ANNEX 1: COPY OF THE PUBLICATIONS


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Questions arising about the future of ecosystem services in tropical countries highlight particular plant species (BIOSERF project funded by the Belgian Science Policy: Sustainability of tropical forest biodiversity and services under climate and human pressure). In this study, we model a set of 11 selected African tree species including several Congolese species with logistic regression, MaxEnt and CARAB models. The two niche-based models rather properly simulate the ranges obtained with the alpha-hull polygon method. CARAB correctly simulates the range of the evergreen species but not of the deciduous trees. We examine how physiological knowledge could be used to improve the model. In particular, we conclude that bud dormancy breaking representation has to be upgraded in the model because this process is likely to control the range of the species. It should act in combination with the specific bioclimatic constraints controlling the hydrological and thermal stress and the germination. Additionally, we examine the evolution of the ranges at the 2050 horizon using one of the most recent socio-economic scenarios.

Dynamic vegetation models (DVMs) are process-based models that simulate plant environment (soil water, light intensity at various heights, etc.) and plant physiology (transpiration, CO2 fixation, photosynthesis, respiration, carbon allocation, etc.) from climate variables, soil properties, and elevation. They can be run at various scales, from global to regional or even local scale, and simulate the growth of plant functional types (PFTs), of biological activity groups (BAGs) or of species. A model like CARAB is able to simulate PFTs and BAGs growth (occurrence and productivity) with rather good accuracy for Western Europe. For the future, the simulations confirm that the physiological effect of CO2 concentration change is dramatic but not easily foreseeable because it depends on overall fertility of the site (Dury et al., 2012). From this conclusion, spatial and temporal variations of fertility

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MOELLING SEED DISPERSAL AND TROPICAL FOREST REGENERATION: AN APPLICATION TO STAUIDA KAMERUNENSIS IN THE WWF LAKE TELE - LAKE TUMBA LANDSCAPE IN DR CONGO

Contact Email address/Address de contact: alain.hambuckers@ulg.ac.be

COOS William, University of Liége, Liége, Belgique DURY Marie, University of Liége, Liége, Belgique TROLLIET Frauds, University of Liége, Liége, Belgique HUYNEN Marie-Claude, University of Liége, Liége, Belgique FRANÇOIS Louis, University of Liége, Liége, Belgique

UNSUSTAINABLE HUNTING AND SLASH-AND-BURN FARMING IN TROPICAL FORESTS CAN LEAD TO THE EMPTY FOREST SYNDROME. IT IS CHARACTERIZED BY THE LOSS OF KEY SPECIES ESSENTIAL IN THE MAINTENANCE AND REGENERATION OF THE FOREST. Indeed the main mechanism of this regeneration is seed dispersal, which for tropical trees is usually driven by animals, and the alteration of this process through a reduction of the disperser population may have serious consequences on forest composition. Computer models are powerful tools to study these processes, not only towards a better understanding of the key mechanisms controlling tropical forest regeneration, but also with the aim of optimising forest management and exploitation to reach a better equilibrium between tropical tree species and their seed dispersers.

This study describes a seed dispersal module ultimately developed to analyze the regeneration of the rainforest in the WWF Lake Tele – Lake Tumba Landscape in RD Congo (BIOSERF project funded by Belgian Science Policy). The module has been developed to upgrade the CARAB dynamic vegetation model, which is used in the BIOSERF project. Data are derived from a field study in which we analyzed seed dispersal of a common tree species (Staudia kamerunensis) and we determined the community of its main dispersers (largely dominated by the hornbill Bycanistes abolittus). Additional data (density of S. kamerunensis, habitat use and retention time in the digestive tract of hornbills to simulate dispersal kernel) were obtained from literature and satellite images. Different simulations were performed to represent seed rain over time and a survival rate was applied to show the regeneration. The module was able to provide a percentage of re-colonization of degraded plots. In the end, this result was compared to field studies, which provide close percentage of re-colonization.

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GENERAL SOLUTIONS FOR FORESTRY PROBLEMS IN AFRICA

Contact Email address/Adresse de contact: yaredxavier@gmail.com

BEYENE KIDANEARIAM Yared, Addis Ababa Youth Association (AYA), Addis Ababa, Ethiopia

The forest resources in Africa have direct and indirect contributions to the environmental, economic and social welfare of Africans. Forests also contribute an important and irreplaceable role in the continent’s environmental, social and economic development. If we properly managed and exploited them, they can protect climate change, soil, water catchments, biodiversity besides to economic benefits. There are general solutions now in after for forestry problems in Africa:

1. Protecting Forest Resources

The life of millions of people in Africa depends on the rainforest found in different parts of the continent. The African Union Commission (AUC) and all Africans jointly and several protect forest resources in Africa by

1.1. Reducing the rate of forest degradation and loss of bio-diversity through protected area management, promoting involvement of the community in forest conservation and development on the basis of benefit sharing with the community. Avoid exclusion of local communities from forest management activities.

1.2. Allocation of the continent’s forest resources in to protected forest areas, production of forests and manage according to management plan.

1.3. Achieving sustainable use of forest by the local inhabitants and protect them from natural and man made calamities.

1.4. Encouraging joint forest management, intensifying forest conservation in highlands, lowlands and pastoralist area and improve forest policies.

1.5. Supporting a network of effectively managed protected areas and promotes women’s participation in forest conservation.

1.6. Organized major logging companies to improve forest management practices.

2. Conserving Forests

Most of Africans’ rural and urban poor people depend on their livelihoods almost entirely on natural resources specifically on forests. The AUC and other stakeholders have a duty to conserve forests in Africa and in surroundings by

2.1. Addressing the links between forests and urban-rural poverty alleviation in Africa by developing alternative business plans that create revenue.
Modelling the Congo basin ecosystems with a dynamic vegetation model

Marie Dury (1), Alain Hambuckers (2), Franck Trolliet (2), Marie-Claude Huynen (2), Damien Haineaux (2), Corentin M. Fontaine (3), Adeline Fayolle (4), and Louis François (1)

(1) Unité de Modélisation du Climat et des Cycles Biogéochimiques, University of Liège, Belgium (marie.dury@ulg.ac.be), (2) Unité de Biologie du Comportement, University of Liège, Belgium, (3) Groupe de Recherche Interdisciplinaire en Développement Durable, University of Namur, Belgium, (4) Unité de Gestion des Ressources Forestières et des Milieux Naturels, University of Liège, Belgium

The scarcity of field observations in some parts of the world makes difficult a deep understanding of some ecosystems such as humid tropical forests in Central Africa. Therefore, modelling tools are interesting alternatives to study those regions even if the lack of data often prevents sharp calibration and validation of the model projections. Dynamic vegetation models (DVMs) are process-based models that simulate shifts in potential vegetation and its associated biogeochemical and hydrological cycles in response to climate. Initially run at the global scale, DVMs can be run at any spatial scale provided that climate and soil data are available. In the framework of the BIOSERF project ("Sustainability of tropical forest biodiversity and services under climate and human pressure"), we use and adapt the CARAIB dynamic vegetation model (Dury et al., iForest - Biogeosciences and Forestry, 4:82-99, 2011) to study the Congo basin vegetation dynamics. The field campaigns have notably allowed the refinement of the vegetation representation from plant functional types (PFTs) to individual species through the collection of parameters such as the specific leaf area or the leaf C:N ratio of common tropical tree species and the localisation of their present-day occurrences from literature and available database.

Here, we test the model ability to reproduce the present spatial and temporal variations of carbon stocks (e.g. biomass, soil carbon) and fluxes (e.g. gross and net primary productivities (GPP and NPP), net ecosystem production (NEP)) as well as the observed distribution of the studied species over the Congo basin. In the lack of abundant and long-term measurements, we compare model results with time series of remote sensing products (e.g. vegetation leaf area index (LAI), GPP and NPP). Several sensitivity tests are presented: we assess consecutively the impacts of the level at which the vegetation is simulated (PFTs or species), the spatial resolution and the initial land cover (potential or human-induced). First, we show simulations over the whole Congo basin at a 0.5° spatial resolution. Then, we present high-resolution simulations (1 km) carried out over different areas of the Congo basin, notably the DRC part of the WWF Lake Tele – Lake Tumba Landscape. Studied in the BIOSERF project, this area is characterized by a forest-savannah mosaic but also by swamp and flooded forest.

In addition, forward transient projections of the model driven with the outputs of about thirty global climate models (GCMs) from the new Coupled Model Intercomparison Project Phase 5 (CMIP5) will permit to outline the likely response of carbon pools to changing climate over the Congo basin during the 21th century.
Une approche participative des interactions entre les hommes, femmes et la biodiversité de la forêt tropicale dans la région du lac Tumba, RDC

Halleux, C.; Dendoncker, N.; Huyven, Marie-Claude; Trottlet, Franck; Van Damme, P.; Baet, A.; Fontaine, C.; François, Louis; Lafontaine, R.-M.; Beudels, R.; Isumbisho, P.; Baloqizi Karhagomba, L.; Bukobero, L.

