I. Lackman-Ancrenaz. 2004. Orangutan nesting behavior in disturbed forest of Sabah, Malaysia: implications for nest census. International Journal of Primatology 25:983–1000.

Basabose, A. K., and J. Yamagiwa. 2002. Factors affecting nesting site choice in Chimpanzees at Tshibati, Kahuzi-Biega National Park: influence of sympatric Gorillas. International Journal of Primatology 23:263–282.

Beaune, D., F. Bretagnolle, L. Bollache, C. Bourson, G. Hohmann, and B. Fruth. 2013. Ecological services performed by the bonobo (*Pan paniscus*): seed dispersal effectiveness in tropical forest. Journal of Tropical Ecology 29:367–380.

Boesch, C. 1996. Social grouping in Taï chimpanzees. Pages 101–113 *in* W. C. McGrew, L. F. Marchant, and T. Nishida, editors. Great Apes Societies. Cambridge University Press, Cambridge.

Brugiere, D., and D. Sakom. 2001. Population density and nesting behaviour of lowland gorillas (*Gorilla gorilla gorilla*) in the Ngotto forest, Central African Republic. Journal of Zoology 255:251–259.

Buckland, S. T. ., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Page 432. Oxford University Press, Oxford.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: A practical information-theoretic approach. Page 353. Springer, New York.

Chapman, C. A., F. J. White, and R. W. Wrangham. 1994. Party Size in Chimpanzees and Bonobos. Pages 41–57 *in* R. Wrangham, W. McGrew, F. de Waal, and P. Heltne, editors. Chimpanzee Cultures. Harvard University Press, Cambridge.

Devos, C., and A. Laguardia. 2011. Local assessment of gorilla nest decay rate at Mikongo Conservation Centre, Lopé National Park: Refining Population Density Estimates. Page 27.

Devos, C., C. Sanz, D. Morgan, J.-R. Onononga, N. Laporte, and M.-C. Huynen. 2008. Comparing Ape densities and habitats in northern Congo: surveys of sympatric Gorillas and Chimpanzees in the Odzala and Ndoki Regions. American Journal of Primatology 70:439–451.

Djoufack, S. D., B. A. Nkongmeneck, J. Dupain, S. Bekah, K. K. Bombome, M. A. Epanda, L. Van Elsacker, and Editeurs. 2007. Manuel d'identification des fruits consommés par les gorilles et les Chimpanzés des basses terres de l'Ouest; Espèces de l'écosystème du Dja (Cameroun). Page 107 (M. A. Epanda and L. Van Elsacker, Eds.).

Dobson, A. J. 2002. An introduction to generalized linear models. Boca Raton [etc.], Chapman & Hall/CRC.

Fox, J., and S. Weisberg. 2011. An R companion to applied regression. Page 472. Sage, Thousant Oaks CA.

Fruth, B. 1995. Nests and nest groups in wild bonobos: ecological and behavioural correlates. PhD Thesis. Ludwig-Maximilian University.

Fruth, B., and G. Hohmann. 1993. Ecological and behavioral aspects of nest building in wild Bonobos (*Pan paniscus*). Ethology 94:113–126.

Fruth, B., and G. Hohmann. 1996. Nest building behavior in the great apes: the great leap forward? Pages 225–240 *in* W. McGrew, L. Marchant, and T. Nishida, editors. Great Apes Societies. Cambridge University Press, Cambridge.

Furuichi, T. 1997. Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. International Journal of Primatology 18:855–875.

Furuichi, T. 2009. Factors underlying party size differences between chimpanzees and bonobos: a review and hypotheses for future study. Primates 50:197–209.

Furuichi, T., and C. Hashimoto. 2002. Why female bonobos have a lower copulation rate during estrus than chimpanzees. Pages 156–167 *in* C. Boesch, G. Hohmman, and L. Marchant, editors. Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, New York.

Furuichi, T., and C. Hashimoto. 2004. Botanical and topographical factors influencing nesting-wste selection by Chimpanzees in Kalinzu Forest, Uganda. International Journal of Primatology 25:755–765.

Furuichi, T., C. Hashimoto, and Y. Tashiro. 2001. Extended application of a marked-nest census method to examine seasonal changes in habitat use by Chimpanzees. International Journal of Primatology 22:913–928.

Furuichi, T., M. Mulavwa, K. Yangozene, B. Motema-salo, G. Idani, and H. Ihobe. 2008. Relationships among fruit abundance, ranging rate, and party size and composition of Bonobos at Wamba. Pages 135–149 *in* T. Furuichi and J. Thompson, editors. The bonobos: Behavior, Ecology, and Conservation. Springer, New York.

Grossmann, F., J. A. Hart, A. Vosper, and O. Ilambu. 2008. Range occupation and population estimates of Bonobos in the Salonga National Park: application to large-scale surveys of Bonobos in the Democratic Republic of Congo. Pages 189–216 *in* T. Furuichi and J. Thompson, editors. The bonobos: Behavior, Ecology, and Conservation. Springer, New York.

Hashimoto, C. 1995. Population census of the chimpanzees in the Kalinzu Forest, Uganda: comparison between methods with nest counts. Primates 36:477–488.

Hernandez-aguilar, R. A. 2006. Ecology and nesting patterns of chimpanzees (*Pan troglodytes*) in Issa, Ugalla, Western Tanzania. PhD thesis. University of Southern California.

Hernandez-Aguilar, R. A., J. Moore, and C. B. Stanford. 2013. Chimpanzee nesting patterns in savanna habitat: environmental influences and preferences. American journal of primatology 75:979–994.

Hickey, J. R., J. Nackoney, N. P. Nibbelink, S. Blake, A. Bonyenge, S. Coxe, J. Dupain, M. Emetshu, T. Furuichi, F. Grossmann, P. Guislain, J. Hart, C. Hashimoto, B. Ikembelo, O. Ilambu, B.-I. Inogwabini, I. Liengola, A. L. Lokasola, A. Lushimba, F. Maisels, J. Masselink, V. Mbenzo, N. M. Mulavwa, P. Naky, N. M. Ndunda, P. Nkumu, V. Omasombo, G. E. Reinartz, R. Rose, T. Sakamaki, S. Strindberg, H. Takemoto, A. Vosper, and H. S. Kühl. 2013. Human proximity and habitat fragmentation are key drivers of the rangewide bonobo distribution. Biodiversity and Conservation 22:3085–3104.

Hohmann, G., A. Fowler, A. Sommer, and S. Ortmann. 2006. Frugivory and gregariousness of Salonga bonobos and Gashaka chimpanzees: the influence of abundance and nutritional quality of fruit. Pages 123–159 *in* G. Hohmann, M. M. Robbins, and C. Boesch, editors. Feeding ecology in apes and other primates. Cambridge University Press, Cambridge.

Hohmann, G., and B. Fruth. 2002. Dynamics in social organization of bonobos (*Pan paniscus*). Pages 138–150 *in* C. Boesch, G. Hohmman, and L. F. Marchant, editors. Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, New York.

Idani, G. 1990. Relations between unit-groups of bonobos at Wamba, Zaire: encounters and temporary fusions. African Study Monographs 11:153–186.

Inogwabini, B., M. Bewa, M. Longwango, M. Abokome, and M. Vuvu. 2008. The Bonobos of the Lake Tumba – Lake Maindombe Hinterland: threats and opportunities for population conservation. Pages 273–290 *in* T. Furuichi and J. Thompson, editors. The bonobos: Behavior, Ecology, and Conservation. Springer, New York.

Inogwabini, B., B. Matungila, L. Mbende, M. Abokome, and T. Tshimanga. 2007. Great apes in the Lake Tumba landscape, Democratic Republic of Congo: newly described populations. Oryx 41:1–7.

IUCN. 2013. IUCN Red List of Threatened Species. www.iucnredlist.org.

IUCN, and ICCN. 2012. Bonobos (*Pan paniscus*): Conservation Strategy 2012-2022. Page 65. IUCN/SSC Primate Specialist Group & Institut Congolais pour la Conservation de la Nature, Gland, Switserland.

Jackman, S. 2012. pscl: classes and methods for R developed in the political science.R package. Computational Laboratory, Stanford University. Department of Political Science, Stanford University, Stanford, California.

Junker, J., S. Blake, C. Boesch, G. Campbell, L. Du Toit, C. Duvall, A. Ekobo, G. Etoga, A. Galat-Luong, J. Gamys, J. Ganas-Swaray, S. Gatti, A. Ghiurghi, N. Granier, J. Hart, J. Head, I. Herbinger, T. C. Hicks, B. Huijbregts, I. S. Imong, N. Kuempel, S. Lahm, J. Lindsell, F. Maisels, M. McLennan, L. Martinez, B. Morgan, D. Morgan, F. Mulindahabi, R. Mundry, K. P. N’Goran, E. Normand, A. Ntongho, D. T. Okon, C.-A. Petre, A. Plumptre, H. Rainey, S. Regnaut, C. Sanz, E. Stokes, A. Tondossama, S. Tranquilli, J. Sunderland-Groves, P. Walsh, Y. Warren, E. A. Williamson, and H. S. Kuehl. 2012. Recent decline in suitable environmental conditions for African great apes. Diversity and Distributions 18:1077–1091.

Kano, T. 1992. The Last Ape: Pygmy Chimpanzee behavior and ecology. Page 248. Stanford University Press, Stanford.

Kano, T., and M. Mulavwa. 1992. Appendix. Pages 225–232 *in* T. Kano, editor. The Last Ape: Pygmy Chimpanzee behavior and ecology. Stanford University Press, Stanford.

Kano, T., and M. Mulawva. 1984. Feeding ecology of the pygmy chimpanzees (*Pan paniscus*) of Wamba. Pages 233–274 *in* R. L. Susman, editor. The Pygmy Chimpanzee, evolutionary bology and behavior. Plenum Press, New York.

Kawamoto, Y., H. Takemoto, S. Higuchi, T. Sakamaki, J. A. Hart, T. B. Hart, N. Tokuyama, G. E. Reinartz, P. Guislain, J. Dupain, A. K. Cobden, M. N. Mulavwa, K. Yangozene, S. Darroze, C. Devos, and T. Furuichi. 2013. Genetic structure of wild bonobo populations: diversity of mitochondrial DNA and geographical distribution. PloS ONE 8:e59660.

Kideghesho, J. R., E. Røskaft, and B. P. Kaltenborn. 2006. Factors influencing conservation attitudes of local people in Western Serengeti, Tanzania. Biodiversity and Conservation 16:2213–2230.

Koops, K. 2011. Elementary technology of foraging and shelter in the chimpanzees (*Pan troglodytes verus*) of the Nimba Mountains , Guinea. PhD Thesis. University of Cambridge.

Koops, K., W. C. McGrew, H. Vries, and T. Matsuzawa. 2012. Nest-building by Chimpanzees (*Pan troglodytes verus*) at Seringbara, Nimba Mountains: antipredation, thermoregulation, and antivector hypotheses. International Journal of Primatology 33:356–380.

Kouakou, C. Y., C. Boesch, and H. Kuehl. 2009. Estimating chimpanzee population size with nest counts: validating methods in Taï National Park. American journal of primatology 71:447–457.

Van Krunkelsven, E. 2001. Density estimation of Bonobos (*Pan paniscus*) in Salonga National Park, Congo. Biological Conservation 99:387–391.

Kuehl, H., F. Maisels, M. Ancrenaz, and E. . Williamson. 2008. Best Practice Guidelines for Surveys and Monitoring of Great Ape Populations. Page 32. Gland, Switzerland.

Kühl, H. S., L. Williamson, C. Sanz, and C. Boesch. 2007. Launch of A.P.E.S. database. Gorilla Journal 34:20–21.

Lacambra, C., J. Thompson, T. Furuichi, H. Vervaecke, and J. Stevens. 2005. Bonobo (*Pan paniscus*). Pages 83–104 *in* J. Caldecott and L. Miles, editors. World atlas of great apes and their conservation. Cambridge Univ Press, London, England.

Laing, S. E., S. T. Buckland, R. W. Burn, and D. Lambie. 2003. Dung and nest surveys : estimating decay rates. Journal of Applied Ecology 40:1102–1111.

Malenky, R. K., and R. W. Wrangham. 1994. A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako Forest, Zaire, and *Pan troglodytes* in the Kibale Forest, Uganda. American Journal of Primatology 32:1–12.

Mathewson, P., S. Spehar, E. Meijaard, Nardiyono, Purnomo, A. Sasmirul, Sudiyanto, Oman, Sulhnudin, Jasary, Jumali, and A. Marshall. 2008. Evaluating orangutan census techniques using nest decay rates: implications for population estimates. Ecological applications : a publication of the Ecological Society of America 18:208–221.

Mohneke, M., and B. Fruth. 2008. Bonobo (*Pan paniscus*) density estimation in the SW-Salonga National Park, Democratic Republic of Congo: common methodology revisited. Pages 151–166 *in* T. Furuichi and J. Thompson, editors. The bonobos: Behavior, Ecology, and Conservation. Springer, New York.

Mulavwa, M., K. Yangozene, M. Yamba-Yamba, B. Motema-Salo, N. Mwanza, and T. Furuichi. 2010. Nest groups of wild Bonobos at Wamba: selection of vegetation and tree species and relationships between nest group size and party size. American Journal of Primatology 71:1–12.

Nyariki, D. M. 2009. Household Data Collection for Socio-Economic Research in Agriculture : Approaches and Challenges in Developing Countries. Journal of Social Sciences 19:91–99.

PEN Prototype Questionnaire. 2008. . http://www.cifor.org/fileadmin/fileupload/PEN/pubs/pdf_files/PEN_Prototype_Questionnaire_-_version_4-4_-_September_2008.pdf. Accessed 10 April 2013

Plumptre, A. J., and V. Reynolds. 1997. Nesting behavior of Chimpanzees: implications for censuses. International Journal of Primatology 18:475–485.

Plumptre, A., and V. Reynolds. 1996. Censusing chimpanzees in the Budongo Forest, Uganda. International Journal of Primatology 17:85–99.

Pruetz, J. D., S. J. Fulton, L. F. Marchant, W. C. McGrew, M. Schiel, and M. Waller. 2008. Arboreal nesting as anti-predator adaptation by savanna chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. American journal of primatology 70:393–401.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Reinartz, G. E., B. I. Inogwabini, M. Ngamankosi, and L. W. Wema. 2006. Effects of forest type and human presence on Bonobo (*Pan paniscus*) density in the Salonga National Park. International Journal of Primatology 27:1229–1231.

Rothman, J. M., A. N. Pell, E. S. Dierenfeld, and C. M. Mccann. 2006. Plant choice in the construction of night nests by Gorillas in the Bwindi Impenetrable National Park, Uganda. American journal of physical anthropology 68:361–368.

Russon, A. E., D. P. Handayani, P. Kuncoro, and A. Ferisa. 2007. Orangutan leaf-carrying for nest-building: toward unraveling cultural processes. Animal cognition 10:189–202.

Samson, D. R., and K. D. Hunt. 2012. A thermodynamic comparison of arboreal and terrestrial sleeping sites for dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at the Toro-Semliki Wildlife Reserve, Uganda. American journal of primatology 74:811–888.

Samson, D. R., M. P. Muehlenbein, and K. D. Hunt. 2013. Do chimpanzees (*Pan troglodytes schweinfurthii*) exhibit sleep related behaviors that minimize exposure to parasitic arthropods? A preliminary report on the possible anti-vector function of chimpanzee sleeping platforms. Primates; journal of primatology 54:73–80.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103–113.

Shibia, M. G. 2000. Determinants of attitudes and perceptions on resource use and management of Marsabit National Reserve, Kenya. Journal of Human Ecology 30:55–62.

Stanford, C. B., and R. C. O'Malley. 2008. Sleeping tree choice by Bwindi chimpanzees. American journal of primatology 70:642–649.

Stewart, F. A. 2011. The evolution of shelter: ecology and ethology of chimpanzee nest building. PhD Thesis. University of Cambridge.

Stewart, F. A., J. D. Pruetz, and M. H. Hansell. 2007. Do Chimpanzees build comfortable nests? American journal of primatology 69:930–939.

Sunderland-Groves, J. L., A. Ekinde, and H. Mboh. 2009. Nesting behavior of *Gorilla gorilla diehli* at Kagwene Mountain, Cameroon: implications for assessing group size and density. International Journal of Primatology 30:253–266.

Tailfer, Y. 1989. La foret dense d'Afrique centrale. Identification pratique des principaux arbres, Tome 1 et 2. C.T.A., Wageningen, Pays-Bas.

Thomas, L., S. T. Buckland, E. a Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. Bishop, T. a Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. The Journal of applied ecology 47:5–14.

Thompson, J. A. M. 1997. The history, taxonomy and ecology of the Bonobo (*Pan paniscus* Schwarz, 1929) with a first description of a wild population living in the forest/savanna mosaic habitat. PhD Thesis. University of Oxford.

Thompson, J. A. M. 2001. The status of Bonobos in their southernmost geographic range. Pages 75–81 *in* B. M. F. Galdikas, N. E. Briggs, L. K. Sheeran, G. L. Shapiro, and J. Goodall, editors. All Apes Great and Small Volume I: African Apes. Kluwer Academic / Plenum Publishers, New York.

Tutin, C., R. Parnell, L. White, and M. Fernandez. 1995. Nest building by lowland gorillas in the Lopé Reserve, Gabon: Environmental influences and implications for censusing. International Journal of Primatology 16:53–76.

Vancutsem, C., J. Pekel, J.-P. Kibamba, X. Blaes, C. de Wasseige, and P. Defourny. 2006. Carte de l'occupation du sol de la République Démocratique du Congo. (P. U. de Louvain, Ed.). Bruxelles.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Page 495. Springer, New York.

Warnes, G. R., B. Bolker, and T. Lumley. 2013. gtools: Various R programming tools.

De Wasseige, C., D. Devers, P. De Marcken, R. Eba'a Atyi, R. Nasi, and P. Mayaux. 2009. The forests of Congo Basin - State of forests 2008. Page 425. Kinshasa.

White, F. J., and K. D. Wood. 2007. Female feeding priority in Bonobos, *Pan paniscus,* and the question of female dominance. American journal of primatology 69:1–14.

White, F. J., and R. W. Wrangham. 1988. Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. Behaviour 105:148–164.

Wilks, C. M., and Y. A. Issembe. 2000. Les arbres de la Guinée Equatoriale: Guide pratique d'identification: région continentale. Projet CUREF, Bata, Guinée Equatoriale. Page 546. Prépresse Communications, France.

Wrangham, R. W. 1993. The evolution of sexuality in chimpanzees and bonobos. Human Nature 4:47–79.

Wrangham, R. W. 2000. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. Pages 248–258 *in* P. M. Kappeler, editor. Primate males: Causes and consequences of variation in group composition. Cambridge University Press, Cambridge.

Zeileis, A., C. Kleiber, and S. Jackman. 2007. Regression models for count data in R. Page 23. Vienna.

CHAPTER 3:

SEASONALITY OF BONOBO DIET AND NUTRITIONAL DRIVERS OF PLANT FOOD SELECTION IN FOREST-SAVANNAH MOSAICS

© WWF- Frédéric Créteur

Serckx A, Huynen M-C, Beudels-Jamar R C, Poncin P, Ortmann S, Fruth B, Hohmann G, Kühl H S. Seasonality of Bonobo diet and nutritional drivers of plant food selection in forest-savannah mosaics. *In prep*.

I RÉSUMÉ

Améliorer nos connaissances de l'écologie alimentaire et de la plasticité des régimes alimentaires des primates est essentiel dans le contexte actuel de modification global des paysages. En effet, la plupart des espèces de primates font actuellement face à de vastes changements de la distribution de leurs habitats et des ressources alimentaires associées. Un nombre grandissant d'études approche ce thème de recherche. Néanmoins, les objectifs nutritionnels conduisant à la sélection des espèces consommées restent peu étudiés, limitant ainsi l'opportunité d'identifier des modifications de stratégies de recherche alimentaire. Dans cette étude, nous présentons la première description du régime alimentaire des bonobos vivant dans les mosaïques de forêts-savanes de l'ouest de la République Démocratique du Congo. Nous étudions en particulier les patterns saisonniers de consommation des ressources alimentaires et les facteurs nutritionnels conduisant à la sélection de ressources. Nos résultats indiquent que le régime alimentaire du bonobo repose sur très peu d'espèces de plantes, sélectionnées pour leur contenu riche en carbohydrates. De manière inattendue, les bonobos consomment préférentiellement des espèces riches en amidon plutôt qu'en sucre, bien que ce nutriment soit peu digestible. Ce résultat, combiné avec la sélection stricte d'un nombre limité d'espèces, toutes riches en carbohydrates, suggèrent que l'accès aux ressources riches en cette source d'énergie est un facteur limitant dans le site d'étude. Nos analyses plus détaillées des espèces les plus consommées ont mis en évidence trois groupes majeurs d'association d'espèces dans le régime alimentaire. Bien que cette combinaison préférentielle d'espèces soit liée aux patterns saisonniers de fructification, nous démontrons également que l'association spécifique de ces espèces permet de maintenir un équilibre d'apport en nutriments constant dans le temps. De manière intéressante, cet équilibre énergétique est également atteint lorsqu'on ne prend en compte que les trois espèces les plus importantes, suggérant que les bonobos favorisent une stratégie alimentaire visant à équilibrer l'apport en nutriments lorsqu'ils sélectionnent leur nourriture. Pour conclure, ces espèces les plus consommées sont également caractéristiques de différents types d'habitat, ce qui suggère que les bonobos ont probablement adapté leur stratégie de recherche alimentaire en réalisant, quotidiennement, de longs déplacements afin de maintenir cet équilibre nutritionnel.

II ABSTRACT

Improving our knowledge of primate feeding ecology and dietary plasticity is crucial in the current context of global landscape modification. Most primate species have to cope with a large shift in the distribution of their habitat and associated food resources. An increasing number of studies are addressing this topic. However, the nutritional goals driving food species selection remains poorly investigated, limiting our understanding of the modifications of efficiency foraging strategy. In this study, we present the first description of bonobo diet in forest-savannah mosaics of western Democratic Republic of Congo by investigating the seasonality patterns of food consumption and the nutritional drivers of food species selection. Our results indicate that bonobo diet relies on few dominant plant species, which are selected for their carbohydrate contents. Unexpectedly, bonobos preferentially consume species with a high proportion of starch, which is less digestible than sugar. This finding, combined with the strict selection of few rich-carbohydrate species, might indicate that the access to carbohydrate source is a limiting factor in our study site. An in-depth investigation of the most consumed species revealed three major groups of plant species association in daily food consumption. Although the preferential combination of species is related to seasonal fruitage, we also demonstrate that the peculiar association of the species enables to maintain constant nutrient balance over time. Interestingly, this balance of energy is also achieved when accounting only for the three most consumed species, suggesting that bonobos might favour a nutrient balancing strategy to select food species. Finally, as the dominant species are characteristics of various habitat types, it suggests that bonobos have to adapt their foraging strategy by traveling large daily distances in order to maintain the nutritional balance.

Key words: bonobo, feeding ecology, diet plasticity, diet seasonality, nutritional goals, right-angled mixture triangle

III INTRODUCTION

Improving our knowledge of primate feeding ecology is crucial in the current context of global landscape modification (Corlett 2011). Primate habitats are facing structure and dynamics changes, due to primary forests' decrease at the expense of secondary forests (Pan et al. 2011). Besides habitat loss, deforestation and forest degradation may also lead to modification of tree species composition and abundance (Wright 2005). As a consequence, most primate species have to cope with a large shift in the distribution of their habitat and the associated food resources (Fahrig 2003, Fischer and Lindenmayer 2007). An increasing number of studies are addressing the impact of habitat fragmentation on primates (Marsh 2003) showing, in feeding ecology, contrasted diet adjustments such as reduced frugivory (guenons: Tutin 1999), food diversification (spider monkey: Chaves and Stoner 2012), increased reliance on low-quality items (collared lemur: Donati et al. 2011) or on fallback resources (sifaka: Irwin 2008). However, such diet adaptations remain poorly investigated regarding nutritional goals driving food species selection (Felton et al. 2009a), which limits our understanding of the modifications of efficiency foraging strategy (Optimal Diet theory, Emlen 1966).

Information on primate nutritional ecology are still restricted because of difficulties in data collection in the wild (Raubenheimer 2011). Estimates of daily nutrient intake usually require continuous direct observations of at least one individual and the assessment of the actual weight of food items ingested (Felton et al. 2009a). Consequently, such study can only be performed on fully habituated populations, consistently limiting the range of potential candidate populations for nutritional analysis. However, recent advances in methodology suggest the possibility to work with proportion-based instead of absolute values of nutrient intakes (Raubenheimer 2011). Such approach has been integrated within the framework of the right-angled mixture triangle analysis and gives promising results on the understanding of the nutritional priorities of animals (Raubenheimer et al. 2009, Felton et al. 2009b, Raubenheimer 2011, Rothman et al. 2011, Köhler et al. 2012, Johnson et al. 2013). Since this methodology only requires food species identification, it might offer new opportunities for studying primate nutritional ecology.

The case of bonobos (*Pan paniscus*) and chimpanzees (*P. troglodytes*) is of particular interest when characterizing primate dietary plasticity. Both species are known to maintain their frugivorous habits even at times of low fruit availability (White and Lanjouw 1992, Wrangham et al. 1998). In turn, *Pan* species require flexibility in ranging and grouping patterns according to the spatio-temporal fluctuations of food patches (Hashimoto et al. 2003, Lehmann et al. 2007, Mulavwa et al. 2008). But, despite this social flexibility to maximise foraging efficiency, chimpanzees living in dry or fragmented environments present largely reduced diversification in diet as compared to populations of dense forests (Hunt and McGrew 2002, Pruetz 2006, McLennan 2013). Consequences of these peculiar environments in bonobo diet are still unknown.

While chimpanzees have been known for decades to live in savannahs, bonobo distribution was thought to be limited to dense rainforests. This changed in the 1990s, when Thompson identified a bonobo population in the southern extremity of their distribution range, inhabiting a transitional ecotone between moist forests and savannahs (Thompson 1997, 2001). Her discovery changed our perception of the ecological limit of the species range, but bonobos within this habitat remained poorly studied. In 2005, a new population living in forest-savannah mosaics was identified in western Democratic Republic of Congo (DRC) (Inogwabini et al. 2007, 2008). First investigations in the region suggest that this population has probably been isolated from other populations since the Pleistocene (Kawamoto et al. 2013) and that fruit availability follows high spatio-temporal variation within forest patches (Serckx et al. 2014). Consequently, this bonobo population could exhibit unique behavioural and ecological features and studies in this region will offer the opportunity to better understand the full spectrum of bonobo adaptations. In particular, they also promise to shed light on bonobo diet plasticity and feeding constraints in fragmented environments, which is urgently needed in the current context of global landscape modification and climate changes.

In this study, we provide a first description of bonobo diet in forest-savannah mosaics of western DRC. We investigate seasonal patterns of fruit consumption and the nutrient drivers of food species selection in this peculiar environment. Our findings offer the first insights into bonobo diet plasticity and the potential nutritional constraints of living in such fragmented habitats.

IV METHODS

IV.1 Study site

The study site is located in the South of the Lake Tumba landscape in the north-western part of the Democratic Republic of Congo, close to the WWF Malebo research station, in forests contiguous to villages known as Nkala and Mpelu (16.41-16.56°E, 2.45-2.66°S, Figure 3-1 – Page 157). This area can be characterized as a forest-savannah mosaic. The altitude ranges from 300 to 700 m (Inogwabini et al. 2008), and the mean daily temperature fluctuates around 25°C (Vancutsem et al. 2006). Annual rainfall oscillates around 1500-1600 mm, and is interrupted by two dry seasons in February and July-August (Inogwabini et al. 2008). Forests are mostly on *terra firma* soils and are characterized by various habitat types, i.e., re-colonizing *Uapaca sp.*, old secondary, mixed mature, old growth mono-dominant, riverine gallery and Marantaceae forests (Inogwabini et al. 2008). At the time of our data collection, the study site encompassed 170 km², made up of 102 km² of forest patches of various shapes and sizes connected by many corridors. Surrounding savannahs were mainly herbaceous and partially used for cattle ranching. Villages and farms were directly adjacent to the forest and zones of slash and burn agriculture was present inside the forests. Two bonobo communities inhabited the forests, and had been, since 2007, the subject of habituation and conservation measures by the WWF-DRC (Inogwabini et al. 2008).

IV.2 Data collection

Between May 2011 and June 2013, we collected feces in Nkala forest, i.e. the home range of the southern community of the study site (32.45 km² of forests, 16.45-16.56°E, 2.58-2.66°S, Figure 3-1 – Page 157). Feces were collected at nesting sites every morning (one fecal sample below each fresh nest, n=2272, in 270 days). Sleeping site was located the previous evening by WWF trackers who daily followed bonobos for the purpose of the habituation program. Feces were stored in plastic bags and brought to Mbou-Mon-Tour farm where all *in situ* analyses were performed within forty eight hours of collection. Each sample was weighted to the nearest gram (Moscovice et al. 2007) and washed in 1-mm mesh sieves. The contents of each sample were divided into five categories: *(i)* fruits with large seeds, i.e. species for which we could count the number of seeds (including seeds, skin and pulp remains), *(ii)* fruits with small seeds, i.e. with uncountable seeds (seeds, skin and pulp remains), *(iii)* foliage (fiber, digested fragments of leaves and flower), *(iv)* fragments of insects or other animal matter and *(v)* other items. The volume percentage of each category was estimated by 5% interval

(Basabose 2002). We also identified clean fruit seeds to the species level and we counted the large seeds. Non-fruit plant items were identified and described as precisely as possible.

In order to complete the description of bonobo diet, we also recorded food remains along the 179.1 km of transects sampled from May to July 2011, Mid-March to Mid-July 2012 and June to August 2013 (114 transects running from west to east, spaced 500 m and of variable lengths, Figure 3-1 – Page 157; for more details on transect design, see Serckx et al. 2014). We identified food remain species, counted them, and noted which plant part had been eaten.

In order to relate feces contents with fruit availability in the forest, we recorded data on the abundance of fruiting trees between May 2011 and June 2013. From May 2011, we monitored 346 trees with a diameter at breast height (DBH) larger than 10 cm, within 14 plots randomly located in the Nkala forest (0.56 ha in total). In May 2012, in order to improve our representation of fruiting trees, we added 8 additional plots (5.75 ha in total) with 2239 additional trees (for more details, see Serckx et al. 2014). Every two weeks, we visited each of the plots and recorded which trees were fruiting by inspecting their crowns and counting fruits on the ground (Basabose and Yamagiwa 2002). We then calculated an index of fleshy fruit availability. Fruit species considered for this index were derived by selecting tree species *(i)* eaten by bonobos (this study, Kano and Mulavwa 1992, Beaune et al. 2013) or *(ii)* producing fleshy fruits (Tailfer 1989, Wilks and Issembe 2000, Djoufack et al. 2007) (Appendix A, Table 1 – Page 184). We used each tree basal area to estimate canopy volume (Strier, 1989 cited in Basabose, 2002) and calculated a fleshy fruit availability index as: $F_m = \sum p_{ki} * ba_k$ where p is the proportion of trees of species k bearing fruits during the plot visit i and and ba is the basal area (in square meters per hectare) of species k in the forest.

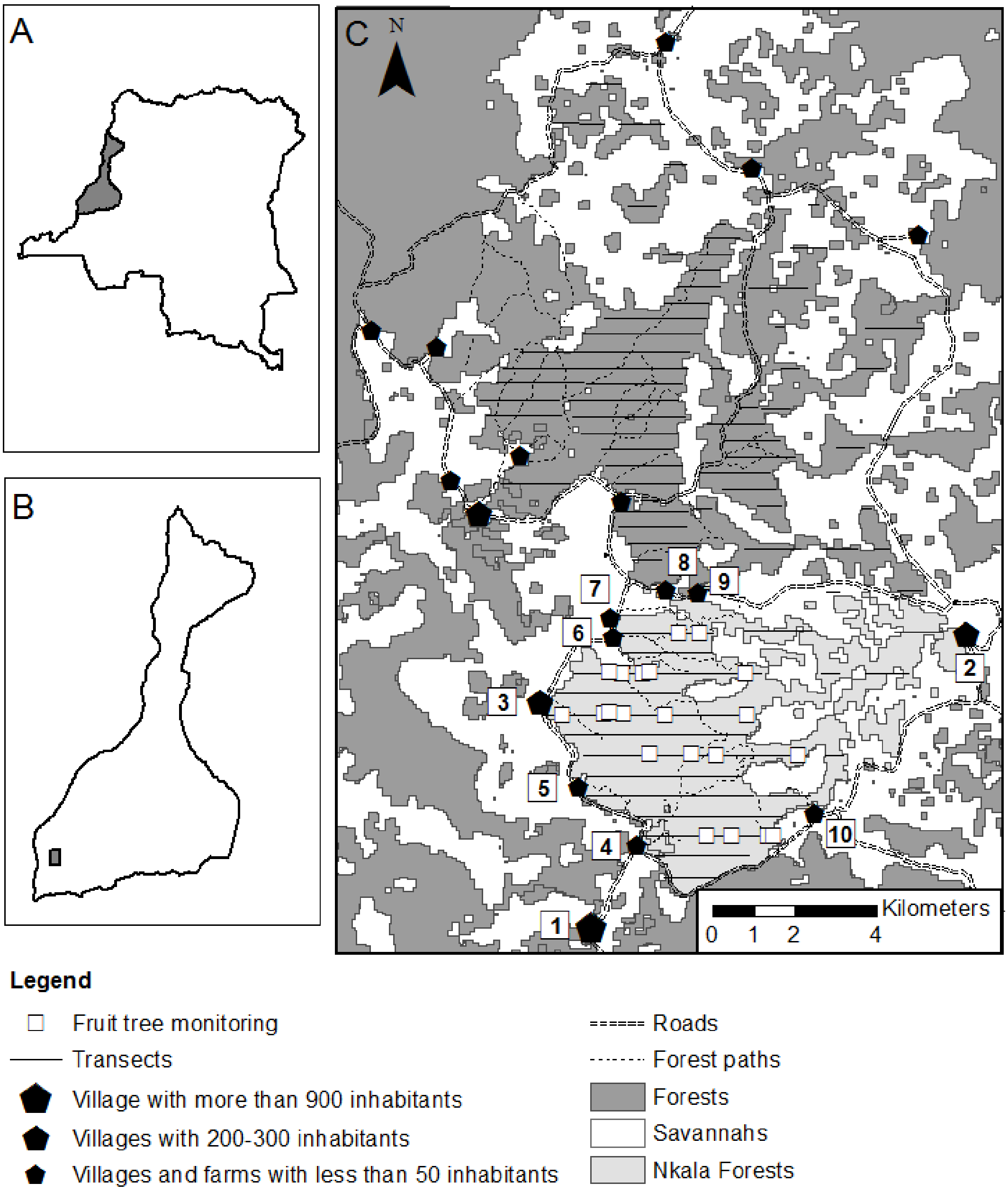


Figure 3-1: Map of the study site (16.41-16.56°E, 2.45-2.66°S, west DRC)

A. Location of the Lake Tumba landscape in Democratic Republic of Congo. B. Location of the study site inside Lake Tumba landscape. C. Map of the study site. Forests are indicated in grey and savannahs in white [the map is based on a non-supervised classification – RED and IR on a Landsat7 (2007), see Serckx et al. In prep.]. The Nkala forest, where lives the bonobo community for which we analysed feces samples, is coloured in pale grey. Villages are figured by black pentagons (numbers 1 to 3 represent villages: (1) Nkoo, (2) Lebomo, (3) Nkala and number 4 to 10 indicate farms: (4) Nkoo clinic, (5) Moza, (6) Mbou-Mon-Tour, (7) Mayi Monene, (8) Motsuemontoro, (9) Bosieli and (10) Lensiana). Parallel dashed lines indicate the roads surrounding the study site, whereas dotted lines indicate the main forest paths. Vertical solid lines depict the 114 line transects (179.1 km) travelled in 2011, 2012 and 2013, and white squares indicate plots of fruit tree monitoring.

IV.3 Analytical methods

IV.3.1 DIET DESCRIPTION

We first described bonobo diet by relating each species identified in feces analysis to its number of occurrence in feces samples (n=2272) and per sampled day (n=270). We evaluated the species of food remains by counting the number of observations on transects (n=311). We verified if our feces analysis was performed for a length of time sufficient to highlight all consumed species by calculating the cumulative number of fruit species observed in feces through the total time of data collection (Basabose 2002). For fecal samples, we tested whether the variation in volume of each fecal content category (fruit with large seeds, fruit with small seeds, foliage, animal matter and other) was correlated with the variation of occurrence in the other categories and whether the two fruit categories were correlated with the fleshy fruit availability index (approximate test of Spearman correlations, derived using a self-written function in R).

We then investigated whether the daily number of consumed fruit species varied over time. We used a generalized linear model with negative binomial error structure and log link function. In order to model the number of daily consumed species and to account for differences in daily sampling efforts, we incorporated the sum of all species observed per feces each day as the response and we included an offset term to control for the variation of sampled feces (the daily number of feces log transformed). We included the sine and cosine of the date, previously converted to a circular variable, to estimate seasonal patterns. We further introduced a temporal autocorrelation term to account for difference in sample size collection according to time. For this, we used the average of the residuals of all other sampled days derived from the full model and weighted by distance as an additional predictor. The weight function had the shape of a Gaussian distribution with a mean of zero (maximal weight at distance equals zero) and a standard deviation chosen such that the likelihood of the full model with the derived variable (autocorrelation term) included was maximized (Fürtbauer et al. 2011). After running the model, we checked various model diagnostics (dfbetas, variance inflation factors and leverage) (Quin and Keough 2002, Field 2005). Dfbetas and variance inflation factors did not reveal any issue (Appendix B1 – Page 194). As the data showed some potentially influential cases of leverage, we used a subset of the data for the analysis (n=254). In order to check the overall effect of seasonality on the number of consumed fruit species daily, we compared the deviance of the full model with the deviance of a null model comprising only the autocorrelation and the offset terms, using a likelihood ratio test.

In order to refine the analysis, we classified fruit species in two categories: "dominant species" if they were present in more than 5 percent of days and "little consumed species" if the species was present in less than 5 percent of days.

IV.3.2 DIET SEASONALITY

In order to test if the consumption of dominant species followed a seasonal pattern, we performed, for each species, a generalized linear model with binomial error structure and logit link function. We used the presence / absence of each dominant species in fecal sample (n=2272) as the response and we incorporated the sine and cosine of the date, previously converted to a circular variable, to estimate seasonal patterns. To account for temporal autocorrelation, we used the average of residuals of all other fecal samples derived from the full model and weighted (with the same function as for the previous model) by temporal distance as an additional predictor. After running the model, we checked various model diagnostics (dfbetas, variance inflation factor and leverage) (Quin and Keough 2002, Field 2005). Dfbetas and variance inflation factors did not reveal any issue (Appendix B2 – Page 194). As the data showed some potentially influential cases of leverage, we used a subset of the dataset for the analysis (Appendix B2 – Page 194). The species "*NID_first.obs: 07.12.2012*" was removed from the analysis as the leverage issue was not rectifiable (the subset of data did not include feces with presence of this species). In order to check the overall effect of seasonality on each species consumption rate, we compared the deviance of the full model with the deviance of a null model comprising only the autocorrelation term, using a likelihood ratio test. In order to come up with a comparable value of the effect of seasonality on consumption of each species, we used the R-squared coefficient of determination (Nagelkerke 1991) which indicates the proportion of variance explained by the regression model.

IV.3.3 ASSOCIATION OF FOOD SPECIES IN DIET

We investigated whether dominant food species present association patterns in diet and whether those patterns could be linked with the related seasonal period of consumption, by using clustering analysis. We first calculated the matrix of Ochiai similarity based on species daily occurrence (presence / absence) in fecal samples (Legendre and Legendre 1998). We clustered species using the Ward's Minimum Variance method. This method defines groups in such a way that the within-group sum of square is minimized (Borcard et al. 2011). The adequate number of groups for representing species association was defined by comparing the original distance matrix to binary matrices computed for the dendrogram cut at various levels and by choosing the level where the matrix Mantel correlation between the two was the highest (Borcard et al. 2011). Matrix Mantel correlations were realised using Spearman correlations, which maximises the highlighting of ecological structure (Legendre and Legendre 1998). In order to check the stability of the clustering, we also tested the Complete Linkage Agglomerative method (Borcard et al. 2011). We further inspected both methods on matrix where Jaccard or Sorenson similarities were calculated and species association remained similar in all cases.

IV.3.4 NUTRITIONAL DRIVERS OF FOOD SPECIES SELECTION

In order to investigate the nutrient balance of plant species consumed by bonobos at the study site, we used the values of nutrient contents from the study of Hohmann et al. (2010). Such data were not available for our own study site but we considered that, even if the absolute values of nutrient contents could vary between study sites, the balance between the different types of nutrients should stay stable within a particular species no matter the site at which the plant has been collected. We used the data of a total of 38 species, collected atSalonga National Park, in DRC, at Gashaka Gumti National Park in Nigeria and at Taï National Park in Ivory Coast (Appendix A, Table 2 – Page 187). Nutrient contents were determined as percent of dry matter (for detailed methods on the phytochemical analyses to calculate nutrient contents, see Hohmann et al. 2010). We selected data on macro-nutrients (protein, crude fat, sugar and starch), fibers (cellulose and hemi-cellulose) and anti-feedants (phenol and tannin). We classified the 38 species within four categories based on their occurrence in bonobo diet: *(cat 1)* the dominant species in bonobo diet at the study site (more than 5% of sampled days in the feces analysis and *Haumania liebrechtsiana* being frequently identified as food remains along transects) (n=12), *(cat 2)* the little consumed species at the study site (less than 5% of sampled days and fibers of *Aframomum sp.* being 6.7% of food remain observations along transects) (n=10), *(cat 3)* the handled or spit species, which are species characterized by seeds too large to be swallowed and consequently not found in feces analysis but that could potentially be eaten by bonobos (n=4), *(cat 4)* the species consumed in other study sites, of which seeds are usually swallowed by bonobos, but that we never found in our feces analysis (Kano and Mulavwa 1992, Djoufack et al. 2007, Beaune et al. 2013) (n=12).

In order to investigate whether nutrient contents explain species food selection at the study site, we used two complementary approaches. We first tested whether the relative proportion of a nutrient or of nutrient groups explains that the species is consumed (*hypothesis 1*) or is dominant (*hypothesis 2*) in the bonobo diet. We then checked whether the variation in nutrient balance followed particular patterns that could help determine nutrient requirements or to understand species associations in bonobo diet. In both approaches, we proceeded at different levels of precision within nutrient categories in order to maximize the number of species for which nutrient data were available. For each level of analysis, we transformed the nutrient percent of dry matter of each nutrient category so that their sum be equal to 100%. We made further references to those values by calling them "relative proportion of nutrient". In a first step, we compared all macro-nutrients with fibers and anti-feedant contents, accounting for these three types of nutrient categories or for all nutrients separately (n=20 species). In a second step, we focused on macro-nutrients by analysing protein, crude fat and carbohydrate contents (n=28). Finally, we detailed carbohydrates by separating them in sugar and starch and analysing it with protein (n=35). We choose to account for protein instead of crude fat as the last one showed only small variation of its relative proportion in macro-nutrients.

We first compared the relative proportion of nutrients between the four categories of species (exact Kruskal-Wallis test, derived using a self-written function in R). Then, in order to test whether nutrients explain species consumption (*hypothesis 1*), we grouped dominant species *(cat 1)*, little consumed species *(cat 2)* and handled or spit species *(cat 3)* together and compared it with the species consumed in other study sites *(cat 4)*. In order to test whether nutrients explain that a species is dominant in bonobo diet (*hypothesis 2*), we used two sets of species groups because we cannot define whether species with large seeds should be considered as dominant or not for bonobos from feces analysis. We compared dominant species *(cat 1)* with a group including little consumed species *(cat 2),* handled or spit species *(cat 3)* and species consumed in other study sites *(cat 4) (hypothesis 2a)*. We also compared a group with dominant species *(cat 1)* and handled or spit species *(cat 3)* with a group composed of the little consumed species *(cat 2)* and the species consumed in other study sites *(cat 4) (Hypothesis 2b)*. All comparisons between two species groups were realised with approximate Mann-Whitney tests.

In order to analyse whether the variations in nutrient balance followed particular patterns, we realised a right-angled mixture triangle (Raubenheimer 2011) for each level of precision of nutrient category analyses.

All analyses were conducted using R (R Development Core Team 2013) and the additional packages car (Fox and Weisberg 2011), MASS (Venables and Ripley 2002), cluster (Maechler et al. 2013) and exactRankTests (Hothorn and Hornik 2013).

V RESULTS

V.1 Diet description

We identified 78 fruit species eaten by bonobos within feces analysis (Appendix A, Table 3 – Page 189). Nonetheless, a large number of those species were rarely consumed: we recorded 13 species present in only one fecal sample, including 8 species represented by only one seed, and 15 other species present in only one sampled day (n=10) or two consecutive sampled days (n=5). Among the other species, 30 species were present in less than 14 days (5% of sampled days). Only 20 species were regularly observed (for more than 5% of sampled days) and were later considered as the "dominant" fruit species (Table 3-1 – Page 163). The distribution of the cumulative number of fruit species through the data collection period underlined the fact that we probably identified all dominant fruit species (plateau reached in Figure 3-2 A2 – Page 165) while numerous other less-consumed species could possibly be identified by increasing the study time duration (no plateau in Figure 3-2 A1). Food remains along transects enabled us to identify 10 species for which stems were eaten, with a large proportion of *Haumania liebrechtsiana* (55% of recorded food remains, Appendix A, Table 3 – Page 190).

Fruits constituted the main diet of bonobos during the study (95.2% of mean volume in fecal samples; range: 10-100%; Table 3-2 – Page 164) and *Musanga cecropioides*, being the only species of the small seed category, was particularly largely consumed (55% of feces, 25.5% of mean volume or 46.2% of mean volume in the subset of fecal samples always including the species). Foliage was much less represented (mean volume of 4.1%, range: 0-90%) with a main proportion of fiber (3.3%). Animal matter appeared in only 4 feces (3 feces with hair, probably of squirrels and 1 feces with chitin; 0.01%). Other items category was composed of soil (0.5%) and small branch (0.2%). When comparing the volume of each content category two by two, we found several significant but weak correlations between categories (Table 3-3 – Page 164). Only the proportion of fruits with large seeds and the proportion of *Musanga cecropioides* were strongly negatively correlated (Spearman, r_s=-0.91, p<0.0001, Figure 3-2B – Page 165). The availability of fleshy fruits in the forest was slightly positively correlated with the proportion of fruits in feces (Spearman, r_s=0.28, p<0.0001) and slightly negatively correlated with the proportion of *Musanga cecropioides* (Spearman, r_s=-0.24, p<0.0001). On average, bonobos consumed 2.8 species per day and the number of consumed fruit species showed a seasonal pattern (comparison between the full and the null model, χ= 17.65, df= 2, p<0.001), with a peak between January and March.

