Diversity of natural forest clearings in Central Africa and their importance for forest mammals and conservation

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von Frau Julia Metsio Sienne, geb. Geßner
geboren am 29.04.1982 in München

Gutachter: Prof. Dr. Rainer Buchwald
Zweitgutachter: Prof. Dr. George Wittemyer

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Abstract

Today, the Central African rain forest and its wildlife are under increasing threat due to growing resource extraction and human pressure. Protection of this unique ecosystem requires informed management. Therefore knowledge on the system including the mammal species inhabiting and altering it is necessary. Bais (natural forest clearings) have been recognised as key habitats for conservation attracting numerous large mammals and providing a ‘window’ on these elusive species’ life. Bai studies have provided essential knowledge on large mammals such as the African forest elephant (*Loxodonta africana cyclotis*) and the western lowland gorilla (*Gorilla gorilla gorilla*). But until now most of these studies have been restricted to single sites and little is known about the differences between bais.

The aim of this thesis was to contribute to a more thorough understanding of plant, mineral and animal aspects of bais diversity and their relevance for conservation and for large mammals in particular. This study took a broad approach surveying 17 bais within the Sangha Trinational Protected Area Complex (Central Africa) during the dry and the rainy season. Results revealed high heterogeneity between bais in respect of general features such as their size and soil moisture. Vegetation surveys were conducted at 14 of these bais. The high diversity of plant species within and between bais was demonstrated indicating that the bais’ vegetation contributes considerably to the overall diversity of the Central African rain forest.

The occurrence of medium-sized to large mammals was investigated using camera traps at seven bais. Concurrently, the study aimed to examine the potential of camera traps for mammal surveys at bais. During three to four weeks of recording at each bai, camera traps provided evidence for the occurrence of altogether 25 mammal species at the bais. The number of species registered at a particular bai represented 65 - 94 % of the mammals known to use it. Camera traps even recorded rare species and nocturnal activity patterns that were missed by direct observational studies. They demonstrated that many large mammals such as the African forest elephant visit bais preferably at night and thus underlined the importance of nocturnal surveys. Hence, evidence was provided that camera traps are cost-effective tools for species inventories and monitoring of medium-sized to large mammals visiting bais. The application of camera traps was recommended especially in remote areas as well as complementary to long-term studies conducting direct observations with the latter allowing more precise individual-based and behavioural data.

The objective of this thesis further was to identify potential factors influencing visitation rates of large mammals at bais. While acknowledging the importance of social factors and human pressure, this study focused on resources provided at bais such as soil, water and plants with respect to their nutritional value. Since forest elephants target soil and especially water at bais, the clay and mineral concentrations of these resources were examined at 15 bais. In comparison to surface water, significantly higher concentrations of nutritionally important minerals (Na, Cl, S, Zn, Ca, Mg, Mn and Fe) were found in water holes excavated by elephants. This demonstrates the importance of mineral rich water resources in bais. In contrast, no evidence was found that soil influences bai visitation since geophagy sites were not differentiated from control samples. Clay could not be identified as target for soil consumption at bais. In accordance with studies on water and soil resources used by mammals worldwide, results indicated that probably not a single mineral, but the composition of several minerals are driving the use of these resources. Finally, the present study revealed considerable differences in mineral concentrations of soil and water resources between bais.

Unlike elephants, western lowland gorillas target plants within bais showing high selectivity for particular plant species and parts. In order to examine this selective behaviour, 14 consumed and non-consumed plant species were collected at 16 bais for nutritional analysis. Consumed species showed significantly higher concentrations of Ca, K and especially Na than non-consumed plants while no differences were found in respect of macronutrients such as lignin and protein. Plant parts of the same species differed in their mineral concentrations reinforcing the assumption that within bais gorillas select for certain mineral compositions. The availability of feeding plants for gorillas and other large mammals was shown to differ distinctly between bais. Once more, this underlined the high heterogeneity of bais with important consequences for wildlife management.

Since bais represent key habitats for large mammals providing important mineral rich resources and considering their heterogeneity, an animal likely relies on several bais in an area in order to fulfil its mineral requirements. The protection of a bai mosaic allowing mammals access to a broad array of resources differing in their mineral content (qualitatively and quantitatively) should therefore be a conservation priority.

Zusammenfassung

Die Bedrohung des zentralafrikanischen Regenwaldes und seiner Tierwelt nimmt aufgrund der wachsenden Ressourcenausbeutung und der anthropogenen Belastung zu. Zum Schutz dieses einzigartigen Ökosystems ist ein Management notwendig, das über gute Kenntnisse des Systems verfügt einschließlich der Säugetiere, welche in ihm leben und es verändern. Bais (natürliche Waldlichtungen) gelten als wichtige Habitate für den Naturschutz. Sie locken zahlreiche große Säugetiere an und bieten gleichzeitig durch das offene Gelände eine gute Möglichkeit, diese Tiere zu erforschen. Studien an Bais haben bedeutende Erkenntnisse zu großen Säugetieren, wie dem Afrikanischen Waldelefanten (*Loxodonta africana cyclotis*) und dem Westlichen Flachlandgorilla (*Gorilla gorilla gorilla*), eingebracht. Bis heute sind die meisten Studien jedoch auf einzelne Lichtungen beschränkt, und nur wenig ist über die Unterschiede zwischen den Lichtungen bekannt.

Das Ziel dieser Dissertation war es, zu einem besseren Verständnis der Diversität der Bais und ihrer Bedeutung für den Naturschutz, insbesondere für größere Säugetiere, beizutragen. Im Rahmen dieser Arbeit wurden 17 Bais innerhalb des Schutzgebietskomplexes Sangha Trinational (Zentralafrika) während der Trocken- und der Regenzeit untersucht. Die Ergebnisse zeigen eine hohe Heterogenität zwischen den Bais hinsichtlich allgemeiner Charakteristika wie der Größe und der Bodenfeuchte. Vegetationsaufnahmen auf 14 der Bais belegen eine hohe Diversität an Pflanzenarten innerhalb und zwischen den Lichtungen. Dies deutet darauf hin, dass die Vegetation der Bais wesentlich zur Diversität des Zentralafrikanischen Regenwaldes beiträgt.

Das Vorkommen von größeren Säugetieren wurde mit Hilfe von Kamerafallen an sieben Bais erforscht. Gleichzeitig wurde dabei das Potenzial von Kamerafallen für die Erfassung von Säugetieren an Bais untersucht. Innerhalb von einer Aufnahmezeit von maximal vier Wochen an jedem Bai erbrachten die Kamerafallen Nachweise für insgesamt 25 Säugetierarten. Die Anzahl an aufgenommenen Arten an einem Bai stellte 65 - 94 % der Säugetierarten dar, deren Vorkommen im jeweiligen Bai belegt ist. Mit den Kamerafallen wurden auch seltene Arten sowie nächtliche Aktivitätsmuster dokumentiert, die im Rahmen von direkten Beobachtungen nicht erfasst wurden. Die Ergebnisse zeigten, dass viele große Säugetiere, wie der Afrikanische Waldelefant, Bais bevorzugt nachts besuchen. Dies unterstreicht die Bedeutung von in der Nacht durchgeführten Untersuchungen. Es wurde gezeigt, dass Kamerafallen kostengünstige und effektive Geräte für die Erfassung von Arten und das Monitoring von größeren Säugetieren an Bais darstellen. Die Anwendung von Kamerafallen wurde insbesondere für entlegene Gebiete empfohlen sowie ergänzend zu direkten Beobachtungen bei Langzeitstudien. Diese erlauben eine genauere Datenerhebung hinsichtlich der Identifizierung von Individuen und dem Verhalten der Tiere.

Das Ziel dieser Arbeit war es zudem, mögliche Faktoren zu identifizieren, welche die Besuchsraten von größeren Säugetieren auf den Bais beeinflussen. Zu diesen Faktoren zählen unter anderem soziale Faktoren sowie Beeinträchtigungen durch den Menschen. Der Fokus der vorliegenden Untersuchung liegt jedoch auf den in einem Bai verfügbaren Ressourcen wie Boden, Wasser und Pflanzen. Da Waldelefanten in Bais Boden und insbesondere Wasser konsumieren, wurde der Tongehalt und der Mineraliengehalt dieser Ressourcen in 15 Bais untersucht. In von Elefanten gegrabenen Wasserlöchern wurden signifikant höhere Konzentrationen wichtiger Mineralien (Na, Cl, S, Zn, Ca, Mg, Mn und Fe) gefunden als im Oberflächenwasser. Dies zeigt die Bedeutung von mineralienhaltigem Wasser in Bais. Im Gegensatz dazu wurde kein Hinweis darauf gefunden, dass Bodenmaterial die Besuchsraten beeinflusst, da geophagische Stellen sich weniger deutlich von Kontrollbodenproben unterschieden. Der Tongehalt konnte nicht als Grund für das Fressen von Bodenmaterial in Bais identifiziert werden. In Übereinstimmung mit weltweiten Studien zu den von Säugetieren genutzten Wasser- und Bodenressourcen deuten die vorliegenden Ergebnisse an, dass nicht ein einzelnes Mineral, sondern die Mischung aus mehreren Mineralien die Nutzung dieser Ressourcen positiv beeinflusst. Die vorliegende Untersuchung deckt zudem deutliche Unterschiede zwischen Bais hinsichtlich der Mineralienkonzentrationen in Boden- und Wasserressourcen auf.

Anders als Elefanten fressen Westliche Flachlandgorillas in den Bais vorwiegend Pflanzen, wobei sie eine hohe Selektivität für bestimmte Arten und Pflanzenteile zeigen. Zur Untersuchung dieses selektiven Verhaltens wurden Futterpflanzen wie auch Pflanzenarten, die nicht von Gorillas gefressen werden, für Nährstoffanalysen in 16 Bais gesammelt (insgesamt 14 Arten). Futterpflanzen wiesen signifikant höhere Konzentrationen an Ca, K und insbesondere Na auf. In Bezug auf Makronährstoffe wie Lignin und Protein wurden keine Unterschiede gefunden. Die Pflanzenteile einer Art unterschieden sich hinsichtlich ihres Mineraliengehaltes. Dies bekräftigt die Annahme, dass Gorillas nach bestimmten Mineralien selektieren.