Date de publication : 2012

Organisme(s) subsidiant(s) : BELSPO

Intitulé du projet de BIOSERF recherche :

Public cible : Chercheurs ; Professionnels du domaine ; Etudiants

URL permanente : http://hdl.handle.net/2268/136398

Commentaires :

International Conference on Governance of Collective Natural Resources

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DOES BIODIVERSITY MATTER? STATE-OF-THE-ART AND FUTURE DIRECTIONS OF FUNCTIONAL BIODIVERSITY RESEARCH IN FORESTS

Contact Email address/Adresse mail de contact: wika@hamburg.de

VENETIEN Kria, Ghent University, Department of Forest and Water Management, Forest & Nature Lab, Gent, Belgium

Forests are biodiversity hotspots worldwide with 70 to 80% of terrestrial biodiversity being linked to forested landscapes. However, deforestation, forest degradation and fragmentation lead to an increasing rate of species extinctions. Hence, predicting the consequences of changes in species numbers, in distribution patterns of taxa, and of shifts in dominance, has become a major challenge for community and ecosystem ecology. However, until now the relationships between biodiversity and ecosystem functioning in forests have been largely underestimated.

Recent research provides increasing evidence that this biodiversity crisis is indeed not only an ethical problem, but a potentially threat to ecosystem processes and services. But until now the relationships between biodiversity and ecosystem functioning in forests have been largely underestimated. Nevertheless, research on this topic could give an answer to important issues for sustainable forest management. Will mixed forests be more productive, have more pronounced microclimate, have more control over energy, water and mineral fluxes, be more resistant to disturbances, and/or host a higher diversity of associated species? Although these questions have puzzled forest ecologists for a very long time, no unequivocal answers have been formulated yet due to methodological problems and the lack of a rigorous conceptual framework. In this lecture I will provide an overview of the mechanisms behind biodiversity – ecosystem functioning relationships. Next, the state-of-the-art of functional biodiversity research in forests will be presented by listing the different research approaches, and the main results that have been obtained so far. I will end by pointing at directions for future research.

THE LEAKY N CYCLE OF TROPICAL FOREST – EVIDENCE FROM NYUNGE FOREST

Contact Email address/Adresse mail de contact: pascal.bouvier@kuleuven.be

BOECKX Pascal, Ghent University, Ghent, Belgium

NYUGUNGU landry, Université Catholique de Bukuva, Bukavu, DR Congo

HUYGENS Dries, Ghent University, Ghent, Belgium

GHANABI GHEISI NASIR, Ghent University, Ghent, Belgium

BUTTERBACH-BALDI Klaus, ULR & Karlsruhe Institute of Technology, Karlsruhe, Germany

CHRISTIAN Werner, Biodiversity and Climate Research Centre, Frankfurt am Main, Germany

KEISE Ralf, Karlsruhe Institute of Technology, Karlsruhe, Germany

ROORBECK Dries, IITA, Nairobi, Kenya

RUTTING Tobias, Gothenburg University, Gothenburg, Sweden

WALANGALULU Jean M., Université Catholique de Bukuva, Bukavu, DR Congo

Nitrogen (N) is mostly limiting gross primary productivity in pristine ecosystems. In forest N input originates from atmospheric N deposition, biological N fixation and decomposition of leaf litter. Surprisingly, humid tropical forests simultaneously develop high N bioavailability and sustained loss of bioavailable N forms. This apparent up-regulation of the N cycle has been conceptually explained via a model wherein biological N fixation is operating in biogeochemical N-poor niches, decoupled from N-rich soil condition (Hedin et al., 2008). To better explain this apparent up-regulation of the N cycle in tropical forests, process-based understanding of soil N transformations, in geographically diverse locations in the tropics, remains paramount. However, field based experimental evidence is very limited and entirely lacking for humid tropical forests on the African continent. We will report on field-based experiments from the Nyungwe tropical forest in Rwanda. During a period of two years N-deposition and N-leaching data were collected in situ N labeling experiments have been carried out and gaseous N losses were modeled via DNDC-Tropica.

Applying a 15N tracing model we confirmed that this tropical mountain forest soil is indeed characterized by an open N cycle, i.e., high gross N mineralisation is followed by high nitrification rates, ammonia (NH4+) production via FAAxox and plant N uptake is dominated by NH4+. In addition the calculation was estimated to emit 27 - 53 kg N-DN-N ha-1 yr-1 and 8 - 50 kg NO3-N ha-1 yr-1, corroborating high gaseous N losses from previous studies in tropical forests. This study provided on the one hand new process understanding of soil N cycling in humid tropical forests and added geographically independent evidence that humid tropical forests are characterized by high N dynamics sustaining bioavailable N loss.

References

Modeling the future range and productivity of African tree species perspectives and limits

Contact Email address/Adresse mail de contact: elain.hambuckier@ulg.ac.be
There remains a lack of information on the future of plant species in many parts of Africa under the threats of climate change with the exception of the mountainous areas. Models are valuable tools to examine this problem because they permit to extrapolate basic information as simple as species occurrence coming from a restricted number of localities to the entire continent. Niche-based models, like logistic regression or MaxEnt, easily allow fitting empirical relationships between environmental variables related to climate and possibly to soil properties. They produce probabilities of occurrence for the present with good accuracy (calibration phase). Projections for the future are made by switching the explanatory data set with future conditions. These models however are limited by the fact that it is almost impossible to integrate physiological response to increasing CO2 air concentration.

Dynamic vegetation models (DVMs) are process-based models that simulate plant environment (soil water, light intensity at various heights, etc.) and plant physiology (transpiration, CO2 fixation, photosynthesis, respiration, carbon allocation, etc.) from climate variables, soil properties, and elevation. They can be run at various scales, from global to regional or even local scale, and simulate the growth of plant functional types (PFTs), of biological affinity groups (BAGs) or of species. A model like CARIB is able to simulate PFTs and BAGs growth (occurrence and productivity) with rather good accuracy for Western Europe. For the future, the simulations confirm that the physiological effect of CO2 concentration change is dramatic but not easily foreseeable because it depends on overall fertility of the sites (Dury et al., 2009; Kroner, 2011). From this conclusion, spatial and temporal variations of fertility would have to be introduced in modelling studies to reach more operational conclusions.

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MODELLING SEED DISPERSAL AND TROPICAL FOREST REGENERATION: AN APPLICATION TO STAUDTIA KAMERUNIENSIS IN THE WWF LAKE TELE – LAKE TUMBA LANDSCAPE IN DR CONGO

Contact Email address/Adresse mail de contact: alain.hambuckers@ulg.ac.be

COOS Wiliam, University of Liège, Liège, Belgique
DURY Marie, University of Liège, Liège, Belgique
TOSSO Fabian, University of Liège, Liège, Belgique
TROLLIET Francois, University of Liège, Liège, Belgique
HUYSEN Marie-Claude, University of Liège, Liège, Belgique
HAINEAUX Damien, University of Liège, Liège, Belgique
FAYOLLE Adeline, University of Liège, Liège, Belgique
FRANCOIS Louis, University of Liège, Liège, Belgique

GENERAL SOLUTIONS FOR FOREST PROBLEMS IN AFRICA

Contact Email address/Adresse mail de contact: bayenebureya@gmail.com

BEYENE KIDANE MARIAM, Taddis Ababa Youth Association (AMVH), Addis Ababa, Ethiopia

The forest resources in Africa have direct and indirect contributions to the environmental, economic and social welfare of Africans. Forests also contribute an important and irreplaceable role in the continent’s environmental, social and economic development. If we properly managed and exploited them, they can protect climate change, soil, water catchments, biodiversity and to economic benefits. There are general solutions more in after for forestry problems in Africa:

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2.1. Addressing the links between forests and urban-rural poverty alleviation in Africa by developing alternative business plans that creates revenue.
The objective of the BIOSERF project is to assess the sustainability of a tropical humid forest ecosystem and the local human communities in southern Congo under future climate, demographic and societal changes. The project focuses on the interactions between flora, fauna and local human population to understand the processes affecting biodiversity and ecosystem services in tropical humid areas, with the objective of setting up mechanisms to preserve local biodiversity. In close collaboration with a local NGO, it will use a dynamic vegetation model (CARAIB) which will be integrated within an agent-based model, to analyze the impacts of different ecosystem services in a tropical humid area, e.g. the production of medicinal plants, of wood and other forest products, or the services provided by the building of natural reserves. The vegetation model will be upgraded to take into account the process of regeneration of several plant species, selected for their use by local human populations, through a quantitative and qualitative description of plant dispersal by the animal community. To do so, a selection of five tree species frequently or traditionally used plants through dispersal by the animal community. These species will allow identifying the main dispersers and the pattern of seed shadow they generate. Integrated into the CARAIB model, these results will allow figuring how the evolution of the dispersal community under pressures of climate change, habitat loss and hunting, but also potentially placed under managed protection could affect the services available to the human community.

Organisme(s) subsidiant(s): Fonds de la Recherche Scientifique (Communauté française de Belgique) - F.R.S.-FNRS
Public cible: Chercheurs ; Professionnels du domaine ; Etudiants
URL permanente: http://hdl.handle.net/2268/136400
Commentaires: Adaptability to Climate Change and Attaining the Millennium Development Goals for Tropical Ecosystems

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FMU 10.944 and on the farmland was realised with the aim of bringing out an in-depth knowledge on the diameter structure, phenology of defoliation, flowering and fruiting as well as the dissemination of the diaspores.

This study was carried out in a natural forest and cultivated 365 species that 47% belong to 55 ev- engram species, its foliation is always present inde- pendent of the climatic seasons the size of fruits does not restrain the species to baronchothy colonial types such as zoochory and anthropoph- orny been observed blossom and fructification take place once a year flower and fruit yield have been different at the leaf of the branches trees and pop- ulation the distribution of trees by diameter classes revealed that the species regenerates easily under the wood but the follow up of the individuals is weak.