Table 3-1: Most common fruit species in bonobo feces analysis (more than 5% of observation day)

Scientific name	**Family**	**Nb feces (%)**	**Nb days (%)**	**Seasonality**			**Group**	**Tree guild**
				χ	**p-value**	**R^2**		
Musanga cecropioides	Urticaceae	1251 (55)	180 (67)	6.16	*	0.05	1	P
Aframomum sp.	Zingiberaceae	855 (38)	167 (62)	120.35	***	0.54	1	--
Marantochloa leucantha	Marantaceae	560 (25)	133 (49)	19.85	***	0.10	1	--
Uapaca sp.	Euphorbiaceae	386 (17)	79 (29)	48.50	***	0.29	3	NPLD
Cissus dinklagei	Vitaceae	342 (15)	76 (28)	120.15	***	0.61	3	--
Landolphia sp3.	Apocynaceae	238 (10)	65 (24)	0.49	N.S.	-	1	--
Piptostigma fasciculatum	Annonaceae	236 (10)	57 (21)	7.63	*	0.05	1	SB
Dialium sp.	Fabaceae - caesalpinoideae	372 (16)	55 (20)	8.35	*	0.08	1	SB
Landolphia sp2.	Apocynaceae	225 (10)	51 (19)	48.84	***	0.44	3	--
Landolphia sp1.	Apocynaceae	336 (15)	48 (18)	92.45	***	0.66	1	--
Polyalthia suaveolens	Annonaceae	193 (8)	46 (17)	69.28	***	0.52	3	SB
NID_local.name: Lenkala	NID	182 (8)	44 (16)	25.88	***	0.20	1	--
Pycnanthus angolensis	Myristicaceae	108 (5)	43 (16)	54.74	***	0.38	2	NPLD
Cordia platythyrsa	Boraginaceae	136 (6)	37 (14)	1.60	N.S.	-	3	NA
Pancovia laurentii	Sapindaceae	141 (6)	35 (13)	1.15	N.S.	-	2	SB
Uvaria sp.	Annonaceae	76 (3)	24 (9)	5.65	N.S.(1)	0.07	1	SB
NID_first.obs: 07.02.2012	NID	78 (3)	22 (8)	NA	NA	NA	1	--
Isolona hexaloba	Annonaceae	49 (2)	19 (7)	2.03	N.S.	-	3	SB
Annona senegalensis	Annonaceae	57 (3)	18 (7)	0.23	N.S.	-	3	Sav.
Myrianthus arboreus	Moraceae	47 (2)	18 (7)	4.69	N.S.	-	2	P

NID=non identified. In the scientific name column, NID is followed either by the local name if identified by the local assistants and if we did not found the scientific name equivalence or by the first date of observation. Seasonality p-values underline the significance of the chi-squared test comparing the fit of the full model and the null model (***: $p<0.0001$, **: $p<0.001$, *: $p<0.05$, N.S.: non significant). Seasonality (R^2) indicates the coefficient of determination, i.e. proportion of variance explained by the regression model. Seasonality of ‘*NID_first.obs*: 07.02.2012’ is not available because the model did not converge after taking into account leverage issues. (1) indicates the positive trend of the effect of seasonality on *Uvaria sp.* ($p=0.059$). Group indicates the result from the cluster analysis. Tree guild is categorized as shade-bearer (SB), pioneer (P), non-pioneer light demanding (NPLD), non-available in the literature (NA) (Hawthorne 1995).

Table 3-2: Description of contents observed in the fecal samples

	Number of feces	*Mean volume (%)*	*Range of volume (%)*
Fruit	**2272**	**95.20**	**10-100**
Big seeds	2137	69.71	0-100
Musanga cercropioides	1254	25.48	0-100
Foliage	**715**	**4.09**	**0-90**
Fiber	579	3.27	0-90
Leave	199	0.78	0-40
Flower	12	0.04	0-15
Animal	**4**	**0.01**	**0-10**
Other items(1)	**170**	**0.68**	**0-45**
Small Branch	47	0.15	0-30
Soil	102	0.48	0-45

(1) Beside the remains of small branch and soil, we also observed in few feces some items for which the identification remains not clear: possibly we found mushroom remains and very small pieces of stone.

Table 3-3: Correlation between feces content categories and with fleshy fruit availability in the forest

	Musanga	*Foliage*	*Animal matter*	*Other items*	*Fleshy fruit availability*
Fruit (w/o Musanga)	-0.92***	-0.27***	0.002	-0.07**	0.28***
Musanga		-0.02	-0.02	-0.09***	-0.24***
Foliage			0.01	0.09***	
Animal matter				0.06*	

Correlations have been calculated using the approximate test of Spearman correlations. *** indicates p-value <0.0001, ** p-value <0.001 and * p-value<0.05.

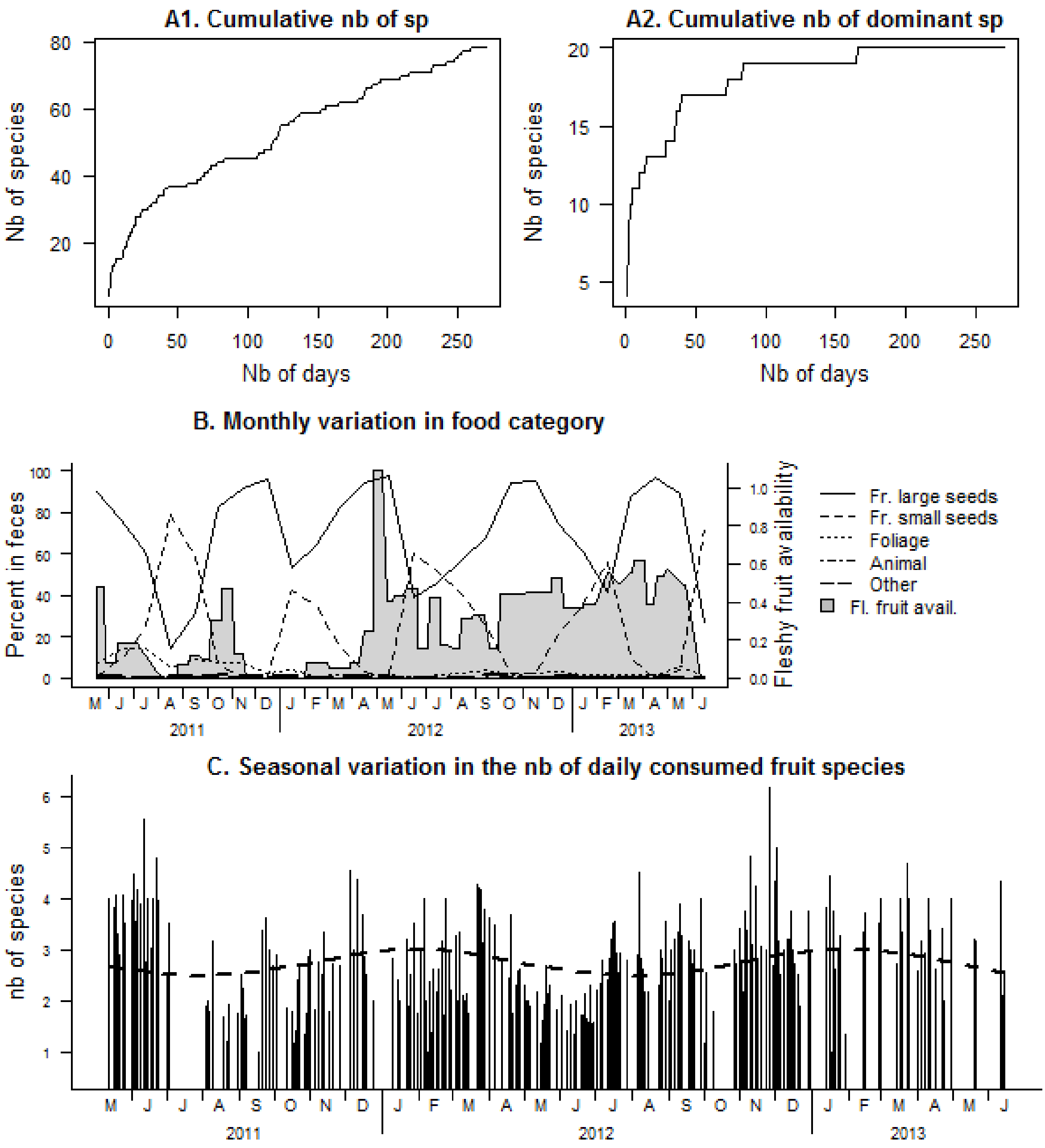


Figure 3-2: Diet description

In Figure A1 and A2, we present the cumulative number of species and dominant species observed in feces over time. Figure B shows the variation of the different food categories (percent of feces volume) that we observed during *in situ* feces analyses (fruit with large seeds, fruit with small seeds, foliage, animal matter and other items). The index of fleshy fruit availability calculated from the data of fruit tree monitoring is superimposed on the figure with its scale on a second y-axis. Figure C shows the mean number of fruit species consumed per day and the fitted model is indicated by the dashed line.

V.2 **Diet seasonality**

Twelve of the 20 dominant fruit species were consumed following a seasonal pattern (likelihood ratio test, Table 3-1 – Page 163) and the effect of seasonality was generally more important for liana and herb species (i.e., *Aframomum sp.*, *Cissus dinklagei*, *Landolphia sp1.* and *Landolphia sp2.*, R^2 in Table 3-1, Figure 3-3 – Page 169). *Musanga cecropioides* and *Marantochloa leucantha* showed small amplitude of seasonality (and small R^2), indicating that they are eaten along all the year.

V.3 **Association of food species in diet**

We found three groups of species presenting a good association pattern between dominant species (Figure 3-4 – Page 170). When comparing the seasonality peak of species within groups, we observed that species from group 1 are essentially consumed between March and August while group 3 had their peak between August and February. We only had seasonal pattern of one species from group 2, preventing us to investigate seasonal associations within this group. Associations based on seasonal patterns became even clearer when looking at subgroups within the three main groups: e.g. the agglomerate between *Aframomum sp.* and *Musanga cecropioides* or between *Cissus dinklagei* and *Uapaca sp*. depict their seasonal synchrony. Interestingly, the three most consumed species during the study, i.e. *Musanga cecropioides*, *Aframomum sp.* and *Marantochloa leucantha*, were the most strongly associated (largest coefficients of similarity), indicating that those species are commonly eaten together.

V.1 **Nutritional drivers of food species selection**

The balance between nutrient groups (macro-nutrients, fibers and anti-feedants) was similar in the four categories of species (Kruskal-Wallis test, Table 3-4 – Page 168). All species included varying proportions of macro-nutrients and fibers but anti-feedants were always minimized (Figures 3-5 and 3-6 – Pages 171 and 172), suggesting that anti-feedants might be present in similar proportions in all species available at the study site. Otherwise, the refined analysis per nutrient type showed that bonobos tend to select species and dominant species with smaller proportion of cellulose (Mann-Whitney, *hyp. 1*: z=60, p=0.055; *hyp. 2a*: z=73, p=0.081; *hyp. 2b*: z=77, p<0.05) and that dominant species (including handled and spit species) tends to be composed of larger proportion of starch (*hyp. 2b*: z=24.5, p=0.076).

When analysing the balance between macro-nutrients, we found that the proportions of carbohydrates were different between species categories (Kruskal-Wallis, H=7.29, p=0.054). In particular, carbohydrates tend to be found in larger proportion in consumed species (Mann-

Whitney, *hyp. 1*: z=73, p=0.055) and in dominant species (including handled or spit species, *hyp. 2b*: z=48, p<0.05) (Figure 3-7 – Page 173). Dominant species (excluding handled or spit species, *hyp 2a*) did not present significantly larger proportion of carbohydrates which might indicate that this category is composed of species having more varying balance compositions between three types of macro-nutrients (Figure 3-7 – Page 173). Overall, the majority of consumed species maximise the balance between carbohydrates and protein, with relatively constant and small proportion of crude fat. However, a few dominant and some of the less consumed species seem to be selected for their intake of crude fat, suggesting that the nutrient content is nevertheless important for bonobos (Figure 3-7 – Page 173).

We then investigated the balance between sugar, starch and protein. Dominant species include larger proportion of starch (Mann-Whitney, *hyp. 2a*: z=84, p=0.063; *hyp. 2b*: z=86, p<0.05) and tend to be composed of less proportion of proteins (Mann-Whitney, *hyp. 2b*: z=208, p=0.066). Those results are confirmed by the graphical representation of nutrient balance which shows that dominant species follow two patterns of nutrient balance: either they offer balanced proportion of sugars and proteins but small proportion of starch, or they maximise starch content with relatively small proportion of sugars and proteins. In opposition, all other food species categories showed a balance between sugar and protein contents with generally small proportion of starch. *Haumania liebrechtsiana* was separated from all the patterns, as mainly composed of protein (Figure 3-7 – Page 173).

We finally looked at particular patterns of macro-nutrient balance within the three clusters of dominant species. Interestingly, their locations in the right-angled mixture triangle suggest that species within groups have contrasting relative proportions of macro-nutrients and so that their combined consumption might enable bonobos to achieve a macro-nutrient balance.

Table 3-4: Species consumption and species dominance based on nutrient contents

	Sp category comparison						**Hyp 1 : sp consumption**				**Hyp 2a: sp dominance**				**Hyp 2b: sp dominance**			
	N_1	N_2	N_3	N_4	H	p	N_1	N_2	z	p	N_1	N_2	z	p	N_1	N_2	z	p
Level 1: Nutrient groups																		
Macro-nutrients	9	3	3	5	1.91	0.594	15	5	27	0.383	9	11	32	0.197	12	8	32	0.232
Fibers					1.82	0.635			48	0.383			65	0.254			65	0.203
Anti-feedants					3.36	0.372			42	0.727			64	0.287			47	0.969
Level 1: Nutrients taken separately																		
Protein	9	3	3	5	0.7	0.879	15	5	36	0.930	9	11	49	1.000	12	8	53	0.728
Starch					3.74	0.312			26.5	0.359			27.5	0.102			24.5	**0.076**
Sugar					2.9	0.448			28	0.432			53	0.820			36	0.375
Cellulose					5.34	0.132			60	**0.055**			73	**0.081**			77	**0.028**
Hemicellulose					0.79	0.863			29	0.485			45	0.761			45	0.847
Crude fat					5.99	0.092			31	0.600			30	0.149			49	0.969
Phenol					3.22	0.381			41	0.793			64	0.287			47	0.969
Tannin					3.91	0.299			45	0.541			65	0.254			48	1.000
Level 2: Macro-nutrients																		
Carbohydrates	11	5	3	9	7.29	**0.054**	19	9	46	**0.055**	11	17	71	0.301	14	14	48	**0.023**
Protein					1.46	0.693			108	0.279			105	0.605			119	0.346
Crude fat					4.13	0.260			103	0.403			92	0.962			123	0.260
Level 3: Carbohydrates and protein																		
Protein	12	8	4	11	6.12	0.115	24	11	174	0.140	12	23	152	0.639	16	19	208	**0.066**
Starch					5.03	0.163			103	0.311			84	**0.063**			86	**0.030**
Sugar					5.11	0.166			114	0.534			161	0.434			132	0.518

The comparisons between species categories have been realised with exact Kruskal-Wallis tests. N indicates the number of species comprised in *category 1*: dominant species, *cat. 2*: little consumed species, *cat. 3*: handled and spit species and *cat. 4*: species consumed in other sites. Test results and p-value are shown in the columns H and p, respectively. We further tested whether nutrients explain species consumption (*Hypothesis 1*), by comparing *categories 1 to 3* with *cat. 4* and whether nutrients explain species dominance (*Hypothesis 2*). For this, we included handled or spit species in the group of species dominance as we do not know their importance in diet from feces analysis. *Hypothesis 2a* compared *cat. 1* with *cat 2 to 4*. *Hypothesis 2b* compared *cat. 1 and 3* with *cat. 2 and 4*. The number of species in each category is indicated in the N columns. Comparisons have been conducted with approximate Mann-Whitney tests (column z and p-values are in column p).

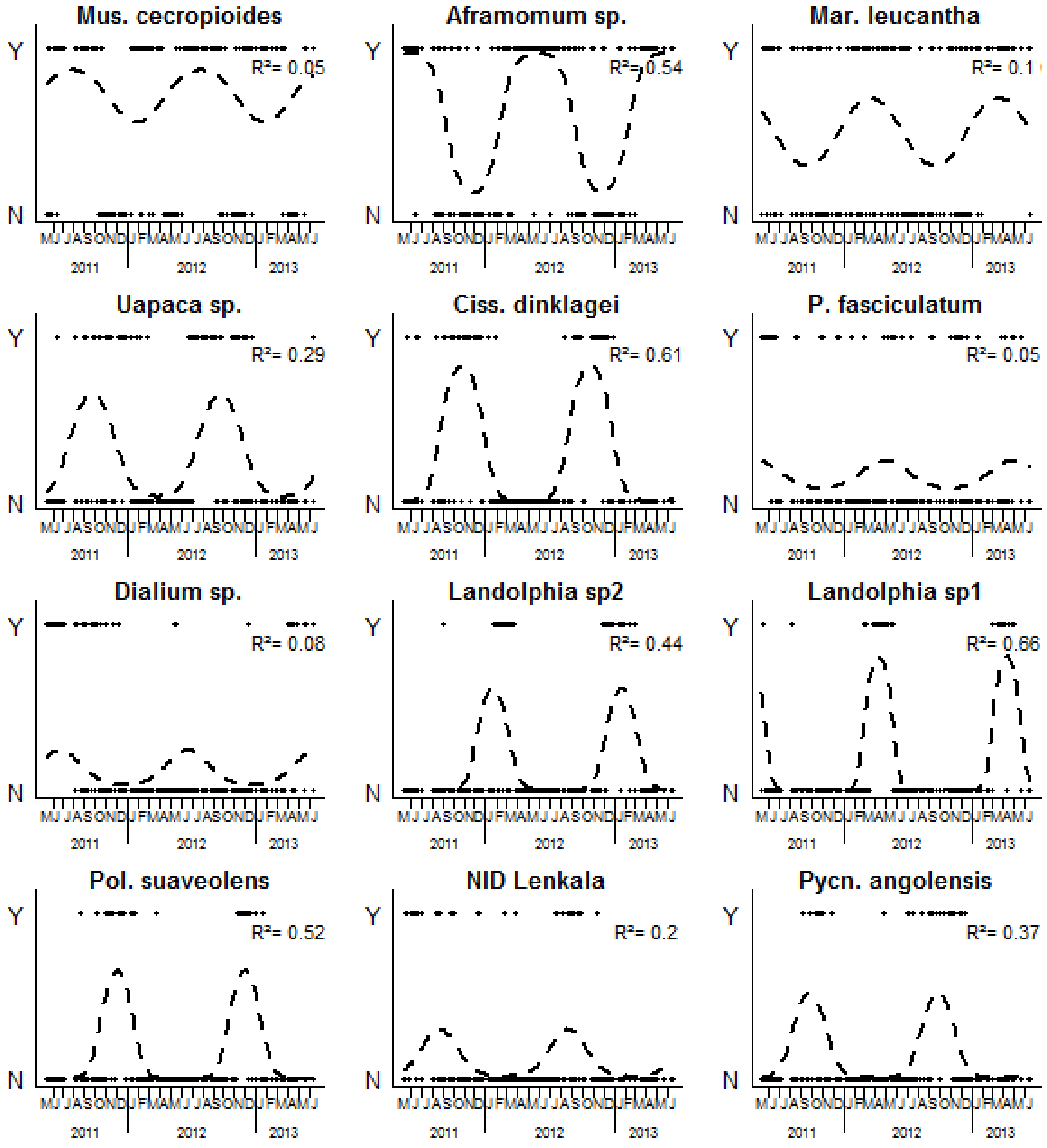


Figure 3-3: Seasonality of dominant fruit species

We only present the fruit species for which we found a significant pattern of seasonality. Fruit species are indicated as present (Y) or absent (N) for each sampled day and the fitted models are indicated by the dashed lines. R^2 are the R-squared coefficients of determination, enabling to make comparisons on the seasonality effect between species.

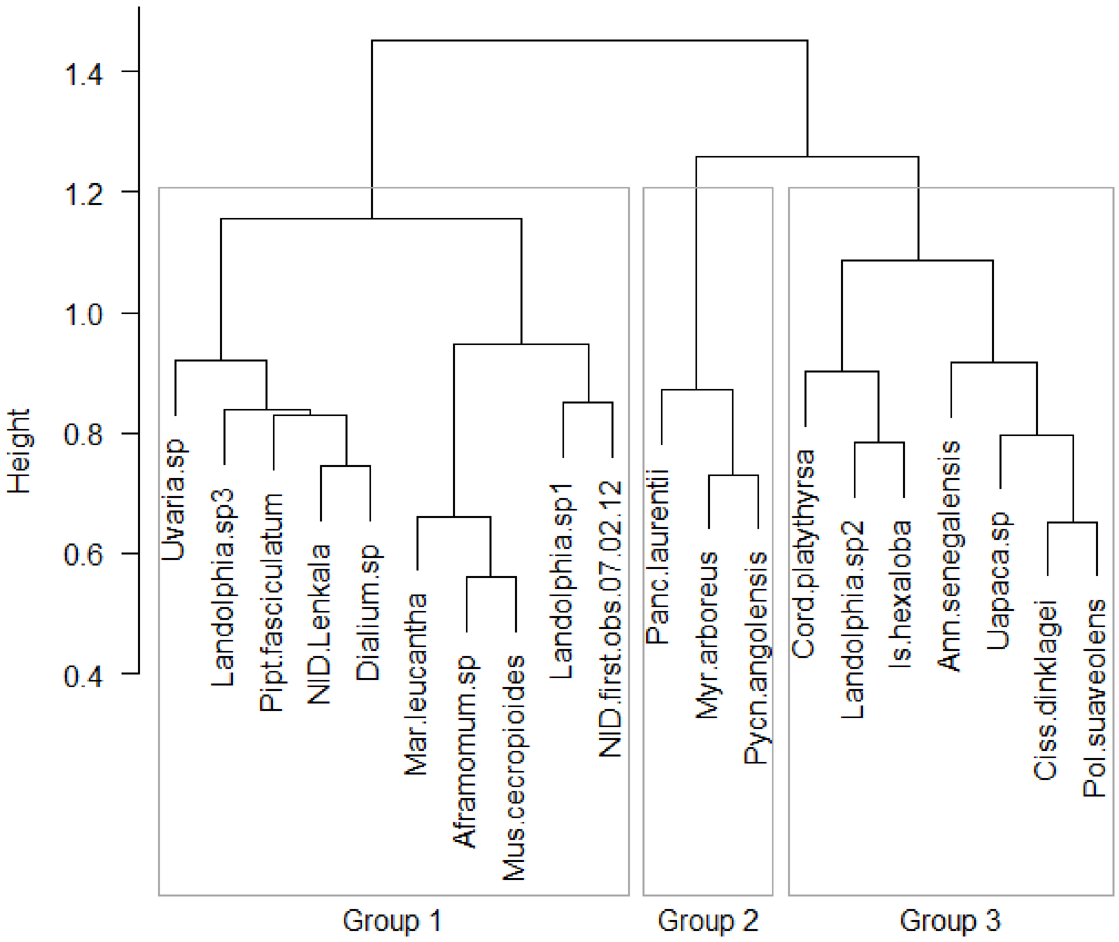


Figure 3-4: Species association in bonobo diet

The height-axis represents the axis of the squared distances (distance = 1 - coefficient of similarity) between groups or species. The nodes between groups / species indicate the squared distances at which groups / species have been agglomerated within the same sub-group. Grey rectangles show the three groups representing adequately the associations between species in bonobo diet.

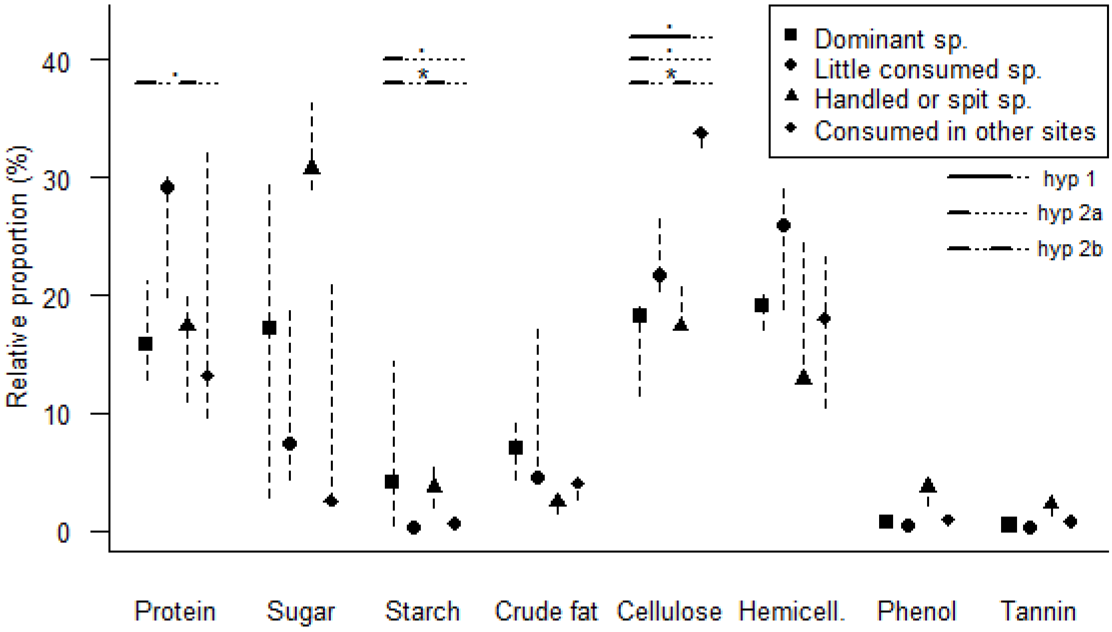


Figure 3-5: Relative proportion of nutrients in food species

Food species are presented per category of occurrence in bonobo diet with different types of points: important species *(cat1)*, little consumed species *(cat2)*, handled and spit species *(cat3)* and species consumed in other study sites *(cat4)*. Points are medians and vertical dashed lines are quartiles. Horizontal lines above nutrients indicate whether Mann-Whitney tests reveal significant differences in the relative proportions of nutrients between the categories of occurrence: we investigated whether dominant species (*cat 1* and including or not the category of handled and spit species – *cat3*) or consumed species (*cat 1 – cat 2 – cat 3*) contain different relative proportions of nutrients by testing them against the other categories. Categories considered as dominant or consumed species in the Mann-Whitney tests are depicted by solid lines and categories representing not consumed or not dominant species are indicated with dotted lines.

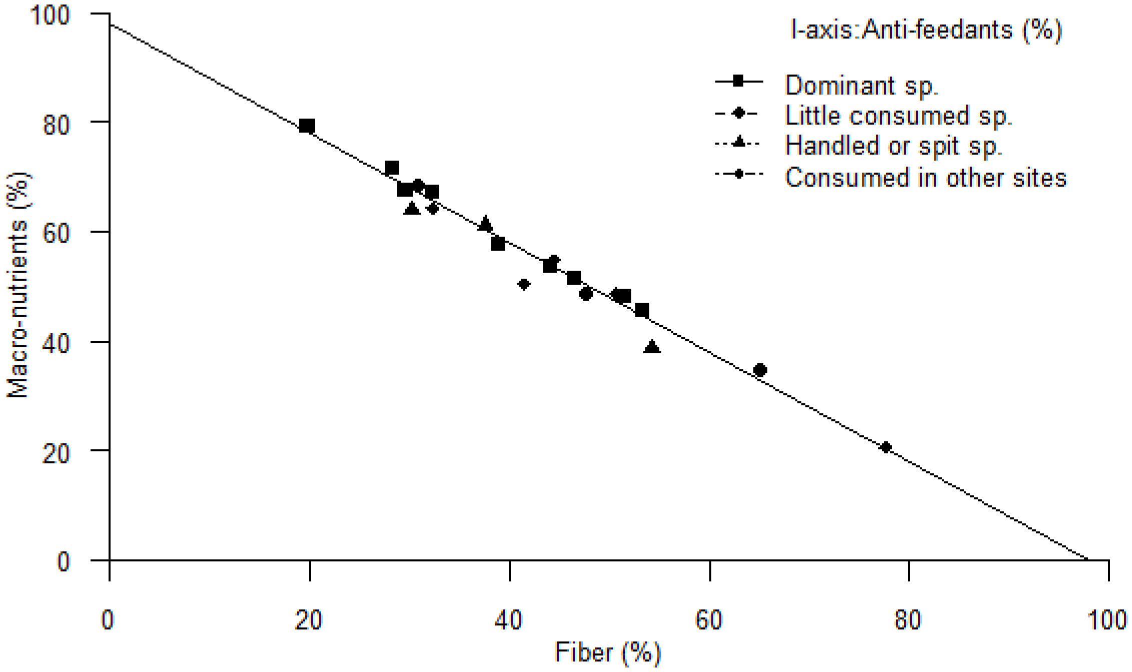


Figure 3-6: Balance of the relative proportion of nutrient groups in food species

Food species are presented per category of occurrence in bonobo diet with different types of points. Nutrients are indicated by their relative proportion in the balance between macro-nutrients (y-axis), fibers (x-axis) and anti-feedants (implicit-axis), so that the sum of the three nutrient groups is equal to 100%. The solid line shows that all species satisfy the same conditions of small proportion of anti-feedants with varying balance between macro-nutrients and fiber.

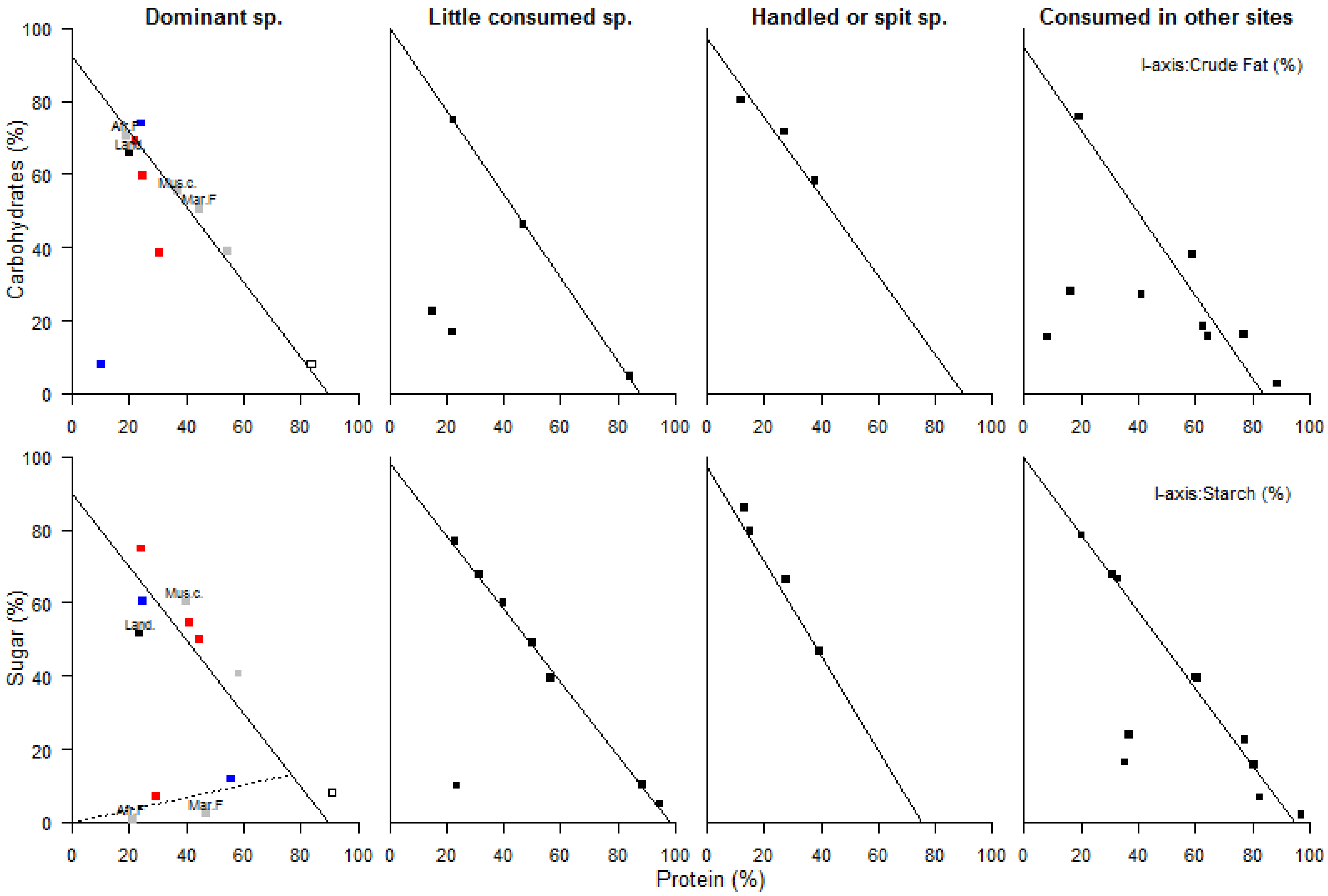


Figure 3-7: Balance of the relative proportion of macro-nutrients in food species (legend on next page)

Figure 3-7: Food species are presented per category of occurrence in bonobo diet in different graphs. The set of figures in the first line shows the nutrient balance between carbohydrates (y-axis), proteins (x-axis) and crude fat (implicit-axis); figures of the second line are the nutrient balance between sugar (y-axis), protein (x-axis) and starch (implicit-axis). The solid lines indicate that species tends to bring similar proportion of the nutrient presented in the implicit axis, with varying balance between nutrients of the x- and y-axis. The dotted line shows that some species follow a different pattern, being composed of larger proportion of the nutrient presented in the implicit axis, and with the same ratio between nutrients of the x- and y-axis. In the category "dominant species", the different colours of points represent the groups of species association: group 1 in grey, group 2 in blue, group 3 in red. *Landolphia sp.* is indicated in black as being part of groups 1 and 3. The non-filled square shows *Haumania liebrechtsiana*. The precise location of *Marantochloa leucantha*, *Aframomum sp.*, *Musanga cecropioides* and *Landolphia sp.*, being the most important species in bonobo diet during the study, is indicated by their name abbreviation.

VI DISCUSSION

The primary aim of this study was to describe the feeding ecology of bonobos living in the forest-savannah mosaic of western DRC by investigating the seasonality patterns of food consumption and the nutritional drivers of food species selection. Our study site is a particularly interesting environment to study bonobo diet plasticity, given its large spatio-temporal variation of resource availability (Serckx et al. 2014). We showed that bonobo diet relies on a few dominant plant species (only 20 species regularly observed in feces), in which liana and herb species take an important place. Dominant species usually follow a seasonal pattern (12 on the 20 dominant species) and we identified three major groups of plant species association in daily food consumption (Figure 3-5 – Page 171). These groups are most likely related to species seasonal availability but we also demonstrated that the peculiar association of these species also enables bonobos to fulfil its macro-nutrient requirements (Figure 3-7 – Page 173). Interestingly, the three most consumed species are typical of disturbed habitats or forest edges and present high proportion of carbohydrates, the major driver of food species selection in the study site. This finding should be investigated in more depth particularly with regards to its implication on bonobo foraging strategy in a fragmented environment.

One particularly interesting finding of our study is the balance between the number of identified fruit species present in the diet (n=78) and the actual number of species regularly eaten (n=20, referred as 'dominant' species). While chimpanzee studies usually demonstrate that populations living in drier environment consumed fewer species than populations evolving in dense forests (Hunt and McGrew 2002, Pruetz 2006, McLennan 2013), this might not be the case for bonobos since we identified a similar number of food species than what had been recorded in dense tropical forests (feces analysis data at Wamba, n=93: Kano 1992; at Lui Kotal in Salonga National Park, n=91: Beaune et al. 2013). However, differences between bonobo populations might appear when comparing the daily number of consumed species (mean= 2.8 in this study vs. 6 at Wamba, Kano 1992, and 2 at Lui Kotal, Beaune et al. 2013) or variation in diet diversity through time. Our study shows that only a very low number of species (n=20) are regularly consumed, including fruits from only 11 tree species. Tree species abundance in the forest does not help explain bonobo selection since only 5 tree species were abundant (i.e., *Musanga cecropioides*, *Uapaca sp.*, *Dialium sp.*, *Pycnanthus angolensis* or *Pancovia laurentii*, Appendix A, Table 1 – Page 185). On the other hand, nutrient balance analysis reveals that dominant species include larger proportion of carbohydrates than other food species (Figure 3-7 – Page 173). The importance of carbohydrates in ape food selection has already been widely demonstrated (Reynolds et al. 1998, Remis 2002, Hohmann et al. 2006, 2010, Rothman et al. 2011) but the strict selection of few rich-carbohydrate species might suggest that the access to this type of energy source is a limiting factor in our study site.

An in-depth investigation within dominant species allowed us to refine our understanding of food species selection. First, we observed that the proportion of starch is significantly higher in dominant species in comparison to other food species of the study site (Table 3-4 – Page 168, Figures 5 and 7 – Pages 171 and 173). This result is quite surprising as recent studies have shown that food species of bonobos and chimpanzees usually contain more sugar but similar starch composition than non-food species (Hohmann et al. 2006, 2010) and that high-starch food species were avoided because the low amylase activity may constrain the digestibility of this polysaccharide by *Pan* species (Perry et al. 2007). This unusual importance of starch should be further investigated with regards to fruit availability of high-sugar content species in order to understand if bonobos still select high-starch food when both are available in the forest. Secondly, our results showed three major groups of species association. Groups are obviously correlated with seasonal fruitage but they also present a combination of species rich in diverse essential macro-nutrients (Figure 3-7 – Page 173). Their peculiar association might then enable bonobos to achieve a constant balance of macro-nutrients through time. More precisely, the particular association of the three most dominant species in feces (*Musanga cecropioides*, *Aframomum sp.* and *Marantochloa leucantha*) and of *Haumania liebrechtsiana* offers a complete balance of sugar, starch, crude fat and protein intakes. This result suggests that bonobos might favour a nutrient balancing strategy to select food species (Felton et al. 2009a), as already demonstrated for other primate populations (Milton 1982, Whiten et al. 1991, Felton et al. 2009b).

However, achieving overall nutrient requirements might imply important constraints for bonobo foraging strategy in forest-savannah mosaics. Frugivorous primates are known to rely on long-term spatial memory to optimize searching strategy within patchy distributed resources (Boyer et al. 2006, Janson and Byrne 2007, Janmaat et al. 2013a) and our study shows that bonobo diet is composed of species typical of various habitat types (Table 3-1 – Page 163). Bonobos will need to use savannahs to feed on *Annona senegalensis* (see also Thompson 1997, 2003), to forage in forests edge / disturbed habitats to find *Musanga cecropioides*, *Aframomum sp.* or *Marantochloa leucantha*, as well as to inspect Marantaceae forest in search of *Pycnanthus angolensis*. While all these habitat types are discarded for nesting (Serckx et al. In prep.), such a strategy likely induces large traveling distance to achieve daily nutrient balance. Direct observations should confirm this hypothesis but WWF trackers already reported that bonobos frequently cross their entire home range to reach particular food trees.

Our study provides a first insight into bonobo food species selection in forest-savannah mosaics but also offers interesting information for conservation programs in the region. We first show the importance of a few selected plant species in this bonobo population's diet. The peculiar selection of food species should be verified within each forested area, but the conservation of the dominant species identified should be integrated in community forest management or benefit from particular attention in logging concessions (Plumptre and Reynolds 1994, Arnhem et al. 2008). Secondly, we demonstrate the importance of high quality food species typical of disturbed and forest edges. While such data might seem comforting for the species survival in fragmented environment, the need to use degraded habitats also constraints bonobos to handle close human proximity. Beside the higher risk of hunting or snare injuries, the co-use of some forested areas might quickly create human-bonobo conflicts, such as crop-raiding in cultivated fields, which is already observed in chimpanzee populations living in close human vicinity (Humle and Matsuzawa 2004, McLennan 2013).

Our overall conclusions should be confirmed by direct observations and nutrient analysis in the study site, but our results already indicate that bonobo's diet in forest-savannah mosaics is highly constrained by the availability of a few selected species. While giving access to new rich food species, adaptation to fragmented environment might force bonobos to adopt foraging strategies to achieve nutrient balance requirements. Data on nutritional ecology are increasingly important and useful for developing conservation strategies (Conklin-Brittain et al. 2001, Chapman et al. 2004, Felton et al. 2010) and new frameworks such as the right-angled mixture triangle offers the opportunity to shed light on the nutritional priorities of animals and the consequences of these priorities (Raubenheimer et al. 2009, Felton et al. 2009b, Raubenheimer 2011, Rothman et al. 2011, Köhler et al. 2012, Johnson et al. 2013). Based on proportion-based instead of absolute values of nutrient intakes (Raubenheimer 2011), such analysis can be applied on indirect observations. It is then possible to rapidly gather additional nutritional information from a wide range of ape populations and give new insights in species diet plasticity. Such nutritional frameworks might also be combined with the concepts of preferred and fallback foods (Marshall and Wrangham 2007, Marshall et al. 2009, Harrison and Marshall 2011) in order to relate food species selection with their frequency in diet, their availability in the forest and their nutritional value.

VII ACKNOWLEDGMENTS

This project was funded by the National Fund for Scientific Research (FNRS, Belgium), the Fonds Leopold III from the Royal Belgian Institute of Natural Sciences (Belgium) and the Ecole Régionale post-universitaire d'Aménagement et de gestion Intégrés des Forêts et Territoires tropicaux (ERAIFT, Democratic Republic of Congo). We would like to thank WWF-DRC for their support in the field, as well as the Minister of Foreign Affairs and International Cooperation of The Democratic Republic of The Congo who permitted us to conduct our research. This research would not have been possible without the help of our local field guides. Ciceron Mbuoli Mbenkira deserves a special thank you for his incredible work during the entire period of data collection. We also thank the Max Planck Society, Roger Mundry for providing us with R scripts and statistical support, Jean-François Bastin and Cleve Hicks for their suggestions during the preparation of this paper. Finally, we thank the anonymous reviewers for their helpful comments.

VIII REFERENCES

Arnhem, E., J. Dupain, R. V. Drubbel, C. Devos, and M. Vercauteren. 2008. Selective logging, habitat quality and home range use by sympatric gorillas and chimpanzees: a case study from an active logging concession in Southeast Cameroon. Folia primatologica 79:1–14.

Basabose, A. K. 2002. Diet composition of Chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. American Journal of Primatology 58:1–21.

Basabose, A. K., and J. Yamagiwa. 2002. Factors affecting nesting site choice in Chimpanzees at Tshibati, Kahuzi-Biega National Park: influence of sympatric Gorillas. International Journal of Primatology 23:263–282.

Beaune, D., F. Bretagnolle, L. Bollache, C. Bourson, G. Hohmann, and B. Fruth. 2013. Ecological services performed by the bonobo (*Pan paniscus*): seed dispersal effectiveness in tropical forest. Journal of Tropical Ecology 29:367–380.

Borcard, D., F. Gillet, and P. Legendre. 2011. Numerical Ecology with R. Page 306. Springer New York, New York.

Boyer, D., G. Ramos-Fernández, O. Miramontes, J. L. Mateos, G. Cocho, H. Larralde, H. Ramos, and F. Rojas. 2006. Scale-free foraging by primates emerges from their interaction with a complex environment. Proceedings of the Royal Society of Biological sciences 273:1743–1750.

Chapman, C. A., L. J. Chapman, and L. Naughton-treves. 2004. Predicting folivorous primate abundance: validation of a nutritional model 69:55–69.

Chaves, M., and K. E. Stoner. 2012. Differences in diet between spider monkey groups living in forest fragments and continuous forest in Mexico. Biotropica 44:105–113.

Conklin-Brittain, N. L., C. D. Knott, and R. W. Wrangham. 2001. The feeding ecology of Apes. Pages 167–174 The Apes: Challenges for the 21st Century, Conference Proceedings of Brookfield Zoo. May 10-13, 2000. Chicago Zoological Society, Chicago.

Corlett, R. T. 2011. How to be a frugivore (in a changing world). Acta Oecologica 37:674–681.

Djoufack, S. D., B. A. Nkongmeneck, J. Dupain, S. Bekah, K. K. Bombome, M. A. Epanda, L. Van Elsacker, and Editeurs. 2007. Manuel d'identification des fruits consommés par les gorilles et les Chimpanzés des basses terres de l'Ouest; Espèces de l'écosystème du Dja (Cameroun). Page 107 (M. A. Epanda and L. Van Elsacker, Eds.).

Donati, G., K. Kesch, K. Ndremifidy, S. L. Schmidt, S. M. Borgognini-tarli, and J. U. Ganzhorn. 2011. Better few than hungry : flexible feeding ecology of collared lemurs *Eulemur collaris* in littoral forest fragments. PloS ONE 6:e19807.

Emlen, J. M. 1966. The role of time and energy in food preference. The American Naturalist 100:611–617.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Felton, A. M., A. Felton, W. J. Foley, and D. B. Lindenmayer. 2010. The role of timber tree species in the nutritional ecology of spider monkeys in a certified logging concession, Bolivia. Forest Ecology and Management 259:1642–1649.

Felton, A. M., A. Felton, D. B. Lindenmayer, and W. J. Foley. 2009a. Nutritional goals of wild primates. Functional Ecology 23:70–78.

Felton, A. M., A. Felton, D. Raubenheimer, S. J. Simpson, W. J. Foley, J. T. Wood, I. R. Wallis, and D. B. Lindenmayer. 2009b. Protein content of diets dictates the daily energy intake of a free-ranging primate. Behavioral Ecology 20:685–690.

Field, A. 2005. Discovering Statistics using SPSS. Sage Publications, London.

Fischer, J., and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation : a synthesis. Global Ecology and Biogeography 16:265–280.

Fox, J., and S. Weisberg. 2011. An R companion to applied regression. Page 472. Sage, Thousant Oaks CA.

Fürtbauer, I., R. Mundry, M. Heistermann, O. Schülke, and J. Ostner. 2011. You mate, I mate: macaque females synchronize sex not cycles. PloS ONE 6:e26144.

Harrison, M. E., and A. J. Marshall. 2011. Strategies for the use of fallback foods in Apes. International journal of primatology 32:531–565.

Hashimoto, C., S. Suzuki, Y. Takenoshita, J. Yamagiwa, A. K. Basabose, and T. Furuichi. 2003. How fruit abundance affects the chimpanzee party size: a comparison between four study sites. Primates 44:77–81.

Hawthorne, W. D. 1995. Ecological profiles of Ghanaian forest trees. Tropical Forestry Papers No. 29.

Hohmann, G., A. Fowler, A. Sommer, and S. Ortmann. 2006. Frugivory and gregariousness of Salonga bonobos and Gashaka chimpanzees: the influence of abundance and nutritional quality of fruit. Pages 123–159 *in* G. Hohmann, M. M. Robbins, and C. Boesch, editors. Feeding ecology in apes and other primates. Cambridge University Press, Cambridge.

Hohmann, G., K. Potts, A. N'Guessan, A. Fowler, R. Mundry, J. Ganzhorn, and S. Ortmann. 2010. Plant foods consumed by *Pan*: exploring the variation of nutritional ecology across Africa. American Journal of Physical Anthropology 141:476–485.

Hothorn, T., and K. Hornik. 2013. exactRankTests: exact distributions for rank and permutation tests. R package version 0.8-27.

Humle, T., and T. Matsuzawa. 2004. Oil palm use by adjacent communities of Chimpanzees at Bossou and Nimba Mountains, West Africa. International Journal of Primatology 25:551–581.

Hunt, K., and W. McGrew. 2002. Chimpanzees in the dry habitats of Assirik, Senegal and Semliki Wildlife Reserve, Uganda. Pages 35–51 *in* C. Boesch, G. Hohmann, and L. Marchant, editors. Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge.

Inogwabini, B., M. Bewa, M. Longwango, M. Abokome, and M. Vuvu. 2008. The Bonobos of the Lake Tumba – Lake Maindombe Hinterland: threats and opportunities for population conservation. Pages 273–290 *in* T. Furuichi and J. Thompson, editors. The bonobos: Behavior, Ecology, and Conservation. Springer, New York.

Inogwabini, B., B. Matungila, L. Mbende, M. Abokome, and T. Tshimanga. 2007. Great apes in the Lake Tumba landscape , Democratic Republic of Congo: newly described populations. Oryx 41:1–7.