Deutliche Unterschiede zeigten sich zwischen den Bais hinsichtlich der Verfügbarkeit von Futterpflanzen für Gorillas und andere große Säugetiere. Dies unterstreicht einmal mehr die starke Heterogenität von Bais und die daraus resultierenden Konsequenzen für das Management. Bais stellen bedeutende Habitate für größere Säugetiere dar und bieten diesen wichtige mineralienreiche Ressourcen. Angesichts ihrer Heterogenität ist es dabei wahrscheinlich, dass ein Tier auf mehrere Bais in einem Gebiet angewiesen ist, um seinen Mineralienbedarf zu decken. Der Schutz eines Mosaiks aus Bais, welches Säugetieren Zugang zu verschiedenen Ressourcen mit unterschiedlichen Mineraliengehalten (qualitativ und quantitativ) ermöglicht, sollte daher eine Priorität des Naturschutzes sein.

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1 Introduction

The Central African rain forest is the world's second largest contiguous forest zone representing about 20 % of the global tropical rain forest. It hosts more than 550 mammal species, approximately 460 reptile species, more than 1000 bird species and holds a high plant species richness (Billand, 2010). About 20 million people, including the indigenous Bambenzele population, rely on this forest for their direct livelihood (e.g. food, medicine, non-timber forest products and cultural functions) (Mayaux et al., 2013). The Central African rain forest further plays an important role in global conservation. It represents a major carbon dioxide sink holding a total carbon stock of 39.2 Gt (78.5 % of Africa's stock) and thus helps to mitigate climate change (Mayaux et al., 2013). The high diversity of animal and plant species found in the Central African forest further underlines its importance for conservation.

Today, however, this unique ecosystem is under enormous threats. The deforestation rate in Central Africa has been estimated at 0.19 % per year for the period 1990 - 2000 and at 0.10 % per year for the period 2000 - 2010 (Mayaux et al., 2013). Despite this slight decline in deforestation over the past decade it is likely that the increased global demand for mineral and wood resources, the resulting investment in infrastructure as well as the increasing human population pressure will accelerate forest degradation (Billand, 2010; Abernethy et al., 2013).

Moreover, deforestation is not the only major impact of logging on the rain forest. Logging companies are encroaching into remote and formerly pristine areas. The roads and infrastructure they construct open up the forest and not only facilitate access to remote areas, but in fact entail a population growth from an immigrant workforce (Mayaux et al., 2013). The demand for wild meat increases as well as an 'extraction to international markets for specialist products like ivory' (Abernethy et al., 2013). Secondary impacts of logging activities such as hunting pressure are assumed to have an even greater ecological impact than habitat alteration through logging that impacts animal densities (Abernethy et al., 2013).

In fact, the decline of African forest elephants (*Loxodonta africana cyclotis*) has been estimated at 62 % between 2002 and 2011 (Maisels et al., 2013) and the demand for ivory is far from declining. Given this negative and rapid trend, Maisels et al. (2013) suggest to uplist the Central African forest elephant subpopulation status on the IUCN Red List of Threatened Species to Critically Endangered. Further targets of commercial hunting are apes that have declined by 50 % between 1984 and 2000 (Abernethy et al., 2013). As seed dispersers and herbivores these large mammals play an important role in the rain forest ecosystem by altering the forest structure. Their dramatic decline and overall changes in species diversity and richness have important implications on the forest system. Mitigating the loss of the megafauna therefore has been identified as a priority for conservation strategies aiming to maintain intact ecosystem functions in tropical forests (Abernethy et al., 2013).

Yet, we still lack major understanding of the exact consequences of the Central African forest megafauna decline and their magnitude. Until today, the Central African rain forest remains poorly studied in comparison to rain forests in Amazonia and Southeast Asia. Very few studies have been conducted on its biomass, species diversity and structure (Abernethey et al., 2013). Political and economic instability have added to logistic constraints and challenging field conditions rendering research difficult. Even studies on the behaviour and ecology of large mammals have been constrained since direct observations of these animals are difficult in the dense forest. Knowledge of the forest megafauna, however, is indispensable for their protection.

Researchers and conservationists have identified natural forest clearings (locally known as ‘bais’) as important features in the Central African rain forest ecosystem. Despite elevated risks such as predation and disease transmission these clearings attract numerous large mammals. This indicates that they play an important role in the life of the megafauna. While it is assumed that their mineral rich resources such as soil, water and plants attract animals to bais (Turkalo & Fay, 1995; Magliocca & Gautier-Hion, 2002), the actual factors still remain unknown. Bais have gained international recognition through long-term studies focusing on large charismatic mammals such as the African forest elephant and the western lowland Gorilla (*Gorilla gorilla gorilla*). These studies, however, have been restricted to only a small number of the numerous, partly still undiscovered bais in Central Africa. Little is known on the bais’ diversity in respect of their structural features, the occurrence of animal and plant species as well as mineral resources.

The present thesis takes a broad approach investigating a number of different bais in the Sangha Trinational area (Central Africa). Its focus lies on bais’ diversity in respect of plant, mineral and animal aspects and their importance for conservation. Prior to presenting the objectives of this study, the current state of knowledge on bais is illustrated. Here a definition of the term ‘bai’ and hypotheses on their origin are provided as well as a briefing on bais in the context of research and conservation up today.

2 Bais (forest clearings)

2.1 Definition of the term ‘bai’

According to the native Bambenzele language of Central Africa, bais are forest clearings with a water outlet (Turkalo & Fay, 1995). Natural forest clearings are considered open areas in the forest with, if at all, only a sparse presence of trees or shrubs that have not been (recently) opened by humans. The name ‘bai’ has been widely used for natural forest clearings in general throughout the Central African rain forest. More precisely, these forest clearings can be classified according to the Bambenzele into three major types: ‘endambas’ found in permanent swamps along watercourses and covered by semi-aquatic plants; ‘bais’ in the strict sense, that are drier clearings on or close to watercourses and usually dominated by species of Cyperaceae and Poaceae; and ‘yangas’ without any running water, though they may be seasonally or permanently flooded (Blake, 2002). Bais in the strict sense have been further subdivided by Elkan & Clark (2005) into ‘elephant bais’, ‘Cyperaceae bais’, ‘Berlinia bais’ and ‘swamp bais’. They further add the term of ‘étang’ to the classification of bais reported by Blake (2002). ‘Étangs’ are supplied by surface water and springs, and are in open exchange with the hydrological system (Elkan & Clark, 2005).

The distinction between different clearings is, however, not always evident and a bai may hold attributes of the different designations cited above. For convenience the term ‘bai‘ will be used in the present thesis for natural forest clearings including bais in the strict sense as well as ‘endambas’, ‘yangas’ and ‘étangs’. The terms of ‘esobe’, ‘bains d’éléphants’ and ‘saline’ that have been designated to forest clearings in the Democratic Republic of Congo and the Republic of Congo (Boupoya-Mapikou, 2010) are cited here solely for the sake of completeness (see also discussion chapter 5).

2.2 Origin of bais

The geographic range of bais is reported for the African forest system from Nigeria to the Eastern Democratic Republic of Congo (Edwards & White, 2000). Until today there is uncertainty as to the origin of these features. It is frequently assumed that they are remnants of savannahs that have been encircled by forest over time (palynological hypothesis; see Boupoya-Mapikou, 2010). DeVivo & Carmignotto (2004) suggest that during the Holocene climatic optimum high precipitation favoured denser vegetation physiognomies and thus forest expansion. The origin of these savannahs has been attributed to particular soil types (pedological hypothesis) unfavourable for forest development (Boupoya-Mapikou, 2010) as well as to climatic changes. The expansion of savannahs from about

3000 B.P. in Congo is possibly the result of a dry Holocene climatic phase combined with fires that are attributed to lightning, but also to human activities in the area (White, 2001). Further explanations for the origin of forest clearings include natural tree-falls of single trees or multiple trees due to storms (Hart, 2001).

Considering the humid character of most bais and their closeness to water courses, it is obvious that soil moisture plays an important role in their maintenance and possibly also their origin (see also Boupoya-Mapikou, 2010). Elephant activity has further been suggested as a contributing factor for forest gaps expanding to forest clearings (Hart, 2001). In fact, multiple factors (direct and indirect) might have contributed to the genesis of a single bai, and given the bais' distinct characteristics it is probable that they differ in their origin.

There is consensus that these clearings are maintained by the activity of large forest mammals such as elephants and buffalo impeding forest succession (Ruggiero & Fay, 1994; Turkalo & Fay, 1995). This is further indicated by elephant feeding traces that are often found at the edge of bais (see Figures 2.2 a-b). Elephants excavate the soil under trees to feed which can occasionally cause trees to fall. On the other hand, the existence of vast savannahs in Africa has been suggested as reason for the survival of large-sized mammals while they went extinct in South America (De Vivo & Carmignotto, 2004). De Vivo & Carmignotto (2004) 'believe that South America and Africa did share similar faunistic patterns until quite recently (middle Holocene) and that vegetation changes associated with fluctuating rainfall levels physiognomically altered habitats available for the open formation fauna'. This indicates the importance of forest clearings for large forest mammals, which is the focus of the present study.

Figures 2.2 a-b Elephants excavate the soil underneath trees at the edge of bais occasionally causing tree-falls.

2.3 Research and conservation at bais

Bais have been recognised as important habitats for numerous mammal species living in the dense rain forest. They offer a unique view on the behaviour of these species that are otherwise hidden in the forest. Consequently, bais have increasingly become the focus of conservation and research in the Central African rain forest. The longest ongoing bai study started in 1990 at the Dzanga clearing in the Central African Republic. The Dzanga bai study focuses on the African forest elephant (*Loxodonta africana cyclotis*) and aims to provide information on the population structure, demographics, morphometrics, genetics, social structure and social behaviour of this species by direct observations (Turkalo & Fay, 2001). During 20 years, Andrea Turkalo has identified more than 3,000 individual elephants visiting Dzanga (Turkalo et al., 2013). Identification of individual elephants at Dzanga and in the northern part of the Nouabale-Ndoki National Park has been further used to study elephant movements between these clearings (Inkamba-Nkulu, 2007). Based on observations at Dzanga and in several bais in Gabon it was suggested that peaks in elephant activity at bais are related to social benefits representing important meeting places and even hotspots for mating (P.H. Wrege, pers. communication). At Dzanga, data on social behaviour has further been collected for other large mammal species such as the bongo antelope (*Tragelaphus euryceros*) (Turkalo & Klaus-Hügi, 1999).

Similarly, data on large mammals has been collected through direct observations from a platform at Mbeli bai since 1995. The Mbeli bai study first focused on observations of the western lowland gorilla (*Gorilla gorilla gorilla*) and provided important information on the social organisation and behaviour of this great ape (Parnell, 2002; Breuer, 2008). Observations at bais further allowed recording of rare events such as tool-use by western lowland gorillas (Breuer et al., 2005). Besides, data on the use of Mbeli bai by other species such as the forest elephant, the forest buffalo (*Syncerus caffer nanus*) and the sitatunga (*Tragelaphus spekeii*) as well as on their behaviour has been collected (Breuer & Ndoundou-Hockemba, 2008; Fishlock et al., 2008).