KEY WORDS: A. FLORIBUNDA, DEP- UTATION, FLOWERING, FRUSTRICA- TION, NATURAL REGENERATION.

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OSTRACODA (CRUSTACEAE) FAUNA OF CONGO RIVER (AFRICA) AND AMAZON RIVER (BRAZIL) CATCHMENTS

Contact Email address/Adresse mail de contact: jo- nathigoud@gmail.com

HIGUITI Janet, Universidad Estatal de Maringá, Brazil &Royal Belgian Institute of Natural Sciences, Brussels, Belgium
MARTENS Koen, Royal Belgian Institute of Natural Sciences, Brussels, Belgium &University of Ghent, Biology, Ghent, Belgium

About 2000 species of recent, non-marine Ostracoda have been described from diverse aquatic environments in the world, of which 275 species (122 endemic) in 56 genera (11 endemic) are known from South America, against 455 species (424 en- demic) in 73 genera (54 endemic) from Africa (based on the counts in the FAUNA network – Martens et al., 2008). In spite of some recent concerted taxonomic activity, the ostracod fauna of both continents re- mains little known. In South American environments, rich pleistocene communities have developed in the rock systems of floating macrophytes, especially in the native Eichhornia crassipes, which meanwhile has become a very common invasive macrophyte species on other continents, including Africa.

Here, we analyse the biodiversity of ostracods from Congo and Amazon Rivers catchments. Ostracoda were collected from 16 environments of the Congo River and the Amazon River basin in 2010 and 2011, respectively. Floating vegetation was hand collect- ed, and roots were thoroughly washed in a bucket to remove the ostracods. The rest were washed in a hand net (mesh size c. 160 μm). The material was preserved in 70% ethanol. Preliminary results recorded 26 taxa of ostracod species in the Ama- zon and 31 species in Congo. Many species of both catchments are new to science. We hypothesized that the introduced Eichhornia in Congo might also have introduced some South American ostracod species, but this appeared not be the case. Ostracod communities in Congo and Amazon were thoroughly dissimilar and all species are mostly likely autochthonous. It appears that local invertebrate faunas have adapted to the alien plant species and exploit the opportunities presented by these form- ing invasive Eichhornia.

Reference

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PREMIERS INVENTAIRES DE BIODIVERSITE DANS LA RESERVE DE NGIR (EQUATEUR)

Contact Email address/Adresse mail de contact: hervi.robin@naturalescences.be

ROBERT Henri, Royal Belgian Institute of Natural Sciences, Brussels, Belgium
BEULDERS Roseline, Royal Belgian Institute of Nat- ural Sciences, Brussels, Belgium
LAFONTAINE René-Marie, Royal Belgian Institute of Natural Sciences, Brussels, Belgium
BANKANZA Michel, WWF, Mbundaka, RD Congo
FUMOTOMO Remi, IUCN, RD Congo
KARONDO Marius, IUCN, RD Congo
BOTEFA Clement, IUCN, Mbundaka, RD Congo

Dans le cadre du projet BIOSEF (Belgique), l’équipe de la Biologie de la Conservation (O.D. Milieux Na- turais) de l’Institut Royal des Sciences Naturelles de Belgique a organisé une mission d’inventaire dans les forêts tropicales humides du bassin de la RD Congo. Le principal objectif du projet BIOSEF est d’identifier les divers services écosystémiques que les forêts tropicales peuvent fournir aux socié- tations locales et une modélisation ultérieure des données recueillies sur le terrain permettra d’evalu- er la durabilité de ces services. Dans ce contexte Roseline C. Beulders-Jamar, René-Marie Lafontaine et Henri Robert ont récemment préparé et participé à une première série d’inventaire faunistique et botanique dans une aire récemment protégée: la réserve de la Nié, située au nord-ouest de Mban- daka, entre la rive Congole et la rivière Oboungou.

En collaboration avec des collègues du WWF- RD Congo et de l’Institut Congolais pour la Conser- vation de la Nature (ICCN), l’équipe a passé près d’un mois au cœur des forêts maniocagèuses de la région et a utilisé plusieurs techniques et pro- tocooles d’évaluation de la biodiversité locale. Une attention particulière a été portée sur les inventaires ornithologiques et mammalogiques ainsi que sur la description des habitats naturels et des différentes formations végétales rencontrées dans cette ré- gion peu prospectée et encore fort méconnue. Les oiseaux et les mammifères jouent, en effet, un rôle important notamment dans la dispersion des graines et sont par conséquent des acteurs indis- pensables de ces processus de régénération des forêts tropicales.

Près de septante pourcent (75 %) de l’espèce de la for- faune potentiellement observable ont été détectés et la présence de bon nombre de mammifères a été observée ou repérée grâce une série d’anémiques menées auprès des chasseurs et des populations locales. Il est à noter que les chercheurs de ces espèces recensées (oiseaux et mammifères) durant cette mission n’avaient jamais été reperto- rées dans cette zone auparavant. Ces nouvelles données apportent donc des informations com- plémentaires importantes sur la distribution de ces espèces.

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AGRICULTURAL INTENSIFICATION IS A STRAT- EGY FOR CLIMATE MITIGATION IN GHANA: AN EVALUATIVE STUDY OF THE COCOBOG HIGH

TECH PROGRAM, RURAL INCOMES, AND FOR- EIGENHUIS IN THE BIA (JUABOS) DIS- TRICT OF G

Contact Email address/Adresse mail de contact: bvanlanwee@cgiar.org

VANLANWEE Bernard, IITA, Nairobi, Kenya GOCKWOKIN JIM, IITA, Ghana
MULERFJAN Sander, IITA, Ghana
ROBLOGIO Valentina, ICRAF, Nairobi, Kenya
FREDDEY ASHYEAM Nana, IITA, Ghana

In the humid tropics of West Africa the expansion of extensive low input agriculture has resulted in significant deforestation resulting in the loss of bio- diversity and greenhouse gas emissions. The inten- sification of agricultural systems is envisioned as a fundamental but not sufficient solution for both the conservation of the remaining West African Guinea rain forest and smallholder income growth. A recently conducted study of cocoa-based tree crop farming systems in the Western region of Ghana reveals the importance of a multidimension- al policy approach for concurrently reducing defor- estation and intensifying production. A set of poli- cies by the Ghana marketing board is estimated to have increased cocoa yields thousandfold from 2000 to 2010 with 8% of the mean yield increase attribut- ed to the adoption of mineral fertilizers by small- holders. Remote sensing quantified the land use transations between forest and agricultural use and found that the rate of deforestation due to agricultural use had reduced by more than twofold from its level prior to intensification. The majority of new deforestation entailed encroachments on protected lands. Outside of these protected domains the for- est has been replaced by an agricultural mosaic of smallholder cropping systems.

The intensification of the cocoa farming systems resulted in substantial income growth approach- ing $3000 per household with many farmers in the study eager to increase the area under cultivation which is most easily achieved by further encroach- ment on protected lands. To achieve the dual objec- tives of environmental conservation and rural eco- nomic growth requires that intensification policies be accompanied by proscriptive land-use policies for protected lands with firm enforcement. Global value streams such as those being discussed un- der the UN-REDD framework from tropical forest assets could be used to support both sustainable intensification and forest protection. Recent a-
Nest Grouping Patterns of Bonobos (Pan paniscus) in Relation to Fruit Availability in a Forest-Savannah Mosaic

Adeline Serckx1,2,3,4, Marie-Claude Huynen1, Jean-François Bastin3,5,6, Alain Hambuckers1, Roseline C. Beudels-Jamar2, Marie Vimond1, Emilien Raynaud1, Hjalmar S. Kühn4,7

1 Behavioural Biology Unit, University of Liège, Liège, Belgium, 2 Conservation Biology Unit, Royal Belgian Institute of Natural Sciences, Brussels, Belgium, 3 École Régionale Post-Universitaire d’Aménagement et de Gestion Intégrés des Forêts et Territoires Tropicaux, University of Kinshasa, Kinshasa, Democratic Republic of the Congo, 4 Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany, 5 Landscape Ecology and Vegetal Production Systems Unit, Université Libre de Bruxelles, Brussels, Belgium, 6 Biodiversity and Landscape Architecture Unit, Gembloux AgroBio-Tech, University of Liège, Gembloux, Belgium, 7 German Centre for Integrative Biodiversity Research, Leipzig, Germany

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.

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 [1], as it permits higher-quality sleep by providing thermoregulation [2,3], reduced vulnerability to predators [2,4,5], more comfortable sleeping postures [4,6,7], and protection against pathogens [2,4,8]. The impact of environmental factors on the location of great ape nests has been the subject of a number of studies [6,9–18], and nest counts are frequently used to estimate ape population density [19–29]. However the functionality of great ape nesting sites in relation to the dynamics of their social organization has been much less well-documented [1]. Bonobo nesting behaviour has not been as thoroughly investigated compared to that of chimpanzees [6,16,30,31]. 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 [1], and that nests could serve as ‘taboo zones’ which can help bonobos avoid conflicts with group members [32]. 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 [1].