Irwin, M. T. 2008. Feeding ecology of Propithecus diadema in forest fragments and continuous forest. International Journal of Primatology 29:95–115.

Janmaat, K. R. L., S. D. Ban, and C. Boesch. 2013. Taï chimpanzees use botanical skills to discover fruit: what we can learn from their mistakes. Animal cognition 16:851–860.

Janson, C. H., and R. Byrne. 2007. What wild primates know about resources: opening up the black box. Animal cognition 10:357–367.

Johnson, C. A., D. Raubenheimer, J. M. Rothman, D. Clarke, and L. Swedell. 2013. 30 Days in the life: daily nutrient balancing in a wild Chacma Baboon. PloS ONE 8:e70383.

Kano, T. 1992. The Last Ape: Pygmy Chimpanzee behavior and ecology. Page 248. Stanford University Press, Stanford.

Kano, T., and M. Mulavwa. 1992. Appendix. Pages 225–232 *in* T. Kano, editor. The Last Ape: Pygmy Chimpanzee behavior and ecology. Stanford University Press, Stanford.

Kano, T., and M. Mulawva. 1984. Feeding ecology of the pygmy chimpanzees (*Pan paniscus*) of Wamba. Pages 233–274 *in* R. L. Susman, editor. The Pygmy Chimpanzee, evolutionary bology and behavior. Plenum Press, New York.

Kawamoto, Y., H. Takemoto, S. Higuchi, T. Sakamaki, J. A. Hart, T. B. Hart, N. Tokuyama, G. E. Reinartz, P. Guislain, J. Dupain, A. K. Cobden, M. N. Mulavwa, K. Yangozene, S. Darroze, C. Devos, and T. Furuichi. 2013. Genetic structure of wild bonobo populations: diversity of mitochondrial DNA and geographical distribution. PloS ONE 8:e59660.

Köhler, A., D. Raubenheimer, and S. W. Nicolson. 2012. Regulation of nutrient intake in nectar-feeding birds: insights from the geometric framework. Journal of comparative physiology B 182:603–611.

Legendre, P., and L. Legendre. 1998. Numerical ecology. Second English Edition. Page 846. Elsevier Science, Amsterdam.

Lehmann, J., A. H. Korstjens, and R. I. M. Dunbar. 2007. Fission–fusion social systems as a strategy for coping with ecological constraints: a primate case. Evolutionary Ecology 21:613–634.

Maechler, M., P. Rousseeuw, A. Struyf, M. Hubert, and K. Hornik. 2013. cluster: cluster analysis basics and extensions. R package version 1.14.4.

Marsh, L. 2003. Primates in fragments: ecology and conservationKluwer. Academic/Plenum Publishers, New York.

Marshall, A. J., C. M. Boyko, K. L. Feilen, R. H. Boyko, and M. Leighton. 2009. Defining fallback foods and assessing their importance in primate ecology and evolution. American journal of physical anthropology 140:603–614.

Marshall, A. J., and R. W. Wrangham. 2007. Evolutionary Consequences of Fallback Foods. International Journal of Primatology 28:1219–1235.

McLennan, M. R. 2013. Diet and feeding ecology of Chimpanzees (*Pan troglodytes*) in Bulindi, Uganda: foraging strategies at the forest–farm interface. International Journal of Primatology 34:585–614.

Milton, K. 1982. Dietary quality and demographic regulation in a howler monkey population. Pages 273–289 *in* E. G. Leigh, A. S. Rand, and M. D. Windsor, editors. The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington DC.

Moscovice, L., M. Issa, K. Petrzelkova, N. Keuler, C. Snowdon, and M. Huffman. 2007. Fruit availability, Chimpanzee diet, and grouping patterns on Rubondo Island, Tanzania. American Journal of Primatology 69:487–502.

Mulavwa, M., T. Furuichi, K. Yangozene, M. Yamba-Yamba, B. Motema-Salo, G. Idani, H. Ihobe, C. Hashimoto, Y. Tashiro, and N. Mwanza. 2008. Seasonal changes in fruit production and party size of Bonobos at Wamba. Pages 121–134 *in* T. Furuichi and J. Thompson, editors. The bonobos: Behavior, Ecology, and Conservation. Springer, New York.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691–692.

Pan, Y., R. A. Birdsey, J. Fang, R. Houghton, P. E. Kauppi, W. A. Kurz, O. L. Phillips, A. Shvidenko, S. L. Lewis, J. G. Canadell, P. Ciais, R. B. Jackson, S. W. Pacala, A. D. McGuire, S. Piao, A. Rautiainen, S. Sitch, and D. Hayes. 2011. A large and persistent carbon sink in the world's forests. Science 333:988–993.

Perry, G. H., N. J. Dominy, K. G. Claw, A. S. Lee, H. Fiegler, R. Redon, J. Werner, F. a Villanea, J. L. Mountain, R. Misra, N. P. Carter, C. Lee, and A. C. Stone. 2007. Diet and the evolution of human amylase gene copy number variation. Nature genetics 39:1256–1260.

Plumptre, A. J., and V. Reynolds. 1994. The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. Journal of Applied Ecology 31:631–641.

Pruetz, J. D. 2006. Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. Pages 161–182 *in* G. Hohmann, M. Robbins, and C. Boesch, editors. Feeding ecology in Apes and other primates. Cambridge University Press, Cambridge.

Quin, G. P., and M. J. Keough. 2002. Experimental designs and data analysis for biologists. Cambrige University Press, Cambrigde.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Raubenheimer, D. 2011. Toward a quantitative nutritional ecology: the right-angled triangle. Ecological Monographs 81:407–427.

Raubenheimer, D., S. J. Simpson, and D. Mayntz. 2009. Nutrition, ecology and nutritional ecology: toward an integrated framework. Functional Ecology 23:4–16.

Remis, M. J. 2002. Food preferences among captive western gorillas (*Gorilla gorilla gorilla*) and Chimpanzees (*Pan troglodytes*). International Journal of Primatology 23:231–248.

Reynolds, V., A. J. Plumptre, J. Greenham, and J. Harborne. 1998. Condensed tannins and sugars in the diet of chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. Oecologia 115:331–336.

Rothman, J. M., D. Raubenheimer, and C. A. Chapman. 2011. Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. Biology letters 7:847–849.

Serckx, A., M.-C. Huynen, J.-F. Bastin, R. C. Beudels-Jamar, A. Hambuckers, M. Vimond, E. Raynaud, and H. Kühl. 2014. Nesting patterns of bonobos (*Pan paniscus*) in relation to fruit availability in a forest-savannah mosaic. PloS ONE:in press.

Strier, K. 1989. Effets of patch size on feeding associations in muriquies (*Brachyteles brachnoides*). Folia primatologica 52:70–77.

Tailfer, Y. 1989. La foret dense d'Afrique centrale. Identification pratique des principaux arbres, Tome 1 et 2. C.T.A., Wageningen, Pays-Bas.

Thompson, J. a M. 2003. A model of the biogeographical journey from *Proto-pan* to *Pan paniscus*. Primates 44:191–197.

Thompson, J. A. M. 1997. The history, taxonomy and ecology of the Bonobo (*Pan paniscus* Schwarz, 1929) with a first description of a wild population living in the forest/savanna mosaic habitat. PhD Thesis. University of Oxford.

Thompson, J. A. M. 2001. The status of Bonobos in their southernmost geographic range. Pages 75–81 *in* B. M. F. Galdikas, N. E. Briggs, L. K. Sheeran, G. L. Shapiro, and J. Goodall, editors. All Apes Great and Small Volume I: African Apes. Kluwer Academic / Plenum Publishers, New York.

Tutin, C. E. G. 1999. Fragmented living: behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. Primates 40:249–265.

Vancutsem, C., J. Pekel, J.-P. Kibamba, X. Blaes, C. de Wasseige, and P. Defourny. 2006. Carte de l'occupation du sol de la République Démocratique du Congo. (P. U. de Louvain, Ed.). Bruxelles.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Page 495. Springer, New York.

White, F. J., and A. Lanjouw. 1992. Feeding competition in Lomako bonobos: variation in social cohesion. Topics in primatology 1:67–79.

Whiten, A., R. W. Byrnel, R. A. Barton, P. G. Waterman, S. P. Henry, K. Hawkes, E. M. Widdowson, S. A. Altmann, K. Milton, and R. I. M. Dunbar. 1991. Dietary and foraging strategies of Baboons. Philosophical Transactions: Biological Sciences 334:187–197.

Wilks, C. M., and Y. A. Issembe. 2000. Les arbres de la Guinée Equatoriale: Guide pratique d'identification: région continentale. Projet CUREF, Bata, Guinée Equatoriale. Page 546. Prépresse Communications, France.

Wrangham, R. W., N. Lou Conklin-Brittain, and K. D. Hunt. 1998. Dietary response of Chimpanzees and Cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. International Journal of Primatology 19:949–970.

Wright, S. J. 2005. Tropical forests in a changing environment. Trends in ecology & evolution 20:553–560.

IX APPENDIX A

Table 1: Number of trees followed in the fruit tree monitoring for species classified as "fleshy fruit"

Species	***Density in the forest (nb/ha)*** $^{(1)}$	***Basal area in the forest (m²/ha)*** $^{(1)}$	***Nb of trees followed between May 2011 and May 2012***	***Nb of trees followed between May 2012 and June 2013***
Anacardiaceae				
Sorindeia africana	11.38	0.33	13	117
Annonaceae				
Annona senegalensis	--	--	0	0
Anonidium mannii	0.89	0.07	12	20
Isolona hexaloba	0.00	0.00	0	0
Polyalthia suaveolens	13.91	0.66	5	93
Annickia chlorantha	1.13	0.02	1	8
Piptostigma fasciculatum	0.09	0.00	2	3
Polyceratocarpus gossweileri	0.00	0.00	0	0
Uvaria sp.	6.58	0.14	2	50
Cleistopholis glauca	4.00	0.23	0	10
Apocynaceae				
Rauvolfia vomitoria	0.36	0.01	0	2
Picralima nitida	1.24	0.04	3	14
Alstonia congensis	0.00	0.00	0	0
Arecaceae				
Elaeis guineensis	2.40	0.23	0	0
Borassus aethiopum	0.00	0.00	0	0
Asparagaceae				
Dracaena mannii	0.09	0.01	0	1
Boraginaceae				
Cordia platythyrsa	0.00	0.00	3	3
Burseraceae				
Dacryodes edulis	7.56	0.34	9	60
Santiria trimera	2.93	0.21	11	22
Canarium schweinfurthii	0.00	0.00	0	0
Chrysobalanaceae				
Parinari excelsa	0.09	0.00	4	5
Clusiaceae				
Symphonia globulifera	4.62	0.33	7	44
Garcinia kola	2.13	0.06	0	23
Garcinia punctata Oliv.	0.62	0.03	0	3
Garcinia sp1	0.00	0.00	0	0
Diospyros ferrea	4.09	0.06	1	41
Diospyros sp1	0.18	0.00	3	5
Diospyros iturensis	0.00	0.00	0	0
Diospyros dendo	0.00	0.00	0	0

Euphorbiaceae				
Plagiostyles africana	33.69	1.73	15	181
Uapaca spp.	9.87	1.31	5	24
Drypetes sp1.	7.22	0.51	2	51
Fabaceae (caesalpinoideae)				
Dialium zenkeri	1.69	0.22	5	19
Bikinia evrardii	0.62	0.11	1	8
Dialium sp1	0.09	0.03	0	1
Dialium pachyphyllum	0.00	0.00	0	0
Fabaceae (Mimosoideae)				
Albizia gummifera	1.07	0.10	0	0
Fabaceae (Papilionoideae)				
Millettia drastica	0.00	0.00	0	0
Flacourtiaceae				
Oncoba mannii	6.93	0.19	2	48
Oncoba welwitschii	4.53	0.09	0	2
Hypericaceae				
Harungana madagascariensis	2.04	0.06	2	2
Irvigiaceae				
Irvingia grandifolia	0.00	0.00	2	2
Irvingia gabonensis	0.53	0.24	1	6
Klainedoxa gabonensis	12.26	3.35	11	91
Malvaceae				
Cola ballayi	21.78	0.40	16	136
Cola griseiflora	0.00	0.00	0	0
Cola gigantea	0.09	0.00	2	3
Cola acuminata	3.20	0.06	1	27
Cola cf. ballayi	0.80	0.02	3	5
Grewia oligoneura	0.00	0.00	0	0
Meliaceae				
Guarea cedrata	0.00	0.00	0	0
Moraceae				
Ficus sp1	0.00	0.00	0	0
Myrianthus arboreus	1.42	0.07	0	15
Ficus sp2	0.00	0.00	0	0
Myristicaceae				
Staudtia kamerunensis var. gabonensis	13.78	0.60	10	92
Pycnanthus angolensis	15.73	1.94	19	95
Olacaceae				
Heisteria parvifolia	14.13	0.72	18	20
Strombosiopsis tetrandra	4.27	0.23	7	54
Ongokea gore	4.96	0.59	0	28
Olax spp.	0.00	0.00	0	0
Pandaceae				

Microdesmis sp.	1.60	0.02	4	20
Rubiaceae				
Nauclea latifolia	0.00	0.00	0	0
Salicaceae				
NID_local.name=Motimanku1	1.60	0.02	4	20
Sapindaceae				
Pancovia laurentii	7.91	0.20	0	78
Eriocoelum microspermum	1.04	0.02	0	12
Sapotaceae				
Baillonella toxisperma	0.09	0.30	0	1
Tieghemella africana	0.00	0.00	0	0
Chrysophyllum lacourtianum	1.60	0.42	0	11
Chrysophyllum africanum	0.00	0.00	0	0
Chrysophyllum beguei	0.00	0.00	0	0
Omphalocarpum elatum	0.53	0.05	0	1
Omphalocarpum lecomteanum	0.00	0.00	0	0
Autranella congolensis	0.00	0.00	0	0
Tiliaceae				
Desplatsia dewevrei	0.00	0.00	1	1
Urticaceae				
Musanga cecropioides	2.76	0.30	4	8
Verbenaceae				
Vitex ferruginea	0.00	0.00	0	0
Vitex congolense	0.00	0.00	3	3
Violaceae				
Rinorea oblongifolia	0.44	0.00	1	3
NID				
NID_local.name=Monsima	0.00	0.00	3	3
NID_local.name=Omonobari	0.00	0.00	0	0
TOTAL			**215**	**1590**

NID=non identified. In the scientific name column, NID is followed by the local name if the species was identified by the local assistants but that we did not found the scientific name equivalence. Species for which density, basal area and number of monitored trees equal zero are species identified as present in the area but never observed in the plots (and then assumed to be present in very small density). (1) see Serckx et al. 2014 for details on the design of the abundance survey.

Table 2: Plant species used for the nutrient analysis

Family	Scientific name	Species category	Site	Type food	Pr.	C.	Cr.f	Ant.f
Annonaceae	Annona senegalensis	Dominant	Gashaka	Fr				
Annonaceae	Anonidium mannii	Handled / spit (a)	SNP	Fr				
Annonaceae	Polyalthia suaveolens	Dominant	SNP	Fr			NA	
Annonaceae	Annickia ambigua (1)	Few cons.	SNP	Fr				
Apocynaceae	Landolphia sp.	Dominant.	SNP	Fr				
Burseraceae	Canarium schweinfurthii	Not eaten (a)	Gashaka	Fr				
Chrysobalanaceae	Parinari excelsa	Handled / spit (a)	SNP	Fr				
Clusiaceae	Garcinia sp.	Few cons.	SNP	Fr	NA		NA	NA
Ebenaceae	Diospyros gilletii (2)	Not eaten (a)	SNP	Fr			NA	
Euphorbiaceae	Uapaca sp.	Dominant	Gashaka	Fr				NA
Fabaceae	Afzelia bella (3)	Not eaten (b)	Taï	Fr				NA
Fabaceae (Caesalpinoideae)	Dialium corbeii (4)	Dominant	SNP	Fr				
Fabaceae (Caesalpinoideae)	Brachystegia eurycoma (5)	Not eaten (b)	Gashaka	Fr				NA
Fabaceae (Caesalpinoideae)	Erythrophleum suaveolens	Not eaten (b)	Gashaka	Fr				
Fabaceae (Papilionoideae)	Millettia sp.	Not eaten (b)	SNP	Fr				
Irvigiaceae	Klainedoxa oblongifolia (6)	Handled / spit (a)	SNP	Fr				
Malvaceae	Cola millenii (7)	Few cons.	Gashaka	Fr				NA
Malvaceae	Grewia mollis (8)	Few cons.	Gashaka	Fr		NA	NA	
Marantaceae	Sarcophrynium sp.	Few cons.	SNP	St			NA	NA
Marantaceae	Haumania liebrechtsiana	Dominant	SNP	St				
Marantaceae	Marantochloa purpurea (9)	Dominant	Gashaka	Fr		NA*	NA*	NA*
Marantaceae	Marantochloa purpurea (9)	Few cons.	Gashaka	St				
Meliaceae	Guarea cedrasta (10)	Not eaten (a)	SNP	Fr			NA	NA
Moraceae	Ficus sp.	Not eaten (a)	SNP	Fr				
Myristicaceae	Staudia sp.	Not eaten (a)	SNP	Fr				NA
Myristicaceae	Pycnanthus angolensis	Dominant	Gashaka	Fr				
Olacaceae	Strombosia gaucenscens (11)	Few cons.	SNP	Fr				
Olacaceae	Strombosiopsis sp.	Not eaten (a)	SNP	Fr	NA			
Rubiaceae	Nauclea latifolia	Not eaten (c)	Gashaka	Fr				NA
Sapindaceae	Pancovia laurentii	Dominant	SNP	Fr				
Sapotaceae	Omphalocarpum sp.	Few cons.	SNP	Fr				NA
Sapotaceae	Autranella sp.	Handled / spit (a)	SNP	Fr			NA	
Tiliaceae	Desplatzia dewevrei	Few cons.	SNP	Fr			NA	
Urticaceae	Musanga cecropioides	Dominant.	SNP	Fr				
Verbenaceae	Vitex doniana (12)	Not eaten (a)	Gashaka	Fr				

Vitaceae	Cissus dinklagei	Dominant	SNP	Fr				
Zingiberaceae	Aframomum sp.	Few cons.	SNP	St			NA	NA
Zingiberaceae	Aframomum sp.	Dominant	Gashaka	Fr				

The table presents the species we used for the nutrient analysis (data from Hohmann et al. 2010). Species followed by numbers indicates when we used the nutrient values of a species to represent another species of the same genus and being present in the study site: (1) *Annickia chlorantha*, (2) *Diospyros ferrea*, *D. dendo*, *D. iturensis*, (3) *Afzelia bipindensis*, (4) *Dialium pachyphyllum*, *D. zenkeri*, (5) *Brachystegia laurentii*, (6) *Klainedoxa gabonensis*, (7) *Cola diversifolia*, (8) *Grewia oligoneura*, (9) *Marantochloa leucantha*, (10) *Guarea cedrata*, (11) *Strombosia pustulata*, *S. grandifolia*, (12) *Vitex ferruginea*, *V. congolense*. Species have been classified in four categories: "dominant" sp, "few cons." = few consumed species, "Handled /spit" = species for which seeds are usually handled or spit and so not observable in feces analysis, "not eaten" = species not eaten in the study site but for which seeds are usually swallowed. The letter after the category indicate the source we used to define whether species are eaten by bonobos and whether seeds are swallowed, spit or handled: (a) Beaune et al. 2013, (b) Kano et Mulavwa, 1992, (c) Djoufack et al. 2007. Site column informs where the species have been collected for the nutrient analysis: "SNP" is Salonga National Park, in DRC, "Gashaka" is Gashaka Gumti National Park in Nigeria and "Taï" is Taï National Park in Ivory Coast. The column 'Type food" specifies the part of the plant on which the nutrient analysis has been done: fruit (Fr) or Stem (St). The four last columns indicate whether the nutrient values were not available for protein (Pr.), carbohydrate (C.), crude fat (Cr.f.) or Anti-feedant (Ant.f) contents. Those species were further removed from the analysis when we needed those particular values. *For the fruit of *Marantochloa*, we had two samples of nutrient contents, one missing carbohydrate and crude fat value, the other missing anti-feedant value: we selected the one with the data we need according to the analysis.

Table 13: Bonobo diet in the Malebo study site

Scientific name	Life form	Tree Guild	Obs. type	Part eaten	Nb feces with seeds (%)	Nb days feces (%)	Nb obs. transects (%)
Anacardiaceae							
Sorindeia africana	Tree	SB	F	Fr	18 (1)	6 (2)	-
Annonaceae							
Annickia chlorantha	Tree	SB	F	Fr	7 (0)	5 (2)	-
Annona senegalensis	Tree	Sav.	F	Fr	57 (3)	18 (7)	-
Isolona hexaloba	Tree	SB	F	Fr	49 (2)	19 (7)	-
Piptostigma fasciculatum	Tree	SB	F	Fr	236 (10)	57 (21)	-
Polyalthia suaveolens	Tree	SB	F	Fr	193 (8)	46 (17)	-
Xylopia hypolampra	Tree	P	F	Fr	6 (0)	3 (1)	-
Uvaria sp.	Tree	SB	F	Fr	76 (3)	24 (9)	-
Apocynaceae							
Landolphia sp2.	Liana		F, Tr	Fr	225 (10)	51 (19)	-
Landolphia sp3.	Liana		F	Fr	238 (10)	65 (24)	-
Landolphia sp1.	Liana		F, Tr	Fr	336 (15)	48 (18)	2 (0.6)
Arecaceae							
Elaeis guineensis			Tr	St	-	-	2 (0.6)
Raphia sp.			Tr	St	-	-	2 (0.6)
Boraginaceae							
Cordia platythyrsa	Tree	NA	F	Fr	136 (6)	37 (14)	-
Burseraceae							
Santiria trimera	Tree	SB	F	Fr	49 (2)	13 (5)	-
Clusiaceae							
Garcinia kola	Tree	SB	F	Fr	1 (0)	1 (0)	-
Symphonia globulifera	Tree	SB	F	Fr	1 (0)	1 (0)	-
Euphorbiaceae							
Plagiostyles africana	Tree	NPLD	F	Fr	7 (0)	3 (1)	-

Uapaca sp.	Tree	NPLD	F	Fr	386 (17)	79 (29)	-
Fabaceae (caesalpinoideae)							
Dialium sp.	Tree	SB	F, Tr	Fr	372 (16)	55 (20)	2 (0.6)
Flacourtiaceae							
Oncoba mannii	Tree	P	F,Tr	Fr	12 (1)	5 (2)	1 (0.3)
Hypericaceae							
Harungana madagascariensis	Tree	P	F	Fr	53 (2)	14 (5)	-
Malvaceae							
Grewia oligoneura	Tree	SB	F	Fr	3 (0)	1 (0)	-
Cola diversifolia	Tree	SB	F	Fr	18 (1)	7 (3)	-
Marantaceae							
Haumania liebrechtsiana	Herb		Tr	Fr	-	-	21 (6.8)
				St	-	-	170 (54.7)
				L	-	-	5 (1.6)
Marantochloa mannii	Herb		Tr	St	-	-	1 (0.3)
Marantochloa leucantha	Herb		F, Tr	Fr	560 (25)	133 (49)	1 (0.3)
			Tr	St	-	-	1 (0.3)
Megaphrynium macrostachyum	Herb		F, Tr	Fr	7 (0)	6 (2)	3 (1.0)
			Tr	St	-	-	38 (12.2)
Megaphrynium trichogynum	Herb		Tr	St	-	-	2 (0.6)
Hypselodelphus violacea	Herb		F	Fr	3 (0)	2 (1)	-
Megaphrynium trichogynum	Herb		F	Fr	4 (0)	4 (1)	-
Sarcophrynium brachystachyum/ schweinfurthianum	Herb		F	Fr	6 (0)	3 (1)	
			Tr	St	-	-	14 (4.5)
Sarcophrynium prionogonium	Herb		F	Fr	17 (1)	7 (3)	-
Thaumatococcus daniellii	Herb		F	Fr	2 (0)	1 (0)	-
			Tr	St	-	-	2 (0.6)
Moraceae							
Myrianthus arboreus	Tree	P	F	Fr	47 (2)	18 (7)	-

Myristicaceae							
Pycnanthus angolensis	Tree	NPLD	F	Fr	108 (5)	43 (16)	-
Olacaceae							
Heisteria parvifolia	Tree	SB	F	Fr	3 (0)	1 (0)	-
Strombosia sp.	Tree	SB	F	Fr	1 (0)	1 (0)	-
Sapindaceae							
Pancovia laurentii	Tree	SB	F	Fr	141 (6)	35 (13)	-
Sapotaceae							
Chrysophyllum lacourtianum	Tree	SB	F	Fr	7 (0)	5 (2)	-
Omphalocarpum elatum	Tree	SB	F	Fr	1 (0)	1 (0)	-
Thymelaceae							
Dicranolepis baertsiana	Tree	NA	F	Fr	4 (0)	2 (1)	-
Tiliaceae							
Desplatsia dewevrei	Tree	NPLD	F	Fr	5 (0)	3 (1)	-
Urticaceae							
Musanga cecropioides	Tree	P	F	Fr	1251 (55)	180 (67)	-
Vitaceae							
Cissus dinklagei	Liana		F	Fr	342 (15)	76 (28)	-
Zingiberaceae							
Aframomum sp.	Herb		F, Tr	Fr	855 (38)	167 (62)	9 (2.9)
Aframomum sp.	Herb		Tr	St	-	-	21 (6.7)
Non identified species							
NID_local.name : Bempura	Liana		F	Fr	11 (0)	5 (2)	-
NID_local.name: Enkwanzala	Liana		F	Fr	24 (1)	10 (4)	-
NID_local.name: Ketshu	Liana		F	Fr	6 (0)	4 (1)	-
NID_local.name: Maniankima	Liana		F	Fr	3 (0)	2 (1)	-
NID_local.name: Mbombal-ngaa	Tree	NID	F	Fr	3 (0)	1 (0)	-
NID_local.name: Mosima	Tree	NID	F	Fr	27 (1)	14 (5)	-
NID_local.name: Motsio	Tree	NID	F	Fr	42 (2)	8 (3)	-

NID_local.name: Omonobari	Tree	NID	F	Fr	8 (0)	5 (2)	-
NID_local.name: Lenkala	Liana		F	Fr	182 (8)	44 (16)	-
NID_first.obs: 18.05.2011	NID		F	Fr	2 (0)	1 (0)	-
NID_first.obs: 21.08.2011	NID		F	Fr	46 (2)	11 (4)	-
NID_first.obs: 04.11.2011	NID		F	Fr	10 (0)	5 (2)	-
NID_first.obs: 07.12.2011	NID		F	Fr	8 (0)	4 (1)	-
NID_first.obs: 13.12.2011	NID		F	Fr	3 (0)	1 (0)	-
NID_first.obs: 19.12.2011	NID		F	Fr	2 (0)	2 (1)	-
NID_first.obs: 07.02.2012	NID		F	Fr	78 (3)	22 (8)	-
NID_first.obs: 27.03.2012	NID		F	Fr	1 (0)	1 (0)	-
NID_first.obs: 18.04.2012	NID		F	Fr	7 (0)	2 (1)	-
NID_first.obs: 18.04.2012	NID		F	Fr	3 (0)	1 (0)	-
NID_first.obs: 18.04.2012	NID		F	Fr	1 (0)	1 (0)	-
NID_first.obs: 19.04.2012	NID		F	Fr	3 (0)	1 (0)	-
NID_first.obs: 25.04.2012	NID		F	Fr	2 (0)	2 (1)	-
NID_first.obs: 25.04.2012	NID		F	Fr	1 (0)	1 (0)	-
NID_first.obs: 16.05.2012	NID		F	Fr	2 (0)	1 (0)	-
NID_first.obs: 18.05.2012	NID		F	Fr	3 (0)	1 (0)	-
NID_first.obs: 21.05.2012	NID		F	Fr	20 (1)	2 (1)	-
NID_first.obs: 06.09.2012	NID		F	Fr	1 (0)	1 (0)	-
NID_first.obs: 10.09.2012	NID		F	Fr	1 (0)	1 (0)	-
NID_first.obs: 12.09.2012	NID		F	Fr	6 (0)	2 (1)	-
NID_first.obs: 12.09.2012	NID		F	Fr	1 (0)	2 (1)	-
NID_first.obs: 05.10.2012	NID		F	Fr	1 (0)	1 (0)	-
NID_first.obs: 21.03.2013	NID		F	Fr	5 (0)	3 (1)	-
NID_first.obs: 16.01.2013	NID		F	Fr	18 (1)	1 (0)	-
NID_first.obs: 16.02.2013	NID		F	Fr	8 (0)	2 (1)	-
NID_first.obs: 18.02.2013	NID		F	Fr	1 (0)	1 (0)	-
NID_first.obs: 05.04.2013	NID		F	Fr	5 (0)	3 (1)	-

Bonobo diet has been recorded in feces analysis (n=2272, 270 days between May 2011 and June 2013) and in observations along transects (179. 1 km travelled in 2011, 2012, 2013). NID means non-identified species. NID is followed (i) by the local name if the species was known and named by the local assistants or (ii) by the first date of observation if local assistants did not recognise the species. Life forms are classified as Tree, Liana, Herb or non-identified (NID). Tree guild is categorized as shade-bearer (SB), pioneer (P), non-pioneer light demanding (NPLD), non-available (NA, when we did not find the information in literature) or non-identified (NID, when the species was not identified with its scientific name) (Hawthorne 1995). Observation type can be in the feces analysis (F) or in the food remains on transects (Tr). Part eaten corresponds to fruits (Fr), stems (St) or leave (L). Feces analysis are presented as the number of feces in which we found the species and the percentage in total feces samples (n=2272) and as the number of day in which we recorded the species presence with the relative percentage of the total sampled days (n=270). Food remains are presented as the number of independent observations, regardless of the number of items counted, and are also indicated as the percentage of total observations (n=311).

X APPENDIX B

Appendix B1: Model diagnostics: Modelling the number of consumed species through time

Table B1-1: DFBetas

	Parameter estimates	DFBeta min	DFBeta max
Intercept	1.657	1.652	1.662
Sin (Date)	-0.111	-0.120	-0.103
Cos (Date)	0.083	0.072	0.091
Ac. term	0.118	0.110	0.130

Ac.term is the temporal autocorrelation term.

Table B1-2: Variance inflation factor (VIF)

	VIF
Sin (Date)	1.018
Cos (Date)	1.010
Ac. term	1.018

Ac.term is the temporal autocorrelation term.

Appendix B2: Model diagnostics: Modelling species seasonality through time

Table B2-1: DFBetas

	DFBetas							
	Intercept		Sin (Date)		Cos (Date)		Ac.term	
	Min	Max	Min	Max	Min	Max	Min	Max
NID_Lenkala	-2.593	-2.509	-1.353	-1.214	-1.193	-1.037	0.715	0.825
Annona senegalensis	-3.873	-3.759	-0.385	-0.176	-0.634	-0.024	0.284	0.682
Myrianthus arboreus	-4.442	-4.196	-1.971	-1.552	0.139	0.807	0.772	1.003
Uapaca sp.	-1.413	-1.347	-2.044	-1.933	-0.389	-0.291	1.129	1.211
Dialium sp.	-2.279	-2.194	0.128	0.334	-1.176	-1.010	2.003	2.167
Marantochloa leucantha	-0.039	-0.007	0.803	0.851	0.197	0.246	0.535	0.610
Landolphia sp1	-6.280	-5.894	7.253	7.660	-1.222	-0.897	0.914	1.059
Landolphia sp2	-3.629	-3.405	1.290	1.515	3.620	3.994	0.892	1.063
Landolphia sp2	-1.397	-1.361	-0.181	-0.107	0.015	0.089	0.876	0.943
Pycnanthus arboreus	-2.892	-2.762	-2.995	-2.816	-0.352	-0.217	0.548	0.623
Pancovia laurentii	-2.792	-2.716	-0.467	-0.209	-0.349	-0.170	0.785	0.947
Isolona hexaloba	-3.616	-3.485	-0.368	-0.060	0.505	0.921	1.509	1.736
Cordia plathyrsa	-3.079	-2.957	-0.158	0.044	0.299	0.457	1.820	1.938
Cissus dinklagei	-1.976	-1.843	-3.275	-3.091	1.233	1.425	0.732	0.857
Uvaria sp.	-3.239	-3.146	0.875	1.055	0.381	0.615	0.494	0.623
Aframomum sp.	0.769	0.850	1.575	1.672	-2.245	-2.120	0.678	0.745
Polyalthia suaveolens	-3.458	-3.243	-2.166	-1.923	3.259	3.623	0.746	0.850
Piptostigma fasciculatum	-1.774	-1.728	0.540	0.635	-0.325	-0.235	0.812	0.877
Musanga cecropioides	1.006	1.076	-0.377	-0.265	-0.813	-0.693	2.153	2.227

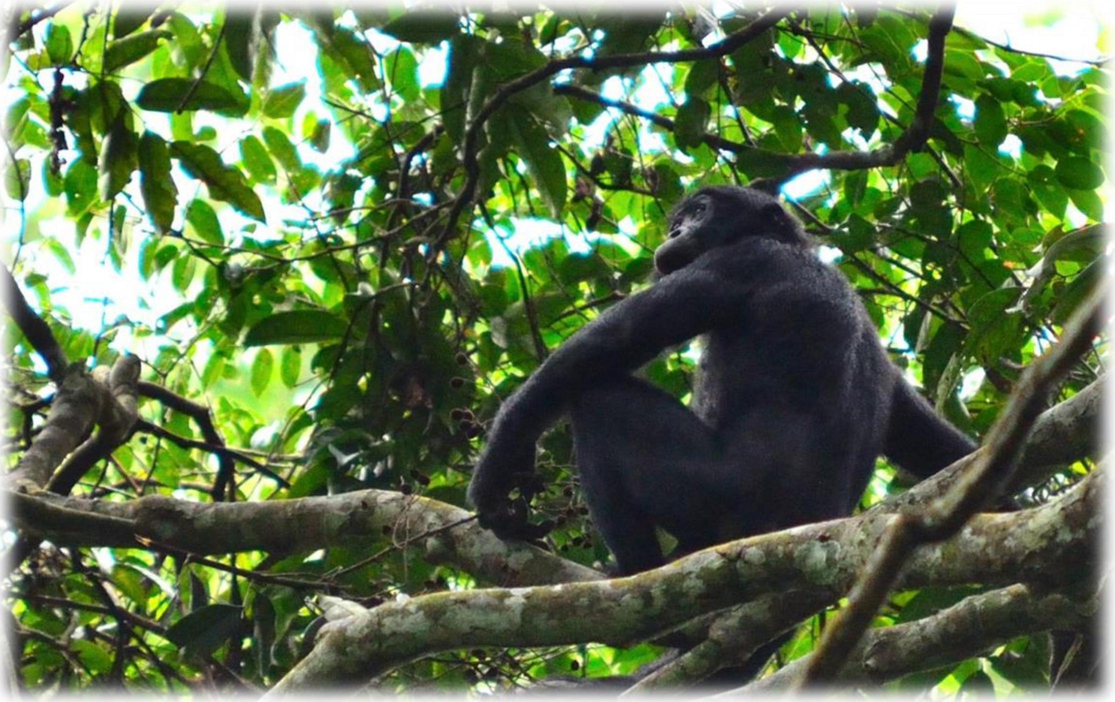
Ac.term is the temporal autocorrelation term.

Table B2-2: Variance inflation factor (VIF) and length of the dataset after correcting for leverage

	VIF sin (Date)	VIF cos (Date)	VIF (ac.term)	Dataset length
NID_Lenkala	1.031	1.042	1.011	256
Annona senegalensis	1.016	1.015	1.024	248
Myrianthus arboreus	1.183	1.063	1.186	228
Uapaca sp.	1.044	1.047	1.003	267
Dialium sp.	1.144	1.006	1.148	261
Marantochloa leucantha	1.011	1.013	1.009	270
Landolphia sp1	1.261	1.229	1.081	265
Landolphia sp2	1.147	1.335	1.176	245
Landolphia sp3	1.006	1.005	1.005	263
Pycnanthus arboreus	1.049	1.045	1.006	260
Pancovia laurentii	1.027	1.021	1.012	242
Isolona hexaloba	1.068	1.320	1.362	256
Cordia plathyrsa	1.086	1.260	1.210	258
Cissus dinklagei	1.091	1.249	1.154	256
Uvaria sp.	1.029	1.029	1.000	248
Aframomum sp.	1.064	1.066	1.008	261
Polyalthia suaveolens	1.227	1.291	1.090	253
Piptostigma fasciculatum	1.058	1.120	1.060	261
Musanga cecropioides	1.074	1.087	1.091	270

Ac.term is the temporal autocorrelation term.

GENERAL DISCUSSION, CONCLUSIONS AND PERSPECTIVES



© WWF – Frédéric Créteur

At the time our research began, only few information was available on bonobos living in the forest-savannah mosaics environment of north-western DRC. Thompson (1997) studied the feeding ecology of a population evolving in a similar environment in the southern extremity of the species distribution range. Inogwabini and his colleagues conducted bonobo surveys in several forest patches of the Lake Tumba Landscape and came up with the first estimates of population density for these westernmost populations (Inogwabini et al. 2007). Other than this, we did not know how bonobos adapted to such forest-savannah environment. Are bonobos using all forest patches, whether they are large or small? Are all habitat types available in the forests suitable for nesting or feeding? How do bonobos manage to survive periods of food scarcity? How can bonobos' socio-ecological traits be compared between those of the forest-savannah mosaics and those of the dense tropical forests? The objective of our research is to begin addressing such questions, putting a particular emphasis on findings that could contribute to the formulation of appropriate recommendations for management of logging concessions in the area, and to help develop sound conservation programs in the region.

In this section, I discuss the main results of my research with regards to the bonobo's ecological requirements and behavioural strategies, results that are detailed in the different chapters. I show also here how these results could be integrated into conservation programs. I point out the new methods we used or developed and which could be applied in a wide range of studies / research topics. I present also some perspectives for future research in the region.

I BONOBO ECOLOGICAL REQUIREMENTS IN FOREST-SAVANNAH MOSAICS

In our study on the influential scale range of environmental variables (Chapter 1), we highlight the fact that bonobos favour large forest patches for nesting (at least 750 m of radius around nest occurrence). Even if it is obvious that forests are indispensable for bonobos, this finding implies that there is a minimal requirement of forest patch size when it comes to sleeping / nesting space needs. This result can be correlated with several characteristics of the preferred habitat for sleeping, i.e., the preferred tree species for nest building (the complete list is provided in Appendix IV – Page 277), the relative small DBH size for nest trees (Chapter 2), the parts of the forest presenting a high fruit availability, and the abundance of a species of Marantaceae, *Haumania liebrechtsiana* (Chapter 1), which were mainly observed in the interior of forest patches. In opposition, when we analysed where feeding remains or ranging indices are observed in the forest (data not shown in this manuscript, but presented in the ATBC Congress in 2011), we found that bonobos use equally all forest parts with regards to the distance to the forest edge. This result is in line with our finding of diet analysis (Chapter 3), where the main species consumed are all characteristic of disturbed or edge habitats, which suggests then that the ecological requirements of the species vary largely according to the type of behaviour: bonobos are dependent on undisturbed forests for sleeping, but rely on all forest types and even savannahs for feeding.

Food availability could be a challenging factor in forest-savannah mosaics. We provide the evidence that fruit availability is seasonal and can vary largely according to the forest patches (significant difference between Mpelu and Nkala forests, Chapter 2), with even quite low occurrence of trees bearing fruits within the forests. Of course, this type of analysis and diet description should be carried out during a much longer time period than our two year research before drawing conclusions, but our findings suggest that bonobos are probably highly constrained by the availability of rich-carbohydrate fruits (Chapter 3). As their diet is restricted to few selected species characteristics of various habitat types, it suggests that bonobos have to adapt their foraging strategy by traveling daily large distances in order to complete the nutritional balance.

It is obvious that we will need direct observations to characterize more precisely food items or the use of the different forest habitat types, but our research already points out that bonobos are probably highly constrained by their ecological requirements and that some measures of forest management is needed to ensure their long term survival in the region.

II BONOBO BEHAVIOURAL STRATEGY IN FOREST-SAVANNAH MOSAICS

In the analysis of variable scale range in species distribution modelling (Chapter 1), we correlate environmental variables with the respective behaviour at which the influential scale range corresponds. We showed that forest structure explains nesting site location at large scale, above 750 m of radius around nest occurrence (and preferentially at least above 1200 m), which reflects bonobo ranging strategies. On the other hand, food availability acts at smaller scales: terrestrial herbaceous vegetation is influential under 300 m and fruit availability under 600 m, corresponding well to scales of sleeping site selection and feeding behaviour around nesting sites, respectively. Such type of analysis is very useful when no direct observations are available and our results correspond quite well with our other findings and observations.

In forest-savannah mosaics, bonobos could have to adapt their ranging strategy in order to satisfy their food requirements by travelling daily over large distance (Chapter 3), by significantly varying the home range size in period of food scarcity (Chapter 2) and by selecting sleeping areas with high fruit availability in a large radius (600 m – Chapter 1). Direct observations should confirm such information as well as studies from other bonobo communities of the forest-savannah mosaic, but this suggests that corridors between forest patches are essential for long term survival of the species even if bonobos do not use such corridors for sleeping, as well as forest patch quality.

In opposition, sleeping behaviour might be more similar to that of bonobo populations living in tropical dense forests, possibly because of the importance of sleeping quality. Nest building, by providing thermoregulation, reduced vulnerability to predators, more comfortable sleeping postures, and protection against pathogens, is one of the factors which have permitted the cognitive evolution of early hominoids. In our research, we show that bonobos chose defined tree species for sleeping (Chapter 2). Even if those tree species are different from those selected in the dense forests, they are also preferentially bearing small leave size. This, in combination with the nest position within the tree (data not shown in this manuscript, but see Master Thesis of Emilien Raynaud), probably explains a selection that favours comfortable posture and thermoregulation (Fruth 1995). Nest height and the lack of accessibility to the nest tree suggest a behavioural attempt to reduce vulnerability to predators, even if leopards probably do not occur in the study site any longer. All those traits are shared by all Great Apes and probably the ancestor of the hominoids, suggesting that sleeping is a highly conservative behaviour.

According to our findings, bonobos' cohesiveness at night also seems to be a conservative trait of the species (Chapter 2). Until now, their socio-ecology was only studied in dense tropical forests. People suggested that high food availability, among others, had permitted the evolution of the bonobo species towards a more cohesive grouping pattern than chimpanzees. At the same time, other studies pointed out that, in similar environments, grouping pattern of both species was very similar (Boesch 1996). We thus decided to test how bonobos of forest-savannah mosaics were socially reacting to periods of fruit scarcity in their habitats. Again, our results should be confirmed by direct observations and completed by data on day grouping patterns, but we observed that variations in fruit availability do not influence bonobo cohesion at night, which could suggest that marked seasonal variations alone do not explain the differences in grouping patterns between bonobos and chimpanzees.

Finally, we have to underline a particular finding from all our analyses: at the study site, human activity did not seem to influence bonobo home range use or cohesiveness (Chapters 1 and 2). While most Great Apes studies point out to human pressure as one of the principal drivers of ape density decline, this result should be taken with precaution and correctly addressed. First, the apparent absence of influence of human proximity might be explained by the fact that the study site is located in the Teke ethnic group territory, a group that has ancestral taboos concerning bonobos, and therefore not a threat for bonobos. Moreover, the bonobo Nkala community is living in the largest study forest patch, with higher food availability, even if located close to the most important village of the study site. Maybe bonobos cannot avoid humans because this patch is too important in term of habitat suitability. We suggest that bonobos are most probably so constrained by their environmental requirements that they cannot avoid human proximity. Finally, when taking into account our predictor on human activity in the forests, we did not find a negative influence on bonobo nest occurrence. It is however possible that we should have integrated a more dynamic predictor to represent human forest use.

III APPLICATIONS OF OUR RESEARCH FOR BONOBO CONSERVATION

While our research suggests that bonobos are already highly constrained by their ecological requirements within the study site, the question of how to integrate our findings in conservation programs is a priority. As part of a process that started less than 10 years ago, local communities have accepted to dedicate some parts of their forests for bonobo conservation, essentially by stopping all hunting in those areas. While hunting regulations are respected readily by the villagers, rules remain too open to individual interpretation. Of course, these communities rely entirely on forests for agriculture and subsistence hunting and fishing, and therefore a ban on forest use is not realistic. However some measures of integrated forests management could be taken, as forest degradation could rapidly become a pressing issue for bonobo survival in these forests.

Our major concern is the current forest degradation induced by the practice of slash-and-burn agriculture. We found out that bonobos have minimal requirements in terms of forest patch size (a minimum of 750 m of radius but preferentially at least 1200 m), a surface already larger than the majority of forest patches in the study site. Human population is currently growing in the region (2.5% at a national level) and cultivated fields are developing almost everywhere along forest edges. Over three years, almost 500 m of the study transects were transformed into cultivated fields; local assistants told me that not so long ago bonobos were often found in tree patches between cultivated fields, which is not the case anymore. Such problems are even more acute in the Nkala forest, where people from other villages are starting to cultivate. The situation is of course quite complex but forest management, such as forest allocation planning for cultivated fields, could help slow down the current dynamic. As we underlined, some areas are preferentially used by bonobos for sleeping and feeding. By improving our knowledge on bonobo ranging patterns and their relative habitats, we could draw a precise forest map and identify forest areas of little interest for the species in order to suggest locations for new cultivated fields. Agricultural techniques, such as rotation system or soil enrichment by natural methods (e.g., use of leguminous plant or of cowpat to improve soil fertility) could also been developed at low cost in order to decrease the needs for new forested lands. As part of the Teke tradition, it is normally the women who cultivate the land in the savannahs. This tradition has been recently discarded because of the development of local cattle ranching concessions. People do not guard their animals and / or do not built night enclosures, which often leads to savannah field degradation by cattle. Increasing awareness and dialogue with ranch owners might enable to re-open agriculture in savannahs.

Despite this worrying situation, the study site could offer a nice opportunity to develop a community natural reserve. Most people wish to help in bonobo conservation but actually do not know what to do. I would suggest working with them on "*reducing their impacts on bonobos*". With this research, we highlighted a number of fruit species that are preferred by bonobos. Human generally do not consume the same fruits but cut trees for house-building, lianas for drinking in the forests or diverse type of building (basket, roof, etc.) and Marantaceae for cooking. In some cases, tree cutting does have a considerable impact. For example, the tree *Piptostigma fasciculatum* or the Marantaceae *Marantochloa leucantha* are highly consumed by bonobos but quite rare within the forests. In contrast, nest tree species are generally abundant in the forests, and are not particularly sought after. By improving our knowledge on the eco-systemic services, we could discuss with the local people on how to adapt their forest practices to decrease the use of some of the species that are used by both humans and bonobos. My personal impression is that the local community would positively accept such capacity building and awareness programs and that this could even improve other conservation actions as people would feel that they actively take part into bonobo conservation. Anecdotally, when I explained to WWF trackers and to my local assistants that, of the two liana species that people use as drinks, one is highly consumed by bonobos, most of them spontaneously stop cutting the species favoured by bonobos.

Finally, the potential impacts of logging concessions in the area should be addressed specifically. Major consequences from logging are generally roads opening, immigrants arrival and canopy gaps leading to forest degradation. Another possible consequence might be that the region could rapidly become a new spot of bushmeat collection for the trade to Kinshasa. Canopy gaps could favour Marantaceae forests which seem to be discarded by bonobos, at least for nesting, in the study site. The impact of all these threats on bonobos should be more largely investigated.