Direct observations have been conducted at other bais such as Maya Nord in the Odzala National Park, Republic of Congo (Magliocca, 2000; Fishlock, 2010) and Langoue bai in the Ivindo National Park, Gabon (Momont, 2007), though with shorter study durations. While medium-sized to large mammals are the focus of these studies, essential information has also been provided on bird species (Ruggiero & Eves, 1998; Turkalo et al., 2003) and on the conservation status of the Congo clawless otter (*Aonyx congicus*) (Jacques et al., 2009). At several bais in Southeast Cameroon data collection has been performed for management purposes monitoring changes in populations of medium-sized to large mammal species (Nzooh Dongmo, 2003). Furthermore, the value of bai studies for the conservation of species such as the African forest elephant has been recognised

(Turkalo et al., 2013). Attracting large numbers of mammals these open spaces represent easy hunting grounds and have been widely used by hunters (Vanleuwee & Gautier-Hion, 1998). The presence of researchers and conservationists may constrain poachers from bais and contribute to the protection of the animals visiting a particular bai.

3 Thesis objectives and outline

3.1 Thesis objectives

The present thesis aims to contribute to a more thorough understanding of plant, mineral and animal aspects of bais diversity and their relevance for conservation.

Its first objective is to investigate the diversity of bais in Central Africa. Do bais differ conspicuously in respect of general features and vegetation? Does the bai vegetation add considerably to the diversity of the Central African rain forest? It further aims to answer the question which mammal species use bais and whether there are clear differences in the use of several bais. For this purpose, the potential of camera traps for species inventories and monitoring of medium-sized to large mammals visiting bais is examined.

The second objective of the study is to analyse resources used by large mammals at bais. It follows the questions whether forest elephants gain particular minerals or clay by the consumption of water and soil resources in bais and whether there are differences in nutrient concentrations of these resources between bais. Similarly, it investigates whether minerals or rather macronutrients influence feeding selectivity in bai plants by gorillas and whether there are differences in the availability of consumed plant species between bais.

The third objective of the study is to identify potential factors influencing visitation rates of large mammals at bais. Its purpose is to assist management planning and to help identifying important conservation sites.

3.2 Thesis outline

The thesis comprises four main chapters (5 – 8) following the introductory chapter and the state of knowledge on bais (chapter 2) as well as a presentation of the study area (chapter 4).

Chapter five discusses bais’ diversity in the light of general features and vegetation. It provides descriptive baseline information on the studied bais that are subject in the following chapters and investigates the richness and diversity of plants at bais. In particular, it focuses on the abundance of large mammals’ feeding plants and whether there are differences in their availability at different bais.

Chapter six addresses the question of which medium-sized to large mammals visit bais. Camera traps are used in order to investigate visitation patterns of large mammals such as elephants and whether there are differences in species richness and visitation patterns between bais. The adequacy of camera traps as tools for species inventories and monitoring at bais is examined as well.

Chapter seven focuses on geophagical soil and water resources that are consumed mainly by elephants. It examines mineral and clay concentrations of these resources and aims to identify potential factors attracting elephants to bais. Thereby it queries whether it is rather soil or water resources that influence elephant visitation rates at bais. Finally, differences between bais regarding mineral and clay concentrations in water and soil resources as well as seasonal differences in the water from holes excavated by elephants are investigated.

Chapter eight enquires concentrations of minerals and macronutrients in feeding plant species at bais. In particular, nutrient concentrations of consumed versus non-consumed plants and plant parts by the western lowland gorilla are examined. The question is raised whether it is minerals rather than macronutrients that drive feeding selectivity by this great ape at bais. Seasonal differences in mineral concentrations are investigated as well as the availability of consumed plants at different bais.

The final synthesis combines the principal findings from the different chapters. It focuses on the diversity of bais as well as on potential factors influencing visitation rates of large mammals at bais. Based on these findings, recommendations for conservation management in the Central African rain forest ecosystem and its wildlife in particular are provided in respect of bais.

4 Study area

The present study focused on 17 bais in Central Africa – five in the Lobeke National Park (Cameroon), ten in the Nouabale-Ndoki National Park (Republic of Congo) and one in its periphery, as well as Dzanga bai in the Dzanga National Park (Central African Republic) (see Figure 4.1). The three National Parks have been created independently by the respective governments; the Dzanga National Park in 1990 and the Nouabale-Ndoki National Park in 1993. Lobeke was designed a protected area in 1995 and declared a National Park in 2001 (TNS, 2012). In the year 2000, the Sangha Trinational Protected Area Complex (TNS) was established comprising the three National Parks and their periphery. It encompasses a total area of approximately 750,000 ha (TNS, 2012). The creation of the TNS followed the Yaoundé Summit, which was held in 1999. At this summit, the presidents and leaders from the Central African region agreed on transboundary collaboration in the TNS protected area complex aiming to ensure the integrity of the forest ecosystem (TNS, 2012). In July 2012, the TNS was declared a World Heritage site by UNESCO because of its large size and intactness including 'the continuous presence of viable populations and natural densities of wildlife' (UNESCO, 2013). Natural forest clearings were recognised as important features in the TNS forest ecosystem contributing to species richness (UNESCO, 2013).

The Nouabale-Ndoki and Dzanga National Parks have never been exploited, while parts of Lobeke (20 %) have been selectively logged up to its declaration as National Park (Stromayer & Ekobo, 1992). The National Parks are surrounded by buffer zones. In the periphery of the protected areas, logging concessions are located and have constructed a network of roads. The density of roads is comparatively high in Cameroon (0.30 km/km²) and lower in the Republic of Congo (0.17 km/km²) and the Central African Republic (0.09 km/km²). Human settlements are mainly situated along roads with a density of approximately 4 persons/km² (TNS, 2012). It is thought that much of the study area has been cultivated up to about 1600 B.P. based on findings of large numbers of palm nuts (*Elaeis guineensis*) that are believed to be restricted to human habitations (White, 2001). Findings from a paleo-ecological study showed that the Northern Republic of Congo harbours one of the most stable and intact forest in Central Africa and has never been degraded to open space for at least 3,300 years (Brncic et al., 2009). Accordingly, the forest was dominated by closed canopy until the climate became drier approximately 1,345 years ago and semi-evergreen forest became dominant with numerous pioneer plant species. For the last 900 years the forest composition has been relatively stable (Brncic et al., 2009).

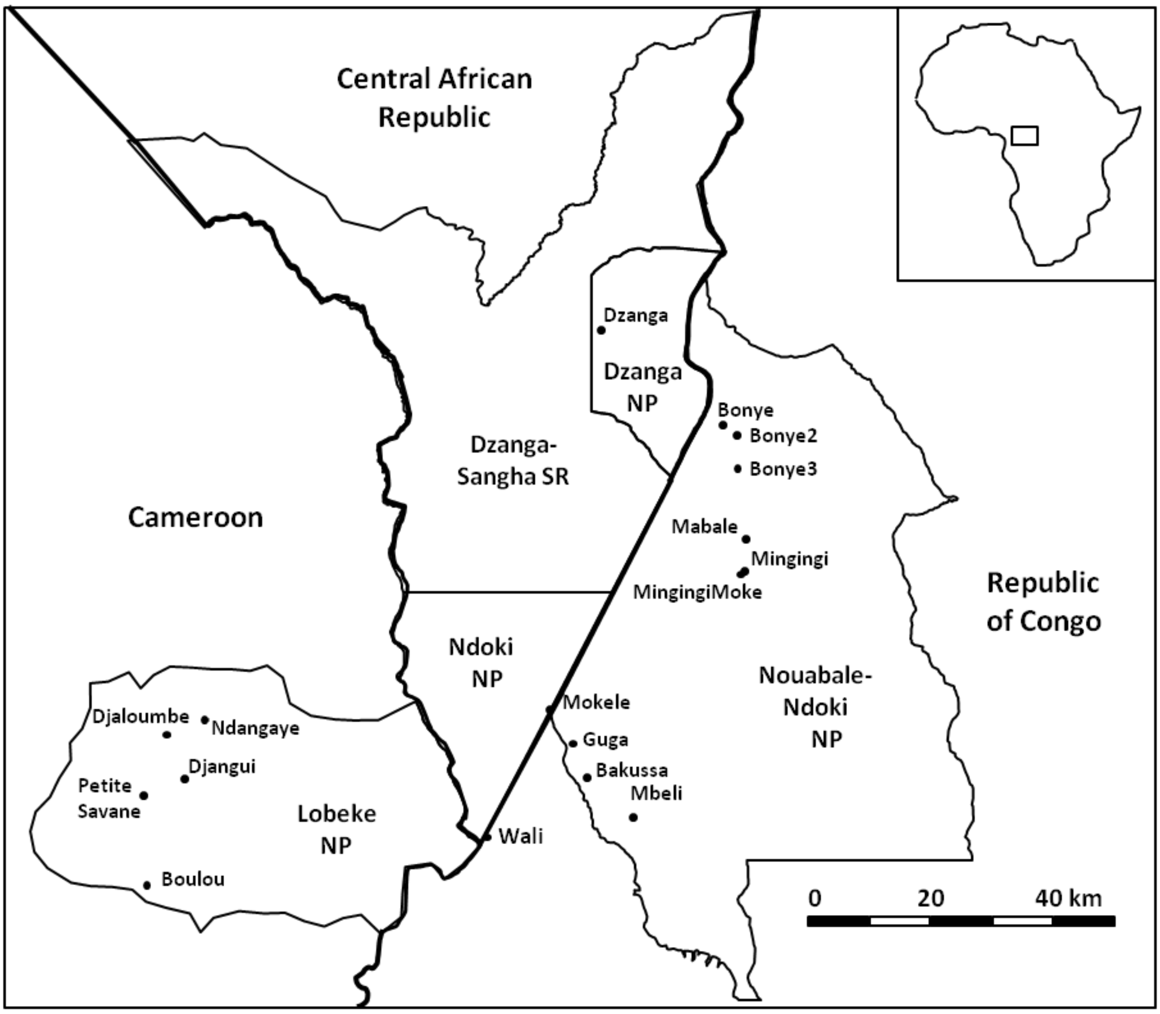


Figure 4.1 Study site in Central Africa. 17 bais were surveyed within the Lobeke National Park (Cameroon), the Nouabale-Ndoki National Park (Republic of Congo) and its periphery, as well as the Dzanga National Park (Central African Republic). These national parks together with the Ndoki National Park are part of the Sangha Trinational Protected Area Complex.