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) [33–36]. 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,
Bonobos’ Nest Grouping Patterns

whereas bonobo parties usually range in the same general area and tend to aggregate towards the evening [37]. 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 [37]), and numerous socio-ecological and environmental factors have been suggested to explain it: prolonged oestrus of bonobo females [30], close association between mothers and their adult sons [39], strong social bonds between females [40], high female social status [39,41], food patch size [30,42], availability of terrestrial herbaceous vegetation [43], and a feed-as-you-go foraging strategy (i.e., foraging during travel between fruit patches) [44]. 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 [37]. 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 Tai (Ivory Coast) were similar to those of bonobos inhabiting similar rainforest study sites [34]. 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 [37].

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 [45,46]. Her discovery changed our perception of the ecological limit of the species range, but bonobos within this habitat remained poorly studied. In 2003, 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) [47,48]. 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 [49]. 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 microhabitats. 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 [50], 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 [29,51], 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 unhabitated 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.

Materials and Methods

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 ethical 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).

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 Mpehu villages (16.41–16.56° E, 2.45–2.66°S, Figure 1). This region can be characterized as a forest-savannah mosaic. The altitude ranges from 300 to 700 m [48], and the mean daily temperature fluctuates around 25°C [52]. Annual rainfall oscillates around 1300–1600 mm, and is interrupted by two dry seasons in February and July-August [48]. 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 Mani Anita forests [48]. 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 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 [48].

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 focusing 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 1).

Rainfall. Between May 2011 and June 2013, rainfall was collected every twenty-four hours with a rain gauge at the Mbou-Bruxelles (“BRLU”), with reference IDs Bastin-Serckx herbarium and botanical library of the Université Libre de Bruxelles (“BRLU”), with ID Bastin-Serckx#1-474.

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 [53,54]. 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 1). 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 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 [54] and Buckland et al. [53]. The three observers were trained together and used a consistent methodology.

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 1). We developed a questionnaire based on the “Poverty and Environment Network (PEN) prototype questionnaire” [55]. We randomly chose a minimum of 30% of adults in all local villages and farms [56–58]. We interviewed a total of 201 adults (Table 3) 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.

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 [6,16]. We counted only fresh nests, i.e., nests built the previous night, with green leaves and traces of feces or urine [59]. 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.

Nest decay time. We conducted a nest decay rate study between August 2011 and May 2013, following previously validated methodology [54,60–63]. 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 [63]. 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 [59]; and finally, (v) disappeared: nest no longer recognizable [27]. We estimated mean nest decay time by using the method proposed by Laing et al. 2003 [61]. 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%.

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.

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’.

**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 [53,64]. 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 1). 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

**Figure 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.

doi:10.1371/journal.pone.0093742.g001
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, [65]). 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 [53]. We used a nest construction rate of 1.37 per day [66] and considered the proportion of nest-builders in the population to be 0.75 [6]. The construction rate and proportion of nest-builders were taken from the literature, as these can only be estimated by following habituated individuals.

**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 Lokosok&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 [67], 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 nest-builders and the nest decay time [53]. We used a nest construction rate of 1.37 per day [66] and considered the proportion of nest-builders in the population to be 0.75 [6]. The construction rate and proportion of nest-builders were taken from the literature, as these can only be estimated by following habituated individuals.

**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 [71,72] (Serckx unpublished data) or (ii) producing fleshy fruits [73–75]. 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’[76] 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 autocorrela-
tion, 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, dfit, leverage, and Variance Inflation Factors) and none of these indicated obvious influential cases or outliers or collinearity problems. Inspection of a q-q 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 site 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 [69] and the additional package car [76].

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 identified 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 (Model 1) or separately for the two forests in which each community was presumed to live (Model 2). 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 (Model 1, n = 9730) or in the forest (Model 2, 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:

\[ Human\text{\_forest\_use} = \frac{\sum_{activity} \sum_{village} (prop\_quest\_adult \ast nb\_adults\_village)}{forest\_part\_area} \]

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
Table 3. Socio-economic data.

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<th>Nb men</th>
<th>Nb women</th>
<th>Nb children</th>
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<th>Women</th>
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<th>Fishermen (W)</th>
<th>Fishermen (M)</th>
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<td>1897</td>
<td>201</td>
<td>119</td>
<td>82</td>
<td>60</td>
<td>76</td>
<td>75</td>
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</table>

The numbers beside the village names were used to locate them on the study site in Figure 1. 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.

doi:10.1371/journal.pone.0093742.t003
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 [6]) 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 nest 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 [69] and the additional packages gtools [77], car [76], and MASS [78]. 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 [79]. 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

Figure 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. doi:10.1371/journal.pone.0093742.g002

Figure 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 for the exact total effort of each year). Villages, roads and main forest paths are represented as in Figure 1. doi:10.1371/journal.pone.0093742.g003
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).

Results

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 4). 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). 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 3).

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 5, p = 0.050), a significant increase between 2012 and 2013 (Table 5, p = 0.043) and no significant difference between 2011 and 2013 (Table 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).

Variation in fruit availability between years

Fruit availability showed high variation between the two years of data collection (Figure 4), with large differences between plots as well (Figure 5). Analysis revealed that the overall effect of seasonality was significant (model including date, forests and their interaction vs. model including only forest, F2,106 = 3.14, p<0.05). The pattern of seasonality was similar in both forests (model including the interaction vs. model without it, F2,106 = 1.90, p = 0.15) and was significant in both forests (model with date and forest vs. model lacking date, F2,106 = 3.51, p<0.05). We also found that fruit availability was significantly higher in the Nkala Forest (Table 6, p<0.001). A representation of fruit availability with the fitted model is presented in Figure 6.

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 7, 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 ($\chi^2 = 11.42$, 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 7, p < 0.05, Figure 8) along with a trend for a positive influence of ‘density of suitable nesting trees’ (Table 7, p = 0.050), but no influence of the ‘fruit availability in the forest’ (Table 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 7).

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 6). 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 7). 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 (81.4 km, 111 km and 108.9 km 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 [80]. 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 4) and the non-significant difference in bonobo density between 2011 and 2013 (Table 5) 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 [81], with overlaps between community home ranges of the same bonobo population [82,83]. Also fruit availability in the Mpelu Forest was significantly lower than in the Nkala Forest ($p<0.001$, Table 6) 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 7). 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 [16,30]. 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 [6,16] (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 [48].

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 7). 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 [16]. 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 4). 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 [31,82]. 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 7), as bonobos from dense forests do [16,30] (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 [37].

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

| Table 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<sub>2,106</sub> = 3.51, p<0.05).

doi:10.1371/journal.pone.0093742.g006
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 [84], 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 [80]. 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.

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/) [85].

Figure 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. doi:10.1371/journal.pone.0093742.g007

Figure 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. doi:10.1371/journal.pone.0093742.g008
Table 7. Effect of the environmental factors on nest community size (Generalized Linear Model Models with negative binomial error structure and log link function).

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<th>P value</th>
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<td>0.249</td>
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<td>−0.388</td>
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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).

doi:10.1371/journal.pone.0093742.t007

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 help in the design of our study. This research would not have been possible without the help of our local field guides. Ciceron Mbueli 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 Brotocone 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.

Author Contributions

Conceived and designed the experiments: AS MCH JFB AH RBJ HSK. Performed the experiments: AS JFB MV ER. Analyzed the data: AS HSK. Wrote the paper: AS.

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45. Thompson JM (1997) The history, taxonomy and ecology of the Bonobo (Pan paniscus)


Référence : Dispersal and regeneration capacity of large-seeded tree species in a forest-savanna ...

Type de document : Colloques et congrès scientifiques : Communication poster
Discipline(s) : Sciences du vivant : Sciences de l'environnement & écologie
Pour citer cette référence : http://hdl.handle.net/2268/136399

Titre : Dispersal and regeneration capacity of large-seeded tree species in a forest-savanna mosaic in Western DR Congo
Langue du document : anglais
Auteur, co-auteur : Trolliet, Franck [Université de Liège - Ulg > Département de Biologie, Écologie et Évolution > Biologie du comportement - Éthologie et psychologie animale ]
Huyven, Marie-Claudie [Université de Liège - Ulg > Département de Biologie, Écologie et Évolution > Biologie du comportement - Éthologie et psychologie animale ]
Hambuckers, Alain [Université de Liège - Ulg > Département de Biologie, Écologie et Évolution > Biologie du comportement - Éthologie et psychologie animale ]

Date de publication : 2012
Peer reviewed : Oui
Sur invitation : Non

Nom de la manifestation : Islands in land- and seascape: the challenges of fragmentation
Date(s) de la manifestation : du 22 février au 25 février 2012
Organisateur(s) de la manifestation : Association for Tropical Biology and Conservation
Ville de la manifestation : Erlangen
Pays de la manifestation : Allemagne

Résumé : It is widely recognized that the Congo Basin is affected by numerous anthropogenic pressures. A number of studies proved that hunting and forest fragmentation diminish the diversity and abundance of large vertebrates, more specifically, of large frugivores. The depletion of these animals can directly affect large-seeded tree species as large seeds closely depend on the community of large frugivorous vertebrates for their dispersal. Thus, the disruption of animal mediated seed dispersal is thought to deeply impact the plant regeneration capacity. The forest-savanna mosaic situated in Western DR Congo is an ecotone characterized by naturally occurring forest fragments which are also subject to numerous anthropogenic pressures. Those are very likely to disrupt seed dispersal mechanisms and to alter forest regeneration processes. To date, few studies have considered the effect of such an ecosystem on plant-animal interaction dynamics such as seed dispersal, and none have been done in this region. This study will examine if the early stages of regeneration of the large-seeded tree species Annonidium mannii, namely the dispersal capacity and seedling establishment is affected by forest fragment size. We predict that the small fragment size will negatively affect the regeneration capacity of this species. To test this assumption, we will work along a gradient of forest fragment sizes to define the composition of the seed disperser community. For each disperser assemblage, we will evaluate the quantitative capacity of seed dispersal by combining direct focal observations and camera trapping. A literature review on each disperser species seed retention time and animal interaction dynamics such as predation will also evaluate the effect of seed ingestion by a presumably important seed disperser, the bonobo, Pan paniscus, on its germination capacity. Seeds will be collected from dung to evaluate the effect of seed ingestion on the rate and velocity of germination. Finally, we will study the predation pressure exerted on dispersed and non-dispersed seeds and seedlings by setting up two sets of seeds below the canopy of parent trees and away from any conspecific trees. One set will be dispersed unprotected to seed predators; another one will be enclosed in a cage and permit seeds to germinate, allowing us to evaluate the herbivores pressure on seedlings.