IV DEVELOPMENT OF NEW METHODOLOGY

During this research, I particularly work on the development of a new methodology for scale search in species distribution modelling. Furthermore, I also used different methods of analyses that could be more widely applied as they offer very interesting results and opportunities of interpretation. These methods include the zero inflated models we realized to study yearly variation of population density and the right-angled mixture triangle to investigate nutritional ecology.

IV.1 Improving scale search in species distribution modelling

In our first chapter, we developed a procedure that enabled us to define the influential scale range of variables in species distribution modelling. The role of spatial scale in ecological pattern formation has been studied for decades. But, even if much progress has been made on how to identify most influential spatial scales, previous methods often relied on misunderstandings: people generally tried to identify one optimal scale instead of an influential scale range. This misunderstanding comes from the fact that they did not represent correctly the predictor influence when extracting their values as they do not account for the decreasing influence of values at increasing distance from the observation point. Those issues often lead to statistical problems and misinterpretations of the result. In our study, we suggested a procedure that allowed us to simultaneously evaluate the influence of multiple scales, predictors and autocorrelation, and to account also for spatial decay effects. Our methods give very interesting results when applied on our bonobo data, highlighting the influential scale ranges of the environmental variables and reflecting the related bonobo behaviours.

Predictor scale search is an essential tool in many applied fields. In various research topics, people are working with spatial or temporal data, wishing to highlight their scale influence in order to interpret the effect of the predictor. In our paper, we suggest that such type of methodology could be largely applied in conservation, e.g. for landscape management. For example, in our study site, it could be helpful for developing forest integrated management plans as we highlighted bonobo minimal ecological requirements for ranging and sleeping. But, the scale search could also be very useful in landscape ecology and this, particularly in the current context of global landscape modification. Numerous studies have been developed to estimate edge effects, effects of patch size or isolation, within-patch and landscape matrix quality. For all those researches, the question of spatial scale is essential but scale was often defined arbitrarily as people do not know in advance the effect of habitat fragmentation on the species studied. Such method could also be promising for studies in temporal domain. We gave the example of research on animal relationships over extensive periods, e.g. to better understand behaviours favouring individual affiliations such as grooming reciprocity in primates.

IV.2 **Modelling population dynamics**

In the second chapter, we studied the variation of population density over the three years of survey with a zero inflated model. We suggested that such modelling could be very interesting when several years of data are available. It enabled us to test, in a first step, if population density estimates are stable over years and then to investigate the possible changes. By comparing the model with different reduced models, we could tell if the home range use was varying (i.e., if animals use different forest areas over years) and if density estimates were significantly changing in the forest areas used by bonobos. With this second step, we had a better understanding of the variations in population estimates and thus we can suggest a possible interpretation. For example, in our study, we showed that bonobos sleep in the same forest areas over the years but that nest density was significantly changing. This finding reveals consistency in home range use, indicating that some areas have more suitable habitats for nesting, i.e. with suitable understory, high food availability or preferred nest tree species. We further investigated the possible explanations of density variation and suggested that our study site probably did not encompass the entire home range, probably because the home range size was varying largely according to food availability.

Such methods could be applied to a wide range of animal surveys for which more than one time-period data is available. It could be particularly useful for elusive species for which direct observations are difficult to make as it can give first insights in habitat preferences or home range use. It could also be interesting to apply to monitoring population dynamics over long time period, e.g. in protected or sensible areas.

IV.3 **Investigating nutritional ecology with the right-angled mixture triangle**

Information on primate nutritional ecology has been restricted for a long time because of difficulties in data collection in the wild. Estimates of daily nutrient intake usually require continuous direct observations of at least one individual and the assessment of the actual weight of the food items ingested. Consequently, such study can only be performed on fully habituated populations, consistently limiting the range of potential candidate populations for nutritional analysis. But, recent advances in methodology suggest the possibility to work with proportion-based instead of absolute values of nutrient intakes and to integrate such data within the framework of the right-angled mixture triangle analysis (Raubenheimer 2011). Such approach has been applied on various animal studies and gives promising results on the understanding of the nutritional priorities of animals. Since this methodology only requires food species identification, it offers new opportunities for studying primate nutritional ecology. It is then possible to rapidly gather additional nutritional information from a wide range of ape populations and give new insights on species diet plasticity.

In the third chapter, we applied the right-angled mixture triangle on our data of feces analysis and found interesting results. Classical analyses, such as testing differences in the distribution of nutrient values between two groups (e.g. food and non-food species), may lead to relatively weak results because of the small size of the dataset, which limits the opportunity to understand species nutrient requirement. But this new approach provides the possibility to graphically look at nutrient intake patterns while accounting for the other nutrient intakes. As a result, this technique indicates possible limiting nutrients and foraging strategy such as nutrient balancing strategy, fiber or anti-feedants minimization or energy maximization. Thanks to such approach, we demonstrate that the carbohydrate source of energy is a limiting factor in our study site and that bonobos usually consume daily a peculiar association of species in order to complete a nutritional balance of important energy source (carbohydrates, crude fate and protein).

V CONCLUSIONS AND PERSPECTIVES

All through my PhD research, my main objective was to provide first insights on the etho-ecological requirements of bonobos living in the forest-savannah mosaics of western DRC. Overall results should be confirmed by direct observations but we already came up with some interesting findings.

While sleeping behaviour and cohesiveness seem to be species conservative traits, bonobos probably had to adapt their foraging strategies and their diet to this particular environment. We only studied the diet of one community. Further studies should analyse bonobo diet plasticity between communities within forest-savannah mosaics and make comparisons with populations of dense forests.

We also showed that bonobos have minimal requirements in terms of forest patch size. Considering the importance of this finding for forest management in conservation, we should further investigate forest patch characteristics that explain bonobo occurrence. For example, we could try to differentiate the effects of patch size from patch shape, patch isolation, within-patch and landscape matrix quality or highlight possible edge effects. Such analysis would be very useful to address more precisely the question of bonobo forest structure requirements in fragmented habitats. A meta-analysis across bonobo distribution range could also help to demonstrate potential plasticity in ranging / foraging strategies.

To conclude, more emphasis should be put on the influence of human activity on bonobos populations in order to identify adequate conservation measures for the region. Until now, few studies have assessed how human resource use practices and local socio-economic systems lead to deforestation, habitat and biodiversity loss. Furthermore, demographic expansion could rapidly disrupt already fragile systems: e.g., habitat fragmentation can lead to a sudden decline in animal abundance around villages, which may trigger higher agricultural expansion to compensate for unsuccessful hunting. Such interactions should be analysed in coupled human-natural systems in order to identify tipping points, as well as human decisions that affect maintenance or loss of sustainability. For example, recent development in agent-based modelling will enable to model social-ecological systems of local communities. This will ultimately help to estimate how human resource use practices impact on bonobo habitats as well as on bonobos' survival, and to analyse how community conservation planning scenarios could impact on socio-ecological system sustainability and bonobo survival in forest-savannah mosaics.

BIBLIOGRAPHY

© Fabrice Dentressangle

Adiseshan, A., T. Adiseshan, and L. A. Isbell. 2011. Affiliative relationships and reciprocity among adult male bonnet macaques (*Macaca radiata*) at Arunachala Hill, India. American journal of primatology 73:1107–1113.

Amman, K. 2001. Bushmeat hunting and the Great Apes. Pages 71–85 *in* B. Beck, T. Stoinski, M. Hutchins, T. Maple, B. Norton, A. Rowan, E. Stevens, and A. Arluke, editors. Great Apes and Humans : the ethics of coexistence. Smithsonian Institution Press, Washingtion DC and London.

Ancrenaz, M., R. Calaque, and I. Lackman-Ancrenaz. 2004. Orangutan nesting behavior in disturbed forest of Sabah, Malaysia: implications for nest census. International Journal of Primatology 25:983–1000.

Ancrenaz, M., A. Marshall, B. Goossens, C. van Schaik, J. Sugardjito, M. Gumal, and S. Wich. 2008. *Pongo pygmaeus*. www.iucnredlist.org. Accessed 19 February 2014

Anderson, P., M. G. Turner, J. D. Forester, J. Zhu, M. S. Boyce, H. Beyer, and L. Sotwell. 2005. Scale-dependent summer resource selection bu reintroduced elk in Wisconsin, USA. The journal of wildlife management 69:298–310.

Araújo, M. B., and A. Guisan. 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography 33:1677–1688.

Arnhem, E., J. Dupain, R. V. Drubbel, C. Devos, and M. Vercauteren. 2008. Selective logging, habitat quality and home range use by sympatric gorillas and chimpanzees: a case study from an active logging concession in Southeast Cameroon. Folia primatologica 79:1–14.

Arroyo-Rodríguez, V., and P. A. D. Dias. 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. American journal of primatology 72:1–16.

Aue, B., K. Ekschmitt, S. Hotes, and V. Wolters. 2012. Distance weighting avoids erroneous scale effects in species-habitat models. Methods in Ecology and Evolution 3:102–111.

Basabose, A. K. 2002. Diet composition of Chimpanzees inhabiting the montane forest of Kahuzi, Democratic Republic of Congo. American Journal of Primatology 58:1–21.

Basabose, A. K. 2004. Fruit availability and chimpanzee party size at Kahuzi montane forest, Democratic Republic of Congo. Primates 45:211–219.

Basabose, A. K., and J. Yamagiwa. 2002. Factors affecting nesting site choice in Chimpanzees at Tshibati, Kahuzi-Biega National Park: influence of sympatric Gorillas. International Journal of Primatology 23:263–282.

Beaune, D., F. Bretagnolle, L. Bollache, C. Bourson, G. Hohmann, and B. Fruth. 2013. Ecological services performed by the bonobo (*Pan paniscus*): seed dispersal effectiveness in tropical forest. Journal of Tropical Ecology 29:367–380.

Van Beest, F. M., I. M. Rivrud, L. E. Loe, J. M. Milner, and A. Mysterud. 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? The Journal of animal ecology 80:771–785.

Boesch, C. 1996. Social grouping in Taï chimpanzees. Pages 101–113 *in* W. C. McGrew, L. F. Marchant, and T. Nishida, editors. Great Apes Societies. Cambridge University Press, Cambridge.

Borcard, D., F. Gillet, and P. Legendre. 2011. Numerical Ecology with R. Page 306. Springer New York, New York.

Bourland, N., L. Koudia Yao, P. Lejeune, B. Sonké, J. Philippart, K. Daïnou, F. Fétéké, and J.-L. Doucet. 2012. Ecology of *Pericopsis elata* (Fabaceae), an endangered timber species in southeastern Cameroon. Biotropica 44:840–847.

Bowyer, R. T., and J. G. Kie. 2006. Effects of scale on interpreting life-history characteristics of ungulates and carnivores. Diversity and Distributions 12:244–257.

Boyce, M. S. 2006. Scale for resource selection functions. Diversity and Distributions 12:269–276.

Boyer, D., G. Ramos-Fernández, O. Miramontes, J. L. Mateos, G. Cocho, H. Larralde, H. Ramos, and F. Rojas. 2006. Scale-free foraging by primates emerges from their interaction with a complex environment. Proceedings of the Royal Society of Biological sciences 273:1743–1750.

Brugiere, D., and D. Sakom. 2001. Population density and nesting behaviour of lowland gorillas (*Gorilla gorilla gorilla*) in the Ngotto forest, Central African Republic. Journal of Zoology 255:251–259.

Buckland, S. T. ., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Page 432. Oxford University Press, Oxford.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference a practical information-theoretic approach. Second edition. Page 488. Springer, New York.

Chapman, C. A., L. J. Chapman, and L. Naughton-treves. 2004. Predicting folivorous primate abundance: validation of a nutritional model 69:55–69.

Chapman, C. A., M. J. Lawes, L. Naughton-Treves, and T. Gillespie. 2003. Primate survival in community-owned forest fragments: are metapopulation models useful amidst intensive use? Pages 63–78 *in* L. K. Marsh, editor. Primates in Fragments. Ecology in Conservation. Kluwer Academic / Plenum Publishers, New York.

Chapman, C. A., F. J. White, and R. W. Wrangham. 1994. Party size in Chimpanzees and Bonobos. Pages 41–57 *in* R. Wrangham, W. McGrew, F. de Waal, and P. Heltne, editors. Chimpanzee Cultures. Harvard University Press, Cambridge.

Chaves, M., and K. E. Stoner. 2012. Differences in diet between spider monkey groups living in forest fragments and continuous forest in Mexico. Biotropica 44:105–113.

Chiarello, A. G. 2003. Primates of the Brazalian Atlantic forest: the influence of forest fragmentation on survival. Pages 99–122 *in* L. K. Marsh, editor. Primates in Fragments. Ecology in Conservation. Kluwer Academic / Plenum Publishers, New York.

Choudhury, A., D. K. Lahiri Choudhury, A. Desai, J. W. Duckworth, P. S. Easa, A. J. T. Johnsingh, P. Fernando, S. Hedges, M. Gunawardena, F. Kurt, U. Karanth, A. Lister, V. Menon, H. Riddle, A. Rübel, and E. Wikramanayake. 2008. *Elephas maximus*. www.iucnredlist.org. Accessed 19 February 2014

Clark, C. J., J. R. Poulsen, R. Malonga, and P. W. Elkan. 2009. Logging concessions can extend the conservation estate for Central African tropical forests. Conservation biology : the journal of the Society for Conservation Biology 23:1281–1293.

Conklin-Brittain, N. L., C. D. Knott, and R. W. Wrangham. 2001. The feeding ecology of Apes. Pages 167–174 The Apes: Challenges for the 21st Century, Conference Proceedings of Brookfield Zoo. May 10-13, 2000. Chicago Zoological Society, Chicago.

Corlett, R. T. 2011. How to be a frugivore (in a changing world). Acta Oecologica 37:674–681.

Devers, D., and J. P. Vande Weghe. 2006. The forests of the Congo Basin - State of the Forest 2006. Page 257. Kinshasa.

Devos, C., and A. Laguardia. 2011. Local assessment of gorilla nest decay rate at Mikongo Conservation Centre, Lopé National Park: refining population density estimates. Page 27.

Devos, C., C. Sanz, D. Morgan, J.-R. Onononga, N. Laporte, and M.-C. Huynen. 2008. Comparing Ape densities and habitats in northern Congo: surveys of sympatric Gorillas and Chimpanzees in the Odzala and Ndoki Regions. American Journal of Primatology 70:439–451.

Djoufack, S. D., B. A. Nkongmeneck, J. Dupain, S. Bekah, K. K. Bombome, M. A. Epanda, L. Van Elsacker, and Editeurs. 2007. Manuel d’identification des fruits consommés par les Gorilles et les Chimpanzés des basses terres de l’Ouest; Espèces de l'écosystème du Dja (Cameroun). Page 107 (M. A. Epanda and L. Van Elsacker, Eds.).

Dobson, A. J. 2002. An introduction to generalized linear models. Boca Raton [etc.], Chapman & Hall/CRC.

Donati, G., K. Kesch, K. Ndremifidy, S. L. Schmidt, S. M. Borgognini-tarli, and J. U. Ganzhorn. 2011. Better few than hungry: flexible feeding ecology of collared lemurs *Eulemur collaris* in littoral forest fragments. PloS ONE 6:e19807.

Doucet, J.-L. 2003. PhD Thesis. L’alliance délicate de la gestion forestière et de la biodiversité dans les forêts du centre du Gabon. University of Liege.

Emlen, J. M. 1966. The Role of Time and Energy in Food Preference. The American Naturalist 100:611–617.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Felton, A. M., A. Felton, W. J. Foley, and D. B. Lindenmayer. 2010. The role of timber tree species in the nutritional ecology of spider monkeys in a certified logging concession, Bolivia. Forest Ecology and Management 259:1642–1649.

Felton, A. M., A. Felton, D. B. Lindenmayer, and W. J. Foley. 2009a. Nutritional goals of wild primates. Functional Ecology 23:70–78.

Felton, A. M., A. Felton, D. Raubenheimer, S. J. Simpson, W. J. Foley, J. T. Wood, I. R. Wallis, and D. B. Lindenmayer. 2009b. Protein content of diets dictates the daily energy intake of a free-ranging primate. Behavioral Ecology 20:685–690.

Field, A. 2005. Discovering Statistics using SPSS. Sage Publications, London.

Fischer, J., and D. B. Lindenmayer. 2006. Beyond fragmentation : the continuum model for fauna research and conservation in human-modified landscapes. Oikos 2:473–480.

Fischer, J., and D. B. Lindenmayer. 2007. Landscape modification and habitat fragmentation : a synthesis. Global Ecology and Biogeography 16:265–280.

Forester, J. D., H. Kyung Im, and P. J. Rathouz. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology 90:3554–3565.

Forstmeier, W., and H. Schielzeth. 2011. Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner’s curse. Behavioral ecology and sociobiology 65:47–55.

Fortin, D., H. Beyer, M. Boyce, and D. Smith. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Fox, J., and S. Weisberg. 2011. An R companion to applied regression. Page 472. Sage, Thousant Oaks CA.

Fruth, B. 1995. Nests and nest groups in wild bonobos: ecological and behavioural correlates. PhD Thesis. Ludwig-Maximilian University.

Fruth, B., J. M. Benishay, B.-I. Inogwabini, S. Coxe, J. Dupain, T. Furuichi, J. Hart, T. Hart, C. Hashimoto, G. Hohmann, M. Hurley, O. Ilambu, M. Mulavwa, M. Ndunda, V. Omasombo, G. Reinartz, J. Scherlis, L. Steel, and J. Thompson. 2008. *Pan paniscus*. www.iucnredlist.org. Accessed 17 February 2014.

Fruth, B., and G. Hohmann. 1993. Ecological and behavioral aspects of nest building in wild Bonobos (*Pan paniscus*). Ethology 94:113–126.

Fruth, B., and G. Hohmann. 1996. Nest building behavior in the great apes: the great leap forward? Pages 225–240 *in* W. McGrew, L. Marchant, and T. Nishida, editors. Great Apes Societies. Cambridge University Press, Cambridge.

Fürtbauer, I., R. Mundry, M. Heistermann, O. Schülke, and J. Ostner. 2011. You mate, I mate: macaque females synchronize sex not cycles. PloS ONE 6:e26144.

Furuichi, T. 1997. Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. International Journal of Primatology 18:855–875.

Furuichi, T. 2009. Factors underlying party size differences between chimpanzees and bonobos: a review and hypotheses for future study. Primates 50:197–209.

Furuichi, T., and C. Hashimoto. 2002. Why female bonobos have a lower copulation rate during estrus than chimpanzees. Pages 156–167 *in* C. Boesch, G. Hohmman, and L. Marchant, editors. Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, New York.

Furuichi, T., and C. Hashimoto. 2004. Botanical and topographical factors influencing nesting-wste selection by Chimpanzees in Kalinzu Forest, Uganda. International Journal of Primatology 25:755–765.

Furuichi, T., C. Hashimoto, and Y. Tashiro. 2001a. Fruit availability and habitat use by Chimpanzees in the Kalinzu Forest, Uganda: examination of fallback foods. International Journal of Primatology 22:929–945.

Furuichi, T., C. Hashimoto, and Y. Tashiro. 2001b. Extended application of a marked-nest census method to examine seasonal changes in habitat use by Chimpanzees. International Journal of Primatology 22:913–928.

Furuichi, T., M. Mulavwa, K. Yangozene, B. Motema-salo, G. Idani, and H. Ihobe. 2008. Relationships among fruit abundance, ranging rate, and party size and composition of Bonobos at Wamba. Pages 135–149 *in* T. Furuichi and J. Thompson, editors. The bonobos: Behavior, Ecology, and Conservation. Springer, New York.

Furuichi, T., T. Sakamaki, and M. N. Mulavwa. 2012. Swamp forest: an indispensable resource for wild bonobos (abstract). XXIV Congress of the International Primatological Society. Cancun, Mexico.

Gerbens-Leenes, P., and S. Nonhebel. 2002. Consumption patterns and their effects on land required for food. Ecological Economics 42:185–199.

Gilbert, K. A. 2003. Primates and fragmentation of the Amazon forest. Pages 145–158 *in* L. K. Marsh, editor. Primates in Fragments. Ecology in Conservation. Kluwer Academic / Plenum Publishers, New York.

Gillespie, T. R., C. A. Chapman, and E. C. Greiner. 2005. Effects of logging on gastrointestinal parasite infections and infection risk in African primates. Journal of Applied Ecology 42:699–707.

Goldsmith, M. L., J. Glick, and N. Evarist. 2006. Gorillas living on the edge: literally and figuratively. Pages 405–422 *in* N. E. Newton-fisher, N. Hugh, J. D. Paterson, and V. Reynolds, editors. Primate of Western Uganda. Springer, New York.

Gomes, C. M., and C. Boesch. 2011. Reciprocity and trades in wild West African chimpanzees. Behavioral Ecology and Sociobiology 65:2183–2196.

Goncalves, E. C., S. F. Ferrari, A. Silva, P. E. G. Coutinho, E. V Menezes, and M. P. C. Schneider. 2003. Effects of habitat fragmentation of the genetic variability of silvery marmosets, *Mico argentatus*. Pages 17–28 *in* L. k Marsh, editor. Primates in Fragments. Ecology in Conservation. Kluwer Academic / Plenum Publishers, New York.

Grossmann, F., J. A. Hart, A. Vosper, and O. Ilambu. 2008. Range occupation and population estimates of Bonobos in the Salonga National Park: application to large-scale surveys of Bonobos in the Democratic Republic of Congo. Pages 189–216 *in* T. Furuichi and J. Thompson, editors. The bonobos: Behavior, Ecology, and Conservation. Springer, New York.

Guisan, A., and T. C. Edwards. 2002. Generalized linear and generalized additive models in studies of species distributions : setting the scene. Ecological Modelling 157:89–100.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147–186.

Harrison, M. E., and A. J. Marshall. 2011. Strategies for the use of fallback foods in Apes. International journal of primatology 32:531–565.

Hart, T. 2007. Searching for bonobos in Congo. http://www.bonoboincongo.com. Accessed 17 February 2014

Hashimoto, C. 1995. Population census of the chimpanzees in the Kalinzu Forest, Uganda: comparison between methods with nest counts. Primates 36:477–488.

Hashimoto, C., S. Suzuki, Y. Takenoshita, J. Yamagiwa, A. K. Basabose, and T. Furuichi. 2003. How fruit abundance affects the chimpanzee party size: a comparison between four study sites. Primates 44:77–81.

Hawthorne, W. D. 1995. Ecological profiles of Ghanaian forest trees. Tropical Forestry Papers No. 29.

Hedley, S. L., and S. T. Buckland. 2004. Spatial models for line transect sampling. Journal of Agricultural, Biological, and Environmental Statistics 9:181–199.

Henry, M., M. Fröchen, J. Maillet-Mezeray, E. Breyne, F. Allier, J.-F. Odoux, and A. Decourtye. 2012. Spatial autocorrelation in honeybee foraging activity reveals optimal focus scale for predicting agro-environmental scheme efficiency. Ecological Modelling 225:103–114.

Hernandez-aguilar, R. A. 2006. Ecology and nesting patterns of chimpanzees (*Pan troglodytes*) in Issa, Ugalla, Western Tanzania. PhD thesis. University of Southern California.

Hernandez-Aguilar, R. A., J. Moore, and C. B. Stanford. 2013. Chimpanzee nesting patterns in savanna habitat: environmental influences and preferences. American journal of primatology 75:979–994.

Hickey, J. R., J. Nackoney, N. P. Nibbelink, S. Blake, A. Bonyenge, S. Coxe, J. Dupain, M. Emetshu, T. Furuichi, F. Grossmann, P. Guislain, J. Hart, C. Hashimoto, B. Ikembelo, O. Ilambu, B.-I. Inogwabini, I. Liengola, A. L. Lokasola, A. Lushimba, F. Maisels, J. Masselink, V. Mbenzo, N. M. Mulavwa, P. Naky, N. M. Ndunda, P. Nkumu, V. Omasombo, G. E. Reinartz, R. Rose, T. Sakamaki, S. Strindberg, H. Takemoto, A. Vosper, and H. S. Kühl. 2013. Human proximity and habitat fragmentation are key drivers of the rangewide bonobo distribution. Biodiversity and Conservation 22:3085–3104.

Hohmann, G., A. Fowler, A. Sommer, and S. Ortmann. 2006. Frugivory and gregariousness of Salonga bonobos and Gashaka chimpanzees: the influence of abundance and nutritional quality of fruit. Pages 123–159 *in* G. Hohmann, M. M. Robbins, and C. Boesch, editors. Feeding ecology in apes and other primates. Cambridge University Press, Cambridge.

Hohmann, G., and B. Fruth. 2000. Use and function of genital contacts among female bonobos. Animal Behavior 60:107–120.

Hohmann, G., and B. Fruth. 2002. Dynamics in social organization of bonobos (*Pan paniscus*). Pages 138–150 *in* C. Boesch, G. Hohmman, and L. F. Marchant, editors. Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, New York.

Hohmann, G., and B. Fruth. 2008. New records on prey capture and meat eating by bonobos at Lui Kotale, Salonga National Park, Democratic Republic of Congo. Folia primatologica; international journal of primatology 79:103–110.

Hohmann, G., U. Gerloff, D. Tautz, and B. Fruth. 1999. Social bonds and genetic ties : kinship, association and affiliation in a community of bonobos (*Pan paniscus*). Behaviour 136:1219–1235.

Hohmann, G., K. Potts, A. N'Guessan, A. Fowler, R. Mundry, J. Ganzhorn, and S. Ortmann. 2010. Plant foods consumed by *Pan*: exploring the variation of nutritional ecology across Africa. American Journal of Physical Anthropology 141:476–485.

Hothorn, T., and K. Hornik. 2013. exactRankTests: exact distributions for rank and permutation tests. R package version 0.8-27.

Humle, T., and T. Matsuzawa. 2004. Oil palm use by adjacent communities of Chimpanzees at Bossou and Nimba Mountains, West Africa. International Journal of Primatology 25:551–581.

Hunt, K., and W. McGrew. 2002. Chimpanzees in the dry habitats of Assirik, Senegal and Semliki Wildlife Reserve, Uganda. Pages 35–51 *in* C. Boesch, G. Hohmann, and L. Marchant, editors. Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge.

Idani, G. 1990. Relations between unit-groups of bonobos at Wamba, Zaire: encounters and temporary fusions. African Study Monographs 11:153–186.

Imong, I., M. M. Robbins, R. Mundry, R. Bergl, and H. S. Kühl. (In review). Informing conservation management about structural vs. functional connectivity: a case study of Cross River gorillas.

Imong, I., M. M. Robbins, R. Mundry, R. Bergl, and H. S. Kühl. 2014. Distinguishing ecological constraints from human activity in species range fragmentation: the case of Cross River gorillas. Animal Conservation: DOI: 10.1111/acv.12100.

Inogwabini, B., M. Bewa, M. Longwango, M. Abokome, and M. Vuvu. 2008. The Bonobos of the Lake Tumba – Lake Maindombe Hinterland : threats and opportunities for population conservation. Pages 273–290 *in* T. Furuichi and J. Thompson, editors. The bonobos: Behavior, Ecology, and Conservation. Springer, New York.

Inogwabini, B., B. Matungila, L. Mbende, M. Abokome, and T. Tshimanga. 2007. Great apes in the Lake Tumba landscape, Democratic Republic of Congo : newly described populations. Oryx 41:1–7.

Inogwabini, B.-I., and B. Matungila. 2009. Bonobo food items, food availability and Bonobo distribution in the Lake Tumba swampy forests, Democratic Republic of Congo. The Open Conservation Biology Journal 3:14–23.

Irwin, M. T. 2008. Feeding ecology of *Propithecus diadema* in forest fragments and continuous forest. International Journal of Primatology 29:95–115.

IUCN. 2013. IUCN Red List of Threatened Species. www.iucnredlist.org. Accessed 17 February 2014

IUCN, and ICCN. 2012. Bonobos (*Pan paniscus*): Conservation Strategy 2012-2022. Page 65. IUCN/SSC Primate Specialist Group & Institut Congolais pour la Conservation de la Nature, Gland, Switserland.

Jackman, S. 2012. pscl: classes and methods for R developed in the political science. R package. Computational Laboratory, Stanford University. Department of Political Science, Stanford University, Stanford, California.

Janmaat, K. R. L., S. D. Ban, and C. Boesch. 2013a. Taï chimpanzees use botanical skills to discover fruit: what we can learn from their mistakes. Animal cognition 16:851–860.

Janmaat, K. R. L., S. D. Ban, and C. Boesch. 2013b. Chimpanzees use long-term spatial memory to monitor large fruit trees and remember feeding experiences across seasons. Animal Behaviour 86:1183–1205.

Janmaat, K. R. L., W. Olupot, R. L. Chancellor, M. E. Arlet, and P. M. Waser. 2009. Long-term site fidelity and individual home range shifts in *Lophocebus albigena*. International Journal of Primatology 30:443–466.

Janson, C. H., and R. Byrne. 2007. What wild primates know about resources: opening up the black box. Animal cognition 10:357–367.

Johnson, C. A., D. Raubenheimer, J. M. Rothman, D. Clarke, and L. Swedell. 2013. 30 Days in the life: daily nutrient balancing in a wild Chacma Baboon. PloS ONE 8:e70383.

Johnson, C., M. Boyce, R. Mulders, and A. Gunn. 2004a. Quantifying patch distribution at multiple spatial scales: applications to wildlife-habitat models. Landscape Ecology 29:869–882.

Johnson, C. J., K. L. Parker, D. C. Heard, M. P. Gillingham, S. E. Applications, and N. Dec. 2004b. A multiscale behavioral approach to understanding the movements of woodland Caribou. Ecological applications 12:1840–1860.

Johnson, C. J., D. R. Seip, and M. S. Boyce. 2004c. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. Journal of Applied Ecology 41:238–251.

Junker, J., S. Blake, C. Boesch, G. Campbell, L. Du Toit, C. Duvall, A. Ekobo, G. Etoga, A. Galat-Luong, J. Gamys, J. Ganas-Swaray, S. Gatti, A. Ghiurghi, N. Granier, J. Hart, J. Head, I. Herbinger, T. C. Hicks, B. Huijbregts, I. S. Imong, N. Kuempel, S. Lahm, J. Lindsell, F. Maisels, M. McLennan, L. Martinez, B. Morgan, D. Morgan, F. Mulindahabi, R. Mundry, K. P. N'Goran, E. Normand, A. Ntongho, D. T. Okon, C.-A. Petre, A. Plumptre, H. Rainey, S. Regnaut, C. Sanz, E. Stokes, A. Tondossama, S. Tranquilli, J. Sunderland-Groves, P. Walsh, Y. Warren, E. A. Williamson, and H. S. Kuehl. 2012. Recent decline in suitable environmental conditions for African great apes. Diversity and Distributions 18:1077–1091.

Kano, T. 1992. The Last Ape: Pygmy Chimpanzee behavior and ecology. Page 248. Stanford University Press, Stanford.

Kano, T., and M. Mulavwa. 1992. Appendix. Pages 225–232 *in* T. Kano, editor. The Last Ape: Pygmy Chimpanzee behavior and ecology. Stanford University Press, Stanford.

Kano, T., and M. Mulawva. 1984. Feeding ecology of the pygmy chimpanzees (*Pan paniscus*) of Wamba. Pages 233–274 *in* R. L. Susman, editor. The Pygmy Chimpanzee, evolutionary biology and behavior. Plenum Press, New York.

Kawamoto, Y., H. Takemoto, S. Higuchi, T. Sakamaki, J. A. Hart, T. B. Hart, N. Tokuyama, G. E. Reinartz, P. Guislain, J. Dupain, A. K. Cobden, M. N. Mulavwa, K. Yangozene, S. Darroze, C. Devos, and T. Furuichi. 2013. Genetic structure of wild bonobo populations: diversity of mitochondrial DNA and geographical distribution. PloS ONE 8:e59660.

Kideghesho, J. R., E. Røskaft, and B. P. Kaltenborn. 2006. Factors influencing conservation attitudes of local people in Western Serengeti, Tanzania. Biodiversity and Conservation 16:2213–2230.

Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, E.R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of Mule Deer. Ecology 83:530–544.

Kingdon, J., and M. Pagel. 1997. The Kingdon field guide to African mammals. Page 273Academic P. London.

Köhler, A., D. Raubenheimer, and S. W. Nicolson. 2012. Regulation of nutrient intake in nectar-feeding birds: insights from the geometric framework. Journal of comparative physiology B 182:603–611.

Koops, K. 2011. Elementary technology of foraging and shelter in the chimpanzees (*Pan troglodytes verus*) of the Nimba Mountains , Guinea. PhD Thesis. University of Cambridge.

Koops, K., W. C. McGrew, H. Vries, and T. Matsuzawa. 2012. Nest-building by Chimpanzees (*Pan troglodytes verus*) at Seringbara, Nimba Mountains: antipredation, thermoregulation, and antivector hypotheses. International Journal of Primatology 33:356–380.

Kouakou, C. Y., C. Boesch, and H. Kuehl. 2009. Estimating chimpanzee population size with nest counts: validating methods in Taï National Park. American journal of primatology 71:447–457.

Van Krunkelsven, E. 2001. Density estimation of Bonobos (*Pan paniscus*) in Salonga National Park, Congo. Biological Conservation 99:387–391.

Kuehl, H., F. Maisels, M. Ancrenaz, and E. . Williamson. 2008. Best Practice Guidelines for Surveys and Monitoring of Great Ape Populations. Page 32. Gland, Switserland.

Kuehl, H. S., C. Nzeingui, S. L. D. Yeno, B. Huijbregts, C. Boesch, and P. D. Walsh. 2009. Discriminating between village and commercial hunting of apes. Biological Conservation 142:1500–1506.

Kühl, H. S., L. Williamson, C. Sanz, and C. Boesch. 2007. Launch of A.P.E.S. database. Gorilla Journal 34:20–21.

Lacambra, C., J. Thompson, T. Furuichi, H. Vervaecke, and J. Stevens. 2005. Bonobo (*Pan paniscus*). Pages 83–104 *in* J. Caldecott and L. Miles, editors. World atlas of great apes and their conservation. Cambridge Univ Press, London, England.

Laing, S. E., S. T. Buckland, R. W. Burn, and D. Lambie. 2003. Dung and nest surveys : estimating decay rates. Journal of Applied Ecology 40:1102–1111.

Lambin, E. F., H. J. Geist, and E. Lepers. 2003. Dynamics of land-use and land-cover change in tropical regions. Annual Review of Environment and Resources 28:205–241.

Lambin, E. F., H. K. Gibbs, L. Ferreira, R. Grau, P. Mayaux, P. Meyfroidt, D. C. Morton, T. K. Rudel, I. Gasparri, and J. Munger. 2013. Estimating the world’s potentially available cropland using a bottom-up approach. Global Environmental Change 23:892–901.

Laurance, W. F., B. M. Croes, N. Guissouegou, R. Buij, M. Dethier, and A. Alonso. 2008. Impacts of roads, hunting, and habitat alteration on nocturnal mammals in African rainforests. Conservation biology : the journal of the Society for Conservation Biology 22:721–732.

Laurance, W. F., M. Goosem, and S. G. W. Laurance. 2009. Impacts of roads and linear clearings on tropical forests. Trends in ecology & evolution 24:659–669.

Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: a 22-Year Investigation. Conservation Biology 16:605–618.

Legendre, P., and L. Legendre. 1998. Numerical ecology. Second English Edition. Page 846. Elsevier Science, Amsterdam.

Lehmann, J., and C. Boesch. 2003. Social influences on ranging patterns among chimpanzees (*Pan troglodytes verus*) in the Tai National Park, Cote d'Ivoire. Behavioral Ecology 14:642–649.

Lehmann, J., A. H. Korstjens, and R. I. M. Dunbar. 2007. Fission–fusion social systems as a strategy for coping with ecological constraints: a primate case. Evolutionary Ecology 21:613–634.

Levin, S. A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. Ecology 73:1943–1967.

Li, B., Z. Jia, R. Pan, and B. Ren. 2003. Changes in distribution of the snub-nosed monkey in China. Pages 29–52 *in* L. K. Marsh, editor. Primates in Fragments. Ecology in Conservation. Kluwer Academic / Plenum Publishers, New York.

Linkie, M., H. T. Wibisono, D. J. Martyr, and S. Sunarto. 2008. *Panthera tigris ssp. sumatrae*. www.iucnredlist.org. Accessed 19 February 2014

Madron, L. D. De, and A. Daumerie. 2004. Diamètre de fructification de quelques essences en forêt naturelle centrafricaine. Bois et Forêts des Tropiques 281:87–95.

Maechler, M., P. Rousseeuw, A. Struyf, M. Hubert, and K. Hornik. 2013. cluster: cluster analysis basics and extensions. R package version 1.14.4.

Maisels, F., S. Strindberg, S. Blake, G. Wittemyer, J. Hart, E. a. Williamson, R. Aba'a, G. Abitsi, R. D. Ambahe, F. Amsini, P. C. Bakabana, T. C. Hicks, R. E. Bayogo, M. Bechem, R. L. Beyers, A. N. Bezangoye, P. Boundja, N. Bout, M. E. Akou, L. B. Bene, B. Fosso, E. Greengrass, F. Grossmann, C. Ikamba-Nkulu, O. Ilambu, B.-I. Inogwabini, F. Iyenguet, F. Kiminou, M. Kokangoye, D. Kujirakwinja, S. Latour, I. Liengola, Q. Mackaya, J. Madidi, B. Madzoke, C. Makoumbou, G.-A. Malanda, R. Malonga, O. Mbani, V. a. Mbendzo, E. Ambassa, A. Ekinde, Y. Mihindou, B. J. Morgan, P. Motsaba, G. Moukala, A. Mounguengui, B. S. Mowawa, C. Ndzai, S. Nixon, P. Nkumu, F. Nzolani, L. Pintea, A. Plumptre, H. Rainey, B. B. de Semboli, A. Serckx, E. Stokes, A. Turkalo, H. Vanleeuwe, A. Vosper, and Y. Warren. 2013. Devastating decline of Forest Elephants in Central Africa. PLoS ONE 8:e59469.

Majolo, B., G. Schino, and F. Aureli. 2012. The relative prevalence of direct, indirect and generalized reciprocity in macaque grooming exchanges. Animal Behaviour 83:763–771.

Malenky, R. K., and E. W. Stiles. 1991. Distribution of terrestrial herbaceous vegetation and its consumption by *Pan paniscus* in the Lomako Forest, Zaire. American journal of primatology 169:153–169.

Malenky, R. K., and R. W. Wrangham. 1994. A quantitative comparison of terrestrial herbaceous food consumption by *Pan paniscus* in the Lomako Forest, Zaire, and *Pan troglodytes* in the Kibale Forest, Uganda. American Journal of Primatology 32:1–12.

Marceau, D. J. 1999. The scale issue in social and natural sciences. Canadian Journal of Remote Sensing 25:347–356.

Marceau, D. J., and G. J. Hay. 1999. Scaling and modelling in forestry: applications in remote sensing and GIS. Canadian Journal of Remote Sensing 25:342–346.

Marsh, L. K. 2003. Primates in Fragments. Ecology in Conservation. Page 404 (L. K. Marsh, Ed.). Kluwer Academic / Plenum Publishers, New York.

Marshall, A. J., C. M. Boyko, K. L. Feilen, R. H. Boyko, and M. Leighton. 2009. Defining fallback foods and assessing their importance in primate ecology and evolution. American journal of physical anthropology 140:603–614.

Marshall, A. J., and R. W. Wrangham. 2007. Evolutionary Consequences of Fallback Foods. International Journal of Primatology 28:1219–1235.

Mathewson, P., S. Spehar, E. Meijaard, Nardiyono, Purnomo, A. Sasmirul, Sudiyanto, Oman, Sulhnudin, Jasary, Jumali, and A. Marshall. 2008. Evaluating orangutan census techniques using nest decay rates: implications for population estimates. Ecological applications : a publication of the Ecological Society of America 18:208–221.

Mayor, A. S. J., J. A. Schaefer, D. C. Schneider, S. P. Mahoney, and S. J. Mayor. 2007. Spectrum of selection: new approaches to detecting the scale-dependent response to habitat. Ecology 88:1634–1640.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Ecoscience 16:238–247.

McGrew, W. C., L. F. Marchant, M. M. Beuerlein, D. Vrancken, B. Fruth, and G. Hohmann. 2007. Prospects for Bonobo insectivory: Lui Kotal, Democratic Republic of Congo. International Journal of Primatology 28:1237–1252.

McLennan, M. R. 2013. Diet and feeding ecology of Chimpanzees (*Pan troglodytes*) in Bulindi, Uganda: foraging strategies at the forest–farm interface. International Journal of Primatology 34:585–614.

Menga, P., N. Bayol, R. Nasi, and A. Fayolle. 2012. Phenology and fructification diameter in wenge, *Millettia laurentii* de wild.: management implications. Bois et Forêts des Tropiques 66:31–42.

Mertens, B., E. Forni, and E. F. Lambin. 2001. Prediction of the impact of logging activities on forest cover : a case-study in the East province of Cameroon. Journal of environmental management 62:21–36.

Meyer, C. B., and W. Thuiller. 2006. Accuracy of resource selection functions across spatial scales. Diversity and Distributions Distributions 12:288–297.

Milton, K. 1982. Dietary quality and demographic regulation in a howler monkey population. Pages 273–289 *in* E. G. Leigh, A. S. Rand, and M. D. Windsor, editors. The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington DC.

Mitchell, M. W., and M. K. Gonder. 2013. Primate speciation: a case study of African Apes. Nature Education Knowledge 4:1. Accessed 17 February 2014.

Mohneke, M., and B. Fruth. 2008. Bonobo (*Pan paniscus*) density estimation in the SW-Salonga National Park, Democratic Republic of Congo: common methodology revisited. Pages 151–166 *in* T. Furuichi and J. Thompson, editors. The bonobos: Behavior, Ecology, and Conservation. Springer, New York.

Moscovice, L., M. Issa, K. Petrzelkova, N. Keuler, C. Snowdon, and M. Huffman. 2007. Fruit availability, Chimpanzee diet, and grouping patterns on Rubondo Island, Tanzania. American Journal of Primatology 69:487–502.

Mulavwa, M., T. Furuichi, K. Yangozene, M. Yamba-Yamba, B. Motema-Salo, G. Idani, H. Ihobe, C. Hashimoto, Y. Tashiro, and N. Mwanza. 2008. Seasonal changes in fruit production and party size of Bonobos at Wamba. Pages 121–134 *in* T. Furuichi and J. Thompson, editors. The bonobos: Behavior, Ecology, and Conservation. Springer, New York.

Mulavwa, M., K. Yangozene, M. Yamba-Yamba, B. Motema-Salo, N. Mwanza, and T. Furuichi. 2010. Nest groups of wild Bonobos at Wamba: selection of vegetation and tree species and relationships between nest group size and party size. American Journal of Primatology 71:1–12.

Mundry, R., and C. L. Nunn. 2009. Stepwise model fitting and statistical inference: turning noise into signal pollution. The American naturalist 173:119–123.

Murai, M., H. Ruffler, A. Berlemont, G. Campbell, F. Esono, A. Agbor, D. Mbomio, A. Ebana, A. Nze, and H. S. Kühl. 2013. Priority areas for large mammal conservation in Equatorial Guinea. PloS ONE 8:e75024.

Murray, C. M., I. C. Gilby, S. V Mane, and A. E. Pusey. 2008. Adult male chimpanzees inherit maternal ranging patterns. Current biology 18:20–24.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691–692.

Nams, V. O. 2012. Shape of patch edges affects edge permeability for meadow voles. Ecological applications 22:1827–1837.

Nams, V. O., G. Mowat, and M. A. Panian. 2006. Determining the spatial scale for conservation purposes – an example with grizzly bears. Biological Conservation 128:109–119.

Nasi, R., A. Billand, and N. van Vliet. 2012. Managing for timber and biodiversity in the Congo Basin. Forest Ecology and Management 268:103–111.

Newton-fisher, N. E., V. Reynolds, and A. J. Plumptre. 2000. Food supply and Chimpanzee (*Pan troglodytes schweinfurthii*) party size in the Budongo Forest Reserve, Uganda. International Journal of Primatology 21:613–628.

Nicholson, M. C., R. T. Bowyer, J. G. Kie, S. Journal, and N. May. 1997. Habitat selection and survival of Mule Deer: tradeoffs associated with migration. Journal of Mammalogy 78:483–504.

Nyariki, D. M. 2009. Household Data Collection for Socio-Economic Research in Agriculture: Approaches and Challenges in Developing Countries. Journal of Social Sciences 19:91–99.

Palagi, E., T. Paoli, and S. Tarli. 2006. Short-term benefits of play behavior and conflict prevention in *Pan paniscus*. International Journal of Primatology 27:1257–1270.

Pan, Y., R. A. Birdsey, J. Fang, R. Houghton, P. E. Kauppi, W. A. Kurz, O. L. Phillips, A. Shvidenko, S. L. Lewis, J. G. Canadell, P. Ciais, R. B. Jackson, S. W. Pacala, A. D. McGuire, S. Piao, A. Rautiainen, S. Sitch, and D. Hayes. 2011. A large and persistent carbon sink in the world's forests. Science 333:988–993.

PEN Prototype Questionnaire. 2008. . http://www.cifor.org/fileadmin/fileupload/PEN/pubs/pdf_files/PEN_Prototype_Questionnaire_-_version_4-4_-_September_2008.pdf. Accessed 10 April 2013

Perry, G.H., N.J. Dominy, K.G. Claw, C. Lee, and A. C. Stone. 2007. Diet and the evolution of human amylase gene copy number variation. Nature genetics 39:1256–1260.

Pita, R., A. Mira, and P. Beja. 2011. Assessing habitat differentiation between coexisting species: The role of spatial scale. Acta Oecologica 37:124–132.

Plumptre, A. J. 2000. Monitoring mammal populations with line transect techniques in African Forests. Journal of Applied Ecology 37:356–368.

Plumptre, A. J., and V. Reynolds. 1994. The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. Journal of Applied Ecology 31:631–641.

Plumptre, A. J., and V. Reynolds. 1997. Nesting behavior of Chimpanzees: implications for censuses. International Journal of Primatology 18:475–485.

Plumptre, A., and V. Reynolds. 1996. Censusing chimpanzees in the Budongo Forest, Uganda. International Journal of Primatology 17:85–99.

Potamochoerus_porcus. 2004. http://www.ultimateungulate.com/Artiodactyla/Potamochoerus_porcus.html. Accessed 1 November 2013

Pruetz, J. D. 2006. Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. Pages 161–182 *in* G. Hohmann, M. Robbins, and C. Boesch, editors. Feeding ecology in Apes and other primates. Cambridge University Press, Cambridge.

Pruetz, J. D., S. J. Fulton, L. F. Marchant, W. C. McGrew, M. Schiel, and M. Waller. 2008. Arboreal nesting as anti-predator adaptation by savanna chimpanzees (*Pan troglodytes verus*) in southeastern Senegal. American journal of primatology 70:393–401.

Prugh, L. R. 2009. An evaluation of patch connectivity measures. Ecological applications 19:1300–1310.

Prugh, L. R., K. E. Hodges, A. R. E. Sinclair, and J. S. Brashares. 2008. Effect of habitat area and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences of the United States of America 105:20770–20775.

Quin, G. P., and M. J. Keough. 2002. Experimental designs and data analysis for biologists. Cambrige University Press, Cambrigde.

R Development Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Raubenheimer, D. 2011. Toward a quantitative nutritional ecology: the right-angled triangle. Ecological Monographs 81:407–427.

Raubenheimer, D., S. J. Simpson, and D. Mayntz. 2009. Nutrition, ecology and nutritional ecology: toward an integrated framework. Functional Ecology 23:4–16.