More than 95 % of the TNS area is covered by forest (TNS, 2012), which belongs to the 'Guineo-Congolian regional centre of endemism' (Harris, 2002). Three subdivisions of this phytochoria are present in the area according to Harris (2002): 'mixed moist semi-evergreen rain forest', 'single dominant moist evergreen and semi-evergreen Guineo-Congolian rain forest' and 'Guineo-Congolian swamp forest and riparian forest'. The forest type Sterculiaceae-Ulmaceae is described as dominant on terra firma with patches of mono-dominant *Gilbertiodendron dewevrei* forest in riparian zones, *Raphia* spp. swamps and Marantaceae (Blake & Fay, 1997; Nzooh Dongmo, 2003). A total of 1,122 plant species have been identified in the area including 556 tree species (TNS, 2012).

Located in the Northeast of the Congo basin, the study area is part of this hydrographical system. Lobeke belongs to the Dja series with late Proterozoic glacigenic formations, while the respective parts of the Central African Republic and the Republic of Congo show Jurassic and

Cretaceous continental deposits (Alvarez, 1995). The typical metamorphic formations of the Dja series consist essentially of tillite, quarzite, schist, calcareous and dolerite (Nzooh Dongmo, 2003). The Lobeke soils are ferralitic with a weak cover of humus as it is typical for many tropical soils (Nzooh Dongmo, 2003). The Dzanga area is covered with alluvial sediments of the Sangha river that are mainly sandstones and quarzites (Klaus, 1998). Soils in the Northern Congo are of a sandy texture and belong mainly to arenosols, ferrasols and gleysols (Blake, 2002). In the whole study area dolerite intrusions are abundant (Vicat et al., 1996).

The climate is typically equatorial in transition between the Congolo-equatorial and the sub-equatorial climatic zones. The major rainy season lasts from August to November and the major dry season from December to February. Mean annual rain fall is about 1,500 mm, the average annual temperature ranges around 24 – 26 °C and the relative humidity of the air varies from 60 to 90 % (TNS, 2012).

5 Diversity of bais: General features and vegetation

Introduction

The present thesis investigates the diversity of natural forest clearings in the Sangha Trinational Protected Area Complex in Central Africa. Differences between bais in mineral resources such as water, soil and plants as well as the occurrence of different mammal species will be discussed in later chapters. This chapter focuses on the heterogeneity of bais regarding general features and vegetation.

‘Biodiversity’, as a contraction of ‘biological diversity’, is a term widely used today and, according to the Convention on Biological Diversity (United Nations, 1992), includes the ‘diversity within species, between species and of ecosystems’. Here I follow Magurran (2006), who assigns two components to biological diversity: species richness and evenness. While species richness simply denotes the number of species, evenness provides information on the variability of species abundance in the unit of study (Magurran, 2006). Both are meaningful for the assessment of the bais’ vegetation in the present study. Species richness can be used to assess the contribution of the bais’ vegetation to the overall number of plant species found in the study area. Evenness, on the other hand, describes the composition of plant species in a bai, distinguishing between bais where species are present in similar abundances and those bais where the abundances of different species differ greatly.

Until today, the vegetation at bais has only been the subject of a few studies in contrast to the high number of studies on large mammals visiting bais. Different groupings and vegetation communities have been described by Deuse (1960) at clearings in the Lac Tumba area, Democratic Republic of Congo, and by Lejoly & Lisowski (1997) within the Odzala National Park, Republic of Congo. In a detailed study, Boupoya-Mapikou (2010) investigated the vegetation of swampy clearings on hydromorphic soils within the Ivindo National Park, Gabon. He distinguished between two principal vegetation types: the central meadow and the edge of a bai. Within the meadow geophytes and therophytes prevail and the major modes of dispersal are zoochory and anemochory. Boupoya-Mapikou (2010) described eight vegetation communities and argued that their occurrence was influenced by the soil moisture, the depth of the mud and their frequentation by animals. Similarly, Neugebaur (2012) reported three communities with several sub-communities for the vegetation in the bais of Djaloumbe, Djangui and Petite Savane (Lobeke National Park) and related their formation to the soil moisture and the degree of disturbance by large mammals. In the Odzala National Park, Republic of Congo, Magliocca (2000) distinguished seven vegetation communities at three bais, which occurrence she also related to the soil moisture of the different areas within each bai.

Magliocca (2000) further investigated the phenology of the ten principal plant species at the clearing Maya Nord, but could not distinguish any seasonality in flowering or fructification of these species.

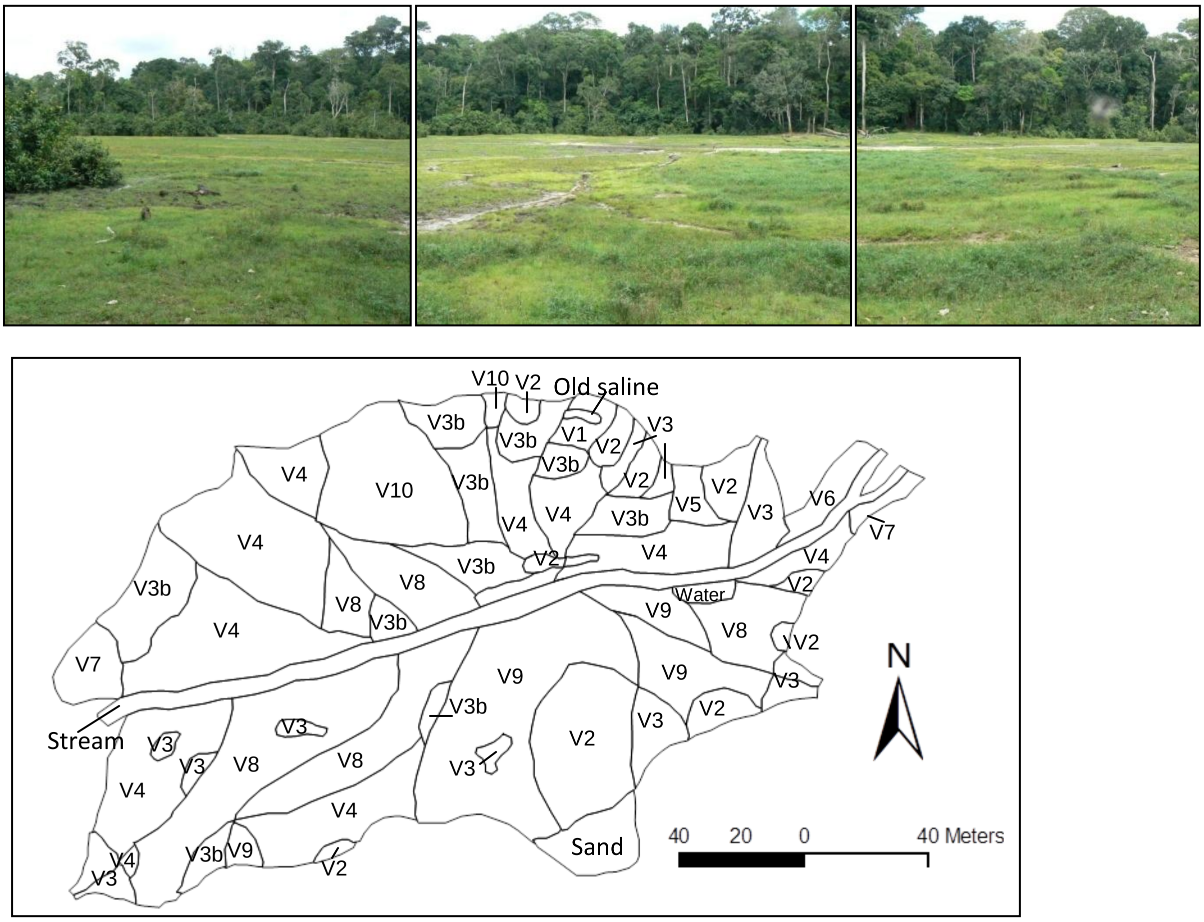
The identification of different plant communities and their classification is beyond the scope of the present study. The aim of this study was to shed more light on the heterogeneity of bais in the Sangha Trinational Area including their floristic diversity. Here, general features and vegetation of different bais are described providing detailed and supplementary information on the surveyed bais that will be the focus of the following chapters. The goal further was to contribute to the knowledge on species richness of these bais and to emphasize their importance regarding the overall diversity of the area. A focus thereby lies on plant species that are consumed by large mammals. The vegetation plays an important role regarding the respective bais' attractiveness for animals. The availability and abundance of feeding plants for different mammal species at different bais will be discussed.

Methods

The study area, namely the Sangha Trinational (TNS) in Central Africa, has been described in detail in chapter 4. During a pilot study in 2010, 17 bais within the TNS were selected for further investigations (see Figure 4.1). Each bai was visited at least once in the rainy and once in the dry season and general data on each bai's characteristics such as the size were collected. Based on observations during both seasons, each bai was assigned a level of soil moisture. According to Boupoya-Mapikou (2010) different classes of soil moisture (hydromorphie) were distinguished: (1) minor, well-draining underground, (2) medium, soil drying slowly after rain, (3) strong, soil periodically inundated and staying saturated for a long time after rain, and (4) permanent, soil saturated even in the dry season. Maps were drawn based on GPS (Global Positioning System) data taken within and on the border of each bai that were processed in ArcGIS version 9.3. Some areas, especially at swampy bais, were inaccessible and the location of essential components such as watercourses and the forest edge were determined using a compass and a laser range finder. The size of Guga bai was estimated for the surveyed area, though the actual area of this bai located along a river likely is larger. The percentage of the water surface out of the total bai area was estimated for each bai in ArcGIS and classified with an estimated accuracy of 5 % (0 - 5, 6 - 10,…, 96 -100 %).

Vegetation mapping was conducted at 14 bais excluding Wali, Mbeli and Dzanga bai due to the inaccessibility of the bais' area (high water level) and the large presence of elephants, respectively. While the area of Bakussa and Guga bai was not accessible, it was possible to survey a large part of the vegetation cover from the edge of these bais due to their small sizes. At each of the surveyed bais different vegetation types were identified by their floristic homogeneity (Figures 5.1 a - b). Within each vegetation type one plot (4 x 6 m^2) was then delimited in a randomly chosen location.

At Ndangaye bai additional four plots were surveyed within a vegetation type that covered more than 10 ha. All species inside a plot were recorded and their abundance estimated according to the method of Braun-Blanquet (Dierschke, 1994) that was slightly simplified as follows: dominant (26 - 100 % of cover), medium (6 – 25 %), rare (1 – 5 %) and sporadic (< 1 %). At each bai, the abundance of each species was estimated as follows. The average of the abundance class of a certain species within a vegetation type (e.g. dominant: 63 %) was calculated and multiplied by the total area of the respective vegetation type. The total area covered by this species in the respective bai was then calculated by summing up the areas covered across all vegetation types. Finally, the percentage of the area covered by a species from the bais total vegetation cover was computed. Besides, species not detected in the surveyed plots were recorded at random, though these lists are not exhaustive.