Organisme(s) subsidiant(s) : FNRS
Public cible : Chercheurs
URL permanente : http://hdl.handle.net/2268/136399
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Abstracts

5th Congress of the European Federation for Primatology
Antwerp, Belgium, September 10–13, 2013
Editors: Kristiaan D’Août, Jeroen Stevens, Antwerp, Belgium

Prevalence of Helminthes Infection among Non-Human Primates in Southwest Nigeria
Aderotimi Adejuyigbe, Babafemi Ogunjemite
Adekunle Ajasin University, Akungba Akoko, and Federal University of Technology, Akure, Nigeria
E-Mail: ogunjemitebg@conserveteam.org

Key Words: Zoological gardens · Parasitic infection · Season

We sampled three selected zoological gardens in southwestern Nigeria with the aim of documenting the prevalence of helminth parasite infections in their non-human primates and assessing the risk of transmission to humans. We subjected freshly voided faecal samples of the primates to diagnostic tests, namely modified formal ether sedimentation, flotation technique and larvae fecal culture method to facilitate helminth identification. Six helminths were identified in the primates. These were Taenia sp., Strongyloides sp., Heterodera sp., Trichuris trichuria, Ancylostoma duodenale and Ascaris sp. We observed the highest prevalence (40%) in the primates at Oyo Themes Parks and Gardens Zoo, followed by 16.6% in the primates at the University of Ibadan Zoo, while 0% was recorded in primates at the Obafemi Awolowo University Zoo. We recorded a high prevalence in the wet season and a low one in the dry season. We also observed that the zoo setting and the number of animals housed influenced the prevalence of helminth infections in the primates.

Gastrointestinal Parasites and Ectoparasites in Wild Javajin Slow Loris (Nycticebus javanicus)
Marlies Albers, Ivona Foitova, Abi Abinawanto, K.A.I. Nekaris
Little Fireface Project/Oxford Brookes University, Oxford, UK, Orangutan Health Project, Sumatra, and Department of Biology, FMIPA, University of Indonesia
E-Mail: albers.marlies@gmail.com

Key Words: Strepsirrhines · Nocturnal · Asia · Faecal flotation

We present the first results of analyses of faecal samples from the free-ranging Javan slow lorises (Nycticebus javanicus), for evidence of gastrointestinal and ectoparasites. Javan slow lo-
environments for effective psychological and physiological rehabilitation. Stereotypic behaviours were prevalent in all sanctuaries with most (>90%) orangutans in the study showing signs of these behaviours. Positional behaviours observed during rehabilitation could be improved through appropriate housing conditions and enrichment. The absence of opportunity to practice energy-efficient modes of travel, such as sway and ride, may be detrimental to fitness after release, especially in times of a negative energy balance. Improving conditions and monitoring methods used for orangutans during rehabilitation is vital to improving, and determining correctly, results after release.

Could Bonobos, *Pan paniscus*, Influence the Dynamic of Forest (Re)Colonization in a Forest-Savanna Mosaic?
Franck Trollet*, Adeline Serckx*, Roseline Beudels-Jamar*, Marie-Claude Huynen*, Alain Hambuckers*

*Behavioral Biology Unit, University of Liège, Liège, and aConservation Biology Unit, Royal Belgian Institute of Natural Sciences, Brussels, Belgium
E-Mail: franck.trollet@ulg.ac.be

Key Words: Bonobos - Seed dispersal - Forest regeneration - Mutualism - Forest-savanna mosaic

The forest-savanna mosaic of Western D.R. Congo is a particular ecotone with forest patches characterized by a high diversity of habitat types and a large proportion of transitional forests at edges. This ecosystem is highly disturbed by human activities, forests being degraded by slash-and-burn agriculture and savanna being used for cattle ranching, though it is inhabited by bonobos, *Pan paniscus*. We investigate how this large frugivore can participate in the natural regeneration of the forest in this fragmented ecosystem. We identified all seed species dispersed by faeces analysis (24 months, 1,977 faeces, 78 spp. identified). To assess the effect of gut transit on germination, we collected seeds in faeces and directly in fruits to conduct germination trials (1,391 seeds of 12 spp.). Habitat use by bonobos was identified with indirect signs over 180 km of transect inventories. Bonobos appear to disperse a large number of viable seeds by endozoocho-ry. Seed transit in gut can have a harmful, neutral or positive effect on germination capacity. Species benefiting from endozoochoery are characterized by varying light demands and shade tolerance. Percentage of germination and germination speed of the most important species in the diet (*Marantochloia leucantha*, *Aframomum* sp., *Musanga cecropioides*) is enhanced when ingested. Bonobos tend to avoid human activity and stay in more remote forested areas for sleeping, whereas direct observations and indirect signs indicate they are not restricted to primary forests but use forest edges and savanna matrix. Through the ingestion of a large number of seeds, the enhancement of germination and the deposition of those seeds to diverse habitats types, bonobos are likely to favour forest regeneration at early and late successional stages.
Référence : Dynamic of seed dispersal by large frugivores in a forest-savanna mosaic subject to a...

Type de document : Colloques et congrès scientifiques : Communication poster

Discipline(s) : Sciences du vivant : Sciences de l'environnement & éthologie

Pour citer cette référence : http://hdl.handle.net/2268/154279

Titre : Dynamic of seed dispersal by large frugivores in a forest-savanna mosaic subject to anthropic pressure in Western D.R. Congo

Langue du document : anglais

Auteur, co-auteur : Trolliet, Franck

Université de Liège - ULg > Département de Biologie, Écologie et Évolution > Biologie du comportement - Ethologie et psychologie animale

Serckx, Alain

Université de Liège - ULg > Département de Biologie, Écologie et Évolution > Biologie du comportement - Ethologie et psychologie animale

Huyven, Marie-Claude

Université de Liège - ULg > Département de Biologie, Écologie et Évolution > Biologie du comportement - Ethologie et psychologie animale

Date de publication : 5-avr-2013

Peer reviewed : Oui

Sur invitation : Non

Manifestation/périodique à portée internationale

Nom de la manifestation : Tropical organisms and ecosystems in a changing world

Date(s) de la manifestation : 02-05 April

Organisateur(s) de la manifestation : Society for Tropical Ecology

Ville de la manifestation : Vienna

Pays de la manifestation : Austria

Mots-clés : [en] seed dispersal ; zoochory ; forest regeneration

Résumé : [en] The Western Congolian forest-savanna mosaic is an ecotone subject to anthropogenic as well as natural fragmentation. Its forests have thus a considerable proportion of edges. This vegetation structure is likely to impact animal and plant communities and its dynamics such as animal mediated seed dispersal. Synergetically, activities such as bush meat hunting deplete large frugivores populations and thus decrease recruitment potential of the plants they disperse. Indeed, zoochory is known to be of great importance for tropical forests and a number of studies proved that large-seeded tree species closely depend on large frugivores for their regeneration. In such a context, we aim to understand how forest edges affect the dynamics of seed dispersal. More precisely, we wonder if the interactions between large seeds and their dispersers and predators are affected when closer to edges and how this can impact plant regeneration capacity. Also, we wonder if the dispersal and regeneration of large-seeded tree species depend on a few disproportionately important frugivores species. Bonobos, Pan paniscus, are among the largest frugivores left in the area and thus likely to be disproportionately important seed dispersers, though, their role as seed dispersers has yet been little investigated. We thus focus on the qualitative role for seed dispersal of the potentially keystone and umbrella ape species, the bonobo. To answer those questions, we study the main steps characteristics of large-seeded tree species regeneration process; namely quantitative seed dispersal, seed deposition pattern, germination capacity after transit in frugivores’ gut and, seed and seedling fate. By studying five different tree species at varying distances from forest edge, we aim to drive an inter-species comparison and to highlight the effect of forest edge on the regeneration process. We first quantify the seed production for each tree species and then evaluate the quantitative capacity of seed dispersal. By combining direct focal observations and camera trapping, we are able to highlight variations in composition of dispersers community and their respective contribution to seed dispersal. A literature review on each disperser species’ seed retention time and habitat use will allow the computation of the seed dispersal kernels. We will also evaluate the effect of seed ingestion by the bonobo on its germination capacity: seeds will be collected from dung to evaluate the effect of seed ingestion on the rate and velocity of germination. Finally, we will study the predation pressure exerted on dispersed and non-dispersed seeds and seedlings by setting up two sets of seeds below the canopy of parent trees and away from any conspecific tree. One set will be dispersed unprotected to seed predators; another one will be enclosed in a cage and permit seeds to germinate, allowing us to evaluate the herbivores pressure on seedings.