Reinartz, G. E., B. I. Inogwabini, M. Ngamankosi, and L. W. Wema. 2006. Effects of forest type and human presence on Bonobo (*Pan paniscus*) density in the Salonga National Park. International Journal of Primatology 27:1229–1231.

Remis, M. J. 2002. Food preferences among captive western gorillas (*Gorilla gorilla gorilla*) and Chimpanzees (*Pan troglodytes*). International Journal of Primatology 23:231–248.

Reynolds, V., A. J. Plumptre, J. Greenham, and J. Harborne. 1998. Condensed tannins and sugars in the diet of chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo Forest, Uganda. Oecologia 115:331–336.

Reynolds, V., J. Wallis, and R. Kyamanywa. 2003. Fragments, sugar, and chimpanzees in Masindi District, Western Uganda. Pages 309–320 *in* L. K. Marsh, editor. Primates in Fragments. Ecology in Conservation. Kluwer Academic / Plenum Publishers, New York.

Rhodes, J., C. McAlpine, D. Lunney, and H. Possingham. 2005. A spatially explicit habitat selection model incorporating home range behavior. Ecology 86:1199–1205.

Rhodes, J. R., C. A. Mcalpine, A. F. Zuur, G. M. Smith, and E. N. Ieno. 2009. GLMM applied on the spatial distribution of Koalas in a fragmented landscape. Pages 469–492 *in* A. F. Zuur, E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith, editors. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.

Riitters, K. H., J. D. Wickham, T. G. Wade, and P. Vogt. 2012. Global survey of anthropogenic neighborhood threats to conservation of grass-shrub and forest vegetation. Journal of environmental management 97:116–21.

Riitters, K., J. Wickham, R. O. Neill, B. Jones, and E. Smith. 2000. Global-scale patterns of forest fragmentation. Conservation Ecology 4:1–18.

Rothman, J. M., A. N. Pell, E. S. Dierenfeld, and C. M. Mccann. 2006. Plant choice in the construction of night nests by Gorillas in the Bwindi Impenetrable National Park, Uganda. American journal of physical anthropology 68:361–368.

Rothman, J. M., D. Raubenheimer, and C. A. Chapman. 2011. Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. Biology letters 7:847–849.

Russon, A. E., D. P. Handayani, P. Kuncoro, and A. Ferisa. 2007. Orangutan leaf-carrying for nest-building: toward unraveling cultural processes. Animal cognition 10:189–202.

Samson, D. R., and K. D. Hunt. 2012. A thermodynamic comparison of arboreal and terrestrial sleeping sites for dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at the Toro-Semliki Wildlife Reserve, Uganda. American journal of primatology 74:811–888.

Samson, D. R., M. P. Muehlenbein, and K. D. Hunt. 2013. Do chimpanzees (*Pan troglodytes schweinfurthii*) exhibit sleep related behaviors that minimize exposure to parasitic arthropods? A preliminary report on the possible anti-vector function of chimpanzee sleeping platforms. Primates; journal of primatology 54:73–80.

Santos-Filho, M., C. a. Peres, D. J. Silva, and T. M. Sanaiotti. 2012. Habitat patch and matrix effects on small-mammal persistence in Amazonian forest fragments. Biodiversity and Conservation 21:1127–1147.

Sawyer, S. C., and J. S. Brashares. 2013. Applying resource selection functions at multiple scales to prioritize habitat use by the endangered Cross River gorilla. Diversity and Distributions 19:943–954.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution 1:103–113.

Searle, K. R., C. J. Stokes, and I. J. Gordon. 2008. When foraging and fear meet: using foraging hierarchies to inform assessments of landscapes of fear. Behavioral Ecology 19:475–482.

Seo, C., J. H. Thorne, L. Hannah, and W. Thuiller. 2009. Scale effects in species distribution models: implications for conservation planning under climate change. Biology letters 5:39–43.

Serckx, A., M.-C. Huynen, J.-F. Bastin, R. C. Beudels-Jamar, A. Hambuckers, M. Vimond, E. Raynaud, and H. Kühl. 2014. Nesting patterns of bonobos (*Pan paniscus*) in relation to fruit availability in a forest-savannah mosaic. PloS ONE:in press.

Shibia, M. G. 2000. Determinants of attitudes and perceptions on resource use and management of Marsabit National Reserve, Kenya. Journal of Human Ecology 30:55–62.

Sokal, R. S., and F. J. Rohlf. 1996. Introduction to Biostatistics. Page 363. W.H. Freeman and Company, New York.

Stanford, C. B., and R. C. O’Malley. 2008. Sleeping tree choice by Bwindi chimpanzees. American journal of primatology 70:642–649.

Stewart, F. A. 2011. The evolution of shelter: ecology and ethology of chimpanzee nest building. PhD Thesis. University of Cambridge.

Stewart, F. A., A. K. Piel, and W. C. McGrew. 2011. Living archaeology: artefacts of specific nest site fidelity in wild chimpanzees. Journal of human evolution 61:388–395.

Stewart, F. A., J. D. Pruetz, and M. H. Hansell. 2007. Do Chimpanzees build comfortable nests? American journal of primatology 69:930–939.

Strier, K. 1989. Effets of patch size on feeding associations in muriquies (*Brachyteles brachnoides*). Folia primatologica 52:70–77.

Sunderland-Groves, J. L., A. Ekinde, and H. Mboh. 2009. Nesting behavior of *Gorilla gorilla diehli* at Kagwene Mountain, Cameroon: implications for assessing group size and density. International Journal of Primatology 30:253–266.

Surbeck, M., A. Fowler, C. Deimel, and G. Hohmann. 2009. Evidence for the consumption of arboreal, diurnal primates by bonobos (*Pan paniscus*). American journal of primatology 71:171–174.

Surbeck, M., and G. Hohmann. 2008. Primate hunting by bonobos at LuiKotale, Salonga National Park. Current biology 18:R906–R907.

Tailfer, Y. 1989. La foret dense d'Afrique centrale. Identification pratique des principaux arbres, Tome 1 et 2. C.T.A., Wageningen, Pays-Bas.

Thomas, L., S. T. Buckland, E. a Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R. Bishop, T. a Marques, and K. P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. The Journal of applied ecology 47:5–14.

Thompson, J. a M. 2003. A model of the biogeographical journey from *Proto-pan* to *Pan paniscus*. Primates 44:191–197.

Thompson, J. A. M. 1997. The history, taxonomy and ecology of the Bonobo (*Pan paniscus* Schwarz, 1929) with a first description of a wild population living in the forest/savanna mosaic habitat. PhD Thesis. University of Oxford.

Thompson, J. A. M. 2001. The status of Bonobos in their southernmost geographic range. Pages 75–81 *in* B. M. F. Galdikas, N. E. Briggs, L. K. Sheeran, G. L. Shapiro, and J. Goodall, editors. All Apes Great and Small Volume I: African Apes. Kluwer Academic / Plenum Publishers, New York.

Thornton, D. H., L. C. Branch, and M. E. Sunquist. 2010. The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies. Landscape Ecology 26:7–18.

Torres, J., J. C. Brito, M. J. Vasconcelos, L. Catarino, J. Gonçalves, and J. Honrado. 2010. Ensemble models of habitat suitability relate chimpanzee (*Pan troglodytes*) conservation to forest and landscape dynamics in Western Africa. Biological Conservation 143:416–425.

Turner, B. L., E. F. Lambin, and A. Reenberg. 2007. The emergence of land change science for global environmental change and sustainability. Proceedings of the National Academy of Sciences of the United States of America 104:20666–20671.

Tutin, C. E. G. 1999. Fragmented living: behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. Primates 40:249–265.

Tutin, C., R. Parnell, L. White, and M. Fernandez. 1995. Nest building by lowland gorillas in the Lopé Reserve, Gabon: Environmental influences and implications for censusing. International Journal of Primatology 16:53–76.

Umapathy, G., and A. Kumar. 2003. Impacts of forest fragmentation on lion-tailed macaque and Nilgiri langur in western Ghats, south India. Pages 163–190 *in* L. K. Marsh, editor. Primates in Fragments. Ecology in Conservation. Kluwer Academic / Plenum Publishers, New York.

United States Census Bureau. International Database. http://www.census.gov/population/international/data/idb/informationGateway.php. Accessed 19 February 2014

Urban, D. L. 2004. Modeling ecological processes across scales. Ecology 86:1996–2006.

Vancutsem, C., J. Pekel, J.-P. Kibamba, X. Blaes, C. de Wasseige, and P. Defourny. 2006. Carte de l'occupation du sol de la République Démocratique du Congo. (P. U. de Louvain, Ed.). Bruxelles.

Vaughan, I. P., and S. J. Ormerod. 2003. Improving the quality of distribution models for conservation by addressing shortcomings in the field collection of training data. Conservation Biology 17:1601–1611.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Page 495. Springer, New York.

De Waal, F. B. M., and F. Lanting. 1997. Bonobo: the forgotten Ape. Page 210. Berkeley: University of California Press, London.

Warnes, G. R., B. Bolker, and T. Lumley. 2013. gtools: Various R programming tools.

De Wasseige, C., D. Devers, P. De Marcken, R. Eba'a Atyi, R. Nasi, and P. Mayaux. 2009. The forests of Congo Basin - State of forests 2008. Page 425. Publications Office of the European Union, Kinshasa.

De Wasseige, C., P. de Marcken, N. Bayol, F. Hiol Hiol, P. Mayaux, B. Desclée, R. Nasi, A. Billand, P. Defourny, and R. Eba'a Atyi. 2012. The Forests of the Congo Basin - State of the Forest 2010. Page 276. Publications Office of the European Union, Luxembourg.

Watling, J. I., A. J. Nowakowski, M. A. Donnelly, and J. L. Orrock. 2011. Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. Global Ecology and Biogeography 20:209–217.

Wheatley, M. 2010. Domains of scale in forest-landscape metrics: implications for species-habitat modeling. Acta Oecologica 36:259–267.

Wheatley, M., and C. Johnson. 2009. Factors limiting our understanding of ecological scale. Ecological Complexity 6:150–159.

White, F. J., and A. Lanjouw. 1992. Feeding competition in Lomako bonobos: variation in social cohesion. Topics in primatology 1:67–79.

White, F. J., and K. D. Wood. 2007. Female feeding priority in Bonobos, *Pan paniscus*, and the question of female dominance. American journal of primatology 69:1–14.

White, F. J., and R. W. Wrangham. 1988. Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. Behaviour 105:148–164.

Whiten, A., R. W. Byrnel, R. A. Barton, P. G. Waterman, S. P. Henry, K. Hawkes, E. M. Widdowson, S. A. Altmann, K. Milton, and R. I. M. Dunbar. 1991. Dietary and foraging strategies of Baboons. Philosophical Transactions: Biological Sciences 334:187–197.

Whittingham, M. J., P. A. Stephens, R. B. Bradbury, and R. P. Freckleton. 2006. Why do we still use stepwise modelling in ecology and behaviour? The Journal of animal ecology 75:1182–1189.

Wich, S. A., G. M. Fredriksson, G. Usher, H. H. Peters, D. Priatna, F. Basalamah, W. Susanto, and H. Kühl. 2012. Hunting of Sumatran orang-utans and its importance in determining distribution and density. Biological Conservation 146:163–169.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Wilkie, D. S. 2001. Bushmeat trade in the Congo Basin. Pages 86–109 *in* B. Beck, T. Stoinski, M. Hutchins, T. Maple, B. Norton, A. Rowan, E. Stevens, and A. Arluke, editors. Great Apes and Humans : the ethics of coexistence. Smithsonian Institution Press, Washingtion DC and London.

Wilks, C. M., and Y. A. Issembe. 2000. Les arbres de la Guinée Equatoriale: Guide pratique d'identification: région continentale. Projet CUREF, Bata, Guinée Equatoriale. Page 546. Prépresse Communications, France.

Woodcock, C. E., and A. H. Strahler. 1987. The Factor of scale in remote sensing. Remote Sensing of Environment 21:311–332.

Wrangham, R. W. 1993. The evolution of sexuality in chimpanzees and bonobos. Human Nature 4:47–79.

Wrangham, R. W. 2000. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. Pages 248–258 *in* P. M. Kappeler, editor. Primate males: Causes and consequences of variation in group composition. Cambridge University Press, Cambridge.

Wrangham, R. W., N. Lou Conklin-Brittain, and K. D. Hunt. 1998. Dietary response of Chimpanzees and Cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. International Journal of Primatology 19:949–970.

Wright, S. J. 2005. Tropical forests in a changing environment. Trends in ecology & evolution 20:553–560.

Ye, X., A. K. Skidmore, and T. Wang. 2013. Within-patch habitat quality determines the resilience of specialist species in fragmented landscapes. Landscape Ecology 28:135–147.

Zeileis, A., C. Kleiber, and S. Jackman. 2007. Regression models for count data in R. Page 23. Vienna.

APPENDICES

© Adeline Serckx

I APPENDIX I: REPORT TO WWF – NOVEMBER 2013

Estimations de densité de population de bonobos dans les forêts de Nkala/Nkoo et Mpelu - 2013

Adeline Serckx[1, 2]

[1] Groupe de Recherche de Primatologie, Unité de biologie du comportement, Université de Liège, Belgique; [2] Unité de Biologie de la Conservation, Institut Royal des Sciences Naturelles de Belgique, Belgique

Rappel de l’objectif de cette étude

Dans le cadre de la thèse de doctorat d’Adeline Serckx, des inventaires ont été réalisés en 2011 et 2012 dans les forêts de Nkala/Nkoo et Mpelu pour estimer la densité de population de bonobos. Ces inventaires, menés dans environ 100km² de forêts, englobaient les forêts dans lesquelles le WWF a entrepris le programme d’habituation depuis 2007. Les résultats de cette étude ont été alarmants puisque nous avons observé une diminution énorme de la taille du groupe de bonobos de Mpelu. En effet, nos estimations indiquaient que près de 20 individus (sur 31) auraient disparu en un an. Après discussions entre le Projet PICBOU de WWF (Petra Lahann) et Adeline Serckx, nous avons décidé de mettre en place une collaboration pour estimer à nouveau la densité de population de bonobos dans ces forêts en 2013. Le programme de travail a été mis en place par Adeline Serckx et réalisé par ses équipes d’assistants locaux précédemment formées en 2011 et 2012, avec l’appui financier du WWF-BE et WWF-NL. Les données ont ensuite été analysées par Adeline Serckx (veuillez noter que les résultats de cette étude font également l’objet d’une publication scientifique soumise en Novembre 2013).

Méthodologie

Collecte de données en forêt

Les données ont été collectées entre Juillet et Septembre 2013 dans la cadre du projet PICBOU de WWF mais ont également été récoltées d'Avril à Juillet 2011 et de mi-Mars à mi-Juillet 2012 dans le cadre de la thèse de doctorat d'Adeline Serckx. En 2011, nous avons réalisé une étude pilote pendant laquelle nous avons enregistré la présence de nids sur des recces (i.e., marche de reconnaissance en forêt pendant laquelle on suit une direction prédéfinie mais où les obstacles sont contournés au contraire des transects où la direction est suivie en permanence) afin de définir l'effort total d'échantillonnage nécessaire pour réaliser un inventaire précis d'estimation de densité de population. Suivant les résultats de cette étude, nous avons créé un design d'échantillonnage de 114 transects allant d'est en ouest, espacés de 500m et de longueur variable (total de 179.1km). Les transects ont été échantillonnés en 2011, 2012 et 2013. Certains transects n'ont pas été échantillonnés chaque année à cause de contraintes externes (dans le cas de 2013, un buffle a empêché de parcourir 3 transects ; voir Tableau 1 les efforts d'échantillonnage totaux par année). Nous avons systématiquement collecté les nids de bonobos et enregistré leur distance au transect avec un décamètre, suivant les guidelines de UICN (Kuehl et al. 2008) et Buckland et al. 2001 (Buckland et al. 2001). Les 3 observateurs ont été entrainés ensemble afin d'utiliser la même méthodologie.

Tableau 1: Superficie et effort total d'échantillonnage, par année, utilisé pour l'estimation de densité de population de bonobos.

	Aire (km²)	**Effort total 2011 (km)**	**Effort total 2012 (km)**	**Effort total 2013 (km)**
Global	93.84	130.1	179.1	175.5
Nkala/Nkoo	32.45	49.9	61.9	61.9
Mpelu	54.26	72.7	109.7	106.1
Lokoso&Mankere	7.13	7.5	7.5	7.5

Les indices de présence humaine et d'autres animaux ont également été notés pendant les 3 années (pour un descriptif des différents types de présence humaine, voir Tableau 2 ; pour le détail des espèces animales identifiées sur les transects, voir Tableau 3). Il est à noter que nous avons adapté le travail de terrain en 2013 en faisant couper les transects par une équipe et en enregistrant les indices 7 à 15 jours plus tard afin de pouvoir être plus silencieux et observer les présences directes d'animaux. Les résultats ne sont donc pas comparables entre les 3 années.

Tableau 2 : Descriptif des différents indices de présence humaine et d'animaux

Indice de présence humaine
Passage de personnes sur une piste
Coupe de Marantacées pour la fabrication de nattes ou pour récupération des feuilles (avec indication de l'espèce), coupe de lianes
Coupe de « poteaux » (petits arbres, pour la construction des maisons)
Indices de présence pour la pêche (avec indication du type de pêche si possible)
Piège (avec indication du matériau utilisé : câble ou nylon ou de l'animal visé)
Cartouche de fusil
Indice de présence pour la chasse au filet
Pistes de forêt (avec précision, si possible, du type de piste : pour les villageois ou pour les pisteurs bonobos)
Trace de feux
Trace de coupe à la machette

Tableau 3 : Liste des différentes espèces animales observées le long des transects

Animaux identifiés sur les transects	**Type d'observation possible**
Antilopes (avec si possible l'identification de l'espèce en nom vernaculaire local)	Piste, trace, observation de feces ou observation de l'animal
Buffle	Piste ou trace
Calao	Cris ou observation (et nb d'individus si possible)
Gazelle	Piste, trace ou observation de l'animal
Musaraigne/rat	Trace
Pangolin	Trace
Perdrix	Trace
Porc-épic	Piste ou trace
Potamochère	Piste, trace, résidus alimentaire, bruit
Petits singes (avec si possible l'identification de l'espèce en nom vernaculaire local)	Cris ou observation (et nb d'individus si possible

Nb : les distances perpendiculaires au transect ont été notées pour l'année 2013

Estimation des densités de population de bonobos

Les estimations de densité de population ont été estimées sur base des données de transects en utilisant le logiciel Distance 6.0 Release 2 (Buckland et al. 2001, Thomas et al. 2010). Nous avons divisé le site d'étude en trois parties pour les analyses: le domaine vital présumé des deux groupes de bonobos ('Nkala/Nkoo' et 'Mpelu') et les patches de forêts *Uapaca sp.* ('Lokoso&Mankere') que nous avons inventorié chaque année mais où nous n'avons jamais observé de traces de bonobos (Figure 1). Nous avons post-stratifié les données pour obtenir des estimations par année. Une estimation globale a été obtenue en pondérant les données suivant la superficie des trois zones. Une estimation globale pour Nkala/Nkoo et Mpelu a été obtenue en analysant indépendamment les données des deux forêts et en pondérant les données suivant l'effort total par année. Les données ont été tronquées de manière à ne garder que les nids dont la probabilité de détection était supérieure à 0.15. Nous avons testé différentes fonctions pour modéliser les données et avons choisi la fonction qui minimisait le AIC (Akaike Information Criterion). Pour convertir les densités de nids en estimation de bonobos, les densités de nids doivent être divisées par le taux de construction de nids, la proportion d'individus construisant des nids au sein d'un groupe (proportion des individus matures du groupe, ne prend donc pas en compte les juvéniles utilisant les mêmes nids que leur mère) et le taux de dégradation des nids. Nous avons utilisé un taux de construction de nids de 1.37 (Mohneke and Fruth 2008) et une proportion d'individus construisant les nids de 0.75 (Fruth 1995) provenant de la littérature (puisque ces informations nécessitent des observations directes). Nous avons utilisé notre propre estimation du taux de dégradation des nids de 183 jours (range : 179-188 jours ; les détails méthodologiques concernant le taux de dégradation des nids peuvent être trouvés dans l'article Serckx et al. 2014). Une analyse de la variation des densités de population pendant les trois années a également été réalisée pour chaque forêt. Nous avons utilisé un modèle (Modèle linéaire généralisé) qui analysait séparément le nombre de transects avec présence de nids (partie 'zero inflated' du modèle), et le nombre de nids sur ces transects (partie 'count' du modèle). Les détails méthodologiques peuvent être trouvés dans l'article Serckx et al. 2014.

Estimation des taux de rencontre des indices de présence humaine et d'animaux

Le taux de rencontre annuel a été calculé en divisant le nombre d'observation de chaque type d'indice par l'effort d'échantillonnage de l'année respective. Le taux de rencontre pour les différents indices d'animaux ont été estimés de manière globale pour le site d'étude puisque nous ne connaissons pas les caractéristiques de déplacements propres à chaque espèce (domaines vitaux, distance parcourue par jour). Les indices de présence humaine ont également été calculés pour l'ensemble de la zone d'étude.

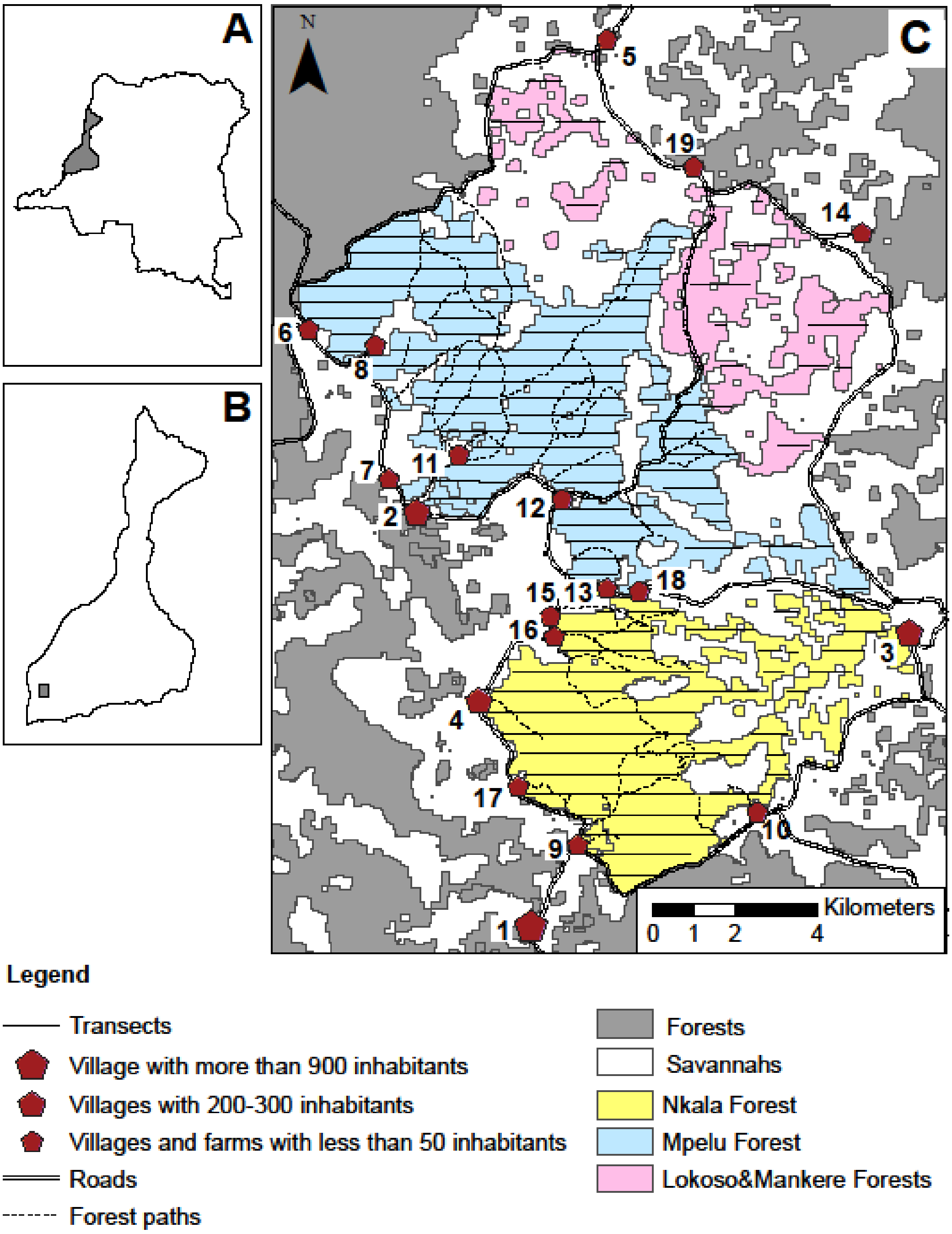


Figure 1 : Carte de la zone d’étude (16.41-16.56°E, 2.45-2.66°S, Ouest de la RDC)

A. Localisation du landscape Lac Tumba en RDC. B. Localisation de la zone d’étude dans le landscape Lac Tumba. C. Carte de la zone d’étude. Les forêts et les savanes sont respectivement indiquées en gris et blanc (cette carte est basée sur une classification non-supervisée – RED et IR de Landsat7(2007), Serckx *non. Publ.*). Pour une compréhension plus aisée de nos subdivisions de la zone d’étude, nous avons colorés les forêts en bleu et jaune pour représenter les domaines vitaux des deux groupes de bonobos et en rose pour représenter la zone de forêts de *Uapaca sp.* Les villages sont indiqués par des pentagones rouges (1 : Nkoo, 2 : Mpelu, 3 : Lebomo, 4 :Nkala, 5 : Malebo, 6 : Mavula, 7 : Bosatore, 8 : Mokoabuo, 9 : Dispensaire de Nkoo, 10 : Ferme de Lensiana, 11 : Biomengele, 12 : Ngandjele, 13 : Motsuemontore, 14 : Ezano, 15 : Mayi Monene, 16 : Mbou-Mon-Tour, 17 : Ferme de Moza, 18 : Bosieli, 19 : WWF-Base). Les lignes parallèles indiquent les routes et les lignes simples représentent les principaux chemins de forêt. Les lignes verticales pleines situent les 114 transects parcourus en 2011, 2012 et 2013.

Résultats et discussions

Estimation des densités de population de bonobos

Pour estimer la densité de bonobos, nous avons tronqué les données à une distance de 35m diminuant le nombre de nids de 1411 à 1341 et nous avons modélisé les données pour une function half-normal cosine. Les densités de bonobos ont été estimées à 0.63, 0.51 et 0.55 individus par kilomètres carrés pour la forêt Nkala/Nkoo (moyenne : 0.51 ind/km²) et à 0.56, 0.21 et 0.32 individus par kilomètres carrés pour la forêt Mpelu (moyenne : 0.37ind/km²), pour respectivement 2011, 2012 et 2013. Comme les résultats montraient de larges différences entre les années et ce, particulièrement pour le groupe de Mpelu, nous avons réalisé une analyse par modélisation pour comprendre la signification des variations.

Tableau 4 : Estimation de densité de populations et nombre d'individus pour 2011, 2012 et 2013, estimé avec Distance 6.0

	ESW	P	% CV	D	D LCL	D UCL	N	N LCL	N UCL
Global estimation[1]	19.1	0.55	14.38	0.41	0.32	0.56	39	30	53
Mpelu (moyenne)	17.1	0.49	29.1	0.37	0.12	1.2	20	7	65
Mpelu 2011	19.1	0.55	36.5	0.56	0.27	1.13	31	15	61
Mpelu 2012	19.1	0.55	27.08	0.21	0.12	0.35	11	7	19
Mpelu 2013	19.1	0.55	26.24	0.32	0.19	0.53	17	11	28
Nkala/Nkoo (moyenne)	21.3	0.61	7.37	0.51	0.40	0.63	17	13	20
Nkala/Nkoo 2011	19.1	0.55	27.85	0.63	0.36	1.12	20	12	36
Nkala/Nkoo 2012	19.1	0.55	22.65	0.51	0.32	0.79	16	11	25
Nkala/Nkoo 2013	19.1	0.55	33.54	0.55	0.28	1.07	17	9	35
Lokoso&Mankere 2011	19.1	0.55	0	0	0	0	0	0	0
Lokoso&Mankere 2012	19.1	0.55	0	0	0	0	0	0	0
Lokoso&Mankere 2013	19.1	0.55	0	0	0	0	0	0	0

Nous avons modélisé les données avec une function half-normal cosine et tronquée les données à 35m. ESW= effective strip width. P= probabilité de détection moyenne. %CV= coefficient de variation des estimations de densité. D= estimation de densité. D LCL= Intervalle de confiance inférieur (95%) de l'estimation de densité. D UCL= Intervalle de confiance supérieur (95%) de l'estimation de densité. N= Nombre d'individus estimé. N LCL= Intervalle de confiance inférieur (95%) de l'estimation d'individus. N UCL= Intervalle de confiance supérieur (95%) de l'estimation d'individus ([1]Estimation globale dérivée en pondérant les données avec la superficie des zones).

Notre analyse par modélisation de la variation annuelle de densités de population a montré que la densité de population à Nkala/Nkoo est stable (chi square=3.27, df=4, p=0.5, comparaison du modèle comprenant l'année comme prédicteur et d'un modèle sans ce prédicteur). Par contre, pour la forêt de Mpelu, nous observons des différences significatives de densité suivant l'année (même comparaison de modèle, chi square=9.59, df=4, p<0.05). Une analyse plus détaillée montre que la distribution des nids sur les différents transects ne changent pas au cours des années (chi square=3.71, df=2, p=0.16, comparaison du modèle comprenant l'année avec un modèle sans ce prédicteur dans la partie 'zero inflated') mais révèle une tendance positive de la variation du nombre de nids sur les transects (chi square=5.03, df=2, p=0.08, comparaison du modèle comprenant l'année avec un modèle sans ce prédicteur dans la partie 'count'). Des comparaisons deux à deux ont démontré une diminution de la densité de population entre 2011 à 2012 (p=0.050, résultat du modèle) et une augmentation de la densité de population entre 2012 et 2013 (p=0.043, résultat du modèle). Notons que la densité de population entre 2011 et 2013 n'est pas significative (p=0.91, résultat du modèle).

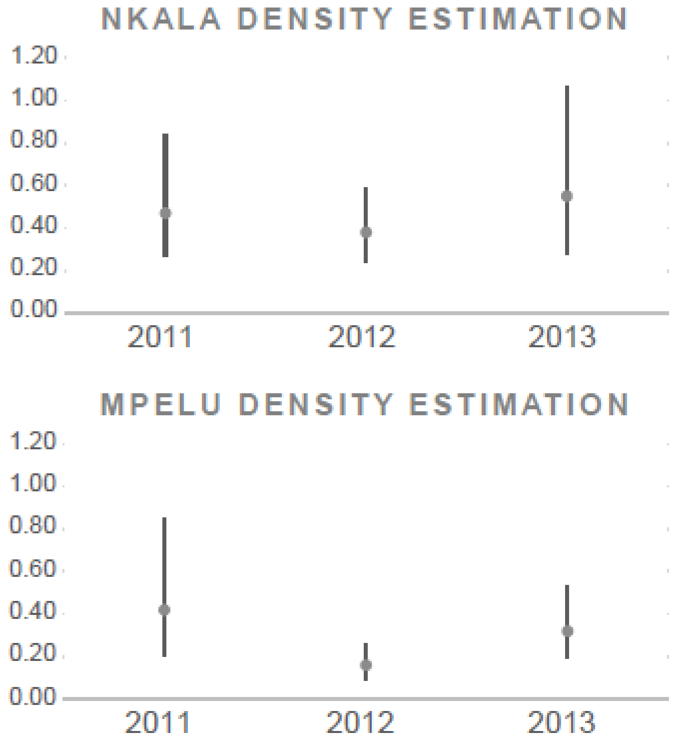


Figure 2 : Représentation des estimations de densités de population pour 2011, 2012 et 2013. Les points indiquent les estimations et les lignes, leur intervalle de 95% confiance

La variation de densités de population peut être expliquée par différences hypothèses. Premièrement, il pourrait être suggéré que cette variation provient d'artefacts de notre échantillonnage. Cette hypothèse est peu probable car nous avons utilisé un effort d'échantillonnage important les trois années (81.4km, 111km et 108.9km pour respectivement 2011, 2012 et 2013) et que notre modèle de variation de densités propose des résultats significatifs et ayant du sens sur base de notre expérience de terrain. Ces modèles indiquent que les bonobos utilisent les mêmes zones de la forêt pour faire leurs nids (effet non significatif de l'année dans la partie 'zero inflated' du modèle, p=0.16), même si la taille du groupe varie. Cette distribution agrégée des nids sur certains transects suggère que les bonobos maximisent leur accès à des zones de hot-spot alimentaires. Cette interprétation est supportée par notre autre étude réalisée dans la zone, qui montrait que la variation de densités de nids le long des transects est expliquée par la disponibilité en arbres avec fruits pulpeux et en plantes herbacées terrestres consommées par les bonobos (Serckx et al. In prep.). Deuxièmement, nous pourrions suspecter que la variation de densités résulte d'un évènement de chasse ou de maladie, deux menaces majeures pour la survie du bonobo (IUCN and ICCN 2012). Cette hypothèse pourrait expliquer la diminution de bonobos entre 2011 et 2012 mais les preuves de tels évènements sont quasiment impossibles à observer sur le terrain (Hohmann pers. comm.) et n'ont pas été confirmées par les pisteurs WWF ou la population locale. Néanmoins, l'augmentation significative entre 2012 et 2013 (0.21 à 0.32 ind/km², correspondant à une augmentation de 6 individus dans le groupe, Tableau 4) et la différence non-significative entre 2011 et 2013 (p=0.91, résultat du modèle) suggère qu'une telle hypothèse n'est pas suffisante pour expliquer les variations de taille de groupe dans cette forêt. Finalement, la variation de densités entre les trois années pourrait être expliquée si la zone inventoriée ne couvre pas l'ensemble des domaines vitaux des deux groupes. De précédentes études ont montré que les domaines vitaux peuvent varier de manière saisonnière ou annuelle (Kano and Mulawva 1984) et que les domaines vitaux de différents groupes d'une même communauté peuvent se recouvrir (Idani 1990, Lacambra et al. 2005). Notre étude de la variabilité en disponibilité en fruits a démontré que cette disponibilité est significativement plus faible dans la forêt de 'Mpelu' que dans la forêt de 'Nkala/Nkoo' pendant les 3 années d'étude (p<0.001, Serckx et al. 2014 suggérant que ce groupe de bonobos doit adaptée sa stratégie de recherche alimentaire (domaine vital, déplacement quotidien) en fonction de la disponibilité en fruits. Une observation de 2013 confirme cela puisque des traces de bonobos allant vers la forêt de 'Moba' (grand patch de forêts à l'ouest de Mpelu). Nos résultats suggèrent que les délimitations de domaines vitaux actuellement utilisées ne reflètent pas la réalité et devraient probablement être adaptées mais ce point devrait définitivement être éclairé grâce aux progrès du programme d'habituation et aux observations directes faites par des scientifiques.

Taux de rencontre des indices de présence d'animaux

Les résultats des taux de rencontre des indices de présence d'animaux sont présentés dans le Tableau 5. Notons que les résultats de 2011 indiquent de très faibles densités pour tous les animaux mais reflètent très probablement un problème méthodologique. En effet, la première année, nos efforts se sont concentrés sur les traces de bonobos et il est donc fort probable que de nombreuses autres traces d'autres animaux n'ont pas été relevées. Notons également que les traces d'oiseaux (calaos et perdrix) ne sont pas disponibles pour 2011 et 2012 car nous n'avions pas demandé aux guides de relever cette information en forêt.

Tableau 5 : Taux de rencontre des indices de présence d'animaux

	2011	2012	2013
Antilope	0.02	0.38	0.37
Buffle	0.03	0.08	0.14
Calao	Na	Na	0.11
Gazelle	0	0	0.06
Musaraigne-Rat	0	0.02	0.03
Pangolin	0	0.01	0.01
Perdrix	Na	Na	0.02
Porc-épic	0	0.31	0.39
Potamochère	0.35	0.79	1.50
Singe	0	0.02	0.17

Soulignons également que les données de 2012 et 2013 ne peuvent pas être comparées puisque la méthodologie a été modifiée (pour rappel, en 2012, les transects étaient coupées et les indices étaient relevés en même temps alors qu'en 2013, nous avons relevé les indices 7 à 15 jours après la coupe). Les résultats sont pourtant assez similaires à l'exception du potamochère et des singes. Il est évident, pour les singes, que la différence provient du changement de méthodologie puisque nos indices sont principalement des observations directes. Dans le cas du potamochère, nous ne les avons pas observés directement en 2013. La différence pourrait donc provenir d'une augmentation de la population (la reproduction de cette espèce étant assez rapide : 120 jours de gestation, 4 mois de soins au petit, 18-21 mois : âge de maturité sexuelle ("Potamochoerus_porcus" 2004)) mais de nouveaux inventaires dans les années à venir seraient nécessaires pour confirmer ce résultat.

A l'heure actuelle, il est difficile de discuter ces résultats mais il serait intéressant de pouvoir les comparer avec des zones de la région dans lesquelles le WWF ne travaille pas directement (futures inventaires) afin de voir si le programme de conservation permet une augmentation des animaux autres que le bonobo et, de faire des comparaisons sur le long terme dans la zone de Nkala/Nkoo et Mpelu pour identifier l'impact du programme de conservation sur la faune locale.

Taux de rencontre des indices humains

Les résultats des taux de rencontre des indices humains sont présentés dans le Table 0-7: Encounter rate of human indices. Les indices de présence en forêt pour la récolte de produits forestiers non ligneux semblent stables dans le temps (coupe de Marantacées, coupe de troncs, trace de machette ou de feu pour la mise en place de champs). On peut observer une augmentation des traces de pêche en 2013. Cette augmentation devrait être suivie sur une plus longue période pour vérifier si elle est significative mais elle pourrait simplement être due au fait que l'inventaire de 2013 s'est déroulé en pleine saison sèche (en comparaison à 2011 et 2012, qui chevauchaient la saison des pluies et la saison sèche) et pourrait donc simplement indiquer l'augmentation de la pêche à cette période de l'année (ce qui correspondrait aux informations récoltées lors de nos questionnaires aux communautés locales en 2012, Serckx, données non publiées).

Tableau 6 : Taux de rencontre des indices humains

	2011	**2012**	**2013**
Passage d'hommes	0.02	0.02	0.02
Coupe de Marantacées	0.08	0.11	0.12
Coupe de troncs (poteaux)	0.01	0	0.01
Trace de pêche	0.02	0.04	0.12
Trace de feu	0	0.01	0.03
Trace de machette	0	0.08	0.05
Piège à câble	0.02	0.05	0.13 (+0.03)[1]
Piège en nylon	0.04	0.13	0.07 (+0.02)[1]
Autres pièges (bois ou non défini)	0.05	0.03	0.02 (+0.01)[1]
Cartouche	0.05	0.03	0.11
Trace de chasse au filet	0	0.11	0.01
Autres traces de chasse	0	0.03[2]	0.01

[1] Le chiffre entre parenthèse indique le taux de rencontre d'anciens pièges n'étant donc plus en usage.[2] Représente 6 indices dont 3 sont des indices de présence de camp de chasse dans la forêt.

Les résultats de trace de chasse semblent par contre moins stables au cours du temps (augmentation des pièges en nylon et des traces de chasse au filet en 2012 ; augmentation des pièges à câble et des cartouches de fusils en 2013). Ces indices devraient être suivis pendant une plus longue période pour tirer des conclusions. Cependant, il faut souligner que l'augmentation des pièges à câble et des cartouches de fusils en 2013 pourraient être corrélée avec une augmentation moyenne du niveau de vie de la population locale : une augmentation de leur pouvoir d'achat pourrait impliquer une modification du choix des techniques de chasse vers des matériaux plus efficaces et plus couteux. Etant donné que les pièges à câble présentent un risque de blessures, parfois mortelles, pour les bonobos, cette observation mérite notre attention dans les années à venir. Soulignons finalement la présence de camps de chasse en 2012 : cette observation est assez étonnante pour la zone d'étude au vu des habitudes de chasses des populations locales (qui partent généralement à la chasse pendant la journée et parcourent de courtes distances, Serckx, données non publiées). Ces camps pourraient donc indiquer la présence de chasseurs ne provenant pas des villages avoisinants les forêts de Nkala/Nkoo et Mpelu.

Conclusions et perspectives

Cette étude a permis de présenter des résultats intéressants et importants concernant les densités de population de bonobos puisque nous avons pu confirmer une diminution de la population de bonobos en 2012 et, ensuite, une augmentation en 2013 dans la forêt de Mpelu. Ces variations de densités étant importantes, il nous faut suggérer un évènement de chasse ou de maladie entre 2011 et 2012 ou une utilisation du domaine vital variable en fonction de l'année et donc probablement en fonction de la disponibilité en fruits de la forêt. Il faut ici souligner que la zone inventoriée pour cette étude était cependant plus grande que la zone dans laquelle les pisteurs de Mpelu font leur suivi quotidien. Notons l'utilisation par les bonobos des forêts de Lekwa (petit patch forestier situé au sud de Ngandjele) et Minkalu (petit patch forestier situé à l'est de la forêt de Mpelu, à côté de la route menant au WWF) dans lesquelles nous avons trouvé chaque année des nids de bonobos et dans lesquelles les pisteurs ont dit ne pas aller. Les progrès du suivi dans le programme d'habituation devraient nous aider à mieux comprendre les zones utilisées par les bonobos et éventuellement mettre en évidence la présence de plusieurs groupes de bonobos dans la forêt de Mpelu. Pour nous aider à répondre à cette question, je voudrais donc préconiser la prise régulière de points GPS lors du suivi des bonobos. Soulignons finalement qu'il est possible que les bonobos de Mpelu aillent parfois dans la forêt de Moba (à l'ouest de la forêt de Mpelu), cette zone n'a jamais pu être inventoriée en raison de problème avec les populations locales à qui appartient cette forêt. Il serait donc intéressant de régler ces problèmes pour permettre de futurs inventaires dans cette zone.

Au vu des résultats et de la variation significative de densités de population des bonobos chaque année pour la forêt de Mpelu, il serait souhaitable de continuer à faire des inventaires réguliers afin de suivre l'évolution de la communauté de bonobos de la zone d'étude. De plus, ces inventaires nous permettront de suivre l'évolution des autres espèces animales présentes, ce qui pourrait être utilisé comme un indice de l'impact du programme de conservation. Ces inventaires aideront également à suivre l'évolution de l'utilisation des forêts par les hommes et notamment, leur habitude de chasse qui semble avoir augmenté en 2013.

Des inventaires dans d'autres forêts de la région nous permettront de faire des comparaisons tant pour les densités de population de bonobos que pour la présence des autres espèces animales et pour l'utilisation de la forêt par les hommes. Nous pourrions ainsi mieux comprendre l'impact du programme de conservation et, éventuellement, mettre en place des zones prioritaires de conservation pour le maintien à long terme des populations de bonobos de la région. Je voudrais finalement proposer que, lorsque de futurs inventaires seront réalisés, nous utilisions la technique de modélisation des densités de nids sur les transects pour mettre en évidence les différences de densités inter-sites.

Bibliographie

Buckland ST., Anderson DR, Burnham KP, Laake JL, Borchers DL, et al. (2001) Introduction to distance sampling: estimating abundance of biological populations. Oxford: Oxford University Press.

Fruth B (1995) Nests and nest groups in wild bonobos: ecological and behavioural correlates. PhD Thesis. Ludwig-Maximilian University.

Idani G (1990) Relations between unit-groups of bonobos at Wamba, Zaire: encounters and temporary fusions. Afr Study Monogr 11: 153–186.

IUCN, ICCN (2012) Bonobos (*Pan paniscus*): Conservation Strategy 2012-2022. Gland, Switserland: IUCN/SSC Primate Specialist Group & Institut Congolais pour la Conservation de la Nature.

Kano T, Mulawva M (1984) Feeding ecology if the pygmy chimpanzees (*Pan paniscus*) of Wamba. *In*: Susman RL, editor. The Pygmy Chimpanzee, Evolutionary Biology and Behavior. New York: Plenum Press. pp. 233–274

Kuehl H, Maisels F, Ancrenaz M, Williamson E. (2008) Best practice guidelines for surveys and monitoring of Great Ape populations. Gland, Switserland.

Lacambra C, Thompson J, Furuichi T, Vervaecke H, Stevens J (2005) Bonobo (*Pan paniscus*). In: Caldecott J, Miles L, editors. World atlas of great apes and their conservation. London, England: Cambridge Univ Press. pp. 83–104.

Mohneke M, Fruth B (2008) Bonobo (*Pan paniscus*) density estimation in the SW-Salonga National Park, Democratic Republic of Congo: common methodology revisited. *In*: Furuichi T, Thompson J, editors. The bonobos: Behavior, Ecology, and Conservation. New York: Springer. pp. 151–166.

Potamochoerus_porcus (2004). Available: http://www.ultimateungulate.com/Artiodactyla/Potamochoerus_porcus.html. Accessed 1 November 2013

Serckx A, Huynen M-C, Bastin J-F, Vimond M, Raynaud E, et al. (2013) Nesting patterns of bonobos (*Pan paniscus*) in relation to fruit availability in a forest-savannah mosaic. PLoS ONE: In press.

Thomas L, Buckland ST, Rexstad E a, Laake JL, Strindberg S, et al. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. J Appl Ecol 47: 5–14.

II APPENDIX II

Maisels et al. 2013. Devastating Decline of Forest Elephants in Central Africa.

PloS ONE: e59469

OPEN ACCESS Freely available online

PLOS ONE

Devastating Decline of Forest Elephants in Central Africa

Fiona Maisels[1,2☯*], Samantha Strindberg[1☯], Stephen Blake[1¤a], George Wittemyer[3,4], John Hart[1¤b], Elizabeth A. Williamson[2], Rostand Aba'a[1¤c], Gaspard Abitsi[1], Ruffin D. Ambahe[1], Fidèl Amsini[1¤d], Parfait C. Bakabana[1¤e], Thurston Cleveland Hicks[6¤f], Rosine E. Bayogo[7], Martha Bechem[1¤g], Rene L. Beyers[8], Anicet N. Bezangoye[9], Patrick Boundja[1], Nicolas Bout[1¤h], Marc Ella Akou[9¤i], Lambert Bene Bene[10†], Bernard Fosso[1], Elizabeth Greengrass[1¤j], Falk Grossmann[1], Clement Ikamba-Nkulu[1], Omari Ilambu[1¤i], Bila-Isia Inogwabini[1¤k], Fortune Iyenguet[1], Franck Kiminou[1], Max Kokangoye[1,9†], Deo Kujirakwinja[1], Stephanie Latour[1,11¤l], Innocent Liengola[1], Quevain Mackaya[1], Jacob Madidi[1¤m], Bola Madzoke[1], Calixte Makoumbou[1¤n], Guy-Aimé Malanda[1¤o], Richard Malonga[1], Olivier Mbani[1¤p], Valentin A. Mbendzo[1,10¤q], Edgar Ambassa[1¤r], Albert Ekinde[1], Yves Mihindou[1], Bethan J. Morgan[2,12], Prosper Motsaba[1], Gabin Moukala[1¤p], Anselme Mounguengui[10], Brice S. Mowawa[1¤s], Christian Ndzai[1], Stuart Nixon[13¤t], Pele Nkumu[1], Fabian Nzolani[1], Lilian Pintea[11], Andrew Plumptre[1], Hugo Rainey[1¤u], Bruno Bokoto de Semboli[7], Adeline Serckx[14], Emma Stokes[1], Andrea Turkalo[1], Hilde Vanleeuwe[1], Ashley Vosper[5,15¤v], Ymke Warren[1†]

1 Global Conservation Program, Wildlife Conservation Society, Bronx, New York, United States of America, **2** School of Natural Sciences, University of Stirling, Stirling, Scotland, United Kingdom, **3** Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, United States of America, **4** Save The Elephants, Karen, Nairobi, Kenya, **5** Lukuru Wildlife Research Foundation, Gombe, Kinshasa, Democratic Republic of Congo, **6** The Institute of Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands, **7** Ministère des Eaux, Forêts, Chasse et Pêche, Bangui, Central African Republic, **8** Beatty Biodiversity Centre, University of British Columbia, Vancouver, British Columbia, Canada, **9** Direction de la Gestion de la Faune et de la Chasse, Ministère des Eaux et Forêts, Libreville, Gabon, **10** Central Africa Regional Programme Office, World Wildlife Fund, Yaoundé, Cameroon, **11** The Jane Goodall Institute, Arlington, Virginia, United States of America, **12** Central Africa Program, Zoological Society of San Diego, Yaoundé, Cameroon, **13** Zoological Society of London, Regents Park, London, United Kingdom, **14** Behavioral Biology Unit, University of Liege, Liege, Belgium, **15** African Wildlife Foundation, Gombe, Kinshasa, Democratic Republic of Congo

Abstract

African forest elephants– taxonomically and functionally unique–are being poached at accelerating rates, but we lack range-wide information on the repercussions. Analysis of the largest survey dataset ever assembled for forest elephants (80 foot-surveys; covering 13,000 km; 91,600 person-days of fieldwork) revealed that population size declined by ca. 62% between 2002–2011, and the taxon lost 30% of its geographical range. The population is now less than 10% of its potential size, occupying less than 25% of its potential range. High human population density, hunting intensity, absence of law enforcement, poor governance, and proximity to expanding infrastructure are the strongest predictors of decline. To save the remaining African forest elephants, illegal poaching for ivory and encroachment into core elephant habitat must be stopped. In addition, the international demand for ivory, which fuels illegal trade, must be dramatically reduced.