Figures 5.1 a-b Example of vegetation mapping: photo of Bonye bai and the respective vegetation map showing limits of the different vegetation types (V1 - V10) recorded during the present study.

Species determination was assisted by Annemarie Neugebaur who identified species collected at three bais in Lobeke (Neugebaur, 2012). Species that could not be identified to the scientific name were given a code including the name of the bai where the species was first recorded and a number. Notes were taken on feeding traces from animals in order to determine plant species consumed by medium-sized to large mammals. The animal species feeding on the respective plants were determined by direct observations and with the help of local assistants. Additionally, information on feeding plant species of certain mammal species from the literature was provided for the analysis of feeding plant abundance at the bais (Nishihara, 1995; Klaus-Hügi, 1998; Magliocca, 2000; Blake, 2002b; Magliocca & Gautier-Hion, 2002; Nowell & Fletcher, 2006). For many plant species, however, the exact consumer species could not be identified and no information was found in the literature. In this chapter, all plants identified as gorilla feeding species during the present study were considered. In contrast, solely species reported as major gorilla feeding plants in the literature were considered consumed species in chapter 8. Consequently, feeding plant availability in chapter 8 reflects only that of major gorilla feeding plants while in the present chapter the availability of major as well as minor feeding plants are considered.

For each species the percentage of bais where they were recorded (within and outside of plots) was converted to a class of relative frequency from 1 (1 - 10 %) to 10 (91 – 100 %) following Boupoya-Mapikou (2010). The Simpson's index of diversity at each bai was calculated by $D' = \Sigma p_i^2$, where p_i is the percentage of vegetation cover for species i (Magurran, 2006). Only the species recorded within plots were used for this analysis since the percentage of vegetation cover for species recorded at random was not known. As recommended by Magurran (2006) the reciprocal ($D = 1/D'$) was used as index since interpretation is more straightforward when diversity increases with an increasing index. Accordingly, the Simpson's measure of evenness was calculated by $E = (1/D')/S$, where S is the number of species recorded within plots at the respective bai. The Jaccard similarity coefficient was used in order to compare similarities in plant species composition between bais. This analysis was conducted in the program R version 2.15.2 (R Foundation for Statistical Computing 2012) producing a distance matrix with the *vegdist* function. Based on this matrix agglomerative clustering was performed with the function *hclust* using the *Ward* linkage. In order to determine the number of different groups, the elbow criterion was used.

Results

The 17 bais surveyed show high variation in size (0.2 - 22.4 ha) as well as in structural characteristics (see Table 5.1). Each bai is unique, yet some general differentiations can be identified especially in respect of the soil moisture. Wali bai resembles a small lake right in the forest and might be classified as 'étang' according to Elkan & Clark (2005) (see Figure 5.2). Forest elephants (*Loxodonta africana cyclotis*), bongo antelopes (*Tragelaphus euryceros*), sitatungas (*Tragelaphus spekeii*) and forest buffalo (*Syncerus caffer nanus*) come to feed on the algae *Spirogyra* spec., often diving with their whole body under water in order to 'graze' on the ground. Guga, Bakussa and in part also Mbeli are swampy bais with most of their surface covered by (semi-)aquatic plant species. Guga and Bakussa are typical ‘endambas’, while Mbeli as well as the remaining clearings surveyed here are ‘bais’ in the strict sense (Blake, 2002), though transition exists in some cases. Ndangaye, Boulou, Mingingi and Djangui are swampy to a lesser degree, less profound and with a steady vegetation cover. At Mabale, Bonye2 and Bonye3 more than 10 % of the area is covered by running water. Similarly, a stream running through Djaloumbe covers approximately 15 % of the bai’s area representing an important location of elephant water holes and geophagical sites at its bank. Next to the stream lies a rather dry area covered by non-aquatic plant species, though (semi-)aquatic species are found in a permanent small lake and seasonal water pits. The bais of Mingingi-Moke, Bonye, Dzanga and Mokele are crossed by small streams and are well-drained by a sandy substrate. The latter bai located next to the Ndoki River becomes swampy towards the river side. At Petite Savane small water streams are only located at the edge of the bai, though it becomes quite muddy in the rainy season.

Figure 5.2 From top left to bottom left: View on Wali bai (étang), Guga bai (endamba) and Bonye bai (bai in strict sense).

Table 5.1 Overview presenting general information on the 17 bais surveyed within the Lobeke National Park, the Noubale-Ndoki National Park (NNNP) and the Dzanga National Park. Different classes of soil moisture have been distinguished following Boupoya-Mapikou (2010) (see methods). The number of plant species identified within and outside of vegetation plots are reported. On the basis of the plant species recorded in vegetation plots the Simpson's diversity index (D = 1/D') as well as the evenness index ($E_{1/D'}$) has been calculated.

	Location	Size [ha]	Soil moisture	Water-surface [%]	Plant species	Number of plots	D	$E_{1/D'}$
Djangui Petite	Lobeke NP	9.6	3	0 - 5	43	10	8.57	0.24
Savane	Lobeke NP	5.7	2 - 3	0 - 5	42	8	3.48	0.09
Djaloumbe	Lobeke NP	2.7	2	11 - 15	40	5	3.91	0.20
Ndangaye	Lobeke NP	22.4	3	0 - 5	46	10	4.54	0.13
Boulou	Lobeke NP	6.7	3 - 4	0 - 5	21	5	3.69	0.28
Bonye2	NNNP	1.8	3	11 - 15	36	5	3.40	0.11
Bonye3	NNNP	0.3	2	11 - 15	21	5	3.48	0.23
Mabale	NNNP	1.4	3	21 - 25	30	3	4.19	0.17
Mingingi-moke	NNNP	1.9	2	6 - 10	29	7	3.96	0.16
Mingingi	NNNP	5.9	3	6 - 10	36	14	7.34	0.24
Bonye	NNNP	2.9	2	0 - 5	49	11	8.35	0.26
Mokele	NNNP	1.6	2	6 - 10	30	6	3.07	0.12
Bakussa	NNNP	0.2	4	0 - 5	11	2	1.64	0.33
Guga	NNNP	> 0.7	4	6 - 10	14	6	2.45	0.22
Mbeli	NNNP	12.9	3 - 4	0 - 5	> 29	-	-	-
Wali	Periphery NNNP	2.3	4	75 - 80	> 12	-	-	-
Dzanga	Dzanga NP	7	2	0 - 5	> 17	-	-	-

In total, 147 plant species were recorded (including 22 possible double counts) from at least 37 families. The Cyperaceae and Poaceae were the dominant families with at least 31 and 16 species, respectively. The number of species recorded at each bai ranged from 11 to 49. Most species occurred in low frequency classes, i.e. they were recorded only in a few bais (see Figure 5.3). Genera of *Commelina and Ludwigia* occurred in most bais (frequency class 9), followed by *Cyperus difformis*, *Paspalum conjugatum*, *Rhynchospora corymbosa*, *Bacopa crenata, Oldenlandia lancifolia, Pycreus lanceolatus* and species of the family Pontederiaceae (frequency class 8). *Cyperus distans*, *Scleria* spec. and three unidentified species were recorded in 61 – 70 % of the bais, *Eleocharis* spec. and *Torenia* spec. in 51 - 60 % of the bais.

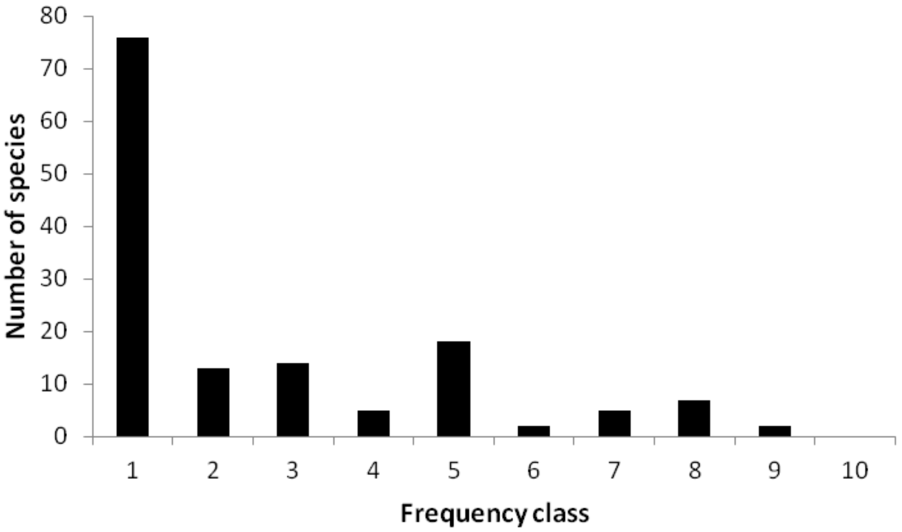


Figure 5.3 Each species is assigned a frequency class according to the percentage of bais the respective plant species was found in from the 14 bais surveyed.

At each of the 14 bais surveyed only two to eight species yielded more than 5 % of cover each and together represented 73 – 94 % of vegetation cover (see Figures 5-A.1 a-n). *Eleocharis* spec. yielded 17 - 50 % of vegetation cover in six bais, *Rhynchospora corymbosa* 9 – 48 % in seven bais and *Kyllinga erecta* 5 – 32 % in five bais. As clearly dominant species *Cyperus pectinatus* presented 60 % of vegetation cover in Guga and *Hydrocharis chevalieri* 76 % in Bakussa. Indeed, the latter two bais showed lowest diversities and Bakussa bai the highest evenness (see Table 5.1). The Simpson's diversity index and evenness are listed for all surveyed bais (Table 5.1).

Highest similarities regarding plant species composition were found between Mabale and Mingingi-Moke. The elbow criterion suggested three major groups and the bais were clustered accordingly (Figure 5.4). One group comprises all bais in the Lobeke National Park, though the vegetation in Djaloumbe and Boulou is quite distinct. Bais in the North and West of the Nouabale-Ndoki National Park showed relatively high Jaccard indices in comparison to the other sites and constitute a second group. The third group includes Guga and Bakussa in the Southwest of the Nouabale-Ndoki National Park that are distinct from the remaining bais due to the strong presence of (semi-)aquatic plant species such as *Hydrocharis chevalieri*. The Jaccard index for both bais is, however, not as high since part of Guga is dominated by *Cyperus pectinatus*, a species that is not found in Bakussa. As mentioned above, species inventories in Guga and Bakussa were only feasible from the edge of the bais and results, therefore, have to be considered with caution.