Organisme(s) subsidiant(s) : BELSPO

Institut du projet de Biodiversity recherche :

Public cible : Chercheurs ; Professionnels du domaine ; Etudiants

URL permanente : http://hdl.handle.net/2268/154279

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INFLUENCE OF HUNTING AND FOREST FRAGMENTATION ON ANIMAL-MEDIATED SEED DISPERSAL IN A FOREST-SAVANNA MOSAIC

Franck Trolliet, Pierre-Michel Forget, Marie-Claude Haynen, Alain Hambuckers

1. Behavioral Biology Unit, University of Liege, Belgium
2. Museum National d'Histoire Naturelle, Brunoy, France

Anthropogenic pressures can have cascading effect on plant-animal interactions. Hunting has been demonstrated as altering frugivore community composition in favor of small, body-sized frugivores, probably releasing interspecific competition for resources and influencing dynamics of animal-mediated seed dispersal. In addition, seed dispersal of bird-dispersed tree species are thought to be more resilient to forest fragmentation than species dispersed by large mammals. Here, we seek to understand how the interplay between hunting and fragmentation might influence seed dispersal of a plant species that is dispersed by primates and hornbills. We collected data in a forest-savanna mosaic in DR Congo across five sites varying in size and hunting pressure. We collected fruits below the canopy of 34 Santalium kamerunense (Myrtaceae) trees in order to evaluate the percentage of seed dispersal failure. Preliminary data analysis suggest that trees surrounded by more forest know higher percentages of efficient seed dispersal, and trees in sites with higher availability of S. kamerunense and higher abundance of primates know higher level of dispersal failure. Also, our first data suggest that abundance of primates is inversely related to that of hornbills which is positively related to higher rate of efficient seed dispersal. These results suggest a possible saturation effect, effective seed dispersal away from conspecific parent plants decreasing at sites with high availability of conspecific parent trees and high level of fragmentation. In addition, hunting might indirectly favor frugivorous birds and increase seed removal of bird-dispersed trees. Results will need to be further discussed in light of multivariate statistical analysis.
Use of camera traps for wildlife studies. A review

Franck Trolliet (1), Marie-Claude Huynen (1), Cédric Vermeulen (2), Alain Hambuckers (1)

(1) Université de Liège. Unité de Biologie du Comportement. 22, Quai Van Beneden. B-4020 Liège (Belgique). E-mail : franck.trolliet@ulg.ac.be

Received on March 13, 2013; accepted on February 11, 2014.

As human threats continue to impact natural habitats, there is an increasing need to regularly monitor the trends in large vertebrate populations. Conservation efforts must be directed appropriately, but field work necessary for data collection is often limited by time and availability of people. Camera traps are used as an efficient method to insure continuous sampling and to work in difficult to access areas. In the present study, we illustrate how this instrument is serving a diverse field of studies, such as animal behavior, population monitoring and fauna-flora interaction. By looking at the material and technical aspects of various models of camera trap for implementation in different field studies in animal ecology, we highlight the need to choose appropriate camera trap models for the target species and to set up solid sampling protocols to successfully achieve study objectives.

Keywords. Wildlife management, population census, animal behaviour, photography, traps, surveillance systems.

1. INTRODUCTION

The observed rapid decline in biodiversity, particularly among large vertebrates, throughout the world and the degradation of natural habitats hosting their populations are nowadays widely accepted as fact. It has therefore never been so important to understand how animal populations respond to modern threats and to document the functioning of ecosystems and intra-community interactions (Barrows et al., 2005) as to be able to implement appropriate management and conservation strategies. Regular updating of data on animal population density and on the degree of interspecies interactions is thus crucial to assess the spatio-temporal variations in populations and communities (Bouché et al., 2012). Camera traps are increasingly being used to study wildlife behavior and to conduct population estimations (Cutler et al., 1999; Long et al., 2008; O’Connell et al., 2011; Rovero et al., 2013). In the present study, we undertook a literature review on camera trapping studies, to present some technical aspects of commercially available camera models and provide an overview of sampling procedures and uses of camera trapping data.

2. MATERIALS AND METHODS

We conducted a general literature review on camera trapping using the SciVerse Scopus® database and Google Scholar®. The list of scientific papers consulted is not exhaustive and we do not claim to document all
the studies dealing with camera trapping. However, the list of documents consulted has enabled us to gain a good overview of the diversity of uses of camera traps over recent decades and of the main issues regarding sampling and data analysis. To conduct our study on the technical aspects of camera traps, we searched for camera trap brands sold and advertised on the Internet, as well as those used in recent scientific publications. We finally consulted TrailCamPro.com® (TrailCamPro.com, 2013) and Camera Traps cc®’s (Camera Traps cc, 2013) websites to retrieve technical information on the different models. Those two companies distribute together 18 brands of camera traps, which, to our knowledge, include the vast majority of camera trap models on the market. We could get the price for 61 different models (15 brands).

3. RESULTS AND DISCUSSION

3.1. Diversity of uses of camera traps

While remote photography has been used for more than a century, as presented by O’Connell et al. (2011), the automated camera trap as it is now known came onto the market at the end of the 1980s. Savidge et al. (1988) used a film camera connected to an infrared transmitter, which was able to shoot a picture as soon as the beam was interrupted by an animal. The system was automatic; after a picture had been taken, the film was reloaded and the camera was ready to take more pictures. This technique was used to identify predators visiting bird nests. Some years later, Carthew et al. (1991) and Kucera et al. (1993) listed the advantages of the automated camera trap system for an array of different field applications such as the study of activity patterns, intra-community interactions and large carnivore populations.

The first studies using camera traps for the purpose of large mammal conservation appeared in the 1990s and focused on the tiger, Panthera tigris (e.g., Griffiths, 1993; Karanth, 1995). Following the designation of P. tigris as endangered (Chundawat et al., 2011), one of the few “flagship” species listed on the IUCN red-list as early as 1986, these studies aimed at estimating home range span and population size. In this way, the use of camera traps to estimate population size greatly helped towards the conservation strategy for the species, and more generally, the monitoring of other threatened populations and communities. This use of camera traps was highlighted in a study on the activity patterns of mammal communities in Indonesian rain forests (van Schaik et al., 1996). The aforementioned early studies of the use of camera traps clearly illustrate the major advantages of using the technique, including being able to observe cryptic or elusive animals living in difficult to access habitats such as dense tropical forests. The use of camera traps has been revolutionary for studying the behavior of carnivores, as they are difficult to observe in their natural habitat due to their solitary nature. The technique has also been the subject of many other scientific papers since the beginning of the 21st century, revealing more about the ecology of rare, nocturnal animals, as well as those highly sensitive to the presence of humans or those living in large home ranges. A good example is the study of Moruzzi et al. (2002), which promotes the use of this technology for estimating carnivore distribution over large area and documenting species-specific habitat preferences.

A large proportion of conservation projects aim at managing threatened species, which implies to monitor populations over time and space. Thus, the majority of studies using camera traps nowadays appear to deal with the estimation of population density (e.g., Kalle et al., 2011; Garrote et al., 2012; Oliveira-Santos et al., 2012) or simply with the presence of species in given areas (e.g., Gil-Sanchez et al., 2011; Gray et al., 2011; Liu et al., 2012). Population characteristics are, to a greater or lesser extent, related to habitat use behaviors and habitat selection. Camera traps are useful for monitoring these aspects as they allow the estimation of home range size (e.g., Gil-Sanchez et al., 2011).

Some studies also deal with activity budget (e.g., van Schaik et al., 1996; Azlan et al., 2006; Gray et al., 2011; Oliveira-Santos et al., 2012) and a smaller number with more specific behaviors. For instance, Soley et al. (2011) reported the storing behavior of non-ripe fruits by a mustelidae, allowing the fruits to mature and to be consumed on future occasions; this is a specific behavior that is very hard to report without camera traps. Blake et al. (2010) studied the importance of salt licks for an animal community in a neotropical forest. Other studies have dealt with animal infant care (e.g., Charruau et al., 2012) or social interaction (Lopucki, 2007; Srbek-Araujo et al., 2012).

Camera traps are also increasingly being used to study plant-animal interactions such as seed dispersal and predation (e.g., Babweteera et al., 2010; Nyiramura et al., 2011; Campos et al., 2012; Koike et al., 2012; Pender et al., 2013). Moreover, focal observations need to be conducted in the study of the seed dispersal capacity of a given plant species, to list the frugivore species interacting with the plants and to define the quantitative contribution of each species in the process of seed dispersal. Camera traps are revolutionary in this regard, as they allow the identification of diurnal, nocturnal, and shy species that would not be seen using other methods such as direct observation. This is exemplified by the study of Nyiramura et al. (2011), who discovered that a species of rodent, the forest giant pouched rat Cricetomys emini (Wroughton, 1910), was responsible for the secondary dispersal of large seeds in an Afro-tropical forest.
3.2. Various technical aspects

More than a decade ago, Cutler et al. (1999) reviewed the advantages and disadvantages of using different film camera trapping equipment depending on the research objectives. Given the rapid advances in such technology, and the great variety of camera trap brands and digital models existing on the market nowadays, film cameras are competed. We present here the most important characteristics to take into account when choosing digital equipment. Characteristics such as trigger speed, detection zone, recovery time, night detection and battery consumption can vary greatly and have a significant impact on the types of data to be collected, such as the number of species detected and photographic rates (Hughson et al., 2010). Therefore, the choice of the most appropriate equipment is an important consideration.