Citation: Maisels F, Strindberg S, Blake S, Wittemyer G, Hart J, et al. (2013) Devastating Decline of Forest Elephants in Central Africa. PLoS ONE 8(3): e59469. doi:10.1371/journal.pone.0059469

Editor: Sergios-Orestis Kolokotronis, Fordham University, United States of America

Received May 28, 2012; **Accepted** February 18, 2013; **Published** March 4, 2013

Funding: For funding of the survey work the authors thank (in alphabetical order) Nancy Abraham, the African Wildlife Foundation, Beneficia Foundation, Busch Gardens, Columbus Zoo, Conservation International, Daniel K. Thorne Foundation, Diane Fossey Gorilla Foundation International, Espèces Phares (European Union), Ecosystèmes Forestiers d'Afrique Centrale (ECOFAC), Fauna and Flora International, Frankfurt Zoological Society, IUCN Netherlands, John D. and Catherine T. MacArthur Foundation, KFW, LifeWeb (Spain), National Fund for Scientific Research (FNRS, Belgium), Offield Family Foundation, Operation Loango, Prince Bernhard Wildlife Fund, RAPAC, The Arcus Foundation, The Aspinall Foundation, The Born Free Foundation, The Institute for Biodiversity and Ecosystem Dynamics at The University of Amsterdam, The Jane Goodall Institute, The Liz Claiborne and Art Ortenberg Foundation, The Lucie Burgers Foundation, The Wasmoeth Wildlife Foundation and Karl Ammann, Total Gabon, United States Agency for International Development (USAID CARPE), USFWS Great Ape Conservation Fund, USFWS African Elephant Conservation Fund, Wildlife Conservation Society, World Wildlife Fund and the Zoological Society of London. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have the following interest: This study was in part supported by the following: Busch Gardens and TOTAL Gabon. CIB (Congolaise Industrielle du Bois) provided some logistical help for the 2006 and 2010–11 surveys in the following northern Congo sites (Pokola, Kabo, Loundougou. This does not alter the authors' adherence to all the PLOS ONE policies on sharing data and materials, as detailed online in the guide for authors.

* E-mail: fmaisels@wcs.org

☯ These authors contributed equally to this work.

¤a Current address: Max Planck Institute for Ornithology, Vogelwarte Radolfzell, Radolfzell, Germany
¤b Current address: Lukuru Wildlife Research Foundation, Gombe, Kinshasa, Democratic Republic of Congo
¤c Current address: Agence Nationale des parcs Nationaux, Libreville, Gabon
¤d Current address: Frankfurt Zoological Society, Frankfurt, Germany
¤e Current address: International Union for Conservation of Nature, Kabo, Republic of Congo
¤f Current address: Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
¤g Current address: MIKE Subregional Office, Yaoundé, Cameroon
¤h Current address: The Aspinall Foundation, Franceville, Gabon
¤i Current address: Central Africa Regional Programme Office, World Wildlife Fund, Yaoundé, Cameroon
¤j Current address: Bradford on Avon, Wiltshire, United Kingdom
¤k Current address: Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden
¤l Current address: Vaucresson, France
¤m Current address: Societé Générale de Surveillance, Bunia, Oriental Province, Democratic Republic of Congo
¤n Current address: Mokabi Société anonyme (Rougier Group), Brazzaville, Republic of Congo
¤o Current address: Odzala-Kokoua National Park, African Parks, Brazzaville, Republic of Congo
¤p Current address: Environment Department, Association Sylvatrop, Conakry, Guinea
¤q Current address: Programme d'Appui à la Conservation des Ecosystèmes du Bassin du Congo, Yaoundé, Cameroon
¤r Current address: Ministry of Forestry and Wildlife, Yaoundé, Cameroon
¤s Current address: Ministère de l'Economie Forestière, Brazzaville, Republic of Congo
¤t Current address: Fauna & Flora International, Cambridge, United Kingdom
¤u Current address: The Biodiversity Consultancy Ltd, Cambridge, United Kingdom
¤v Current address: Global Conservation Program, Wildlife Conservation Society, Bronx, New York, United States of America

† Deceased.

Introduction

The basic information required for effective conservation management of a species includes population status and distribution, identification and prioritization of threats, and trends in all of the above [1]. These metrics are the basis by which the IUCN Red List assesses the conservation status of species [2], and conservation policymakers and managers in the field decide on the management strategies which best serve the taxon in question. However, these requirements are notoriously difficult to ascertain and, therefore, lacking for numerous species including one of the world's largest terrestrial mammals, the African forest elephant.

There are two distinct types of African elephants, often considered to be two species: savannah elephants *Loxodonta africana* (Blumenbach, 1797) and forest elephants *L. cyclotis* (Matschie, 1900). In 2003, the IUCN African Elephant Specialist Group (AfESG) listed them as subspecies *(L. a. cyclotis* and *L. a. africana,* respectively), due to perceived data gaps [3]. However, in 2008 they suggested that further research may reveal more than one African elephant species [4]. It was proposed that they should be considered two species on morphological grounds [5] and are considered as such by the Convention on Migratory Species [6]. Genetic evidence also supports this view [7–15]. The AfESG do, however, stress that it is important to recognize the different challenges to the conservation of forest and savannah elephants [3,16].

African forest elephants have deep ecological differences from savannah elephants. They are highly frugivorous [17–20] and thus play an important role in one of Earth's primary carbon-sequestering forests [17,21,22]. They can move great quantities of large seeds many kilometres from the parent tree [17] and are thus integral for maintaining forest structure and diversity. They also maintain [23], and possibly create, forest clearings in mineral-rich soil, on which a wide variety of African forest fauna are dependent [24,25].

The history of African elephant abundance and distribution is strongly linked to the commerce in ivory, and their decline since the 1800s has been documented across the continent [26–28]. Even in the forests of Central Africa, a century ago, there were very few elephants remaining anywhere along the Gabonese coast, or around Brazzaville, in what is now the Republic of Congo [29]. It was thought that there was a slow decline in elephant populations during the 19th century, flattening off in the first half of the 20th century, and then a steep drop between 1950 and 1989 [28]. Modern African elephant density, based on data up to 2007, has recently been shown to be correlated with human factors rather than ecological factors [30].

The elephant subpopulation of Central Africa (which included some savannah populations in Chad and northern Cameroon) was recognized in 2008 as Endangered by the IUCN [4]. In 2010, the African Elephant Action Plan [31] drawn up by all of the African elephant range states, ranked poaching and illegal trade in elephant products as the top threat to elephants across the continent. In the last few years there have been very large and frequent ivory seizures in Africa and Asia, and the combination of seizure data analysed by the Elephant Trade Information System (ETIS) and of elephant carcass data documented and analysed by the Monitoring the Illegal Killing of Elephants (MIKE) programme demonstrate that the illegal trade is escalating [16,32–36]. This increasing trade has been linked to increasing demand and value of ivory in China [37,38]. The proportion of elephant carcasses found that had been killed illegally in 2010 was the highest on record [39] only to be exceeded by 2011 levels [16,35]. Elephant meat is an important by-product, but ivory is the primary reason for elephant poaching [40]. It is now clear that elephants in general, and especially the elephants of Central Africa, are under serious threat [33] and that the poaching since 2011, may be at the level at which all elephant populations are in net decline [16,31].

The scale of historical forest elephant decline, although substantial [28,41], has been difficult to quantify due to a lack of comprehensive, range-wide information on distribution and density. Previous analyses, collected over a relatively short period and limited in geographic extent relative to their range, suggested a growing crisis for elephants in the Central African forests [42]. It is critical that a broader assessment is provided to understand range and demographic trends [16]. The Central African forest block covers about 95% of the current "known" and "possible" range of forest elephants [43]; the remaining 5% are in the forests of West Africa, to the west of the Cameroon-Nigeria border. We present the analysis of eighty surveys carried out over the nine-year period between 2002–2011 across the Central African forest block. The area stretches from the western Cameroon across to the eastern border of the Democratic Republic of Congo (DRC). The analysis responds to recent demands for a rigorous, range-wide assessment of forest elephant conservation status [16,31]. Trends

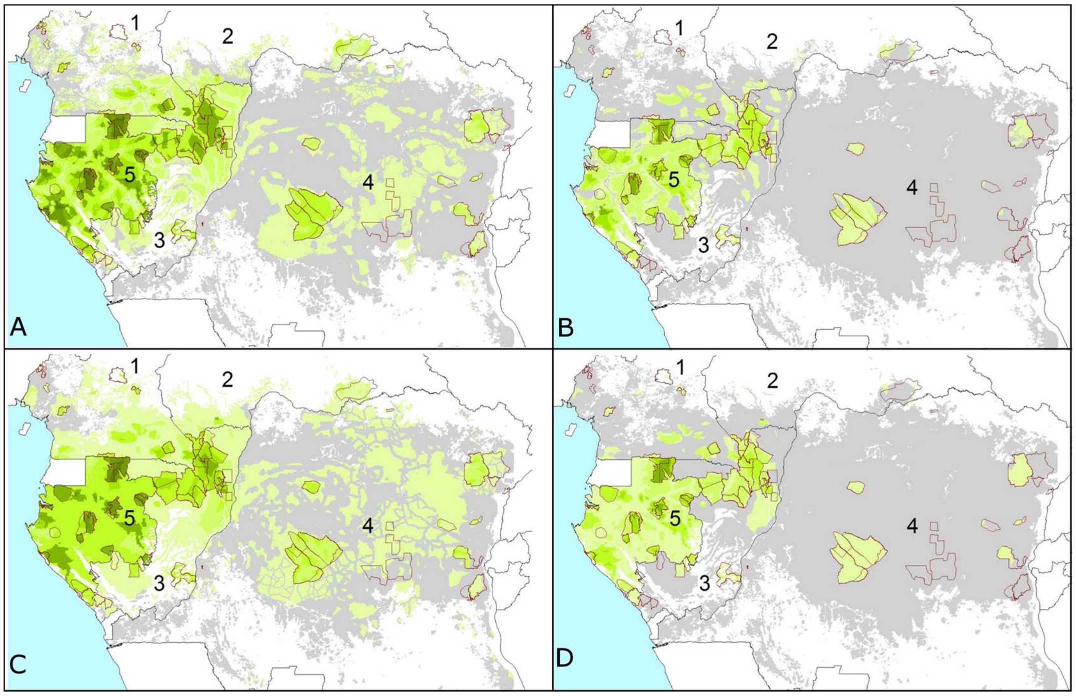


Figure 1. Elephant dung density and range reduction across the Central African forests. Predictions are shown for (A) 2002 and (B) 2011 for the model with variables: survey year^, Human Influence Index***, corruption*** and the presence/absence of guards***, and (C) 2002 and (D) 2011 for the model with variables: survey year^, proximity to road^, human population density***, corruption*** and the presence/absence of guards*** (P-values are: '***' $<$0.001 and '^' $<$0.1). Increasingly darker shades of green correspond to higher densities, grey represents extremely low elephant density range (the first interval: 0–100 elephant dung piles/km^2) and white is non-habitat (80 survey sites outlined in red). Cutpoints are: 0; 100; 250; 500; 1,000; 1,500; 3,000; 5,000; and 7,500 dung piles/km^2. Countries 1–5 are: Cameroon; Central African Republic; Republic of Congo; DRC; Gabon.
doi:10.1371/journal.pone.0059469.g001

inferred from dung surveys are presented. In addition, landscape covariates correlated with dung density (a proxy for elephant density) were analyzed and results discussed with the aim of providing information to enhance effective conservation policy and management.

Results

Our results demonstrate a widespread and catastrophic decline in numbers of forest elephants, in the order of 62%, and a corresponding range contraction of approximately 30%, during the nine-year period 2002–2011 represented by this study (Figs. 1 and 2; Tables S2 and S3). Forest elephants now have likely declined to extremely low density over 75% of their potential range (Tables S3, S6), and probably have been extirpated from large sections of this range. Considering 2002–2011 range contraction relative to elephant habitat per country, ca. 95% of DRC's forests are likely to be almost empty of elephants, a country historically thought to have held the highest numbers (Table S3). About half of the surviving elephants are in Gabon, and under a fifth in DRC, despite these countries covering 13% and 62% of the total forest area, respectively (Table S6). In 2011, less than 2% of the Central African forest contained elephants at high density (Table S3). Even for Gabon, in 2011 high density populations were found in only 14% of the forest (a decline of over 18% between 2002 and 2011). No high density areas remained in DRC even in 2002.

Correlates of Decline in Multi-variable Models

The overall top-ranked multi-variable model of elephant dung pile density by increasing Un-Biased Risk Estimator (UBRE) score included the explanatory variables: hunter-sign frequency, survey year, proximity to roads, human population density, corruption, and presence or absence of wildlife guards (Table S5, and Fig. 3). Site-specific dung-encounter rates and hunter-sign frequency were significantly negatively correlated–elephants occur where people do not–and both were strongly influenced by guard presence/absence (Figs. 4, 5, and 6). Survey year and corruption were included in almost all of the top-ranking models that included hunter sign. Models that included hunter-sign frequency were always better when considering UBRE score than otherwise identical models that excluded this variable and able to explain on average 50% of the variability in the data with satisfactory model fit diagnostics (Table S5, and Fig. 3). The top-ranking models without the hunter sign covariate were similar to each other in terms of UBRE score and were able to explain on average 45% of the variability in the data with satisfactory model fit diagnostics with models including the HII (Human Influence Index: [44]), in place of road proximity and human population density, generally a few percentage points lower; (Table S2, and Fig. S1). Again, survey year and corruption were included in almost all of these models. While hunter sign was clearly an important variable, it was one of the few for which data were collected directly during the surveys at each site (rather than extracting the information from GIS data layers, for example). Because it was site collected and not part of a global dataset such as the HII, it was not available at all locations across the Central African forests. Therefore, models containing hunter sign could not be used to

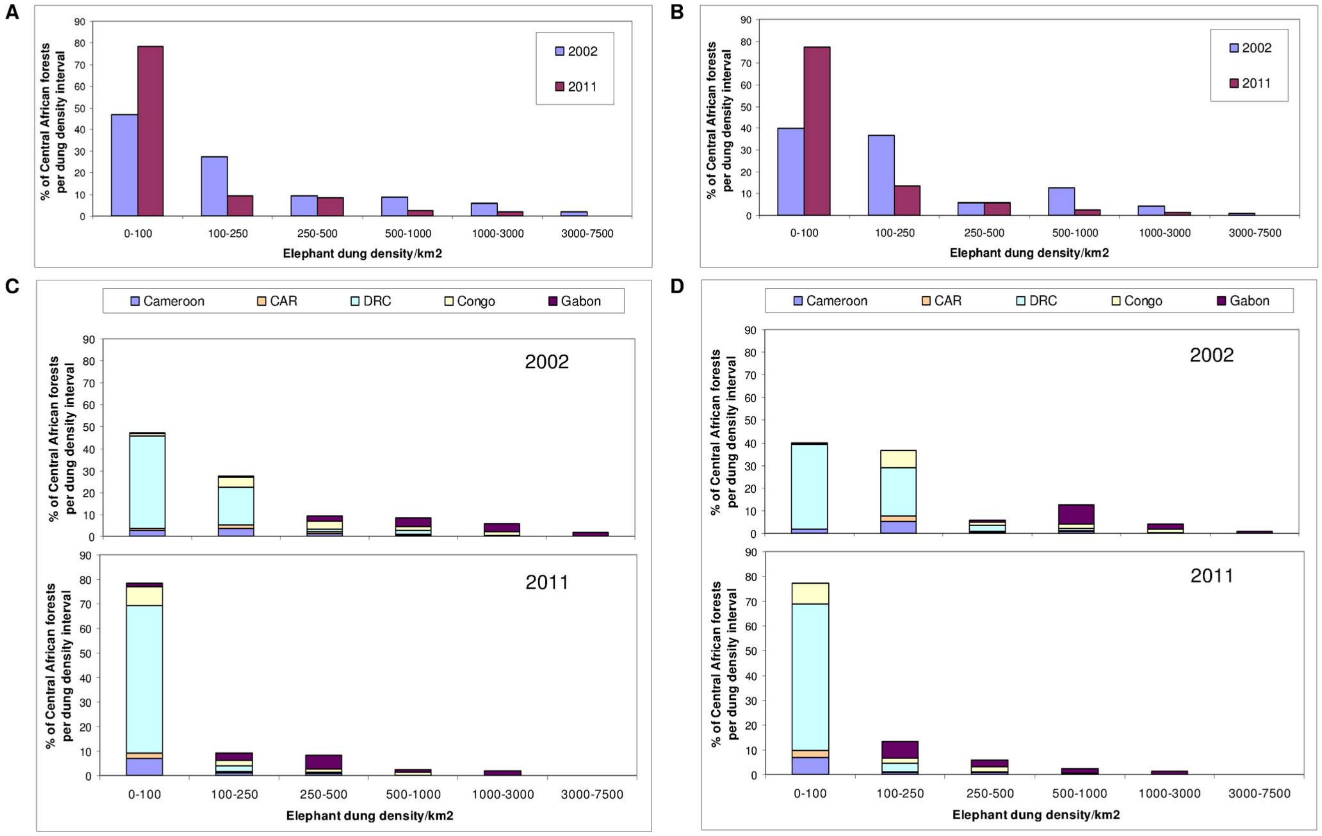


Figure 2. Estimated change in elephant dung density (/km^2) distribution during 2002–2011 across the Central African forests. Results are shown as a percentage of the total area of potential elephant habitat overall (A & B) and by country (C & D) for the predictive model with variables: (A & C) survey year, Human Influence Index, corruption and the presence/absence of guards, and (B & D) survey year, proximity to road, human population density, corruption and the presence/absence of guards. The dung density (per km^2) intervals are unequal and correspond to the following elephant population categories: extremely low density (0–100), very low (100–250), low (250–500), medium (500–1,000), high (1,000–3,000) and very high (3,000–7,500). With the loss of very high elephant populations in 2011, there is a significant shift into the lower density intervals over the nine years.

doi:10.1371/journal.pone.0059469.g002

produce predicted dung density surfaces and to estimate elephant range and abundance across the entire area of interest.

For the set of top-ranked models that used the variables across Central Africa, dung density was significantly higher at sites with wildlife guards and with a designated official protection status (Fig. 4). Dung density was inversely correlated with corruption as measured by Transparency International's Corruption Perception Index (CPI) [45]; with more widespread distributions and higher densities in less corrupt countries: Gabon was significantly higher and DRC significantly lower than the roughly similar Cameroon, Central African Republic (CAR) and Republic of Congo (Congo) (Table S3). The regional proxy variables latitude and longitude appeared frequently among the top-ranking models and also captured significant variation. Longitude was the better covariate. In most of the models including either of these variables, these proxies indicated higher dung densities closer to the equator and significant decreases further east, which potentially represents site differences not accounted for by other variables, such as political instability in the Southeast (Eastern DRC) of the study area [46].

The inclusion of variables such as human population density, HII, and the presence/absence of wildlife guards always improved the UBRE score and were always statistically significant. Inclusion of variables such as proximity to roads, survey year and corruption in the models also improved the UBRE score, but these variables were occasionally non-significant. Either the HII or the combination of proximity to roads and human population density was used (with only human population density in some models), as the composite variable HII was highly correlated with the other two variables that comprise two of several variables used to generate the HII [44]. When considering the relative performance of the significantly correlated variables official protection and the presence/absence of guards (where official protection was low, there were no guards), the latter was much better in terms of improvements to the UBRE score and its effect on deviance explained, and was thus the preferred variable in top-ranking models. Corruption, as measured by the CPI was very highly correlated and almost identical to the country factor in terms of improvements to the UBRE score and its effect on deviance explained; with the added benefit of providing insights on how corruption, conceptually associated with poaching, may be influencing elephant distribution and density by country.

Correlates of Decline in Single-variable Models

The single variable modelling results were similar to the multivariable models, where all variables considered were significantly related to elephant dung density (Fig. S2 and Table S4). Univariate models with the variables longitude, country, corruption, and survey year were highly ranked, whereas the model with official protection received the lowest ranking (the UBRE scores for the remaining variables are also shown in Table S4).

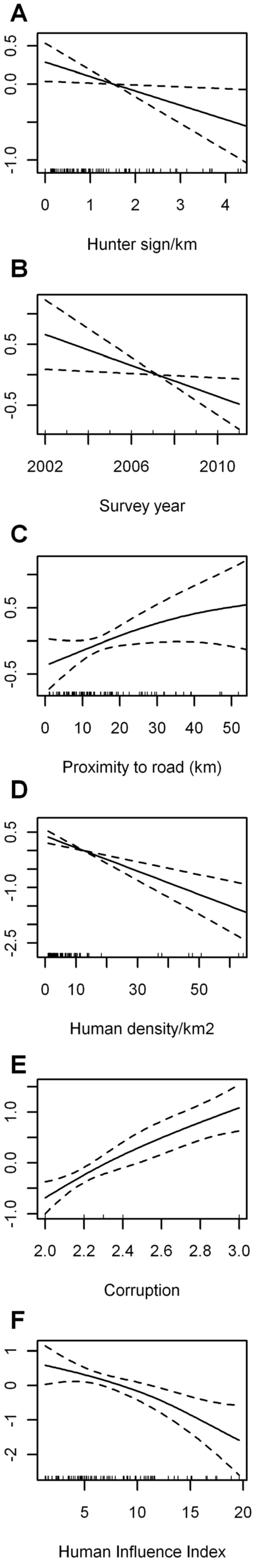


Figure 3. Estimated conditional dependence of elephant dung density for top-ranked multi-variable models including hunter sign. Results are shown for the top-ranked model with variables: (A) hunter sign*, (B) survey year*, (C) proximity to roads^, (D) human population density***, (E) corruption*** (higher values = less corrupt) and presence/absence of guards***. Also shown is (F) the Human Influence Index (HII) for the model with proximity to road and human population density variables replaced by the HII, i.e. one of the top-ranking models with variables: hunter sign**, survey year*, HII*, corruption***, and presence/absence of guards***. P-value significance codes are: '***'<0.001, '**'<0.01, '*'<0.05, and '^'<0.1. Plot components are: Estimates on the scale of the linear predictor (solid lines) with the y-axis scale for each variable selected to optimally display the results, confidence intervals (dashed lines), and explanatory variable values of observations with a focus on the core 95% of values for hunter sign, proximity to road and human population density (rug plot - short vertical bars along each x-axis showing the x value for each site).
doi:10.1371/journal.pone.0059469.g003

Univariate models predicted that dung density decreased by (i) 89% as hunter-sign frequency increased from zero to four per km, (ii) 85% when guards were absent, (iii) 30% or 76% as proximity to road decreased from 50 to 25 or zero km, (iv) 48%, 75% or 92% as human density increased from one to five, 10 or 20 people/km^2, and (v) 17% for each unit increase in the HII. Among the survey site specific variables, human population density had the highest value for deviance explained, followed by the hunter-sign frequency, the presence/absence of guards, and the HII. For the remaining site specific variables (official protection status, proximity to roads, and survey year) the values were considerably smaller. The highest deviance explained corresponded to country-level variables, such as country itself and corruption. The proxy variable longitude also had one of the largest values for deviance explained, whereas latitude did not (Table S4).

Predictive Modelling of Decline

We used the top-ranking multi-variable models with available regional data to predict forest elephant dung density across Central Africa (Fig. 1 and Table S2). We chose to highlight two models including predictor variables that elephants might be responding to directly, rather than latitude and longitude, so as to avoid using spatial location as a proxy for other processes. These models also include survey year as a covariate, which allows for predictions by year and comparisons over time. Results were consistent across models, and predicted dung density across Central Africa reflected the map of actual dung encounter rate (Fig. 5) and also most of the "Known" range described by the African Elephant Database (AED) [47]. Broadly speaking, whether using the HII or a combination of road proximity and human population density, the forested regions of Gabon, northern Congo, southwestern CAR and southeastern Cameroon contained the region's highest elephant densities and almost all the nationally important elephant populations, while most of DRC, eastern Congo and southern CAR had very low densities (Fig. 1). The most country-specific important sites for elephants are as follows: in Gabon, most of the National Parks and their surroundings (often Forest Stewardship Council (FSC)-certified logging concessions), especially all of those in the centre and northeast of the country, plus a long section along the coast. In Congo, about half of the north of the country can be classed as an important elephant site, including not only the National Parks of Odzala and Nouabale-Ndoki (and the soon-to-be declared Ntokou-Pikounda National Park) but several huge areas of FSC certified timber concessions that connect and surround these Parks. In the Central African Republic, the Dzanga-Sangha National Park, and in Cameroon the whole of the southeast corner of the country, which

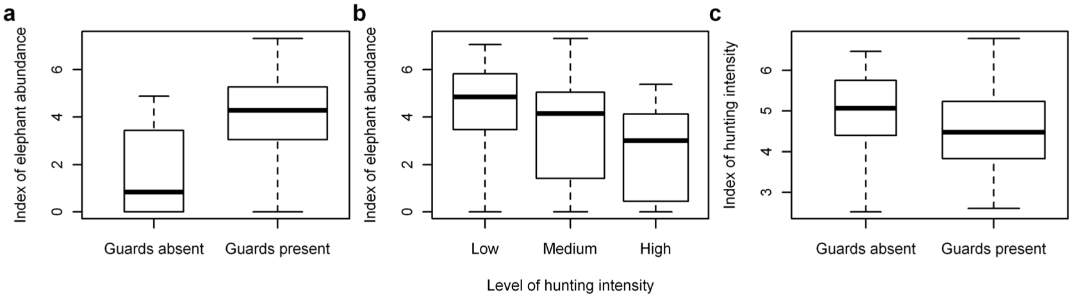


Figure 4. Boxplots of indices of elephant abundance and hunting intensity. Summaries shown are the natural logarithm of: (A) elephant dung encounter rate per 100 km grouped by the presence/absence of wildlife guards, (B) elephant dung encounter rate per 100 km grouped by the level of hunting intensity (group cutpoints are 0.6 and 1.75 hunter sign/km), and (C) hunter-sign frequency per 100 km grouped by the presence/absence of wildlife guards. Box-widths are proportional to the number of observations in each group.
doi:10.1371/journal.pone.0059469.g004

includes three National Parks and large areas of FSC-certified logging concessions. Finally, the two significant sites in DRC are the Okapi Faunal Reserve and the Salonga National Park, with smaller but still significant numbers in some of the other forest areas (including one which may soon be gazetted as a protected area, known as the Tshuapa-Lomami area).

In areas where there is little or no poaching, elephant density is usually 0.5–1.0/km^2 (data included in this study). Using a conservative density of 0.5 elephants/km^2, historically the 2.2 million km^2 Central African forest could have harboured over a million individuals [28,41] (Fig. 7). Even in 1993, it was estimated that roughly half of this projected original population remained [41] (based on their model predictions). Our analysis suggests that in 2011 just 10% (ca. 100,000 individuals) still survive (99,869 with 95% bootstrapped confidence interval (49,867–187,340) for the predictive model shown in Fig. 1B). Gabon maintains 30–50% of its probable historical numbers; DRC only 1% - it was thought that DRC originally contained almost 60% of all forest elephants, and had 40% in 1989 [41].

Discussion

Elephants have been recently extirpated from extensive areas of Africa [30,34,46,47,48] and even sites thought to be well-protected are no longer safe from ivory poaching [32]. Bouché et al.'s (2011) study examined the West and Central African savannahs, and showed that the once large savannah elephant populations had been reduced to several small pockets of a few hundred animals in many cases, with only about 7,000 individuals remaining in total. Shortly after that publication, in early 2012, several hundred elephants were killed in a matter of a few months, in the Park holding most of Cameroon's savannah elephants [49,50]; the poachers were well-armed and on horseback. In mid-November 2012, the same poachers were heading back to the same Park – but the Cameroon army were alerted before they arrived [51]. In February 2013, the Gabonese Government announced the loss of at least half of the elephants in Minkebe National Park; as many as 11,000 individuals may have been killed between 2004 and 2012 [52]. The rapid increases in demand for, and price of, ivory in China, and the ease of sale of ivory in China [37,38], the persistent

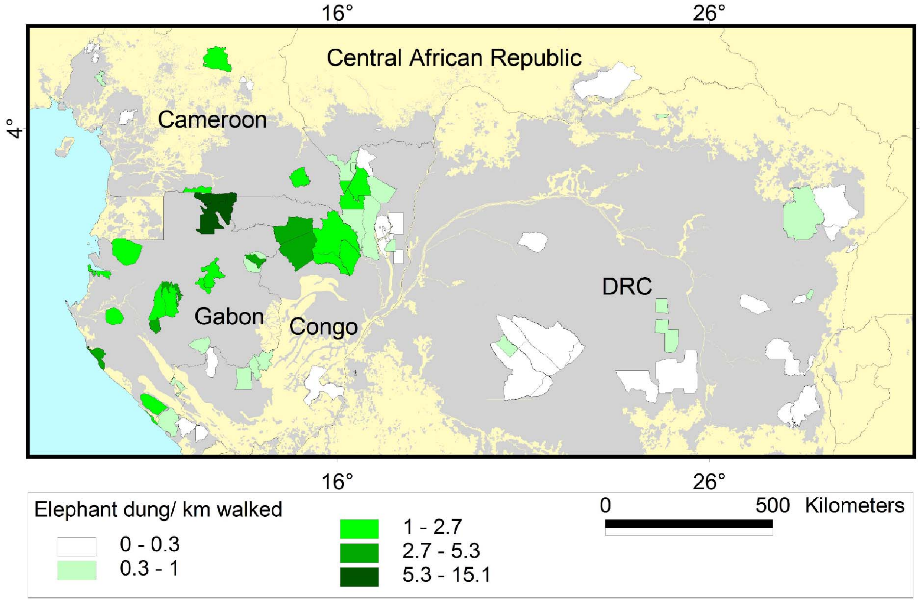


Figure 5. Encounter rate of elephant dung per kilometre. Results are shown for the 80 survey sites in Central Africa included in this study. Grey shading represents forest cover.
doi:10.1371/journal.pone.0059469.g005

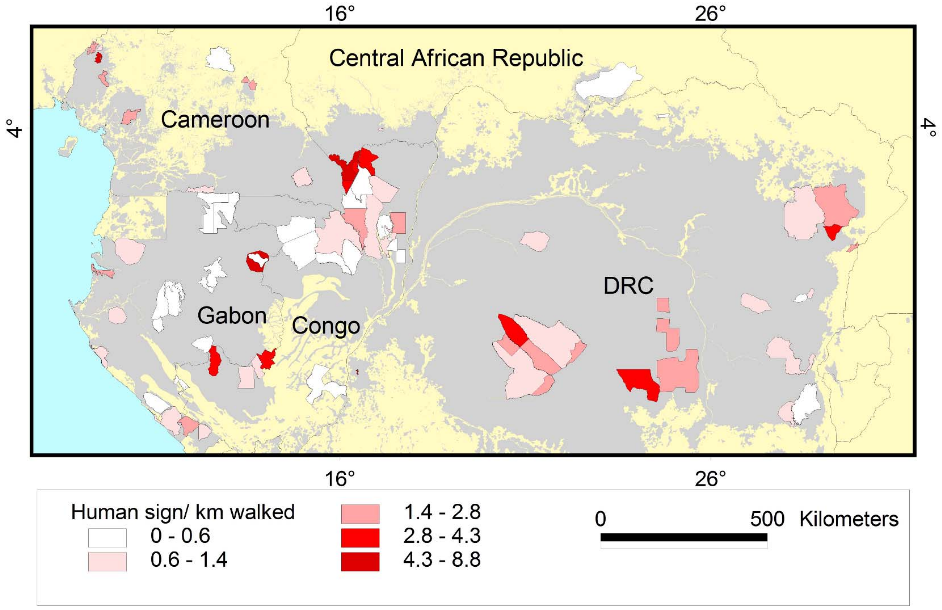


Figure 6. Encounter rate of hunter sign per kilometre. Results are shown for the 80 survey sites in Central Africa included in this study. Grey shading represents forest cover.
doi:10.1371/journal.pone.0059469.g006

lack of effective governance in Central Africa [53] and a proliferation of unprotected roads that provide access to hunters [54,55] combine to facilitate illegal ivory poaching, transport and trade. Forest elephant population and range will continue to decline unless conditions change dramatically.

Other threats and management issues also affect forest elephants. Unlike other tropical forests, deforestation is very low in Central Africa, although increasing [56,57]. Nevertheless, land use pressure, habitat loss, and human-elephant conflict also threaten this species [16] and will likely increase as industrial agriculture, such as oil palm for biofuel production, develops in the near future in Africa in general and Central Africa in particular [58,59]. While these management issues will likely increase with accelerating land use changes, the immediate, and very serious threat to the persistence of this species remains ivory poaching.

Our analysis identified several factors likely to contribute to decline and demonstrated the importance of law enforcement for persistence of elephants. Similar factors were also found to be important in recent analyses of a very different dataset- carcass data from the MIKE sites [16,33] – where higher levels of elephant poaching, as expressed by the proportion of illegally killed elephants (PIKE) were associated with sites where law enforcement capacity was lower, and in countries with poor governance. Governance in our study was represented by the CPI [45], whereas the MIKE analysis up to 2009 [33] incorporated both CPI and several government effectiveness indicators used by the World Bank (which can be found in their website http://info.worldbank.org/governance/wgi/). However, in 2012, the MIKE analysis used only the CPI as the proxy for governance [16]. Because the CPI is strongly associated with other factors within

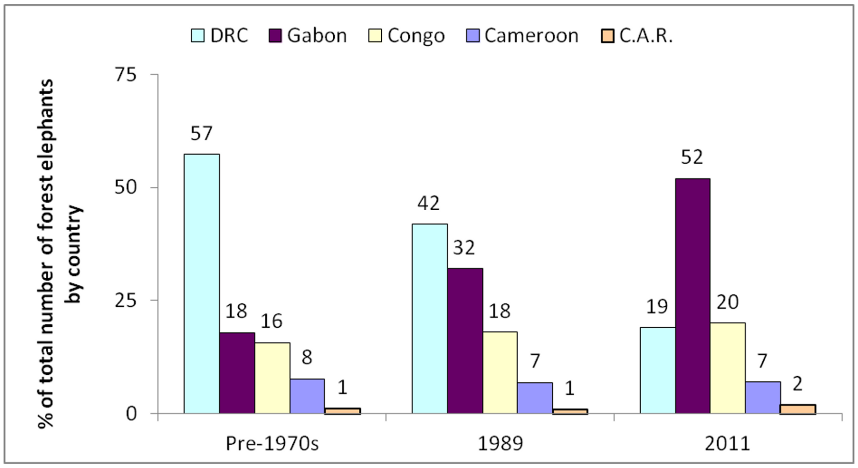


Figure 7. Percentage breakdown of the total number of forest elephants by country. Results are shown for 3 time periods: pre-1970s and 1989 [41] and 2011 (this study).
doi:10.1371/journal.pone.0059469.g007

countries (rule of law, governance, development), it may be considered as a proxy for overall functioning of civil society of each country, and indeed development variables associated with poverty were also found to be associated with PIKE in both 2009 and 2012 [16,33]. A previous analysis using data from the African Elephant Database [60] suggesting a link between elephant decline and poor governance was criticized [61], because latitude was a better explanatory variable and the data were collected using different methods of varying quality [4,47]. The more recent analysis using the 2007 AED showed that the "country" variable, a complex interaction of human development and governance factors, explained elephant density very well [30]. In contrast to the AED's quite variable data, we used highly comparable data obtained within a single vegetation type (closed canopy forest). Corruption in general is increasingly a focus of international attention, whether in the wildlife realm [62–64] or more broadly [65].

Currently the Red List classifies African elephants (*L. africana*) as Vulnerable, and the Central African population as Endangered [4]. Current losses (62% between 2002–2011) combined with previous losses [28,41] indicate a decline of more than 80% in less than two elephant generations, ca. 25 years [47]. The criterion for listing a species as Critically Endangered is when that species has declined by >80% in ten years, or three generations, whichever is the longer. If, conservatively, there were half a million forest elephants in the Congo Basin in 1937 (three elephant generations ago) then about 80% have now been lost. The causes of the decline are unlikely to abate in the short term, and indeed may worsen. This strongly suggests consideration of an uplisting of the Central African forest elephant subpopulation status to Critically Endangered, under the IUCN red list criteria A4b,d (population reduction, and current and projected levels of exploitation) [66].

Remaining large landscapes of major importance for elephants comprise national parks embedded in land-use matrices including logging concessions, where wildlife guards operate in both park and concession [67,68]. However, current site-based interventions in the region are generally inadequate to protect elephants, because conservation budgets are below that needed to achieve management success [42,69] and local interventions do not mitigate macro-scale threats (i.e. infrastructure development, governance issues, and ivory demand). Effective multi-level action is imperative to save forest elephants. We strongly agree with the recommendations of the African Elephant Action plan, of which the highest priority objective was the reduction of poaching and trade in elephant products.

In 2012, China submitted a document to CITES on how it will improve its internal ivory trade [70], as internal and international awareness of the problem grows [16,35,36,71]. China's wildlife officials, among others, attended a wildlife anti-trafficking workshop in Gabon in early 2012 [72]. At the 2012 World Conservation Congress, two specific resolutions were passed [73,74] to enhance the protection of elephants both in the range states and in the ivory-consuming countries, and a specific wildlife-crime related resolution was passed at the same time [75]. In November 2012, the US State department clearly outlined a zero-tolerance approach to wildlife crime [76,77] and many governments, INTERPOL, the World Customs Association and others are collaborating in international efforts to curb ivory (and other wildlife product) trafficking [63,78]- partly for the wildlife itself, and also because the strong links with global organised crime and security are recognised [64,79]. These diplomatic efforts are critical, but we emphasize the importance of *in situ* enforcement investment to protect the remaining populations of this species. However, curbing demand for ivory is key, if forest elephants are to survive.

Materials and Methods

Ethics Statement

All research was conducted using observation of indirect signs of forest elephants (dung).

Data Collection and Standardization

We modelled temporal and spatial trends using data collected during 13,000 km of elephant-dung foot-surveys in 80 sites during 91,600 person-days from 2002 to 2011 (Fig. S3 shows temporal coverage). Field protocol followed the standardized 2003 methods of the Monitoring the Illegal Killing of Elephants (MIKE) [80] program of the Convention on International Trade in Endangered Species (CITES). Surveys covered the five countries holding the majority (95%) [43] of extant forest elephant range: Cameroon, Central African Republic (CAR), Republic of Congo (Congo), Democratic Republic of Congo (DRC) and Gabon, across 257,145 km^2 (about 12% of Central Africa's forests; Table S1, Figs. 5 and 6). There were 9, 5, 25, 22 and 19 surveys in each country with ca. 11%, 2%, 26%, 43% and 18% of total effort (13,000 km) and ca. 4%, 6%, 32%, 41% and 17% of the total area covered (257,145 km^2). For sites surveyed more than once, only the most recent data was used. In just over 25% of sites surveyed wildlife guards were absent.

All surveys were carried out independently for site-based or landscape-based conservation needs. Limited resources for these purposes resulted in surveys being restricted to areas known or suspected to harbour wildlife, but with very variable elephant densities. Over half of the surveys were of existing or prospective protected areas, and the rest were areas in logging concessions, or with potential for wildlife conservation. Although there were some sites where elephant populations were known to be very low, few sites thought to be completely devoid of them were surveyed. Survey data was obtained across the range of values for each of the covariates considered in the analysis.

Either standard systematic line-transect distance sampling surveys (perpendicular distance to each dung pile recorded) [81], or systematic reconnaissance surveys [82] (elephant dung only recorded within a metre of the centre line) were walked. Both transect and recce survey designs allowed for random placement of the sampling units being drawn up using Distance software [83], and orientation of both transects and recces were perpendicular to roads, and major rivers to potentially improve precision. Usually at least 15 transects per stratum were used; usually more, giving reasonable replication to ensure a representative sample was obtained. Transects and recces were usually placed systematically with a random start across the entire area surveyed. At some sites both recces and transects were walked; we have used only the transect data for these sites. Data from recce surveys were used when straight lines were walked, thereby ensuring minimal bias. Other data from less strict recces (where roads or elephant paths might have been used) were not used in the analysis. Most recces were from areas known to have high hunting pressure (and thus low wildlife density). This is because transects are much more expensive to implement than recces. Occasionally, recces were done in areas where resources for a transect survey were not available at the time. Transect data were truncated to one metre of the centre line using the Distance software and the resulting plot checked to ensure that detection was 100% within that distance [83]. For reconnaissance data, detectability of dung piles was assumed certain within the narrow sampling strip (one metre each side of the observer).

Data Analysis

Statistical modeling. We assessed known or suspected drivers of elephant density and distribution [16,17,30,33,54,55] using Generalized Additive Models (GAMs) [84] due to their flexibility and capacity for non-linear responses.

The standardized response variable was elephant dung pile counts within one metre of the centre line, adjusted for survey effort. GAMs were fit to elephant dung pile count data of the form:

$$E(n_i) = \exp\left\{\ln(2l_i) + \beta_0 + \sum_{j=1}^{q} f\left(z_{ij}\right)\right\}$$

where for the i^{th} survey site: n_i denotes number of elephant dung piles detected, l_i aggregate survey effort, $2l_i$ area effectively surveyed, β_0 the intercept, and $f(z_{ij})$ a smooth function of the j^{th} explanatory variable$z$. By including area surveyed as an offset term in the model, elephant dung density is in effect being modelled. A negative binomial distribution was used to deal appropriately with severe over-dispersion in the count data. The scale parameter theta of the negative binomial was treated as unknown and an interval of (1,3) over which to search for theta was specified. Thin plate regression splines were used to fit the smooth functions, where the 'performance iteration' method was used for smoothing parameter estimation. To avoid overfitting, given the limited number of data points (80 survey sites), the gamma parameter was set to a value of 1.4 for all models, which forced the model to be smoother than it might otherwise have been [84]. With the limited number of data points (80 sites across years) it was not possible to account for the nested nature of sites within countries by means of a hierarchical model structure; instead country was simply included as a factor variable. The models were fit in R [85] using the *mgcv* package.

Competing models, i.e. those with different covariates, were ranked by increasing Un-Biased Risk Estimator (UBRE) criterion [84]. The significance of explanatory variables (based on the P-values returned for each of the terms in the GAM), percent deviance explained by the model and model fit diagnostics (Normal Q-Q, residuals vs. linear predictor, histogram of residuals, response vs. fitted values) were also considered [84]. Model selection was based on the UBRE criterion [84].

Models where survey year was modelled by country served to examine country-specific changes over the period 2002–2011. There were indications of country specific changes over time (Fig. S4 shows how the decline in DRC is potentially more extreme than in Gabon, for example). However, given the sparseness of the time series for Cameroon and in particular CAR and the lack of data points for Congo and DRC at the beginning of the period (Fig. S3), we did not incorporate country specific changes over time in the final models used to predict dung density across the Central African forests. Instead we restricted our predictions to models with the same smooth function for temporal change across the Central African forests.

Given the similarity in UBRE scores for the top models, we estimated elephant dung density using each of them (Table S2). The bootstrapped 95% confidence intervals are also shown. The confidence limits are wide and the percent coefficients of variation were frequently larger than 100 (this was particularly the case for models including HII with the exception of models HII 3 and HII 5 in 2011). When models contained survey year (the proxy for temporal change), we estimated elephant dung density in both 2002 and in 2011, rather than just obtaining an average for the 2002–2011 period, which allowed us to calculate rates of decline and percent range loss from these models; estimates of the percentage of extremely low elephant density range overall and by country for 2002 and 2011 are also given (Table S3).

Variance and percentile confidence intervals of elephant abundance estimates were estimated using a combination of nonparametric and parametric bootstrapping [86]. A total of 999 bootstraps were conducted during which replicate survey sites, assumed to be independently and identically distributed, were resampled at random and with replacement until each bootstrap resample was the same size as the original number of 80 survey sites (nonparametric component). Dung abundance estimates were obtained from these resampled data conditioned on the original model fit. Dung abundance estimates were converted to elephant abundance by applying conversion factors (described below) with associated total variance obtained by incorporating the variance associated with the conversion factors. During each iteration of the bootstrap routine, conversion factor values were generated from a normal distribution with mean equal to the estimated value of the conversion factor and the variance equal to the squared value of the associated standard error (parametric component). Estimates of elephant numbers were ordered from smallest to largest and the 25th and 975th value was used to define the percentile confidence interval. The coefficient of variation was obtained by dividing the square root of the variance of the abundance estimates from the resampled data predictions by the mean of those abundance estimates.

We defined extremely low density areas where dung density fell between 0–100 dung piles/km^2 (in practice this approximates to >0.1 dung pile encountered per km walked) based on knowledge of areas within Central Africa which have extremely few or no elephants remaining (in part relying on design-based estimates of dung abundance). All of the areas where we already knew that there were extremely few or no elephants (from historical surveys, from some of these surveys included here, or from other surveys not included in this dataset), such as the majority of the southern Republic of Congo, and the majority of the forests in western Cameroon, fell into this density class, giving us confidence in the model's ability to predict elephant range where there are almost no elephants left.

Conversion factors. Dung density estimates were converted to elephant numbers using estimated production and decay rates since actual rates are notoriously difficult to collect ([87]) and were not available at every site. A production rate of 19.77 dung piles/day (standard error (SE) = 0.23) [88], also suggested by the rainfall regime of much of the area [89], was used. The same rate was also used to assess historical forest elephant loss up to 1989 [41], ensuring comparative differences were not a function of this model assumption. To ensure that the decay rate used in the conversion was representative of our sites that ranged widely in space and time, we used the mean (81.82 days, SE = 6.68 days) of fourteen estimates of dung disappearance time for different seasons, habitats and sites. No particular geographical pattern for decay rate from west to east across the basin was evident in these studies, and the associated variance was low enough to make us more confident in our application of this as a standard conversion factor, whilst recognising that there is variation within decay rates associated with season, sunspots, and rainfall [90,91,92]. To convert dung to elephant density, only dung piles not in a late stage of decomposition ("class E" of [93] are generally included. For this dataset dung density was reduced by 32.1% (SE = 3.7%), the mean percent of dung piles classified as "E", before estimating elephant density.