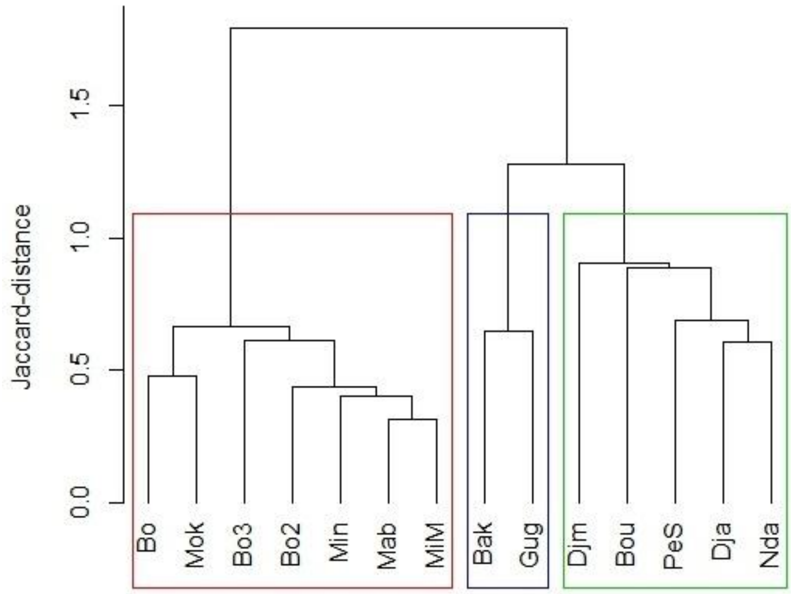


Figure 5.4 The cluster dendrogramm indicates similarities between plant species composition of the different bais. Group one (red) comprises bais in the North and West of the Nouabale-Ndoki NP (NNNP), group two (blue) swampy bais in the Southwest of NNNP and group three (green) bais in the Lobeke NP. The analysis was performed in R with the *vegdist* method, Jaccard function and *Ward* linkage.

Plant species that are known to be consumed by medium-sized to large mammal species represented 5 - 25 species in the respective bais and accounted for 66 - 100 % of vegetation cover (Figure 5.5). None of these species, however, is known to be consumed by all seven large to medium-sized mammal species mentioned here. For the respective mammal species the percentage of feeding plants from the total vegetation cover at each bai is shown in Figures 5-A.2 a-n. Gorilla feeding plants represented 27 – 91 % of the total vegetation cover at nine bais and less than 25 % at five bais. At nine bais buffalo feeding plants represented 25 – 86 % of vegetation cover, at seven bais elephant feeding plants represented 32 – 79 % of vegetation cover and at the remaining bais less than 25 %. Sitatunga feeding plants covered 25 – 76 % of vegetation at nine bais and feeding plants of the giant hog (*Hylochoerus meinertzhageni*) 33 – 59 % at six bais. Feeding plants known to be consumed by the red river hog (*Potamochoerus porcus*) and the bongo represented only a small percentage of vegetation cover at all bais. A large number of species (up to 69 % of vegetation cover) were identified as feeding plants by traces though it could not reliably be determined by which animal species they were consumed.

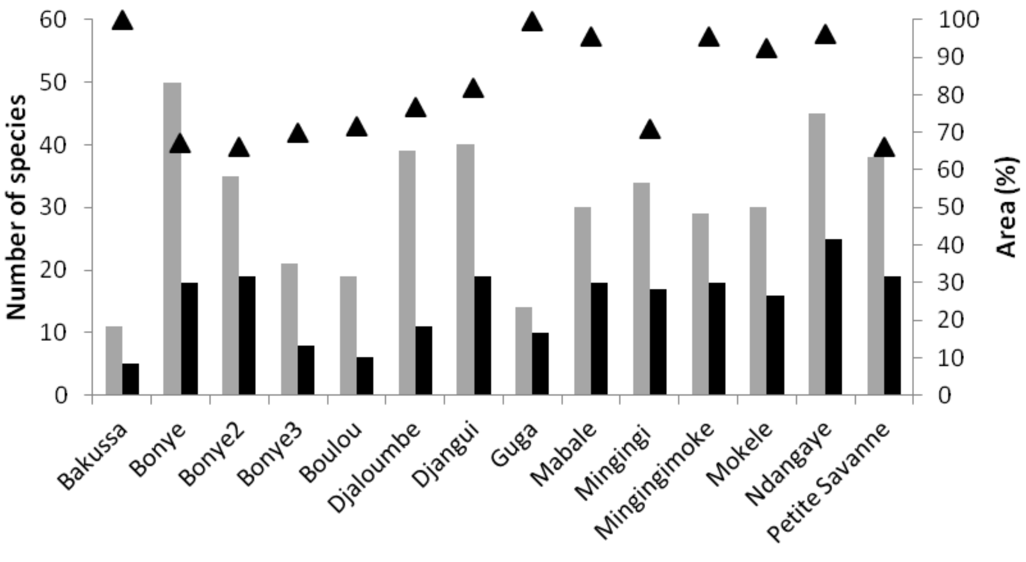


Figure 5.5 The number of plant species recorded within and outside of plots at each bai (grey bars) as well as the number of plant species that are known to be consumed by medium-sized to large mammals (black bars) are displayed. For each bai the area covered by vegetation was measured (total area of vegetation cover). The percentage of area covered by feeding plant species from this total area of vegetation cover was calculated and is shown on the secondary axes (triangles).

Discussion

Bais have gained international recognition due to bai studies allowing long-term observations of flagship species such as the African forest elephant and the western lowland gorilla. Less well known is the high heterogeneity of bais throughout the Central African rain forest and its importance for mammals. The aim of this chapter was to describe the heterogeneity of bais in the Sangha Trinational region with regard to general features and vegetation. This heterogeneity is further discussed in the light of its possible influence on the occurrence of large mammals at bais.

The most obvious differences are found in the size of the surveyed bais, ranging from 0.2 to 22.4 ha. The size of bais possibly influences frequentation by certain mammal species (Klaus, 1998). Large bais offer more space and vegetation and consequently are more attractive notably for herbivores such as buffalo and sitatunga (Klaus, 1998). This, however, also depends on the resources the respective bai provides and on its soil moisture.

The soil moisture differs strongly between bais as described above. Besides the lake-like Wali, they range from permanently to seasonally inundated bais with water-courses of different size. Naturally, the presence and level of water has a direct impact on the respective bai’s suitability for particular mammal species according to their ecology and in part also to their size. A red river hog, for example, will rather avoid a highly swampy bai though this bai might provide valuable nutrition. In contrast, for an adult elephant even deep swamps are no obstacle, though their offspring is likely to stay on the forest edge. The soil moisture further has an important influence on the plant species present in a bai and their respective abundance.

Bais contribute to the floristic diversity

Bais represent distinct habitats in the rain forest that differ conspicuously from the surrounding forest in terms of their vegetation (see also Neugebaur, 2013). In the present study we distinguished 147 plant species from at least 37 families, though this list is unlikely to be exhaustive. Considering the small size of bais, this number is high in comparison to 1,122 plant species that have been identified in the Sangha Trinational area so far (TNS, 2012). Moreover, in the present study we focused on herbaceous plants and disregarded the specific vegetation at the edge of bais in the transition zone to the forest. In a detailed vegetation survey at ten bais in Gabon, Boupoya-Mapikou (2010) reported that 122 out of 229 species were only detected at the edge of bais. In this transition zone a high diversity is promoted by its heterogeneity, different gradients of the microclimate and soil moisture as well as vegetation dynamics (Boupoya-Mapikou, 2010). Consequently, the number of species whose presence is related to the surveyed bais likely was underestimated by the present study. Furthermore, this study focused on no more than 14 bais for vegetation surveys. Considering that many bais are located in the Central African rain forest, this further illustrates the important contribution of bais' vegetation to the diversity of the Central African rain forest.

Floristic diversity between bais

The surveyed bais differ in the number of species recorded as well as in their species composition. The fact, that 54 % of the species were detected only in one bai (see Figure 5.3) indicates a high diversity between bais. The possibility, however, that species with low abundance might have been missed during surveys has to be considered. Species recorded at more than 60 % of bais included species of the genus *Commelina* and *Ludwigia* as well as *Cyperus difformis*, *Paspalum conjugatum*, *Rhynchospora corymbosa*, *Bacopa crenata, Oldenlandia lancifolia,* species of the family Pontederiaceae*, Pycreus lanceolatus, Cyperus distans*, *Scleria* spec. and *Eleocharis* spp. These findings are consistent with the characterisation of Cyperaceae and Poaceae as typical families found in bais (Boupoya-Mapikou, 2010). In her classification of seven vegetation groupings at the clearing Maya Nord in the Odzala National Park, Republic of Congo, Magliocca (2000) described similar species (*Bacopa crenata*, *Ludwigia stolonifera*, *Paspalum conjugatum*, *Rhynchospora corymbosa* and *Cyperus* spp. besides others) as dominant. The number of species (45) recorded by Magliocca (2000) at Maya Nord lies within the range of 11 - 49 species identified at bais during the present study. Given the fact that Boupoya-Mapikou (2010) determined species also at the edge of bais it is likely that his reported numbers of 16 - 109 herbal species at ten bais in Gabon represent numbers of species within the bai (excluding the edge) similar to those reported by Magliocca (2000) and the present study. Further evidence for the high diversity between bais is given by hierarchical cluster analysis using the Jaccard index. Thereby it has to be noted that the Jaccard index regards the species richness and not the abundance of the respective species. As it might have been expected, bais in the same area, e.g. the Lobeke National Park and the northern part of the Nouabale-Ndoki National Park, show highest similarities. Certain bais within these areas, such as Djaloumbe and Boulou, are, however, very distinct in their vegetation. This indicates that not only the geographic location, but also other factors such as the soil moisture influence each bai's vegetation (see also Magliocca, 2000; Boupoya-Mapikou, 2010; Neugebaur, 2012). The grouping of Guga and Bakussa apart from the remaining bais in the Nouabale-Ndoki National Park further confirms this. Data collection at both bais was hindered by the depth of mud rendering access to the bais' centre difficult. Due to the relatively small size of both bais it was, however, possible to identify the dominance of semi-aquatic plants. These species distinguish Guga and Bakussa from the other bais surveyed and explain their separate grouping. Altogether, these results illustrate a high diversity between bais since most bais share less than 50 % of species with another bai.