Trigger speed. Trigger speed is the time delay necessary for the camera to shoot a picture once an animal has interrupted the infrared beam within the camera’s detection zone. This delay can vary from between 0.197 seconds for the Reconyx HC500 model to 4.206 seconds for the Stealth Cam Rogue IR model. Given the relatively narrow field of view of most camera trap lenses (42 mm), a slow trigger speed does not allow the photographing of fast moving animals (Scheibe et al., 2008). Thus, depending on the study goals and the target animal species, this time delay could be a crucial characteristic to consider. For example, if a camera is set up at a random location for a wildlife survey (Pereira et al., 2012), fast moving animals are likely to pass in front of the camera trap without stopping. In this case, a very reactive camera (with a fast trigger speed) would be necessary so it could shoot pictures of the detected animal before it left the camera’s field of view. In their comparative study of motion-activated cameras for wildlife investigation, Hughson et al. (2010) showed that some camera models (such as the fast Reconyx) can detect up to 86% more animal species. If the trigger speed is too slow, the camera may frame only a part of the animal or may even take empty pictures (pictures not showing what the beam has detected). Hughson et al. (2010) observed that, in comparison with other models, Leaf River cameras took the highest percentage of empty pictures. In the case of a camera installed in front of a bird nest, a bait, or a lure, visiting animals are more likely to stay longer (to either depredate the nest or interact with the bait) and to trigger more photographs (Garrote et al., 2012; Trolle et al., 2003) even if the camera has a relatively long time delay (low reactivity). Using lures to attract large carnivores can also allow a better identification of individuals (Gil-Sanchez et al., 2011). This risk of taking empty pictures does not only depend on the speed of the camera in taking a picture; the detection zone as well as the field of view are also primary criteria to consider.

The detection zone. The detection zone is the zone covered by the camera’s infrared beam in which movement can be detected. The zone varies in width and depth, depending on the model (Table 1). This criterion is probably the most important in determining detection rate (Rowcliffe et al., 2011) and therefore the number of pictures that will be taken in a given event.

The field of view. The field of view is the zone covered by the camera lens, and which appears on the pictures. The field of view is generally 42° but there are rare exceptions such as with the Leupold brand, which goes up to 54° (Table 1) and the Moultrie panoramic model, which covers an angle of 150°. The detection zone can vary greatly according to the brand and the model. We thus find models with a detection zone wider than the field of view (e.g. DLC Covert Extreme) and models with the detection zone narrower than the field of view (e.g. Cuddeback Ambush). Where the detection zone is wider than the field of view (Figure 1a), the advantage lies in being better able to capture fast moving animals. The limitation in this case is that the camera is also likely to take empty pictures when animals enter the detection zone (thus passing through the infrared beam and triggering the camera) but without making it into the field of view. Where the detection zone is narrower than the field of view (Figure 1b), the detection zone is centered relative to the field of view of the camera, and so the advantage can be seen in gaining well centered pictures. This can be very useful for the identification of large mammals. However, the limitation in this case is that relatively fewer pictures per visit can be shot, as animals are likely to occupy the field of view without crossing the detection zone. As presented in Table 1, the detection zone can be described with a given width (angle) and a given distance from the camera at which it will detect an animal. The detection distance of a camera is an important aspect to consider when focusing on animal species of either large or small body mass. Larger animals will be more easily detected at further distances than smaller animals. However, speed of movement seems to be less correlated with detection distance (Rowcliffe et al., 2011).

Recovery time. Recovery time is the amount of time necessary for the camera to prepare to shoot the next picture after the previous one has been recorded. Given the wide differences in recovery time for different models, this characteristic must be taken into account, as it can be a very important aspect for some study goals. The fastest camera can take a picture every 0.5 second (Reconyx HC 500 model) while the slowest
Use of camera traps for wildlife studies. A review

needs up to 60 seconds before taking a new picture of an animal still occupying the detection zone (Moultrie I-35s model). A camera able to take numerous pictures within a few seconds is very useful when needing to record a complete sequence of a feeding behavior and to note the number of fruits manipulated (Seufert et al., 2010). Also, having different views of a species of carnivore can greatly help in the process of identifying individuals (Trolle et al., 2003). By contrast, when the aim is only to carry out a diversity census, and only one picture per species is needed, a slow recovery time will be less problematic (Lantschner et al., 2012).

**Table 1.** Main technical characteristics of some camera trap models found on the market at the time of study — Principales caractéristiques techniques de modèles de pièges photographiques disponibles sur le marché au moment de l'étude.

<table>
<thead>
<tr>
<th>Brand</th>
<th>Model</th>
<th>Angle (°)</th>
<th>Distance (m)</th>
<th>Total area (m²)</th>
<th>Field of view (°)</th>
<th>Trigger speed (s)</th>
<th>Recovery time (s)</th>
<th>Resolution (Mpx)</th>
<th>Price range (USD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cuddeback</td>
<td>Ambush IR,V</td>
<td>7.6</td>
<td>11</td>
<td>8</td>
<td>42</td>
<td>5</td>
<td>0.25</td>
<td>NA</td>
<td>100-200</td>
</tr>
<tr>
<td>Scoutguard</td>
<td>SG565 IR,V</td>
<td>64.7</td>
<td>14</td>
<td>116</td>
<td>42</td>
<td>8</td>
<td>1.31</td>
<td>5.1</td>
<td>100-200</td>
</tr>
<tr>
<td>Moultrie</td>
<td>Panoramic 150 IR,V</td>
<td>150</td>
<td>NA</td>
<td>NA</td>
<td>150</td>
<td>8</td>
<td>0.95</td>
<td>6.2</td>
<td>200-300</td>
</tr>
<tr>
<td>Moultrie</td>
<td>I-35s IR</td>
<td>40</td>
<td>9</td>
<td>31</td>
<td>40</td>
<td>4</td>
<td>2.5</td>
<td>60</td>
<td>100-200</td>
</tr>
<tr>
<td>Wildgame Innovation</td>
<td>micro 6 IR,V</td>
<td>15.1</td>
<td>24</td>
<td>76</td>
<td>42</td>
<td>6</td>
<td>1.08</td>
<td>NA</td>
<td>100-200</td>
</tr>
<tr>
<td>Uway</td>
<td>UM562 IR,V,C</td>
<td>60.5</td>
<td>16</td>
<td>133</td>
<td>42</td>
<td>5</td>
<td>1.2</td>
<td>NA</td>
<td>300-400</td>
</tr>
<tr>
<td>Leupold</td>
<td>RCX-1 IR,V,C</td>
<td>48.2</td>
<td>10</td>
<td>42.5</td>
<td>54</td>
<td>8</td>
<td>0.93</td>
<td>2.8</td>
<td>100-200</td>
</tr>
<tr>
<td>Reconyx</td>
<td>HC 500 IR,V</td>
<td>33.4</td>
<td>18.6</td>
<td>100</td>
<td>42</td>
<td>3.1</td>
<td>0.2</td>
<td>1</td>
<td>400-500</td>
</tr>
<tr>
<td>Spypoint</td>
<td>Live 3G IR,V,I</td>
<td>41.9</td>
<td>17</td>
<td>110</td>
<td>42</td>
<td>8</td>
<td>2.7</td>
<td>10</td>
<td>400-500</td>
</tr>
<tr>
<td>Primos</td>
<td>Truth Cam X</td>
<td>45.2</td>
<td>13.7</td>
<td>456</td>
<td>42</td>
<td>1.3</td>
<td>1.2</td>
<td>5</td>
<td>200-300</td>
</tr>
<tr>
<td>Spypoint</td>
<td>Pro X</td>
<td>50</td>
<td>21</td>
<td>82.5</td>
<td>39</td>
<td>12</td>
<td>1.76</td>
<td>10</td>
<td>400-500</td>
</tr>
</tbody>
</table>

Bold characters indicate minima and maxima values found for each respective feature — Les caractères en gras indiquent les valeurs minimales et maximales trouvées pour chaque caractéristique.

**Nighttime pictures.** Nighttime pictures are very useful, as a wide range of taxa exhibit exclusive nocturnal activity. Two methods exist for camera trap night photography: incandescent flash and infrared light. Incandescent flash allows color pictures to be taken, which are generally of better resolution and quality. In this method, the amount of light captured is greater than with infrared light, and this can be critical for individual animal identification with the use of tags or natural marks. The limitation of this method is that the flash has a strong risk of scaring the animal (Sequin et al., 2003; Wegge et al., 2004). The infrared method is much more discrete, and is consequently very useful. Indeed, infrared cameras are more widely used by wildlife researchers than incandescent flash (Meek et al., 2012). The infrared light emitted by a series of Light Emitting Diodes (LEDs), which allows the camera to take black-and-white pictures, is hardly visible, although the red light of the LEDs is slightly visible. The most discrete and best solution to avoid scaring wildlife is to use a camera with a “no-glow” infrared flash (e.g., Bushnel Trophy Cam Black, Covert Black 60, Reconyx Hyperfire SM750, etc.). These cameras basically function in the same way as normal infrared cameras, shooting black and white pictures, but using LEDs that emit no visible light at all.