Explanatory variables. Explanatory variables used in the GAM analysis were (Table S4) [94]: (i) *site-level* at the scale of individual sampling units, (ii) *country-level* (including country itself), and (iii) *regional proxies* latitude and longitude to capture possible geographical gradients in density not captured by other variables. Variables were either recorded at each survey site (hunter-sign frequency, survey year, presence/absence of guards), retrieved from reports (official protection reflecting the degree of potential protection) and online databases (Transparency International's Corruption Perceptions Index [45], or from GIS data layers (distance-based for poacher access, i.e., proximity to major roads; pressure-based for poacher numbers, i.e., human population density [95], the Human Influence Index [44]. Square root transformations for hunter-sign frequency and human population density were considered due to possible undue leverage from the few high values. The predicted likely influence on elephant density for each of the explanatory variable is given (Table S4). Assumptions implicit in the choice of these variables were based on previous work [16,17,33,54,55]. We assumed that both direct hunting pressure (as measured by encounter rate of hunter sign) and measures of human population density and activity (as measured by distance to the nearest road, human population density, and the human influence index) results in elephants moving away from human-dominated areas and/or being killed by poachers. We assumed that official protection of a site (such as National Park status) would reflect real protection, in other words that elephants would be more likely to be at higher densities in such sites. We assumed that if guards were present at a site, that they were actually effective in deterring poaching. We assumed that our measure of governance (CPI) reflected the suite of social, economic, and development factors associated with each country; governance and development had previously been shown to be associated with elephant poaching by the two MIKE analyses in 2009 and 2012 [16,33].

Pearson's product-moment correlation tests (two-sided) with null hypothesis that true correlation is equal to zero were conducted for each pair-wise combination of explanatory variables considered. Variables were considered significantly correlated at the 5% level. Correlations between variables were taken into account to avoid the inclusion of highly correlated variables in the same model. Model prediction was limited to Central African forested regions, including swamp forest [96], in the five countries with survey sites. GIS grids were created at a resolution of approximately 1x1 km^2, and prediction was carried out at the same resolution.

Reporting results. Generally, averaged estimates from the set of top-ranking predictive models were given. Potential elephant range was defined by forest cover. Elephant range and high density elephant areas were estimated as the aggregate of areas with >100 and >1,000 elephant dung piles/km^2, respectively.

Supporting Information

Figure S1 Estimated conditional dependence of elephant dung density for top-ranking multi-variable models without hunter-sign used for prediction across the Central African forests, using the variables available across Central Africa either as GIS layers or in country-specific databases. Plots shown are for models with variables (A) survey year^, Human Influence Index***, and corruption***, and (B) survey year^, proximity to roads^, human population density***, and corruption***. Presence/absence of wildlife guards was also included as a factor covariate in both models and dung density was significantly more - P<0.001 - at sites where guards were present. P-value significance codes are: '***'<0.001 and '^'<0.1. Plot components are: Estimates on the scale of the linear predictor (solid lines) with the y-axis scale for each variable selected to optimally display the results, confidence intervals (dashed lines), and explanatory variable values of observations with a focus on the core 95% of the data for proximity to road and human population density (rug plot - short vertical bars along each x-axis).
(PDF)

Figure S2 Estimated conditional dependence of elephant dung density for single variable models. Results are shown for (A) hunter sign***, (B) survey year**, (C) proximity to roads*, (D) human population density***, (E) Human Influence Index***, (F) official protection*** (higher values = less protected), (presence/absence of wildlife guards is a factor covariate and thus not shown here, however, dung density was significantly higher - P<0.001 - at sites where guards were present), (G) corruption*** (higher values = less corrupt), (H) latitude*, and (I) longitude***. P-value significance codes are: '***' <0.001, '**' <0.01, and '*' <0.05. Plot components are: Estimates on the scale of the linear predictor (solid lines) with the y-axis scale for each variable selected to optimally display the results, confidence intervals (dashed lines), explanatory variable values of observations with a focus on the core 95% of values for a, c and d (rug plot - short vertical bars along each x-axis).
(PDF)

Figure S3 The number of survey sites per country by survey year. Results are shown for the 80 survey sites in Central Africa.
(PDF)

Figure S4 Estimated conditional dependence of elephant dung density considering survey year by country for a multi-variable models including hunter sign. Survey year by country focusing on the Democratic Republic of Congo (DRC) and Gabon for the model with variables hunter sign*, survey year by country*, proximity to roads, human population density***, corruption*** and presence/absence of guards*** (dung density was significantly more - P<0.001 - at sites where guards were present). P-value significance codes are: '***'<0.001, '**'<0.01, '*'<0.05, and '^'<0.1. Plot components are: Estimates on the scale of the linear predictor (solid lines) with the y-axis scale for each variable selected to optimally display the results, confidence intervals (dashed lines), and explanatory variable values of observations (rug plot - short vertical bars along each x-axis).
(PDF)

Table S1 Details of the 80 survey sites included in the analysis.
(PDF)

Table S2 Analysis results for top-ranking predictive models (excluding hunter sign as an explanatory variable), which included (a) the Human Influence Index (HII), or (b) human population density and proximity to road (SPD). Details of the variables included in each model are given and percent deviance explained and UBRE score value. Estimated average elephant dung density (/km^2) from model predictions across the Central African forests and bootstrapped 95% confidence intervals are shown. If the model included the survey year variable then prediction is for the endpoints of the time series (2002 and 2011); otherwise the prediction can be interpreted as an average over the 2002–2011 time period. Also shown for the models that permit temporal prediction is the overall percent decline and overall percent range loss for the period 2002–2011

(elephants are assumed to be absent when dung density falls below 100 elephant dung piles/km^2; see Table S3 and Figure 2 for details, including a breakdown by country).
(PDF)

Table S3 Estimates of percentage extremely low density elephant range across the Central African forests and by country (relative to each country's forested area) for 2002 and 2011 for the top-ranking predictive models, which included the survey year variable. Elephants are assumed to be almost absent when dung density falls below a threshold value of 100 elephant dung piles/km^2. Also shown are estimates of the percentage of potential habitat at high elephant density (defined as $>$1,000 elephant dung piles/km^2). The average across all models for 2002 and for 2011 is shown, as well as the range Table S6 for a breakdown of forest cover by country.
(PDF)

Table S4 Description of spatial variables, data source, method of calculation, likely influence on elephant density, UBRE score and deviance explained for the single variable models.
(PDF)

Table S5 Analysis results for top-ranking models which included the hunter sign variable. Hunter sign was not included in the predictive model across the Central African forests, as it was unavailable at that scale.
(PDF)

Table S6 Estimated forest cover by country as defined by Iremonger et al. (1997) [96].
(PDF)

Acknowledgments

The research authorities and wildlife departments from the Republic of Congo, Republic of Cameroon, Gabon, the Democratic Republic of Congo, and the Central African Republic are thanked for permissions and collaboration. The Central Africa roads dataset came from Global Forest Watch supplemented with local knowledge for some recently built road segments. For support of the survey work we thank (in alphabetical order) Nancy Abraham, the African Wildlife Foundation, Beneficia Foundation, Busch Gardens, CITES-MIKE, Columbus Zoo, Conservation International, Daniel K. Thorne Foundation, Diane Fossey Gorilla Foundation International, Espèces Phares (European Union), Ecosystèmes Forestiers d'Afrique Centrale (ECOFAC), Fauna and Flora International, Frankfurt Zoological Society, IUCN Netherlands, John D. and Catherine T. MacArthur Foundation, KFW, LifeWeb (Spain), National Fund for Scientific Research (FNRS, Belgium), Offield Family Foundation, Operation Loango, Prince Bernhard Wildlife Fund, RAPAC, The Arcus Foundation, The Aspinall Foundation, The Born Free Foundation, The Institute for Biodiversity and Ecosystem Dynamics at The University of Amsterdam, The Jane Goodall Institute, The Liz Claiborne and Art Ortenberg Foundation, The Lucie Burgers Foundation, The Wasmoeth Wildlife Foundation and Karl Ammann, Total Gabon, United States Agency for International Development (USAID CARPE), USFWS Great Ape Conservation Fund, USFWS African Elephant Conservation Fund, Wildlife Conservation Society, World Wildlife Fund and the Zoological Society of London. We thank the following who made extremely useful suggestions for improvements to the MS: David Wilkie, Josh Ginsberg, James Deutsch and Anthony Rylands, and three anonymous referees.

This paper is dedicated to the wildlife guards who have lost their lives across the African continent whilst defending the elephants and other wildlife in their countries, to our co-authors Lambert Bene Bene, Ymke Warren and Max Kokangoye, whose contributions to wildlife conservation live on after them, and to those brave individuals who continue to protect elephants.

Author Contributions

Commented on the MS and organised fieldwork: AB AE AP AS AT AV BBds BF B-II BJM BM BSM TCH CI-N CM CN DK EA EAW EG ES FA FG FI FK FM FN GA G-AM GM GW HR HV IL JH JM LP MA MB MK NB OI OM PB PCB PM PN QM RA RLB REB RDA RM SB SL SN SS VAM YM. Conceived and designed the experiments: AP AS AV BJM TCH DK ES FA FG FI FM G-AM HR HV JH RA SB SL SN SS YW. Performed the experiments: AB AE AM AP AS AV BBds B-II BJM BM BSM TCH CI-N CM CN DK EA EAW EG FA FG FI FK FM FN GA G-AM GM HV JH JM LB MA MB MK NB OI OM PB PCB PM PN QM RA REB RDA SB SL SN VAM YM YW. Analyzed the data: SS FM GW. Wrote the paper: AP AT AV B-II BJM TCH EAW EG ES FI FM GW HR HV JH NB PB RLB RM SB SL SN SS.

References

1. IUCN/SSC (2008) Strategic planning for species conservation- a handbook. The species conservation planning task force. Species Survival Commission, IUCN. Gland, Switzerland: IUCN Species Survival Commission. 104. Available: http://data.iucn.org/dbtw-wpd/edocs/2008-047.pdf. Accessed 2013 Feb 20.
2. IUCN (2012) IUCN Red List of threatened species. Version 2012.2. Cambridge, UK: IUCN. Available: http://www.iucnredlist.org/. Accessed 2013 Feb 20.
3. AfESG (2003) Statement on the taxonomy of extant *Loxodonta*, December 2003. IUCN. 2. Available: www.iucnredlist.org/documents/AfESGGeneticStatement.pdf. Accessed 2013 Feb 20.
4. Blanc J (2008) *Loxodonta africana*. IUCN Available: http://www.iucnredlist.org/documents/attach/12392.pdf. Accessed 2013 Feb 20.
5. Grubb P, Groves CP, Dudley JP, Shoshani J (2000) Living African elephants belong to two species: *Loxodonta africana* (Blumenbach, 1797) and *Loxodonta cyclotis* (Matschie, 1900). Elephant 2: 1–4.
6. CMS (2012) Appendices I and II of the Convention on the conservation of Appendix I migratory species of wild animals. Available: http://www.cms.int/documents/appendix/appendices_e.pdf. Accessed 2013 Feb 20.
7. Ishida Y, Georgiadis N, Hondo T, Roca A (2012) Triangulating the provenance of African elephants using mitochondrial DNA. Evolutionary Applications 6: 253–265.
8. Ishida Y, Demeke Y, de Groot PJvC, Georgiadis NJ, Leggett KEA, et al. (2011) Distinguishing forest and savanna African elephants using short nuclear DNA sequences. Journal of Heredity 102: 610–616.
9. Roca AL, Georgiadis N, O'Brien SJ (2007) Cyto-nuclear genomic dissociation and the African elephant species question. Quaternary International 169: 4–16.
10. Rohland N, Reich D, Mallick S, Meyer M, Green RE, et al. (2010) Genomic DNA sequences from mastodon and woolly mammoth reveal deep speciation of forest and savanna elephants. PLoS Biology 8: e1000564.
11. Ishida Y, Oleksyk TK, Georgiadis NJ, David VA, Zhao K, et al. (2011) Reconciling apparent conflicts between mitochondrial and nuclear phylogenies in African elephants. PLoS One 6: e20642.
12. Brandt AL, Ishida Y, Georgiadis NJ, Roca AL (2012) Forest elephant mitochondrial genomes reveal that elephantid diversification in Africa tracked climate transitions. Molecular Ecology 21: 1175–1189.
13. Roca AL, Georgiadis N, Pecon-Slattery J, O'Brien SJ (2001) Genetic evidence for two species of elephant in Africa. Science 293: 1473–1477.
14. Roca AL, O'Brien SJ (2005) Genomic inferences from Afrotheria and the evolution of elephants. Current Opinion in Genetics & Development 15: 652–659.
15. Roca AL, Georgiadis N, O'Brien SJ (2005) Cytonuclear genomic dissociation in African elephant species. Nature Genetics 37: 96–100.
16. CITES (2012) Convention on international trade in endangered species of wild fauna and flora- Elephant conservation, illegal killing and ivory trade in ivory. SC62 Doc 46.1 (Rev 1). 29. Available: http://www.cites.org/eng/com/sc/62/E62-46-01.pdf. Accessed 2013 Feb 20.
17. Blake S, Deem SL, Mossimbo E, Maisels F, Walsh P (2009) Forest elephants: tree planters of the Congo. Biotropica 41: 459–468.
18. Blake S (2002) The ecology of forest elephant distribution and its implications for conservation [PhD]. Edinburgh: University of Edinburgh. 319 Available: http://www.savetheelephants.org/files/pdf/publications/2002%20Blake%20The%20Ecology%20of%20Forest%20Elephant%20Distribution%20and%20its%20Implications%20for%20Conservation.pdf. Accessed 2013 Feb 20.
19. White LJT, Tutin CEG, Fernandez M (1993) Group composition and diet of forest elephants, *Loxodonta africana cyclotis* Matschie 1900, in the Lope Reserve, Gabon African Journal of Ecology 31: 181–199.
20. Short J (1981) Diet and feeding behaviour of the forest elephant. Mammalia 45: 177–185.

21. Lewis SL, Lopez-Gonzalez G, Sonke B, Affum-Baffoe K, Baker TR, et al. (2009) Increasing carbon storage in intact African tropical forests. Nature 457: 1003–1006.
22. Campos-Arceiz A, Blake S (2011) Megagardeners of the forest - the role of elephants in seed dispersal. Acta Oecologica 37: 542–553.
23. Turkalo A, Fay JM (1995) Studying elephants by direct observations: preliminary results from the Dzanga clearing, Central African Republic. Pachyderm 20: 45–54.
24. Klaus G, Klaus-Hugi C, Schmid B (1998) Geophagy by large mammals at natural licks in the rain forest of the Dzanga National Park, Central African Republic. Journal of Tropical Ecology 14: 829–839.
25. Turkalo A, Fay JM (2001) Forest elephant behaviour and ecology: observations from the Dzanga saline. In: Weber W, White L, Vedder A, Naughton L, editors. Conservation and ecology of the African rain forest. Ithaca: Yale University Press. 207–213.
26. Douglas-Hamilton I (1979) African elephant ivory trade study final report Final Report to US Fish and Wildlife Service. 138. Available: http://www.savetheelephants.org/files/pdf/publications/1979%20Douglas-Hamilton%20African%20Elephant%20Ivory%20Trade%20Study.pdf. Accessed 2013 Feb 20.
27. Douglas-Hamilton I (1987) African elephants: population trends and their causes. Oryx 21: 11–24.
28. Milner-Gulland EJ, Beddington JR (1993) The exploitation of elephants for the ivory trade-an historical perspective. Proceedings of the Royal Society of London - Series B: Biological Sciences 252: 29–37.
29. Cuvillier-Fleury H (1904) La mise en valeur du Congo francais. These de Doctorat [Doctorat.]. Paris Universite de Paris. 290 Available: http://ia600301.us.archive.org/6/items/lamiseenvaleurdu00cuviuoft/lamiseenvaleurdu00cuviuoft.pdf. Accessed 2013 Feb 20.
30. de Boer WF, van Langevelde F, Prins HHT, de Ruiter PC, Blanc J, et al. (2013) Understanding spatial differences in African elephant densities and occurrence, a continent-wide analysis. Biological Conservation 159: 468–476.
31. CITES (2010) African elephant action plan: document CoP15 Inf. 68. 24. Available: http://www.cites.org/common/cop/15/inf/E15i-68.pdf. Accessed 2013 Feb 20.
32. Wittemyer G, Daballen D, Douglas-Hamilton I (2011) Rising ivory prices threaten elephants. Nature 476: 282–283.
33. Burn RW, Underwood FM, Blanc J (2011) Global trends and factors associated with the illegal killing of elephants: A hierarchical Bayesian analysis of carcass encounter data. PLoS One 6: e24165.
34. Bouché P, Douglas-Hamilton I, Wittemyer G, Nianogo AJ, Doucet JL, et al. (2011) Will elephants soon disappear from west African savannahs? PLoS One 6: e20619.
35. Milliken T, Burn RW, Underwood FM, Sangalakula L (2012) The Elephant Trade Information System (ETIS) and the Illicit Trade in Ivory: A report to the 16th meeting of the Conference of the Parties to CITES (Cop 16) cites.org/eng/cop/16/doc/E-CoP16-53-02-02.pdf. TRAFFIC. 30.
36. CITES (2012) Interpretation and implementation of the Convention- Species trade and conservation: Elephants. Monitoring of illegal trade in ivory and other elephant specimens : report of the secretariat. CoP16 Doc. 53.2.1. 10. Available: http://www.cites.org/eng/cop/16/doc/E-CoP16-53-02-01.pdf. Accessed 2013 Feb 20.
37. Vigne L, Martin E (2011) Consumption of elephant and mammoth ivory increases in southern China. Pachyderm 49: 79–89.
38. Martin EB, Vigne L (2011) The ivory dynasty: A report on the soaring demand for elephant and mammoth ivory in southern China. Elephant Family, The Aspinall Foundation and Columbus Zoo and Aquarium Available: http://www.elephantfamily.org/uploads/copy/EF_Ivory_Report_2011_web.pdf. Accessed 2013 Feb 20.
39. CITES (2011) Convention on international trade in endangered species of wild fauna and flora- Status of elephant populations, levels of illegal killing and the trade in ivory: a report to the standing committee of CITES. SC61 Doc. 44.2 (Rev. 1) Annex 1. Available: http://www.cites.org/eng/com/sc/61/E61-44-02-A1.pdf. Accessed 2013 Feb 20.
40. Stiles D (2011) Elephant Meat Trade in Central Africa. Gland, Switzerland: IUCN. 104 Available: http://cmsdata.iucn.org/downloads/ssc_op_045.pdf. Accessed 2013 Feb 20.
41. Michelmore F, Beardsley K, Barnes R, Douglas-Hamilton I (1994) A model illustrating the changes in forest elephant numbers caused by poaching. African Journal of Ecology 32: 89–99.
42. Blake S, Strindberg S, Boudjan P, Makombo C, Bila-Isia I, et al. (2007) Forest elephant crisis in the Congo Basin. PLoS Biology 5: 945–953.
43. IUCN/SSC (2008) African Elephant *Loxodonta africana:* Further Details on Data Used for the Global Assessment. African Elephant Specialist Group. Available: http://www.iucnredlist.org/documents/attach/12392.pdf. Accessed 2013 Feb 20.
44. WCS/CIESIN (2005) Last of the wild data version 2: Global Human Influence Index (HII). Wildlife Conservation Society (WCS) and Center for International Earth Science Information Network (CIESIN). Available: http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-geographic. Accessed 2013 Feb 20.
45. Corruption_Perceptions_Index (2011) Corruption Perceptions Index 2011. Transparency International. Available: http://files.transparency.org/content/download/313/1264/file/CPI2011_DataPackage.zip. Accessed 2013 Feb 20.
46. Beyers R, Sinclair T, Hart J, Grossman F, Dino S, et al. (2011) Resource wars and conflict ivory. The impact of civil conflict on elephants in the Okapi Faunal Reserve: 1995–2006. PLoS One 6: e27129.
47. Blanc J, Barnes RFW, Craig GC, Dublin HT, Thouless CR, et al. (2007) African elephant status report 2007: an update from the African elephant database. Gland, Switzerland: IUCN/SSC African Elephant Specialist Group. pp vi +276 Available: http://www.african-elephant.org/aed/pdfs/aesr2007.pdf. Accessed 2013 Feb 20.
48. Bouche P, Mange RNM, Tankalet F, Zowoya F, Lejeune P, et al. (2012) Game over! Wildlife collapse in northern Central African Republic. Environmental Monitoring and Assessment 184: 7001–7011.
49. Omondi P, Bitok EK, Tchamba M, Mayienda R, Lambert BB (2008) The total aerial count of elephants and other wildlife species in Faro, Benoue and Bouba Ndjidda National Parks and adjacent hunting blocks in northern Cameroon National Parks and adjacent hunting blocks in northern Cameroon. Yaounde, Cameroon: WWF and Cameroon Ministry of Forestry and Wildlife. 75. Available: http://www.mintour.gov.cm/index.php/content/download/1858/19444/version/1/file/Rapport+de+Denombrement+des+Aires+Proteges.pdf. Accessed 2013 Feb 20.
50. Platt J (2012) Cameroon elephant massacre shows poaching, ivory trade require an international response. Available: http://blogs.scientificamerican.com/extinction-countdown/2012/03/20/cameroon-elephant-massacre-poaching-ivory-trade/. Accessed 2013 Feb 20.
51. WWF (2012) Cameroon sends army to defend borders from Sudanese poachers Available: http://wwf.panda.org/wwf_news/?206742/Cameroon-sends-army-to-defend-borders-from-Sudanese-poachers.Accessed 2013 Feb 20.
52. ANPN (2013) Wildlife and poaching assessment in northeast Gabon-preliminary results. ANPN, WCS, WWF. 23. Available: http://awsassets.panda.org/downloads/preliminary_results_of_minkebe_pilot_study.pdf. Accessed 2013 Feb 20.
53. Lemieux AM, Clarke RV (2009) The international ban on ivory sales and its effects on elephant poaching in Africa. British Journal of Criminology 49: 451–471.
54. Blake S, Deem SL, Strindberg S, Maisels F, Momont L, et al. (2008) Roadless wilderness area determines forest elephant movements in the Congo Basin. PLoS One 3: e3546.
55. Yackulic CB, Strindberg S, Maisels F, Blake S (2011) The spatial structure of hunter access determines the local abundance of forest elephants (*Loxodonta africana cyclotis*). Ecological Applications 21: 1296–1307.
56. Potapov PV, Turubanova SA, Hansen MC, Adusei B, Broich M, et al. (2012) Quantifying forest cover loss in Democratic Republic of the Congo, 2000–2010, with Landsat ETM+data. Remote Sensing of Environment 122: 106–116.
57. Hansen MC, Stehman SV, Potapov P (2011) Quantification of global gross forest cover loss. Proceedings of the National Academy of Sciences of the United States of America 107: 8650–8655.
58. Fitzherbert EB, Struebig MJ, Morel A, Danielsen F, Bruhl CA, et al. (2008) How will oil palm expansion affect biodiversity? Trends in Ecology & Evolution 23: 538–545.
59. Senelwa K, Etiégni L, Osano O, Balozi K, Imo M (2012) Environmental Impacts of biofuel production in Africa. In: Janssen R, Rutz D, editors. Bioenergy for Sustainable Development in Africa: Springer Netherlands. 237–245.
60. Smith RJ, Muir RDJ, Walpole MJ, Balmford A, Leader-Williams N (2003) Governance and loss of biodiversity. Nature 426: 67–70.
61. Barrett CB, Gibson CC, Hoffman B, McCubbins MD (2006) The complex links between governance and biodiversity. Conservation Biology 20: 1358–1366.
62. UNODC (2012) Corruption, environment and the United Nations Convention against corruption. United Nations Office on Drugs and Crime. 94. Available: http://www.unodc.org/documents/eastasiaandpacific/indonesia/publication/Corruption_Environment_and_the_UNCAC.pdf. Accessed 2013 Feb 20.
63. INTERPOL (2012) Environmental crime Interpol. Available: http://www.interpol.int/Crime-areas/Environmental-crime/Environmental-crime. Accessed 2013 Feb 20.
64. United States Senate Committee on Foreign Relations (2012) Ivory and insecurity: the global implications of poaching in Africa. U.S. Senate Committee on foreign relations hearing, May 24, 2012. Washington DC, USA: U.S. Senate Committee on Foreign Relations. Available: http://www.foreign.senate.gov/hearings/ivory-and-insecurity_the-global-implications-of-poaching-in-africa. Accessed 2013 Feb 20.
65. INTERPOL (2012) INTERPOL group of experts on corruption. Interpol. Available: http://www.interpol.int/Crime-areas/Corruption/INTERPOL-Group-of-Experts-on-Corruption. Accessed 2013 Feb 20.
66. IUCN (2011) Guidelines for using the IUCN Red List categories and criteria - verson 9.0. Cambridge, U. K: Prepared by the Standards and Petitions Subcommittee in September 2011. Available: http://intranet.iucn.org/webfiles/doc/SSC/RedList/RedListGuidelines.pdf. Accessed 2013 Feb 20.
67. Stokes EJ, Strindberg S, Bakabana PC, Elkan PW, Iyenguet FC, et al. (2010) Monitoring great ape and elephant abundance at large spatial scales: measuring effectiveness of a conservation landscape. PLoS One 5: e10294.
68. Clark CJ, Poulsen JR, Malonga R, Elkan PW (2009) Logging concessions can extend the conservation estate for central African tropical forests. Conservation Biology 23: 1281–1293.

69. Blom A (2004) An estimate of the costs of an effective system of protected areas in the Niger Delta - Congo Basin forest region. Biodiversity and Conservation 13: 2661–2678.
70. CITES-China (2012) Convention on international trade in endangered species of wild fauna and flora- Control of trade in ivory in China. SC62 Inf. 8. 3. Available: http://www.cites.org/eng/com/sc/62/inf/E62i-08.pdf. Accessed 2013 Feb 20.
71. Xinhua (2012) Police uncover 700 illegal wildlife trade cases Available: http://www.chinadaily.com.cn/china/2012-04/28/content_15172209.htm.Accessed 2013 Feb 20.
72. U.S.Embassy (2012) Regional wildlife workshop Chair summary April 2012: Central African sub-regional workshop on wildlife trafficking and dismantling transnational illicit networks. Libreville, Gabon. Available: http://libreville.usembassy.gov/latest_embassy_news3/wildlife-workshop-chair-summary-april-2012.html. Accessed 2013 Feb 20.
73. IUCN (2012) WCC-2012-RES-025-EN; Conservation of African elephants. 2. Available: http://portals.iucn.org/docs/iucnpolicy/2012-resolutions%5Cen/WCC-2012-Res-025-EN%20Conservation%20of%20African%20elephants.pdf. Accessed 2013 Feb 20.
74. IUCN (2012) WCC-2012-Res-024-EN: Enhancing anti-poaching and wildlife resource protection efforts, using rhino and elephant as indicators. 2. Available: http://portals.iucn.org/docs/iucnpolicy/2012-resolutions%5Cen/WCC-2012-Res-024-EN%20Enhancing%20anti-poaching%20and%20wildlife%20resource%20protection%20efforts,%20using%20rhino%20and%20elephant%20as%20indicators.pdf. Accessed 2013 Feb 20.
75. IUCN (2012) WCC-2012-Res-133-EN: Improving capacity for enforcement of legislation relating to wildlife crime. 2. Available: http://portals.iucn.org/docs/iucnpolicy/2012-resolutions%5Cen/WCC-2012-Res-133-EN%20Improving%20capacity%20for%20enforcement%20of%20legislation%20relating%20to%20wildlife%20crime.pdf. Accessed 2013 Feb 20.
76. Department US (2012) Clinton at partnership meeting on combating wildlife trafficking. Available: http://iipdigital.usembassy.gov/st/english/texttrans/2012/11/20121108138454.html#ixzz2CJcgMSv5. Accessed 2013 Feb 20.
77. Department US (2012) U.S. efforts to combat wildlife trafficking and promote conservation. Available: http://www.state.gov/r/pa/prs/ps/2012/11/200354.htm. Accessed 2013 Feb 20.
78. Government U (2012) Wildlife crime - environmental audit committee: 2 International wildlife crime London: UK Government. Available: http://www.publications.parliament.uk/pa/cm201213/cmselect/cmenvaud/140/14005.htm#a5. Accessed 2013 Feb 20.
79. House of Commons Environmental Audit Committee (2012) Wildlife crime: third report of session 2012–13. Volume II. Additional written evidence London: UK Government. 94. Available: http://www.publications.parliament.uk/pa/cm201213/cmselect/cmenvaud/140/140vw.pdf. Accessed 2013 Feb 20.
80. MIKE (2005) Monitoring the illegal killing of elephants- Central African forests: Final report on population surveys (2003–2004). Washington DC, USA: MIKE-CITES- WCS. 122. Available: http://www.cites.org/common/prog/mike/survey/central_africa_survey03-04.pdf. Accessed 2013 Feb 20.
81. Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers D, et al. (2001) Distance sampling: estimating abundance of biological populations. Oxford: Oxford University Press. 432 p.
82. Hall JS, White LJT, Inogwabini B-I, Omari I, Simons Morland H, et al. (1998) Survey of Grauer's gorillas (*Gorilla gorilla graueri*) and Eastern chimpanzees (*Pan troglodytes schweinfurthi*) in the Kahuzi-Biega National Park lowland sector and the adjacent forest in eastern Democratic Republic of Congo. International Journal of Primatology 19: 207–235.
83. Thomas L, Buckland ST, Rexstad EA, Laake JL, Strindberg S, et al. (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47: 5–14.
84. Wood SN (2006) Generalized additive models: an introduction with R. Boca Raton, USA: Chapman & Hall/CRC Press. 391 p.
85. R Development Core Team (2011) R: A language and environment for statistical computing. 2.13.1 Vienna, Austria: R Foundation for Statistical Computing.
86. Buckland ST (1984) Monte-Carlo confidence intervals. Biometrics 40: 811–817.
87. Laing SE, Buckland ST, Burn RW, Lambie D, Amphlett A (2003) Dung and nest surveys: estimating decay rates. Journal of Applied Ecology 40: 1102–1111.
88. Tchamba M (1992) Defaecation by the African forest elephant *Loxodonta africana cyclotis* in the Santchou Reserve, Cameroon. Mammalia 56: 155–158.
89. Theuerkauf J, Gula R (2010) Towards standardisation of population estimates: defecation rates of elephants should be assessed using a rainfall model. Annales Zoologici Fennici 47: 398–402.
90. Breuer T, Hockemba MN (2007) Forest elephant dung decay in Ndoki Forest, northern Congo. Pachyderm 43: 43–51.
91. Barnes RFW, Asamoah-Boateng A, Naada Majam J, Agyei- Ohemeng J (1997) Rainfall and the population dynamics of elephant dung-piles in the forests of southern Ghana. African Journal of Ecology 35: 39–52.
92. Barnes RFW, Dunn A (2002) Estimating forest elephant density in Sapo National Park (Liberia) with a rainfall model. African Journal of Ecology 40: 159–163.
93. Barnes R, Jensen K (1987) How to count elephants in forests. Technical Bulletin of African Elephant and Rhino Specialist Group 1: 1–6.
94. Burnham KP, Anderson DR (2002) Model selection and inference: a practical information-theoretic approach. New York: Springer. 353 p.
95. CIESIN/CIAT (2005) Gridded population of the world, version 3 (GPWv3). Center for International Earth Science Information Network (CIESIN), Columbia University; and Centro Internacional de Agricultura Tropical (CIAT). Palisades, NY: Socioeconomic Data and Applications Center (SEDAC), Columbia University. Available: http://sedac.ciesin.columbia.edu/gpw. Accessed 2013 Feb 20.
96. Iremonger S, Ravilious C, Quinton T (1997) A statistical analysis of global forest conservation. Including: GIS files of forests and protected areas, version 2. CD-ROM In: Iremonger S, Ravilious C, Quinton T, editors. A global overview of forest conservation. 2 ed. Cambridge, U.K: CIFOR and WCMC.

III APPENDIX III: QUESTIONNAIRE TO THE LOCAL COMMUNITY

Questionnaire pour une étude socio-économique des communautés locales autour des zones communautaires de conservation dans le Sud du Landscape du Lac Tumba, Ouest de la RDC

Adeline Serckx

Assistée sur le terrain par Fido

Réalisé entre avril et juillet 2012

Ce questionnaire a été élaboré sur base d'un questionnaire fourni par Inaoyom Sunday Imong, du département de Primatologie de l'Institut Max Planck à Leipzig (Allemagne). Il a ensuite été modifié avec l'aide de Remy-Bernard Beya, responsable socio-économique de la base WWF à Malebo, et Menard Mbende, chef de station de la base WWF à Malebo, de manière à adapter les questions aux problématiques de la région. Certaines questions du questionnaire réalisé en 2010 par Fanny Huth, pour son mémoire de Master en gestion des ressources végétales et animales en milieu tropicaux, ont également été reprises afin d'observer si des évolutions ont eu lieu dans la région au cours des 2 dernières années.

Dans ce questionnaire, le terme « ***ménage*** » fait référence à l'ensemble des personnes qui partagent une même cuisine au sein de la parcelle. Un ménage peut donc être constitué de plusieurs foyers et plusieurs maisons ayant chacune un chef de maison. Seul le chef du ménage est propriétaire de la parcelle. Les maisons sont occupées sans redevance financière, le système de location n'existe donc pas dans la zone.

A. Mituna pona mokolo ndako - *Questionnaire posé à l'homme chef de maison*

1. Mituna pona mboka - *Informations sur la communauté locale*

Les questions de ce chapitre ne sont posées qu'une seule fois par village

1. Nkombo ya lisanga ya mikomboso ya pene *Nom du groupe de bonobos le plus proche*	
2. Nkombo ya mboka *Nom de la communauté locale*	
3. *Coordonnés géographique du centre du village*	
4. *Nombre d'habitants du village*	
5. *Nombre de ménages dans le village*	
6. *Nombre de maisons dans le village*	
7. Classe ezali boni (ya bana na ya mikolo) *Nombre d'écoles primaires/secondaires dans le village*	Prim…………….. Sec...............
8. Mulayi boni ya mboka ? *Distance du village avec l'école primaire/ secondaire la plus proche*	Prim……………..km ………...……hrs Sec………..………km ………..………hrs
9. Mulayi boni ya mboka ezali pene na wenze ? *Distance du village avec le plus proche marché où sont vendus des produits forestiers et agricoles*	……………km ……..………hrs
10. Wenze nini ezalaka na mboka *Type de marché dans le village*	Monene mwa monene moke *grand moyen petit*
11. Nkombo ya mboka pe ya wenze ya monene ya pene *Nom du village où le grand marché le plus proche est localisé*	
12. Mulayi ya mboka na zamba ya mikomboso *Distance du village à la lisière la plus proche de la forêt protégée pour les bonobos*	………..km ………hrs
13. Mulayi ya mboka na zamba misusu *Distance du village à la lisière la plus proche des autres forêts*	………..km ………hrs

14. Lolenge ya kokoma na mboka *Type d'accès routier au village* *(Choisir une proposition)*	1. Nzela mituka elekelaka mikolo nionso *Route utilisable par les véhicules en toute saison* 2. Nzela moto elekelaka mikolo nionso *Route utilisable par les motos en toute saison* 3. Nzela moto elekelaka te mikolo nionso *Chemin non utilisable par les motos en toute saison*

2. Mituna pona libota ya kuku moko - *Informations sur le ménage*

15. *Code de la maison/Position dans le village*	
16. Motuya ya bato bafandi na libota *Nombre de personnes habitant dans le ménage*	
17. Mokolo libota mobali to mwasi *Sexe du chef de ménage*	
18. Mbula ya mokolo libota *Age du chef de ménage*	
19. Nkombo ya ekolo *Nom de la tribu à qui appartient le ménage*	
20. Classe mokolo libota asukeli *Niveau le plus haut d'éducation du chef de ménage* *	
Codes: 0=pas d'éducation formelle, 1=école primaire débuté mais non terminée, 2= école primaire terminée, 3 école secondaire débutée mais non terminée, 4= école secondaire terminée, 5=niveau supplémentaire débuté mais non terminé, 6= niveau supplémentaire terminé	
21. Mosala ya mokolo libota *Occupation principale du chef de ménage*	*(Ecrire 1 pour l'occupation la plus importante, 2 pour la seconde, etc.)*
- Bokila *(Chasse)*	
- Koloba *(Pêche)*	
- Bilanga *(Exploitation agricole)*	
- Kobimisa biloko na zamba *(Récolte de produits forestiers pour usage personnel)*	
- Koteka biloko ya zamba *(Commerce de produits forestiers)*	
- Mosala na WWF/SEBO *(Emploi WWF/SEBO)*	
- Mosala mosusu *(Emploi hors de la forêt (à préciser))*	
22. Misala efutaka tango nionso mpe malamu ? *Ces activités donnent-elles lieu à des revenus réguliers ou ponctuels ?*	

23. Mokolo libota mpe moto mosusu na kati ya libota asalaka na WWF/SEBO mpe esika mosusu ? Bato boni ? *Est-ce que le chef de ménage ou un autre membre est employé par le WWF/SEBO/autre? Combien ?*	Oui/Non

3. Mituna pona libota ya ndako moko - *Informations sur le foyer*

3.1. Mokolo ndako - Chef de maison

24. Motuya ya bato bavandi na libota *Nombre de personnes habitant le foyer*	
25. Mokolo ndako mobali to mwasi *Sexe du chef de maison*	
26. Mbula ya mokolo ndako *Age du chef de la maison*	
27. Classe mokolo libota asukeli *Niveau le plus haut d'éducation du chef de ménage* *	
28. Mosala ya mokolo ndako *Occupation principale du chef de ménage*	*(Ecrire 1 pour l'occupation la plus importante, 2 pour la seconde, etc.)*
- Bokila (*Chasse)*	
- Koloba *(Pêche)*	
- Bilanga *(Exploitation agricole)*	
- Kobimisa biloko na zamba *(Récolte de produits forestiers pour usage personnel)*	
- Koteka biloko ya zamba *(Commerce de produits forestiers)*	
- Mosala na WWF/SEBO *(Emploi WWF/SEBO)*	
- Mosala mosusu *(Emploi hors de la forêt (à préciser))*	
29. Misala efutaka tango nionso mpe malamu ? *Ces activités donnent-elles lieu à des revenus réguliers ou ponctuels ?*	

**Codes: 0=pas d'éducation formelle, 1=école primaire débuté mais non terminée, 2= école primaire terminée, 3 école secondaire débutée mais non terminée, 4= école secondaire terminée, 5=niveau supplémentaire débuté mais non terminé, 6= niveau supplémentaire terminé*

3.2. Bozwi mabele - Possession de terre

30. Monene nionso ya mabele bazali na yango o libota (hectare)

Quantité totale de terres possédées (ha), incluant des terres louées (qui sont louées pour leur utilisation ou qu'on loue à quelqu'un)

Catégories	Monene *Superficie* (# de terrain de football)	Monene *Superficie* (ha)	Mokolo esika *Propriétaire* *(privé, partagé avec un autre membre de la famille ou locataire)*	Milona misato elonami na mbula eleki *3 produits principaux plantés ou récoltés dans les 12 derniers mois*		
				Mulona ya liboso *Produit 1*	Mulona ya mibale *Produit 2*	Mulona ya misato *Produit 3*
i. Zamba (*Forêt)*						
ii. Ferme *(Ferme)*						
iii. Bivu *(Jachère)*						
iv. Esobe *(Savane)*						
Total des terres possédées (i+ii+iii)						

31. Tina boponaki mabele ya kosala bilanga ?

Pourquoi avez-vous choisi les emplacements précédemment cités pour faire vos champs ?

3.3. Biloko ya mokolo ndako - *Biens du chef de maison*

32. Mokolo libota azala na ndako? *Est-ce que le chef de maison possède une maison? **	
33. Ndako etongami na nini ? *Quel matériel constitue la majorité des murs ?* *	
34. Biloko nini eleki ebele na motondo ya ndako? *Quel matériel constitue la majorité du toit ?**	
35. Monene ya ndako *Quelle est la superficie de la maison (m^2)?*	*Longueur………(m)* *largeur……..(m)*

** Codes:*

Chef de maison: 0 = le chef de maison n'est pas le propriétaire; 1 = le chef de maison est l'unique propriétaire des lieux; 2 = la maison est une copropriété; 9 = autres (à préciser)

Ndako *(Murs): 1* = potopoto/mabele *(boue/terre);* 2 = nzete *(bois);* 3 = manzanza *(taule);* 4 = briques *(briques, béton);* 5 = bambu *(végétaux/bambou);* 9 = biloko mosusu *(autres (à préciser))*

Motondo ya ndako *(Toit):* 1 = Matiti *(chaume);* 2 = nzete *(planche de bois);* 3 = manzanza *(taule);* 4 = ndele *(pailles) ;* 9 = biloko mosusu *(autres (à préciser))*

36. Bisalili ya bilanga mpe miloko mosusu ya motuya na libota

Outillage agricole et gros matériel possédés par le ménage et le foyer

Item	Motuya na libota *Nombre d'unité dans le ménage*	Motuya na ndako *Nombre d'unité dans le foyer*
Tukutuku *(Moto)*		
Kinga *(Vélo)*		
Alloallo *(Téléphone)*		
Television *(TV)*		
Radio (*Radio)*		
Dividi *(Magnétoscope/ lecteur DVD)*		
Mbabula (*Foyer amélioré)*		
Munduki *(Armes à feux)*		
Mpusu (*Brouette)*		
Groupe (*Générateur électrique)*		
Batterie *(Batterie)*		
Panneau solaire *(Panneau solaire)*		
Mbeto ya mabaya *(Vrai lit en bois)*		
Kiti ya mabaya *(Chaises en bois)*		
Kiti ya kopale (*Chaises en plastique)*		
Biloko mosusu *(Autres (préciser))*		

4. **Kosalela biloko ya zamba-** ***Utilisation des ressources forestières***

37. Na libota na bino boloni banzete na mbula mitano eleki ? *Est-ce que votre ménage a planté des arbres durant les 5 dernières années ?*		
38. Soki mbongo: tina ezalaki nini? *Si oui : quel était l'objectif principal de cette plantation?* *Indiquer les 3 raisons les plus importantes*	Biyano *Raisons*	Rang 1-3
	Koni ya kolambela *(Bois de chauffe pour usage domestique)*	
	Koni ya koteka *(Bois de chauffe à vendre)*	
	Grume mpe nzete ya kosalela na ndako (*Grume/Piquet pour usage domestique)*	
	Grume mpe nzete ya koteka *(Grume/piquet à vendre)*	
	Mbuma ya kolia *(Fruits pour usage domestique)*	
	Mbuma ya koteka *(Fruits à vendre)*	
	Tina mosusu pona libota *(Autres usages domestiques)*	
	Tina mosusu pona koteka *(Autres produits à vendre)*	
	Ndelo ya mabele *(Délimitation des terres)*	
	Pona kokolisa motuya ya mabele	

	Pour augmenter la valeur de ma terre	
	Pona kotikela bana mpe bakoko bamona yango *Pour permettre à mes enfants/petits-enfants de voir ses arbres*	
	Biloko misusu *(Autres, précisez)*	

39. Soki solo : olonaki yango wapi ? *Si oui : où avez-vous planté ces arbres ? (forêt, savane, village, etc.)*	
40. Na libota bolokotaka biloko na zamba ? *Est-ce que le ménage collecte des produits forestiers non ligneux, ex. fruits ?*	Oui/Non
41. Soki solo : ezalaka mikolo boni na poso moko ? *Si oui : combien de jours par semaine les membres du ménage utilisent à cette collecte ?*	*………jours*
42. Mikolo boni na bana boni balokotaka yango ? *Combien d'adultes et d'enfants collectent ses produits?*	*Ad..... enf.....*
43. Na zamba nini bokendaka kolokota yango ? *A quels endroits de la forêt allez-vous pour récolter ces produits ? Citez les noms des forêts*	
44. Na libota na bino bozali kolokota biloko mingi to moke na zamba ? *Est-ce que votre ménage passe aujourd'hui plus ou moins de temps à collecter ses produits ?* *Codes: 1=plus; 2=environ le même temps; 3=moins*	
45. Est-ce que biloko na zamba ekiti na mbula mitano oyo ewuti koleka ? *Est-ce que la disponibilité en produits forestiers non-ligneux a changé au cours de ces 5 dernières années ?* *Codes: 1=diminution; 2=environ la même chose; 3=augmentation*	
46. Pona nini ? *Pourquoi ?*	

47. Soki eketi ndege nini libota bazali kopesa eyano pona kosila ya biloko wana ? *Si diminution, comment le ménage a-t-il répondu au déclin de disponibilité de ces produits ?* *(Indiquer les réponses par ordre croissant d'importance)*	*Biyano Réponses*	Rang 1-3
	Komatisa ngonga na zamba *Augmentation du temps de récolte en forêt (ex : en allant plus loin de la maison)*	
	Kosomba biloko ya zamba *Achat (de plus) de produits forestiers*	
	Kokitisa bosaleli zamba *Restreindre l'accès/ l'utilisation de la forêt*	
	Kobatela nzete pona mbula ekoya *Conservation des arbres sur pied pour le futur*	
	Kolona banzete *Plantation de ces produits*	
	Biloko misusu *Autres (préciser)*	

5. Bokati zamba - *Défrichage de la forêt*

48. Est-ce que libota bakati zamba na mbula eleki ? *Est-ce que le ménage a défriché la forêt pendant ces 12 derniers mois ?*	Oui/Non

49. Soki solo : *Si oui:*	Bakati bonene boni ya elanga ? *Quelle quantité de forêt fut défrichée ?*	Motuya boni ya bilanga Monene boni *# champs= ha=*		
	Ntina ya kokata ezali nini ? *Quel était le but du défrichage ?* Codes: 1=bilanga *(culture)*; 2=kolona nzete *(plantation d'arbre)*; 3=	Rang1	Rang2	Rang3

	kobokola bibwele *(pâturage)*; 4=Pona misala mosusu oyo ezali ya bilanga te *(usage non agricole)*			
	Soki tina ezali ya bilanga, miluna nini ya motuya oyo ebemi ? *Si le but était la culture, quelles principales cultures ont poussé ?*	Rang1	Rang2	Rang3
	Zamba ya ndenge nini okataki ? (bivu, zamba mosusu) *Quel type de forêt avez-vous défriché ?* *(jachères/galeries forestières/intérieur de la forêt…)*			
	Esika nini (nkombo ya zamba) otaki na ba mbula eleki ? *Où avez-vous défriché pendant ces dernières années ?*			
	Mulayi boni na mboka ? *A quelle distance du village est située cette forêt défrichée ?*	*…km (ou …hrs)*		
50. Est-ce que libota bakati zamba na mbula mitanu eleki ? *Est-ce que le ménage a défriché la forêt pendant ces 5 dernières années ?*		Oui/non		
51. Soki solo : monene boni ekatamaki ? *Si oui : quelle quantité a approximativement été défrichée ?* *Note: Ceci inclut la zone défrichée au cours des 12 derniers mois et indiqué ci-dessus ?*		*……..ha*		
52. Monene ya Bilanga boni basaleli pe batika na mbula mitanu eleki ? *Quelle superficie utilisée par le ménage ont été abandonnées au cours de ces 5 dernières années (pour régénération) ?*		*……..ha*		