Floristic diversity within bais

Diversity is not only pronounced between bais, but also within bais. The highest numbers of species were found in Bonye, Ndangaye, Djangui, Petite Savane and Djaloumbe with more than twice the number of species that were found in Boulou and Bonye3. The Simpson's index indicates not only species richness, but also takes the dominance of species into account. Accordingly, the diversity – considering the number of species and the variation in abundance - is highest in Djangui, Bonye and Mingingi. The lowest diversity is found in Bakussa and Guga. It is possible that this is partly due to the fact that data collection was only feasible from the edge of these bais providing imprecise information for the remaining part of each bai. Besides, the extreme site conditions regarding the swampy nature of these bais likely favour fewer species. Overall, high diversity within the surveyed bais is further underlined by a low Simpson's index of evenness (Table 5.1). This is also illustrated by Figures 5-A.1 a-n showing the dominance of one or two species in most bais. Altogether, only 6 – 22 % of species recorded in vegetation plots represented each more than 5 % of vegetation cover at the respective bai.

Feeding plants

At all bais surveyed feeding plant species were abundant, dominating in the vegetation cover (66 – 100 %). Indeed, the plant species recorded at more than 60 % of bais (cited above), are known feeding plants for medium-sized to large mammals. Information on feeding plant species for different mammal species are based on long-term bai studies, conducting in general direct observations, as well as on feeding traces recorded during the present study. Plant species known to be consumed by the western lowland gorilla are abundant at most bais, though this is not the case for the major gorilla feeding plant species (see chapter 8). These are subject to a more detailed study including investigations of their nutritional value that will be presented and discussed in chapter 8.

The presence of forest buffalo has been related to the location of forest clearings (Melletti et al., 2007b) and it is assumed that as bulk grazers they depend on bai vegetation. Indeed, almost all bais surveyed here provide buffalo with abundant feeding plants. Buffalo have been observed grazing and ruminating most of the time they spent within a bai (Blake, 2002b; J.M.S. pers. observation); this further emphasizes the importance of bai vegetation for buffaloes. Buffaloes frequently visit the lake-like clearing Wali and dive deep into the water in order to feed on the algae *Spirogyra* spec. The most frequent visitor at Wali, however, is the forest elephant spending hours feeding on these tiny algae. Intriguingly, Wali bai represents an outstanding case since at most bais elephants have been observed spending only little time feeding on vegetation. Though plant species known to be consumed by elephants are abundant at most bais, the resources mostly consumed by elephants at bais are the mineral-rich water and soil (see chapter 7).

Plant species known to be consumed by the giant hog were found at rather low abundances at the surveyed bais and the presence of known feeding plant species for the red river hog were negligible. The distinction of feeding traces from the two pig species is, however, very difficult and it is likely that many species reported as feeding plants for the giant hog are also consumed by the red river hog. Moreover, in the field feeding traces for plant species could often not be assigned to a particular animal species. Plant species identified as feeding plants without knowledge on the exact consumer(s) were abundant at most bais. Traces often indicated ungulates such as the bongo and the buffalo as well as pigs as possible consumers. Therefore it is likely that the abundance of feeding plants for these and other species is underestimated. The relatively low number of feeding plant species reported in the literature for bongos, sitatungas, red river hogs and giant hogs probably reflects the fact that these mammals have been less studied than the western lowland gorilla, the forest elephant or the forest buffalo.

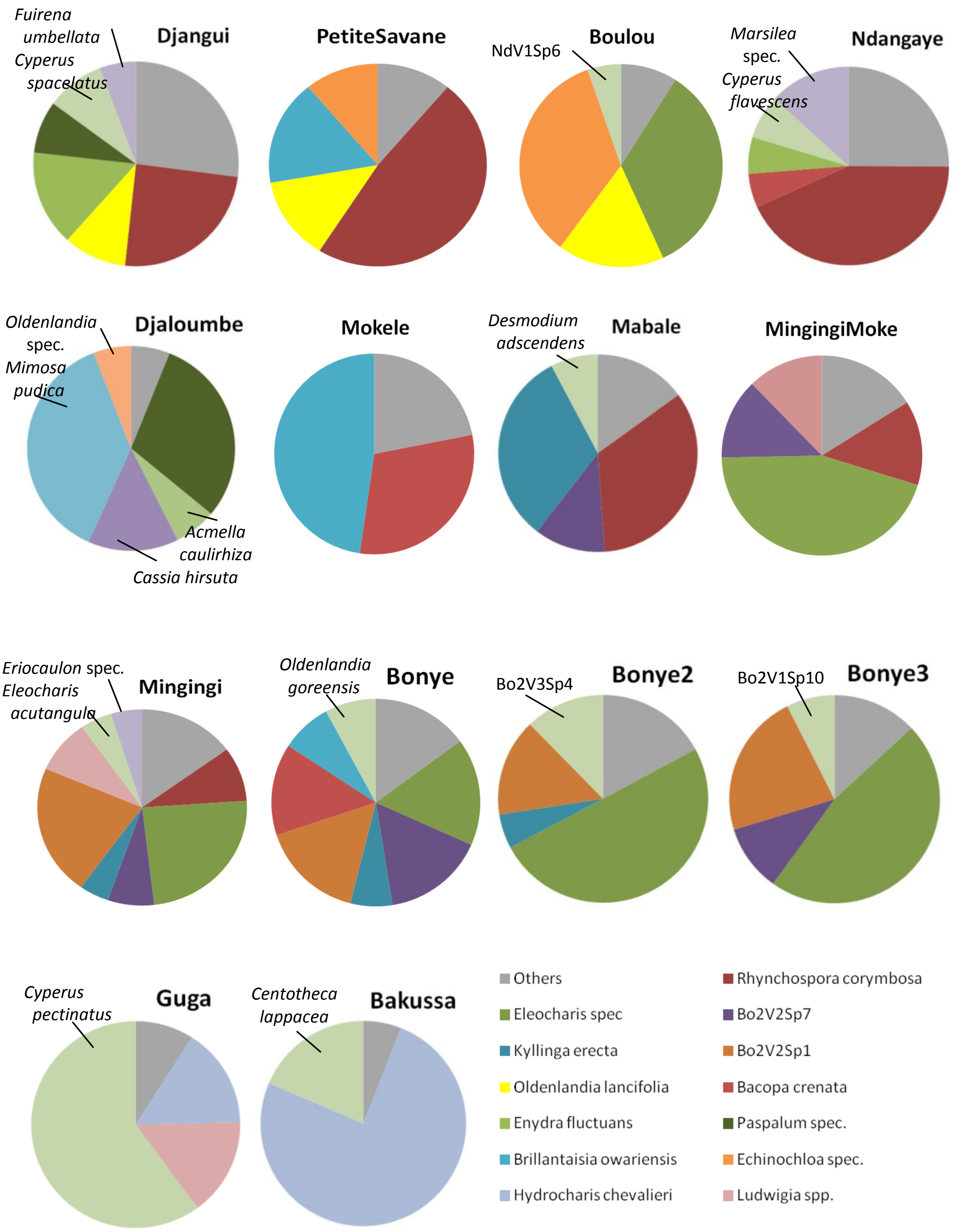
Feeding plants of the sitatunga were, however, abundant at most bais and are likely also consumed by its relative, the bongo. Though a timid species, bongos have been reported as regular visitors to bais that are central points in their home range (Klaus-Hügi, 1998). Bongos consume soil and supplement their diet feeding on grasses and herbs at bais (Klaus-Hügi, 1998). Like elephants and buffaloes, bongos have been reported to feed on *Spirogyra* spec. at Wali bai (Elkan, 2003). Altogether, the number of 21 feeding plant species, which could not be assigned to certain mammal species, demonstrates that we still lack essential information on feeding plants, especially for secretive species such as the bongo and small to medium-sized species such as the red river hog and the giant hog. The high heterogeneity of bais illustrated here emphasizes the need for further studies on feeding plants.