**Battery consumption.** Battery life can also be a crucial point to consider when preparing field work with camera traps, especially in remote areas. Several

![Figure 1](image-url)
characteristics need to be taken into account, such as the level of energy consumption in monitoring mode (when the camera is on and ready to take pictures if it detects movement) and the level of energy consumption for day and nighttime picture processing. These variables can vary greatly depending on the available models and will then vary in suitability depending on the habitat, the faunal composition present in the habitat and accessibility of the camera for the changing of batteries. For example, in the case of an arid habitat with few nocturnal species, no diurnal animals species, and difficult access, it would be better to use a camera that requires little energy in monitoring mode (as battery replacement is not as frequent) and for nighttime picture taking (as only nocturnal pictures are taken). Thus, battery life will be maximized. By contrast, in the case of a study taking place in a habitat with a high level of diurnal activity, a model that uses as little energy as possible for the processing of daytime pictures would be preferred. To extend battery life, some brands (e.g., Reonx, Scoutguard, Spypoint) also provide solar panels.

**Picture resolution.** Picture resolution, expressed in megapixels (Mpx), can vary more than 10 fold between models. Some Primos models take pictures of relatively low resolution (1.3 Mpx), whereas the Spypoint Pro-X takes pictures up to 12 Mpx. The advantage of lower resolution images is that they are less heavy to store so more pictures can be saved on a given memory card but, as having less pixels, they tend to have less details and be less precise. Given the large storage capacity of memory cards nowadays, we would recommend to select for models with higher resolution pictures and especially when individual identification is needed. A more detailed and precise picture can surely help being more accurate when looking at differences in fur patterns and marks to differentiate between individuals. However, the number of pixels advertised by manufacturers must be considered cautiously because it is not the only factor affecting picture’s quality. Image sensor, the component housing the pixels, is also very important in determining picture quality. For a given sensor size, an increase in the number of pixels is automatically associated with a decrease in pixel size. Yet smaller pixels are less sensitive to light, produce more noise (unwanted signal) and have a narrower dynamic range (i.e. the range of light intensities being captured) (Nakamura, 2005). It is therefore possible that a camera with fewer pixels but a larger sensor can produce pictures of higher quality than a camera with more pixels packed into a smaller sensor. Unfortunately, information on sensor size is so far poorly documented by manufacturers and would need further investigation and comparison.

**Camera cost.** At the time of writing, cameras traps cost from about USD 40 to 1,200, though more than half (54%) of the models compared in this study cost between USD 100 to 200. While the cheapest models can have an infrared flash (Hunter GSC35-20IR; Wildgame Innovations Red4), the most expensive ones can provide instant recovery time (Reonxyx) and are able to transmit pictures to cell phones or email (Reonxyx, Spypoint, Covert).

In addition to these main characteristics, various additional options serving specific research needs deserve consideration, such as the programmable burst mode allowing a series of up to five pictures to be taken of the same trigger event. Some cameras also record video, with or without sound, which can be useful for reporting on behavior repertoires (Scheibe et al., 2008).

### 3.3. Sampling methods

**Individual behavior.** Studies aiming to report on specific behaviors (feeding, reproduction, territoriality, social interaction, etc.) must direct sampling efforts to places of interests (e.g., salt licks uses: Blake et al., 2010; carcass scavenging: Bauer et al., 2005; specific habitat use: Sequin et al., 2003). To date, only few studies use camera traps data to study individual ranging behavior and estimate home range size (e.g., Gil Sanchez et al., 2011). Those often have to be completed with data collected using other protocols such as telemetry or indirect animal clues (feeding residuals, latrines, nests, etc.), which could explain the relatively small number of studies estimating home range size.

**Population level studies.** Studies dealing with population monitoring usually need stronger sampling effort and more complex sampling design. To do so, camera traps are increasingly used as an alternative to other more traditional methods. However, Gompper et al. (2006) proved camera traps to be inefficient at detecting small canids, which were otherwise detected by scat surveys, DNA analysis and/or snowtracking. When comparing different methodologies for the census of population diversity and abundance, camera trapping appear to be the most appropriate method in difficult to access areas compared to line transect or animal track survey (Silveira et al., 2003). Using camera traps to estimating population density can involve complex sampling design and be subject to numerous biases. Firstly, it is important to consider the bias of disproportionally samples more easily accessible or more attractive places for wildlife where detection probability is increased (Foster et al., 2011). The typical procedure to characterize an animal population in a given habitat consists of setting up the sampling effort (camera traps) in a random or systematic way (Foster et al., 2011). As explained by Rowcliffe et al. (2013),
In the case of seed dispersal studies, the camera is often set up so that the visual field includes the fruits or seeds of interest to maximize the chances of photographing frugivores (Seufert et al., 2010; Nyiramana et al., 2011). Variables of interest here are frequency of visits and the relative contribution of different animal species to seed removal.

From personal experience, two remaining limitations can, however, be identified. The first limitation occurs when the camera is positioned close to a fruit/seed sample so observers can easily quantify the number of items manipulated by animals. Here, the focal distance might be too close to being able to photograph all the animals visiting the area. The camera would then record a limited number of visiting species and individual animals. By contrast, the second limitation occurs when the camera is positioned to sample the widest area possible below a fruiting tree canopy, in order to systematically record all visiting animals. In this scenario, the focal distance might be too high to allow observers to see accurately the number of fruits/seeds manipulated. An alternative could be to set up two or more cameras at a same location to sample both the tree canopy’s shadow and a fruit sample on the floor. In the latter case, an alternative to evaluate species-specific contribution to seed removal could be to consider visit frequencies per species in the area. Additionally, seed removal rate can be indirectly assessed with an exclusion experiment (Culot et al., 2009).

**Data analysis.** The identification of individual animals is generally made by natural fur marks, injuries, and coloration patterns (dots, bands). This identification is, however, always subjective and likely to vary according to the observer and thus likely to affect the precision of estimates. To diminish the risk of mistaken identification, different computer models are able to help matching pictures of marked individuals (Kelly, 2001; Mendoza et al., 2011). Such tools allow observers to improve their ability to recognize individual animals and to be more precise in making population density estimates.

Individual identification is a crucial step in making population estimate. The spatially explicit capture-recapture technique is increasingly used for this purpose (e.g., Efford, 2011; Kalle et al., 2011; O’Brien et al., 2011). This technique assumes that animals are independently distributed in space and that they use defined home ranges. Thus, a model must be run, which considers, on the one hand, a population parameter (population density) and, on the other hand, a process of individual recognition. The detection process is itself driven by a mathematical function describing the probability of detecting an animal, which decreases as the center of a given home range gets further away from a camera trap (Kalle et al., 2011).

Camera trap data are also used to generate abundance indices and get quick insight into population size. However, the power of such indices is limited compared to true estimates of population density for different reasons. Firstly, variations in indices cannot necessarily be attributed to true variations in
population size. Indeed, to use and be able to compare such indices one needs to make the assumption that wildlife detectability is constant over time, space and between species, however, this is either not tested, nor true (Sollman et al., 2012). Secondly, those indices are rarely calibrated with the actual population and thus only give little information on the true dynamic of population size (Sollman et al., 2012). Moreover, a too low number of traps set up (replicas) does not allow the calculation of a confidence interval (variance) necessary to estimate the exactitude of indices (Azlan et al., 2006), though Bengsen et al. (2011) adapted a General Index Model able to account for variance when calculating population abundance indices.

Camera traps data such as species detection/non-detection can also be used in occupancy model (e.g., MacKenzie et al., 2003; Long et al., 2011) to predict species occurrence and determine population dynamic parameters. Such models generate detection probability data and thus prevent the recording of false absence. This has very helpful implications for monitoring elusive species for which observations are scarce.

4. CONCLUSION

Depending on the data to be collected, the target animal species and the type of ecosystem, it is essential to first choose the appropriate equipment to collect the data needed, as not all camera models will be suitable for a specific research objective. Given the increasing use of camera trapping by scientists, we believe that the available technologies should and will know improvements in the future. Higher image resolution resulting from larger sensor and more efficient infrared beam would allow a better identification of individuals, especially for marked nocturnal species. Even more discrete and faster cameras would prevent spooking animals and get more unblurred pictures. Next, the implementation of appropriate sampling protocols must be seriously considered. In a general way, we believe that homogenization of detection probability could improve the use of camera traps data by diminishing biases and allowing stronger inter-site and inter-species data comparison. This could be done:

– at the camera scale, by using camera models having similar features (detection zone, field of view, trigger speed, etc.),
– at the ecosystem scale by implementing standardized sampling scheme (number of cameras, spacing, and placement).

Having a standard sampling protocol would also permit more solid use of statistical models and interpretation of results. The use of computer tools to improve the scientific value of pictures is increasingly common but all does still not agree basic assumption requirements. Future development of computer tools for population density, abundance and site occupancy estimates would need to rely on empirical validated results on individual habitat use behavior and population dynamics.

Acknowledgements

This study took place in the context of the BIOSERF project funded by the “Politique Scientifique Fédérale Belge” (BELSPO).

Bibliography


Use of camera traps for wildlife studies. A review


(61 ref.)