6. Bilanga na Kobokola - *Culture et élevage*

6.1. Bilanga - Culture

53. Tango milona oyo bosalelaka mingi *Citez les cultures de votre ménage dont vous vous occupez*	
54. Ntina nini bosalelaka yango ? *A quoi sont destinées les cultures de votre ménage ?*	1) koleyisa libota *(consommation du ménage)*; 2) koteka *(vente)*
55. Soki koteka, monene boni ? *Si vente, quelles quantités vendez-vous ?* *Pourcentage de la récolte vendue*	
56. Wapi botekaka ? *Où écoulez-vous vos produits ?*	1) na mboka *(au village)*; 2) na mboka ya mpembeni *(dans les villages avoisinants)*; 3) na zando (nini ?) *(au marché (lequel ?))*

6.2. Kobokola - *Elevage*

57. Ebuele nini bobokolaka ? *Quelles espèces élevez-vous ?* *Citez par ordre d'importance*	
58. Soki obokolaka te, pona nini ? *Si pas d'élevage, expliquez pourquoi ?*	1) kozanga misolo *(pas de capitaux /trop cher)*; 2) kozanga ngonga *(temps)*; 3) kozanga koyeba *(manque de compétences)*; 4) kobela *(maladie)*; 5) kazanga esika ya kobokola *(manque de pâturage)*; 6) biloko misusu *(autres)*
59. Ntina nini bokokolaka ? *A quoi est destiné l'élevage de votre ménage ?*	1) koleyisa libota *(consommation du ménage)*; 2) koteka *(vente)*
60. Soki koteka, monene boni ? *Si vente, quelles quantités vendez-vous ?* *Quantité par mois*	

61. Wapi botekaka ? *Où écoulez-vous vos produits ?*	1) na mboka *(au village)*; 2) na mboka ya mpembeni *(dans les villages avoisinants)*; 3) na zando (nini ?) *(au marché (lequel ?))*
62. Mituya na nyama ezali boni ? *Quelle est la taille de votre cheptel ?*	
63. Banyama na bino eliaka yango moko ? *Vos animaux sont-ils en divagation ? Rentrent-ils le soir, et où ?*	
64. Bopesaka bango biloko ya kolia mpe nkisi mosusu ? *Donnez-vous un supplément alimentaire ou d'autres soins ?*	
65. Bosepelaka na ebokoleli na bino ya mikolo oyo ? Bokoki kobongisa yango ? Ata esengi mosala makasi mpe mbongo? *Etes-vous satisfait de votre technique d'élevage actuelle ? Seriez-vous prêt à l'améliorer ? Y compris si cela implique plus de travail et plus de frais ?*	
66. Bibwele nini bosepelaka kobokola makasi ? Pona nini? *Si vous pouviez élever toutes les espèces, quelles sont celles que vous choisiriez en priorité et pourquoi ?*	

7. **Kosala biloko ya zamba - *Utilisation des ressources naturelles***

7.1. Kosala na nyama ya zamba - Consommation de viande de brousse

67. Mikolo boni na poso boliaka mosuni ya zamba ? *A quelle fréquence mangez-vous de la viande de brousse ? (Nombre de fois par semaine ou mois ou années)*	
68. Bozuaka yango ndege nini ? *Comment faites-vous pour vous la procurer ?*	1) Mingi na bokilaya batu na ndako *(principalement grâce à la chasse des membres de la maison)*; 2) ndambo na bokila, ndambo na kosomba *(50% chasse et 50% achat)*; 3) mingi kosomba *(principalement acheté)*
69. Soki mingi ezali ya kosomba, pona nini ? *Si plus de 50% de la viande de brousse consommée par le ménage est achetée, précisez pourquoi?*	1) kozanga chasseur na ndako *(pas de chasseur dans la maison)*; 2) Ntalo muke ya kosomba te kosala bokila *(moins cher d'acheter que de chasser)*; 3) ekomi pasi na bokila *(devenu trop dur de chasser)*
70. Nyama ya zamba oyo bozali kosomba ewutaka wapi ? (Nkombo ya mboka mpe ya wenze) *D'où vient la viande de brousse que vous achetez ? Citez le nom des endroits où vous achetez*	1) mingi na mboka *(principalement du village)*; 2) mboka mosusu *(en dehors du village)*
71. Bosali kolia mingi mosuni ya zamba lolenge moko na bambula mitanu ewuti koleka ? *Mangez-vous de la viande de brousse plus souvent, pareil ou moins souvent qu'il y a 5 ans ?*	1) mingi *(plus souvent)*; 2) ndenge moko *(autant)*; 3) moke *(moins souvent)*
72. Pona nini *Pourquoi ?*	

73. Nyama nini boliaka mingi ? *Quelles espèces d'animaux mangez-vous le plus souvent ?* (Ordonnez) Nkombo ya makaku mpe ya nkulupa nini *Citez les espèces de singes et antilopes*	1) makaku *(singes)*; 2) nkulupa *(antilopes)*; 3) yiko *(porcs-épics)*; 4) simbiliki *(potamochères)*; 5) biloko mosusu *(autres (préciser))*
74. Osepeli kolia nyama nini ya liboso ? *Quelles espèces d'animaux préférez-vous manger?* Nkombo ya makaku mpe ya nkulupa nini *Citez les espèces de singes et antilopes*	1) makaku *(singes)*; 2) nkulupa *(antilopes)*; 3) yiko *(porcs-épics)*; 4) simbiliki *(potamochères)*; 5) biloko mosusu *(autres (préciser))*
75. Okoki kotika kolia nyama ya zamba soki lolenge mosusu ya kozua mosuni ezali ? *Arrêteriez-vous de manger de la viande de brousse si des alternatives étaient disponibles ? (ex : poulet, chèvre, poissons, vaches)*	Oui /Non
76. Soki solo, pona nini ? *Si oui, pourquoi ?*	1) ezali mingi *(plus facilement disponible)*; 2) talo moke *(moins cher)*; 3) pona mobeko *(à cause de la loi)*; 4) pona kobetela banyama *(pour conserver les espèces)*;
77. Soki te, pona nini ? *Si non, pourquoi ?*	1) posa *(goût)*; 2) lolenge ya coutume *(raisons culturelles)*; 3) talo moke *(coûte moins cher de chasser)*; 4) biloko mosusu *(autre (préciser))*
78. Nini bospeli kosala pona kobatela nyama na zamba ? *Quelle serait votre alternative préférée à la viande de brousse? (Ordonnez)*	1) soso *(poulet)*; 2) ntaba *(chèvre)*; 3) ngombe *(vache)*; 4) mbisi *(poisson)*; 5) mosusu *(autre (préciser))*
79. Bokosepela kolia nyama na zamba soki bobokoli yango, nyama nini, pona nini ? *Accepteriez-vous de manger des animaux de forêts élevés ? Lesquels ? Pourquoi ?*	

7.2. Lolenge ya kolia mbisi - Consommation de poissons

80. Mikolo boni na poso boliaka mbisi ? *A quelle fréquence mangez-vous du poisson ?* *(Nombre de fois par semaine ou mois ou années)*	
81. Bozuaka yango ndege nini ? *Comment faites-vous pour vous la procurer ?*	1) Mingi na koloba ya batu na ndako *(principalement grâce à la pêche des membres de la maison)*; 2) ndambo na koloba, ndambo na kosomba *(50% pêche et 50% achat)*; 3) mingi kosomba *(principalement acheté)*
82. Soki mingi ezali ya kosomba, pona nini ? *Si plus de 50% du poisson consommé par le ménage est achetée, précisez pourquoi ?*	1) kozanga pêcheur na ndako *(pas de pêcheur dans la maison)*; 2) Ntalo muke ya kosomba te kosala koloba *(moins cher d'acheter que de pêcher)*; 3) ekomi pasi na koloba *(devenu trop dur de pêcher)*

83. Mbisi oyo bozali kosomba ewutaka wapi ? *D'où vient le poisson que vous achetez ?*	1) mingi na mboka *(principalement du village)*; 2) mboka mosusu *(en dehors du village)*
84. Bosali kolia mingi mbisi lolenge moko na bambula mitanu ewuti koleka ? *Mangez-vous du poisson plus souvent, pareil ou moins souvent qu'il y à 5 ans ?*	1) mingi *(plus souvent)*; 2) ndenge moko *(autant)*; 3) moke *(moins souvent)*
85. Pona nini ? *Pourquoi ?*	
86. Mbisi nini boliaka mingi ? *Quelles espèces mangez-vous le plus souvent ?*	

7.3. Bokila - Chasse

87. Mbanda tango nini bosala bokila ? *Depuis combien de temps chassez-vous ?*	1) mbula moko *(1 an)*; 2) mbula mitano *(5 ans)*; 3) mbula zomi *(10 ans)*; 4) mbula ntuku mibale *(20 ans)*; 5) koleka ntuku mibale *(>20ans)*
88. Mikolo boni bokendaka bokila ? *A quelle fréquence chassez-vous ?*	1) mikolo nioso *(tous les jours)*; 2) mbala mibale na poso *(au moins 2 fois par semaine)*; 3) mokolo moko na poso mibale *(une fois toute les 2 semaines)*; 4) mokolo moko na sanza moko *(une fois par mois)*
89. Bobomaka nyama boni na mokolo moko ? *Combien d'animaux tuez-vous à chaque fois ?*	
90. Mulayi boni bokendaka bokila *Indiquer la distance la plus lointaine dont vous vous éloigniez du village pour chasser dans la forêt (en km ou heures)*	
91. Ntanga nkombo na nyama obomi liboso, mibale, misato na mbula eleki? *Nommez la première, seconde et troisième espèce que vous avez le plus tué sur l'année dernière ? (ex singes, antilopes, porc-épic, potamochère, autres (préciser) (Ordonnez).*	
92. Bokila nini bosalaka ? *Quelles sont les techniques de chasse que vous utilisez ?*	
93. Tanga ngombo ya zamba oyo bokendaka bokila ? Lolenge nini ya bokila bosalaka mpe banyama nini bobomaka ? *Quels sont les endroits où vous chassez aujourd'hui ? Expliquez le type de chasse et l'animal visé*	
94. Liboso ya kobetela ya mikomboso, tanga ngombo ya zamba oyo bokendaka bokila ? Lolenge nini ya bokila bosalaka mpe banyama nini bobomaka ? *Quels sont les endroits où vous chassiez avant la mise en place des zones communautaires de conservation ? Expliquez le type de chasse et l'animal visé* *Citez chaque nom de forêt et voir ce qu'ils chassent*	
95. Nyama bobomaka bosalaka na yango nini ? *Que faites-vous des produits de votre chasse ?*	1) Koleyisa libota *(Consommation du ménage)*; 2) ndambo kolia, ndambo koteka *(50% consommation, 50% vente)*;

	3) koteka *(vente)*
96. Wapi botekelaka nyama bobomaka ? *Où vendez-vous les produits de votre chasse ?*	1) na mboka *(au village)*; 2) na mboka ya pene *(dans les villages avoisinants)*; 3) na wenze (nkombo ?) *(au marché (lequel ?))*
97. Botambolaka mulayi ya boni pona koteka nyama *Indiquez les distances que vous pouvez parcourir pour vendre vos produits*	… km …. Hrs
98. Bokutanaka na ba chasseur ya mboka na bino mpe ya bamboka mosusu na zamba ? *Rencontrez-vous des chasseurs de votre village ou d'autres villages dans la forêt ?*	Oui/Non
99. Bokutani na bino emati to ekiti na mbula mituna eleki? *La rencontre de ces personnes a-t-elle augmenté, diminué ou est resté la même pendant ces 5 dernières années ?*	1) emati *(augmentation)*; 2) ekiti *(diminution)*; 3) ndenge moko *(identique)*
100. Na bambula mitano eleki, bokila na bino emati, ekiti, to ezali ndenge moko ? *Par rapport à il y a 5 ans diriez vous que votre succès de chasse a augmenté, diminué ou est resté le même ?*	1) emati *(augmentation)*; 2) ekiti *(diminution)*; 3) ndenge moko *(identique)*
101. Soki ekiti to emati, pona nini ? *Si augmentation ou diminution, quelles en sont les raisons selon vous ?*	
102. Eloko nini eleki motuya oyo ekoki kopekisa yo kosala bokila (koboma nyama) ? *Quelle est la chose la plus importante qui vous ferait arrêter de chasser ?*	1) kozua mosala *(avoir un emploi)*; 2) kozala na bibuele oyo ekoki kopesa mosuni *(avoir à disposition des produits alternatifs à la viande de brousse)*; 3) mosusu *(autres (préciser))*
103. Bomonaka nyama mosusu koleka motuya ? *Considérez vous certains animaux comme spéciaux ?*	Oui /Non
104. Ntanga misato *Nommez en trois*	1) 2) 3)
105. Pona nini ? *Expliquez pourquoi ?*	
106. Okoki kotika koboma yango ? *Seriez-vous prêt à arrêter de les chasser ?*	Oui /Non
107. Pona nini ? *Pourquoi ?*	

7.4. Pêche

108. Mbanda tango nini bosala koloba ? *Depuis combien de temps pêchez-vous ?*	1) mbula moko *(1 an)*; 2) mbula mitano *(5 ans)*; 3) mbula zomi *(10 ans)*; 4) mbula ntuku mibale *(20 ans)*; 5) koleka ntuku mibale *(>20ans)*
109. Mikolo boni bokendaka koloba ? *A quelle fréquence pêchez-vous ?*	1) mikolo nioso *(tous les jours)*; 2) mbala mibale na poso *(au moins 2 fois par semaine)*; 3) mokolo moko na poso mibale *(une fois toute les 2 semaines)*;

	4) mokolo moko na sanza moko *(une fois par mois)*
110. Mulayi boni bokendaka koloba *Indiquer la distance la plus lointaine dont vous vous éloigniez du village pour pêcher (en km ou heures)*	
111. Koloba nini bosalaka ? *Quelles sont les techniques de pêche que vous utilisez ?*	
112. Tanga ngombo ya zamba oyo bokendaka koloba ? Lolenge nini ya koloba bosalaka *Quels sont les endroits où vous pêchez aujourd'hui ? Indiquez le type de pêche*	
113. Liboso ya kobetela ya mikomboso, tanga ngombo ya zamba oyo bokendaka koloba ? Lolenge nini ya koloba bosalaka *Quels sont les endroits où vous pêchiez avant la mise en place des zones communautaires de conservation ? Indiquez le type de pêche*	
114. Mbisi bolobaka bosalaka na yango nini ? *Que faites-vous des produits de votre pêche ?*	1) Koleyisa libota *(Consommation du ménage)*; 2) ndambo kolia, ndambo koteka *(50% consommation, 50% vente)*; 3) koteka *(vente)*
115. Wapi botekelaka mbisi bolobaka ? *Où vendez-vous les produits de votre pêche ?*	1) na mboka *(au village)*; 2) na mboka ya pene *(dans les villages avoisinants)*; 3) na wenze (nkombo ?) *(au marché (lequel ?))*
116. Botambolaka mulayi ya boni pona koteka mbisi *Indiquez les distances que vous pouvez parcourir pour vendre vos produits*	… km …. Hrs
117. Bokutanaka na ba pêcheur ya mboka na bino mpe ya bamboka mosusu na zamba ? *Rencontrez-vous des pêcheurs de votre village ou d'autres villages ?*	Oui/Non
118. Bokutani na bino emati to ekiti na mbula mituna eleki? *La rencontre de ces personnes a-t-elle augmenté, diminué ou est resté la même pendant ces 5 dernières années ?*	1) emati *(augmentation)*; 2) ekiti *(diminution)*; 3) ndenge moko *(identique)*
119. Soki ekiti to emati, pona nini ? *Si augmentation ou diminution, quelles en sont les raisons selon vous ?*	
120. Osepeli koloba wapi ? Na ebale mpe na etima/liziba ? Pona nini ? *Où est-ce que vous préfèreriez pêcher : en rivière ou en étang ? Pourquoi ?*	
121. Boponaka ba mbisi mosusu bokangaka ? *Faites-vous un tri dans vos prises ou gardez-vous tous les poissons que vous obtenez ?*	
122. Okoki kotika koloba ? *Seriez-vous prêt à arrêter de pêcher ?*	Oui /Non
123. Eloko nini eleki motuya oyo ekoki kopekisa yo kosala koloba ? *Quelle est la chose la plus importante qui vous ferait arrêter de pêcher?*	1) kozua mosala *(avoir un emploi)*;

	2) kozala na bibuele oyo ekoki kopesa mosuni *(avoir à disposition des produits alternatifs)*; 3) mosusu *(autres (préciser))*

8. Lolenge bato ba mizaleli - *Perceptions du bien-être et du capital social*

124. Na mabota mosusu, okanisi ete ozali lolenge nini ? (1) mabe, (2) ndenge moko, (3) malamu *Par rapport aux autres ménages habitant le village, comment vous situez vous ? plutôt mal loti (1), aux environs de la moyenne (2), plutôt bien loti (3)*		
125. Ozali (1) mabe, (2) ndenge moko, (3) malamu banda mbula mitano eleki? *Etes-vous moins bien loti (1), au même niveau (2), mieux loti (3) qu'il y a 5 ans ?*		
126. Soki bokeseni ezali, pona nini ? *En cas d'amélioration ou de dégradation, indiquez quelles sont les principales raisons de ce changement* *(Numérotez par ordre d'importance jusqu'à trois raisons après avoir écouté les gens donner librement leurs impressions)*	*Raison: Changement au niveau de …*	Rang 1-3
	1. Emploi (hors travail agricole)	
	2. terres (ex achat, vente, expulsion)	
	3. ressources forestières	
	4. prix de vente de certains produits (forestiers, agricoles,…)	
	5. aide extérieure (gouvernement, ONG,…)	
	6. versement d'argent vers un tiers	
	7. coût de la vie (ex inflation)	
	8. conflits dans le village (non violent)	
	9. changement dans la situation familiale (ex décès d'un membre, départ d'une personne qui contribuait beaucoup au revenu)	
	10. maladie	
	11. accès (ex nouvelle route,…)	
	12. augmentation / réduction de la surface cultivable détenue pour la production agricole	
	13. début d'une nouvelle activité commerciale / perte ou diminution de cette activité	
	14. bétails (augmentation ou perte)	
	15. biens matériels incluant l'habitation (augmentation ou perte)	
	16. augmentation des réglementations	
	17. éducation / accès à un nouveau savoir	
	18. engagement dans le commerce	
	19. perte de récolte (météo, animaux,…)	
	20. changement dans les ressources naturelles	
	21. mise à son propre compte (ne plus être salarié)	
	22. avoir plus de temps disponible pour travailler	
	23. avoir rejoint une coopérative	
	24. être obligé à voyager pour pallier à des problèmes familiaux	
	25. le feu a tout détruit	
	26. changement de travail	
	27. autre (préciser)	
127. Nani abombaka bozui ya libota ? *Qui s'occupe de la gestion du patrimoine du ménage (argent) ?*		

9. Likanisi ya zamba babatelaka - *Perceptions locales et attitudes vis-à-vis des zones communautaires de conservation et des ressources naturelles*

128. Zamba babatelaka ezalaka ya nani ? *Comment considérez-vous la forêt dans les zones communautaires de conservation en termes de propriété ?*	*Appartient à:* 1) Mboka *(communauté (au village))*; 2) l'état *(gouvernement)*; 3) mboka mpe l'état (gouvernement & communauté)

129. Osepeli to te kobatela ndambo ya zamba na bino ? *Etes-vous pour ou contre la mise en place d'une partie de la forêt proche de votre communauté comme zones communautaires de conservation ?*	1) bosepeli mingi *(appui fort)*; 2) bosepeli moke *(faible appui)*; 3) bosepeli te mwa moke *(légèrement contre)*; 4) bosepeli ata moke te *(fortement contre)*
130. Pona nini ? *Pourquoi ?*	
131. bozeli na bino ezali nini likolo ya kobatela zamba ? *Quelles sont vos attentes par rapport aux zones communautaires de conservation ?* *Choisir une possibilité ou plusieurs*	1) Komatisa bozui ya libota *(amélioration du niveau de vie/création de projets alternatifs pour gagner sa vie)*; 2) kozua misala *(opportunité d'emploi)*; 3) Komatisa makanisi pona kobatela *(augmentation de la conscientisation pour la conservation)*; 4) Kosunga pona kobetela zamba *(aide pour protéger les ressources de nos forêts)*; 5) kobetela zamba pona biloko oyo ezali na kati *(préserve la forêt pour la récolte de produits forestiers non ligneux)*; 6) Kozua misolo likolo ya ba touristes *(apport de revenus pour la communauté à l'aide du tourisme)*; 7) Kosunga mboka mobimba *(apports d'équipements collectifs)*; 8) mosusu *(autres (préciser))*
132. Okoki kokitisa esaleli ya bokila to ya peche ? *Seriez-vous prêt à restreindre vos périodes de pêche et de chasse ?*	Oui/Non
133. Pona nini ? Nanti na nini ? *Pourquoi ? A quelles conditions ?*	

10. Mikomboso - *Bonobos*

134. Nini boyebi lolenge ya mikomboso ? *Que connaissez-vous du bonobo ?*	
135. Boyebi ete ekoki kolungwa mokolo mosusu ? *Savez-vous qu'il peut disparaitre un jour ?*	Oui/Non
136. Boyebi ete bonobo ezali kaka na mokili ya RDC ? *Savez-vous que le bonobo est une espèce qu'on ne trouve qu'uniquement en RDC ?*	Oui/Non
137. Bokanisi ete bokoki kobetela yango ? Pona nini ? *Pensez-vous qu'il faut le conserver ? Pourquoi ?*	Oui/Non
138. Boyebi masolo oyo ezali likolo ya mikomboso (ntango ya bakoko) ? *Connaissez-vous des histoires, des légendes sur le bonobo ?*	

B. Mituna pona mwasi - *Questionnaire posé à la femme de la maison*

11. Mituna pona libota ya ndako moko - *Informations sur le foyer*

139. Lolenge bozali na mokolo libota *Lien de parenté avec l'homme sondé*	
140. Mbula ya mwasi *Age de la femme*	
141. Motuya ya bana *Nombre d'enfants*	
142. Classe mokolo libota asukeli *Niveau le plus haut d'éducation du chef de ménage* *	
143. Mosala ya mokolo ndako *Occupation principale du chef de ménage*	*(Ecrire 1 pour l'occupation la plus importante, 2 pour la seconde, etc.)*
- Koloba *(Pêche)*	
- Bilanga *(Exploitation agricole)*	
- Kobimisa biloko na zamba *(Récolte de produits forestiers pour usage personnel)*	
- Koteka biloko ya zamba *(Commerce de produits forestiers)*	
- Mosala na WWF/SEBO *(Emploi WWF/SEBO)*	
- Mosala mosusu *(Emploi hors de la forêt (à préciser))*	
29. Misala efutaka tango nionso mpe malamu ? *Ces activités donnent-elles lieu à des revenus réguliers ou ponctuels ?*	

**Codes: 0=pas d'éducation formelle, 1=école primaire débuté mais non terminée, 2= école primaire terminée, 3 école secondaire débutée mais non terminée, 4= école secondaire terminée, 5=niveau supplémentaire débuté mais non terminé, 6= niveau supplémentaire terminé*

12. Utilisation des ressources forestières

145.Libota bakataka nzete ya kolambela na zamba ? *Est-ce que le ménage collecte du bois de chauffage dans la forêt ?*	
146. Soki solo, mikolo boni na poso moko ? *Si oui, combien de jours par semaine ?*	
147. Bato boni mikolo to bana bakataka nkoni ? *Combien d'adultes et d'enfants collectent le bois de chauffage ?*	Adultes………. Enfants……….
Nzete ya lolenge nini bokataka nkoni ? *Quels types de bois utilisez-vous comme bois de chauffe ?*	1) Nzete ya kokawuka *(Bois mort)*; 2) Nzete mobesu *(Bois sur pied)*; 3) Bitape *(Branches)*
148. Lelo, bokati nkoni eleki to ekiti to ndenge moko kobanda mbula mitano eleki ? *Aujourd'hui, la récolte du bois de chauffe nécessite-t-elle plus, moins ou autant de temps qu'il y a 5 ans ?* *Codes: 1 = plus; 2 = identique ; 3 = moins*	
149. Kozua nkoni ezali lolenge moko kobanda mbula mitano eleki ? *Est-ce que la disponibilité du bois de chauffage a décliné, augmenté ou est resté la même depuis 5 ans ?* *Codes: 1 = décliné; 2 = identique; 3 = augmenté*	

150. Soki esili, libota na bino bokosalela nini ? *En cas de déclin, comment votre ménage a-t-il pallié à celui-ci ?*	*Réponse*	
	Komatisa ngonga pona koloka *Augmenter le temps passé pour la collecte (ex : aller le chercher plus loin du village)*	
	Kosomba nkoni to makala	

Numéroter les 3 plus importantes réponses par ordre croissante, 1 étant la plus importante	*Acheter (plus) de bois de chauffage et/ou du charbon*	
	Tokitisa posa ya nkoni *Diminuer le besoin de bois de chauffage (ex : utiliser un foyer amélioré)*	
	Tokitisa kosasela ya nkoni *Diminuer la consommation de bois de chauffage*	
	Tokitisa kolia biloko ya moto *Diminuer le nombre de repas chauds*	
	Kosalela biloko mosusu ya zamba *Augmenter l'utilisation de produits forestiers alternatifs*	
	Kokitisa bosaleli zamba *Restreindre l'accès/ l'utilisation de la forêt*	
	Kobatela nzete pona kosalela yango mikolo ekoya *Conserver les arbres sur pied pour une utilisation future*	
	Kosala makala *Faire du charbon de bois*	
	Biloko mosusu *Autres (préciser):*	
151. Na libota na bino boloni banzete na mbula mitano eleki ? *Est-ce que votre ménage a planté des arbres durant les 5 dernières années ?*		
152. Soki mbongo : tina ezalaki nini ? *Si oui : quel était l'objectif principal de cette plantation?* *Indiquer les 3 raisons les plus importantes*	Biyano *Raisons*	Rang 1-3
	Koni ya kolambela *(Bois de chauffe pour usage domestique)*	
	Koni ya koteka *(Bois de chauffe à vendre)*	
	Grume mpe nzete ya kosalela na ndako (*Grume/Piquet pour usage domestique)*	
	Grume mpe nzete ya koteka *(Grume/piquet à vendre)*	
	Mbuma ya kolia *(Fruits pour usage domestique)*	
	Mbuma ya koteka *(Fruits à vendre)*	
	Tina mosusu pona libota *(Autres usages domestiques)*	
	Tina mosusu pona koteka *(Autres produits à vendre)*	
	Ndelo ya mabele *(Délimitation des terres)*	
	Pona kokolisa motuya ya mabele *Pour augmenter la valeur de ma terre*	
	Pona kotikela bana mpe bakoko bamona yango *Pour permettre à mes enfants/petits-enfants de voir ses arbres*	
	Biloko misusu *(Autres, précisez)*	
153. Soki solo : olonaki yango wapi ? *Si oui : où avez-vous planté ces arbres ? (forêt, savane, village, etc.)*		
154. Na libota bolokotaka biloko na zamba ? *Est-ce que le ménage collecte des produits forestiers non ligneux, ex. fruits ?*		Oui/Non
155. Soki solo : ezalaka mikolo boni na poso moko ? *Si oui : combien de jours par semaine les membres du ménage utilisent à cette collecte ?*		………*jours*
156. Mikolo boni na bana boni balokotaka yango ?		*Ad..... enf.....*

Combien d'adultes et d'enfants collectent ses produits?		
157. Na zamba nini bokendaka kolokota yango ? *A quels endroits de la forêt allez-vous pour récolter ces produits ? Citez les noms des forêts*		
158. Na libota na bino bozali kolokota biloko mingi to moke na zamba ? *Est-ce que votre ménage passe aujourd'hui plus ou moins de temps à collecter ses produits ?* *Codes: 1=plus; 2=environ le même temps; 3=moins*		
159. Est-ce que biloko na zamba ekiti na mbula mitano oyo ewuti koleka ? *Est-ce que la disponibilité en produits forestiers non-ligneux a changé au cours de ces 5 dernières années ?* *Codes: 1=diminution; 2=environ la même chose; 3=augmentation*		
160. Pona nini ? *Pourquoi ?*		
161. Soki eketi ndege nini libota bazali kopesa eyano pona kosila ya biloko wana ? *Si diminution, comment le ménage a-t-il répondu au déclin de disponibilité de ces produits ?* *(Indiquer les réponses par ordre croissant d'importance)*	*Biyano Réponses*	Rang 1-3
	Komatisa ngonga na zamba *Augmentation du temps de récolte en forêt (ex : en allant plus loin de la maison)*	
	Kosomba biloko ya zamba *Achat (de plus) de produits forestiers*	
	Kokitisa bosaleli zamba *Restreindre l'accès/ l'utilisation de la forêt*	
	Kobatela nzete pona mbula ekoya *Conservation des arbres sur pied pour le futur*	
	Kolona banzete *Plantation de ces produits*	
	Biloko misusu *Autres (préciser)*	

13. **Bilanga na Kobokola - *Culture et élevage***

13.1. Bilanga - Culture

162. Tango milona oyo bosalelaka mingi *Citez les cultures de votre ménage dont vous vous occupez*	
163. Ntina nini bosalelaka yango ? *A quoi sont destinées les cultures de votre ménage ?*	1) koleyisa libota *(consommation du ménage)*; 2) koteka *(vente)*
164. Soki koteka, monene boni ? *Si vente, quelles quantités vendez-vous ?* *Pourcentage de la récolte vendue*	
165. Wapi botekaka ? *Où écoulez-vous vos produits ?*	1) na mboka *(au village)*; 2) na mboka ya mpembeni *(dans les villages avoisinants)*; 3) na zando (nini ?) *(au marché (lequel ?))*

13.2. Kobokola - Elevage

166. Ebuele nini bobokolaka ? *Quelles espèces élevez-vous ?* *Citez par ordre d'importance*	
167. Soki obokolaka te, pona nini ? *Si pas d'élevage, expliquez pourquoi ?*	1) kozanga misolo *(pas de capitaux /trop cher)*; 2) kozanga ngonga *(temps)*; 3) kozanga koyeba *(manque de compétences)*; 4) kobela *(maladie)*; 5) kazanga esika ya kobokola *(manque de pâturage)*;

	6) biloko misusu *(autres)*
168. Ntina nini bokokolaka ? *A quoi est destiné l'élevage de votre ménage ?*	1) koleyisa libota *(consommation du ménage)*; 2) koteka *(vente)*
169. Soki koteka, monene boni ? *Si vente, quelles quantités vendez-vous ?* *Quantité par mois*	
170. Wapi botekaka ? *Où écoulez-vous vos produits ?*	1) na mboka *(au village)*; 2) na mboka ya mpembeni *(dans les villages avoisinants)*; 3) na zando (nini ?) *(au marché (lequel ?))*
171. Mituya na nyama ezali boni ? *Quelle est la taille de votre cheptel ?*	
172. Banyama na bino eliaka yango moko ? *Vos animaux sont-ils en divagation ? Rentrent-ils le soir, et où ?*	
173. Bopesaka bango biloko ya kolia mpe nkisi mosusu ? *Donnez-vous un supplément alimentaire ou d'autres soins ?*	
174. Bosepelaka na ebokoleli na bino ya mikolo oyo ? Bokoki kobongisa yango ? Ata esengi mosala makasi mpe mbongo? *Etes-vous satisfait de votre technique d'élevage actuelle ? Seriez-vous prêt à l'améliorer ? Y compris si cela implique plus de travail et plus de frais ?*	
175. Bibwele nini bosepelaka kobokola makasi ? Pona nini? *Si vous pouviez élever toutes les espèces, quelles sont celles que vous choisiriez en priorité et pourquoi ?*	

14. Kosala biloko ya zamba - *Utilisation des ressources naturelles*

14.1. Kosala na nyama ya zamba - Consommation de viande de brousse

176. Mikolo boni na poso boliaka mosuni ya zamba ? *A quelle fréquence mangez-vous de la viande de brousse ?* *(Nombre de fois par semaine ou mois ou années)*	
177. Bozuaka yango ndege nini ? *Comment faites-vous pour vous la procurer ?*	1) Mingi na bokilaya batu na ndako *(principalement grâce à la chasse des membres de la maison)*; 2) ndambo na bokila, ndambo na kosomba *(50% chasse et 50% achat)*; 3) mingi kosomba *(principalement acheté)*
178. Soki mingi ezali ya kosomba, pona nini ? *Si plus de 50% de la viande de brousse consommée par le ménage est achetée, précisez pourquoi ?*	1) kozanga chasseur na ndako *(pas de chasseur dans la maison)*; 2) Ntalo muke ya kosomba te kosala bokila *(moins cher d'acheter que de chasser)*; 3) ekomi pasi na bokila *(devenu trop dur de chasser)*

179. Nyama ya zamba oyo bozali kosomba ewutaka wapi ? (Nkombo ya mboka mpe ya wenze) *D'où vient la viande de brousse que vous achetez ? Citez le nom des endroits où vous achetez*	1) mingi na mboka *(principalement du village)*; 2) mboka mosusu *(en dehors du village)*
180. Bosali kolia mingi mosuni ya zamba lolenge moko na bambula mitanu ewuti koleka ? *Mangez-vous de la viande de brousse plus souvent, pareil ou moins souvent qu'il y a 5 ans ?*	1) mingi *(plus souvent)*; 2) ndenge moko *(autant)*; 3) moke *(moins souvent)*
181. Pona nini *Pourquoi ?*	
182. Nyama nini boliaka mingi ? *Quelles espèces d'animaux mangez-vous le plus souvent ?* (Ordonnez) Nkombo ya makaku mpe ya nkulupa nini *Citez les espèces de singes et antilopes*	1) makaku *(singes)*; 2) nkulupa *(antilopes)*; 3) yiko *(porcs-épics)*; 4) simbiliki *(potamochères)*; 5) biloko mosusu *(autres (préciser))*
183. Osepeli kolia nyama nini ya liboso ? *Quelles espèces d'animaux préférez-vous manger?* Nkombo ya makaku mpe ya nkulupa nini *Citez les espèces de singes et antilopes*	1) makaku *(singes)*; 2) nkulupa *(antilopes)*; 3) yiko *(porcs-épics)*; 4) simbiliki *(potamochères)*; 5) biloko mosusu *(autres (préciser))*
184. Okoki kotika kolia nyama ya zamba soki lolenge mosusu ya kozua mosuni ezali ? *Arrêteriez-vous de manger de la viande de brousse si des alternatives étaient disponibles ? (ex : poulet, chèvre, poissons, vaches)*	Oui /Non
185. Soki solo, pona nini ? *Si oui, pourquoi ?*	1) ezali mingi *(plus facilement disponible)*; 2) talo moke *(moins cher)*; 3) pona mobeko *(à cause de la loi)*; 4) pona kobetela banyama *(pour conserver les espèces)*;
186. Soki te, pona nini ? *Si non, pourquoi ?*	1) posa *(goût)*; 2) lolenge ya coutume *(raisons culturelles)*; 3) talo moke *(coûte moins cher de chasser)*; 4) biloko mosusu *(autre (préciser))*
187. Nini bospeli kosala pona kobatela nyama na zamba ? *Quelle serait votre alternative préférée à la viande de brousse? (Ordonnez)*	1) soso *(poulet)*; 2) ntaba *(chèvre)*; 3) ngombe *(vache)*; 4) mbisi *(poisson)*; 5) mosusu *(autre (préciser))*
188. Bokosepela kolia nyama na zamba soki bobokoli yango, nyama nini, pona nini ? *Accepteriez-vous de manger des animaux de forêts élevés ? Lesquels ? Pourquoi ?*	

14.2. Lolenge ya kolia mbisi - Consommation de poissons

189. Mikolo boni na poso boliaka mbisi ? *A quelle fréquence mangez-vous du poisson ?* *(Nombre de fois par semaine ou mois ou années)*	
190. Bozuaka yango ndege nini ? *Comment faites-vous pour vous la procurer ?*	1) Mingi na koloba ya batu na ndako *(principalement grâce à la pêche des membres de la maison)*;

	2) ndambo na koloba, ndambo na kosomba *(50% pêche et 50% achat)*; 3) mingi kosomba *(principalement acheté)*
191. Soki mingi ezali ya kosomba, pona nini ? *Si plus de 50% du poisson consommé par le ménage est achetée, précisez pourquoi?*	1) kozanga pêcheur na ndako *(pas de pêcheur dans la maison)*; 2) Ntalo muke ya kosomba te kosala koloba *(moins cher d'acheter que de pêcher)*; 3) ekomi pasi na koloba *(devenu trop dur de pêcher)*
192. Mbisi oyo bozali kosomba ewutaka wapi ? *D'où vient le poisson que vous achetez ?*	1) mingi na mboka *(principalement du village)*; 2) mboka mosusu *(en dehors du village)*
193. Bosali kolia mingi mbisi lolenge moko na bambula mitanu ewuti koleka ? *Mangez-vous du poisson plus souvent, pareil ou moins souvent qu'il y à 5 ans ?*	1) mingi *(plus souvent)*; 2) ndenge moko *(autant)*; 3) moke *(moins souvent)*
194. Pona nini ? *Pourquoi ?*	
195. Mbisi nini boliaka mingi ? *Quelles espèces mangez-vous le plus souvent ?*	

14.3. Pêche

196. Mbanda tango nini bosala koloba ? *Depuis combien de temps pêchez-vous ?*	1) mbula moko *(1 an)*; 2) mbula mitano *(5 ans)*; 3) mbula zomi *(10 ans)*; 4) mbula ntuku mibale *(20 ans)*; 5) koleka ntuku mibale *(>20ans)*
197. Mikolo boni bokendaka koloba ? *A quelle fréquence pêchez-vous ?*	1) mikolo nioso *(tous les jours)*; 2) mbala mibale na poso *(au moins 2 fois par semaine)*; 3) mokolo moko na poso mibale *(une fois toute les 2 semaines)*; 4) mokolo moko na sanza moko *(une fois par mois)*
198. Mulayi boni bokendaka koloba *Indiquer la distance la plus lointaine dont vous vous éloigniez du village pour pêcher (en km ou heures)*	
199. Koloba nini bosalaka ? *Quelles sont les techniques de pêche que vous utilisez ?*	
200. Tanga ngombo ya zamba oyo bokendaka koloba ? Lolenge nini ya koloba bosalaka *Quels sont les endroits où vous pêchez aujourd'hui ? Indiquez le type de pêche*	
201. Liboso ya kobetela ya mikomboso, tanga ngombo ya zamba oyo bokendaka koloba ? Lolenge nini ya koloba bosalaka *Quels sont les endroits où vous pêchiez avant la mise en place des zones communautaires de conservation ? Indiquez le type de pêche*	

202. Mbisi bolobaka bosalaka na yango nini ? *Que faites-vous des produits de votre pêche?*	1) Koleyisa libota *(Consommation du ménage)*; 2) ndambo kolia, ndambo koteka *(50% consommation, 50% vente)*; 3) koteka *(vente)*
203. Wapi botekelaka mbisi bolobaka ? *Où vendez-vous les produits de votre pêche ?*	1) na mboka *(au village)*; 2) na mboka ya pene *(dans les villages avoisinants)*; 3) na wenze (nkombo ?) *(au marché (lequel ?))*
204. Botambolaka mulayi ya boni pona koteka mbisi *Indiquez les distances que vous pouvez parcourir pour vendre vos produits*	… km …. Hrs
205. Bokutanaka na ba pêcheur ya mboka na bino mpe ya bamboka mosusu na zamba ? *Rencontrez-vous des pêcheurs de votre village ou d'autres villages ?*	Oui/Non
206. Bokutani na bino emati to ekiti na mbula mituna eleki? *La rencontre de ces personnes a-t-elle augmenté, diminué ou est resté la même pendant ces 5 dernières années ?*	1) emati *(augmentation)*; 2) ekiti *(diminution)*; 3) ndenge moko *(identique)*
207. Soki ekiti to emati, pona nini ? *Si augmentation ou diminution, quelles en sont les raisons selon vous ?*	
208. Osepeli koloba wapi ? Na ebale mpe na etima/liziba ? Pona nini ? *Où est-ce que vous préfèreriez pêcher : en rivière ou en étang ? Pourquoi ?*	
209. Boponaka ba mbisi mosusu bokangaka ? *Faites-vous un tri dans vos prises ou gardez-vous tous les poissons que vous obtenez ?*	
210. Okoki kotika koloba ? *Seriez-vous prêt à arrêter de pêcher ?*	Oui /Non
211. Eloko nini eleki motuya oyo ekoki kopekisa yo kosala koloba ? *Quelle est la chose la plus importante qui vous ferait arrêter de pêcher?*	1) kozua mosala *(avoir un emploi)*; 2) kozala na bibuele oyo ekoki kopesa mosuni *(avoir à disposition des produits alternatifs)*; 3) mosusu *(autres (préciser))*

15. Lolenge bato ba mizaleli - *Perceptions du bien-être et du capital social*

212. Na mabota mosusu, okanisi ete ozali lolenge nini ? (1) mabe, (2) ndenge moko, (3) malamu *Par rapport aux autres ménages habitant le village, comment vous situez vous ? plutôt mal loti (1), aux environs de la moyenne (2), plutôt bien loti (3)*		
213. Ozali (1) mabe, (2) ndenge moko, (3) malamu banda mbula mitano eleki? *Etes-vous moins bien loti (1), au même niveau (2), mieux loti (3) qu'il y a 5 ans ?*		
214. Soki bokeseni ezali, pona nini ? *En cas d'amélioration ou de dégradation, indiquez quelles sont les principales raisons de ce changement*	*Raison: Changement au niveau de …*	Rang 1-3
	1. Emploi (hors travail agricole)	
	2. terres (ex achat, vente, expulsion)	
	3. ressources forestières	
	4. prix de vente de certains produits (forestiers, agricoles,…)	
	5. aide extérieure (gouvernement, ONG,…)	
	6. versement d'argent vers un tiers	

(Numérotez par ordre d'importance jusqu'à trois raisons après avoir écouté les gens donner librement leurs impressions)	*7. coût de la vie (ex inflation)*	
	8. conflits dans le village (non violent)	
	9. changement dans la situation familiale (ex décès d'un membre, départ d'une personne qui contribuait beaucoup au revenu)	
	10. maladie	
	11. accès (ex nouvelle route,…)	
	12. augmentation / réduction de la surface cultivable détenue pour la production agricole	
	13. début d'une nouvelle activité commerciale / perte ou diminution de cette activité	
	14. bétails (augmentation ou perte)	
	15. biens matériels incluant l'habitation (augmentation ou perte)	
	16. augmentation des réglementations	
	17. éducation / accès à un nouveau savoir	
	18. engagement dans le commerce	
	19. perte de récolte (météo, animaux,…)	
	20. changement dans les ressources naturelles	
	21. mise à son propre compte (ne plus être salarié)	
	22. avoir plus de temps disponible pour travailler	
	23. avoir rejoint une coopérative	
	24. être obligé à voyager pour pallier à des problèmes familiaux	
	25. le feu a tout détruit	
	26. changement de travail	
	27. autre (préciser)	
215. Nani abombaka bozui ya libota ? *Qui s'occupe de la gestion du patrimoine du ménage (argent) ?*		

16. **Likanisi ya zamba babatelaka** - ***Perceptions locales et attitudes vis-à-vis des zones communautaires de conservation et des ressources naturelles***

216. Zamba babatelaka ezalaka ya nani ? *Comment considérez-vous la forêt dans les zones communautaires de conservation en termes de propriété?*	*Appartient à:* 1) Mboka *(communauté (au village))*; 2) l'état *(gouvernement)*; 3) mboka mpe l'état (gouvernement & communauté)
217. Osepeli to te kobatela ndambo ya zamba na bino ? *Etes-vous pour ou contre la mise en place d'une partie de la forêt proche de votre communauté comme zones communautaires de conservation?*	1) bosepeli mingi *(appui fort)*; 2) bosepeli moke *(faible appui)*; 3) bosepeli te mwa moke *(légèrement contre)*; 4) bosepeli ata moke te *(fortement contre)*
218. Pona nini ? *Pourquoi?*	
219. bozeli na bino ezali nini likolo ya kobatela zamba ? *Quelles sont vos attentes par rapport aux zones communautaires de conservation?* *Choisir une possibilité ou plusieurs*	1) Komatisa bozui ya libota *(amélioration du niveau de vie/création de projets alternatifs pour gagner sa vie)*; 2) kozua misala *(opportunité d'emploi)*; 3) Komatisa makanisi pona kobatela *(augmentation de la conscientisation pour la conservation)*; 4) Kosunga pona kobetela zamba *(aide pour protéger les ressources de nos forêts)*; 5) kobetela zamba pona biloko oyo ezali na kati *(préserve la forêt pour la récolte de produits forestiers non ligneux)*;

	6) Kozua misolo likolo ya ba touristes *(apport de revenus pour la communauté à l'aide du tourisme)*; 7) Kosunga mboka mobimba *(apports d'équipements collectifs)*; 8) mosusu *(autres (préciser))*
220. Okoki kokitisa esaleli ya bokila to ya peche ? *Seriez-vous prêt à restreindre vos périodes de pêche et de chasse ?*	Oui/Non
221. Pona nini ? Nanti na nini ? *Pourquoi ? A quelles conditions ?*	

17. Mikomboso - *Bonobos*

222. Nini boyebi lolenge ya mikomboso ? *Que connaissez-vous du bonobo ?*	
223. Boyebi ete ekoki kolungwa mokolo mosusu ? *Savez-vous qu'il peut disparaitre un jour ?*	Oui/Non
224. Boyebi ete bonobo ezali kaka na mokili ya RDC ? *Savez-vous que le bonobo est une espèce qu'on ne trouve qu'uniquement en RDC ?*	Oui/Non
225. Bokanisi ete bokoki kobetela yango ? Pona nini ? *Pensez-vous qu'il faut le conserver ? Pourquoi ?*	Oui/Non
226. Boyebi masolo oyo ezali likolo ya mikomboso (ntango ya bakoko) ? *Connaissez-vous des histoires, des légendes sur le bonobo ?*	

IV APPENDIX IV: TREES SPECIES PREFERRED FOR NEST BUILDING

Family	**Scientific name**
Flacourtiaceae	Oncoba mannii Oliv.
Olacaceae	Strombosia pustulata Oliv.
Olacaceae	Heisteria parvifolia Sm.
Olacaceae	Strombosia grandifolia Hook.f.
Olacaceae	Strombosiopsis tetrandra Engl.
Euphorbiaceae	Plagiostyles africana (Müll.Arg.) Prain
Euphorbiaceae	Uapaca guineensis Müll.Arg.
Chrysobalanaceae	Parinari excelsa Sabine.
Ebenaceae	Diospyros sp1
Meliaceae	Entandrophragma sp
Irvigiaceae	Irvingia gabonensis (Aubry-LeComte ex O'Rorke) Baill.
Annonaceae	Anonidium mannii Oliv.
Anacardiaceae	Sorindeia africana Engl.
Fabaceae (caesalpinoideae)	Brachystegia laurentii (De Wild.) Louis ex Hoyle
Fabaceae (caesalpinoideae)	Daniellia pynaertii De Wild.
Fabaceae (caesalpinoideae)	Erythrophleum suaveolens (Guill. & Perr.) Brenan
Ochnaceae	Rhabdophyllum arnoldianum (De Wild. & T.Durand) Tiegh.
Lecythidiaceae	Petersianthus macrocarpus (P.Beauv.) Liben
Pandaceae	Microdesmis cf. puberula
Chrysobalanaceae	Marantes glabra
Dichapetalaceae	Dichapetalum sp1
Annonaceae	Polyalthia suaveolens Engl. & Diels
Annonaceae	Piptostigma fasciculatum De Wild.
Sapindaceae	Eriocoelum microspermum Gilg ex Radlk.