Classification of bais

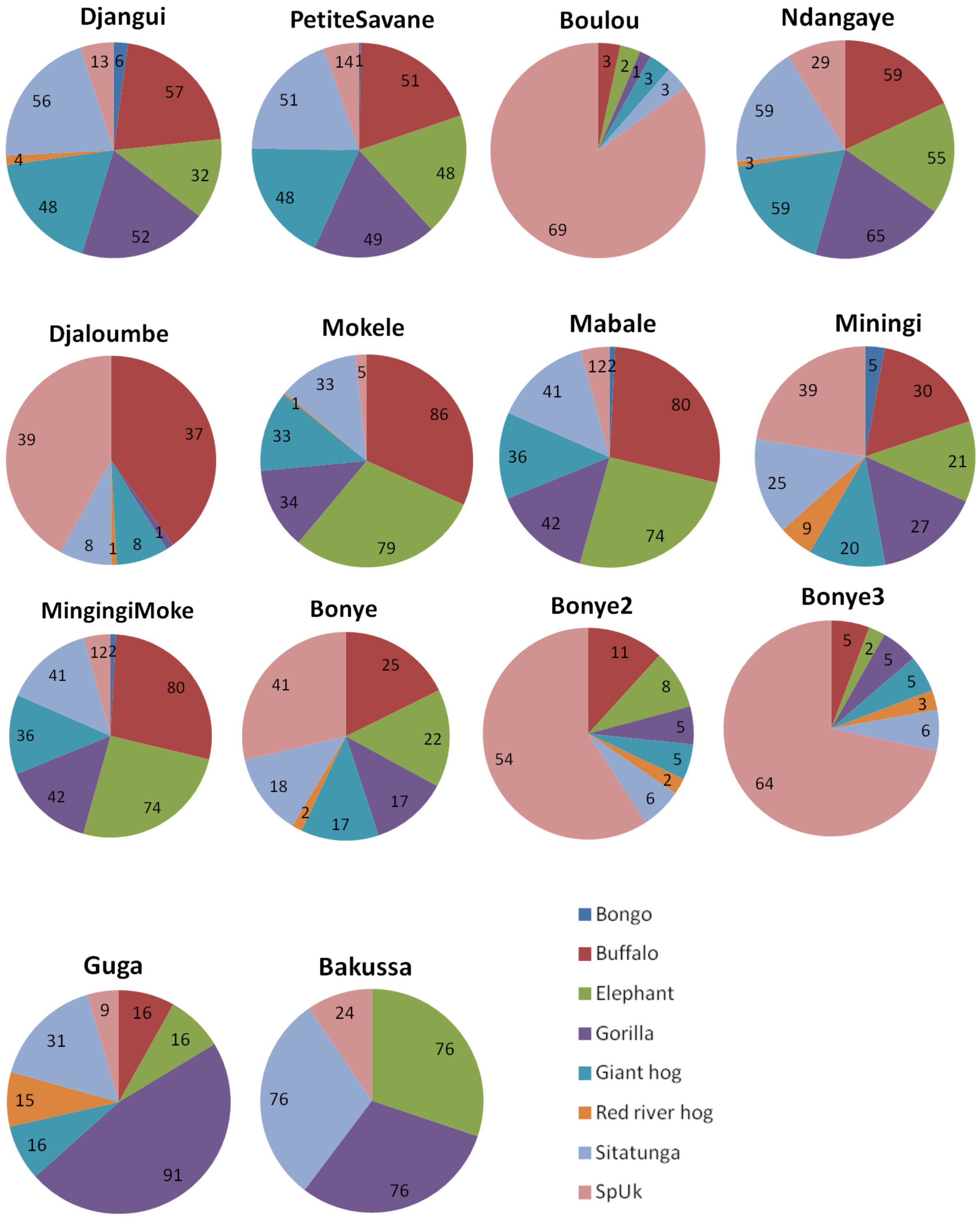
Finally, the high diversity of bais as well as their broad regional distribution explains the variety of terms applied for clearings. Natural forest clearings in the Central African rain forest have been designated different names and have been classified by different authors (see chapter 2.1). Another classification that is often used (TNS, 2012) is the one by Maisels (1996), who distinguishes two main types: elephant bais and gorilla bais 'not greatly visited by elephants'. According to Maisels (1996) the former are visited by elephants and other mammals, with a monotonous flora including *Rhynchospora corymbosa* and other Cyperaceae as well as clear signs of elephant activity such as digging and include almost all bais next to rivers. In contrast, 'gorilla bais' located in valleys (generally not beside major rivers) are wetter and hold a more diverse flora including many dicotyledonous species (Maisels, 1996). This classification appears reasonable since in the field it may be straightforward to distinguish rather dry bais with many signs of elephant activity from wetter bais without those signs but with a high abundance of plant species that supposedly make these bais more attractive for gorillas. There are, however, several reasons to caution against this classification regarding bais in our study area. First, many plant species, including *Rhynchospora corymbosa*, are consumed both by gorillas and elephants rendering a distinction between bais based on feeding plants of either species difficult. Second, in the case of many bais it will be difficult to compare the visitation frequency of gorillas and elephants. The swampy Mbeli bai, for example, is highly frequented by gorillas, yet many elephants visit this bai as well in order to consume water from the bottom of deep pits. Many individual elephants have been identified at Mbeli through direct observations (Fishlock et al., 2008) and results from camera traps suggest that even higher numbers of elephants are visiting during the night (see chapter 6). In fact, little is known about the presence and visitation rates of large mammals such as elephants and gorillas at most bais, except for a small number of bais where long-term bai studies are ongoing (see chapter 6). Besides, in some cases the suitability of a bai regarding nutritional resources, e.g. for gorillas, may be concealed by possible species interactions. Given the lack of data on species presence and abundance for multiple bais due to logistical and financial constraints care has to be taken when classifying bais according to the presence of certain mammal species. A classification based on features such as the soil moisture and vegetation appears therefore more convenient and more informative.

In conclusion, the heterogeneity of structural features and vegetation at bais illustrated here contributes to the high complexity of the system. It is likely that some bais are more attractive for particular mammal species, such as gorillas or elephants. Yet, this deserves more detailed investigations, especially on the presence and visiting rates of mammal species at different bais. In chapter 6, the potential of camera traps to provide such data is explored. The nutritional value and availability of important resources such as soil and water (chapter 7) and plant species (chapter 8) will be investigated.

Appendix



Figures 5-A.1a-n Percentage of vegetation cover for plant species with more than 5 % of coverage.



Figures 5-A.2a-n Percentage of total vegetation cover for feeding plants known to be consumed by certain mammal species at different bais. SpUk: not known by which mammal these plants are consumed.

6 Assessing species occurrence and species-specific use patterns of bais (forest clearings) in Central Africa with camera traps

Julia Gessner, Rainer Buchwald, George Wittemyer

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Assessing species occurrence and species-specific use patterns of bais (forest clearings) in Central Africa with camera traps

Julia Gessner[1]*, Rainer Buchwald[1] and George Wittemyer[2]

[1] *Vegetation Science and Nature Conservation Group, Carl von Ossietzky University, 26111 Oldenburg, Germany and* [2] *Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO 80523,U.S.A.*

Abstract

The impacts of increasing resource extraction on biodiversity in the Central African rainforest are largely unknown, in part due to the lack of baseline data on species occurrence across the basin. Natural forest clearings (bais) in this region are key habitats for a variety of vertebrates and offer opportunities for monitoring species distribution. Information on species composition, however, is lacking from the majority of areas (except for long-term study sites). Approaches and protocols for short-term bai assessments can greatly advance such baseline knowledge. This study demonstrates that camera traps provide an effective method for species inventories (species occurrence and temporal activity patterns) and monitoring at bais across the broader region. In comparison with direct observational studies, they performed especially well regarding rare and nocturnal species. Camera traps during sampling sessions of 4 weeks or less recorded previously undocumented, and 65–94% of the mammals known to use each of seven Central African bais. Results indicate that many mammal species, in particular African forest elephants (*Loxodonta africana cyclotis*), visit bais preferentially at night. This underlines the urgent need for monitoring tools providing both diurnal and nocturnal data to provide baseline data that address conservation and management objectives.

Key words: activity patterns, bais, camera traps, Central Africa, mammals, monitoring

Résumé

Les impacts de l'extraction croissante des ressources sur la biodiversité de la forêt pluviale d'Afrique centrale sont encore fort méconnus, notamment en raison du manque de données de référence sur la présence des espèces dans tout le bassin. Les clairières naturelles (bais) de cette région sont des habitats cruciaux pour toute une variété de vertébrés et elles offrent de bonnes possibilités de suivre la distribution de certaines espèces. Pourtant, les informations manquent pour la majorité des endroits (à l'exception des sites d'études à long terme). Approches et protocoles pour des évaluations des bais à court terme peuvent faire progresser fortement ces connaissances de base. Cette étude montre que les pièges photographiques constituent une méthode efficace pour des inventaires d'espèces (présence d'espèces et schémas temporels des activités) et pour le suivi dans les bais au-delà de la région frontalière. En comparant avec des études par observations directes, ils ont donné des résultats particulièrement bons pour des espèces rares et nocturnes. Des pièges photographiques utilisés pendant les sessions d'échantillonnage ont enregistré des espèces jusque-là non documentées et de 65 à 94 % des mammifères connus pour fréquenter chacun des sept bais d'Afrique centrale. Les résultats indiquent que de nombreuses espèces animales, et particulièrement les éléphants de forêt (*Loxodonta africana cyclotis*), visitent de préférence les bais pendant la nuit. Ceci souligne le besoin urgent d'instruments de suivi qui fournissent à la fois des données diurnes et nocturnes, afin d'obtenir des données de référence pour répondre aux objectifs de la conservation et de la gestion.

Introduction

In the Central African rain forest basin, biodiversity is facing increasing threats from habitat alteration caused by resource exploitation and accompanying increased

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**Correspondence:* E-mail: julia_gessner@gmx.net

poaching. Meanwhile, there is a lack of baseline data on animal species occurrence and density across the basin. As such, there is an urgent need for species distribution monitoring programmes, but the best approach to monitor biodiversity across this vast remote system remains unresolved. Natural forest clearings, locally known as bais, in the Central African rain forest have been identified as key sites for research on the regions fauna (Turkalo & Fay, 1995). These geophysical features attract large numbers of otherwise forest dwelling species (birds, mammals and reptiles), allowing a unique opportunity for behavioural observation, census and sampling of cryptic species. Direct observations at bais provide important monitoring data on mammal populations and insight in the ecology of numerous species, including large mammals such as the African forest elephant (*Loxodonta africana cyclotis*) and the western lowland gorilla (*Gorilla gorilla gorilla*) (Turkalo & Fay, 1995; Breuer *et al.*, 2008). But logistic and financial constraints restrict such observational studies to a relatively small number of bais. Little is known regarding the species composition and distribution across the broader region, despite the importance of such information for conservation and management objectives. Consequently, development of monitoring protocols best suited for short-term bai studies is needed.

Elephants are known to visit bais more frequently during the night than day (Turkalo & Fay, 2001; Momont, 2007), and it is speculated that such nocturnal behaviour is common to many forest species. Due to difficulties in data collection during the night, few studies of night-time bai use or species activity have been conducted. Wrege *et al.* (2012) used acoustic monitoring tools to assess the numbers of elephants for long time periods at several bais in Gabon. Inference on the age and sex classes of this vocal species can be drawn from acoustic data (Wrege *et al.*, 2012), but this approach is less suitable for nonvocal species or where external factors such as human activities impact vocalization rates.

This study is the first to use camera traps to investigate the diurnal and nocturnal use of bais in Central Africa by medium to large-sized mammals. Here, we present results from a camera trap study at seven bais in Cameroon and the Republic of Congo, conducted during both the wet and dry seasons. Species composition and activity patterns of large mammals visiting the different bais were summarized. We compare camera-trap-based data with that from observations and discuss the efficacy of our study protocols and the potential of camera traps as a bai monitoring tool.

Material and methods

Clearings within the Lobeke (Cameroon) and the Nouabale-Ndoki (Republic of Congo) National Parks (NP) as well as the latter's surrounding area were the focus of this study (Fig. 1). Both parks are part of the Sangha Trinational protected areas complex in Central Africa. The Nouabale-Ndoki NP has never been exploited, while part of Lobeke has been selectively logged before its declaration as National Park in 2001 (Stromayer & Ekobo, 1992; MINEF, 2004); logging concessions are located adjacent to both protected areas. The climate is equatorial with mean annual rainfall around 1600 mm and an average annual temperature of about 25°C. The major dry season (<100 mm rainfall per month) lasts from December to February, and the major rainy season from September to November (MINEF, 2004). The area hosts important populations of large mammals such as the African forest elephant, the bongo antelope (*Tragelaphus euryceros*) and the western lowland gorilla (Stokes *et al.*, 2010).

Infrared camera traps (Reconyx hyperfire HC500, Holmen, WI, USA) were set-up around seven bais during the rainy and dry season for approximately 2 weeks for each season. The bais (two in Lobeke, five in Nouabale-Ndoki and its periphery) were selected based on accessibility, representativeness in terms of size and distribution in terms of spatial separation between bais. Due to an ongoing long-term bai study at Mbeli, camera traps were employed only once in the rainy season for 3 weeks to minimize disturbance of animals. As direct sunlight may influence the cameras' performance, cameras were installed in the adjacent forest facing animal trails leading into the respective bai. At each bai, two to six camera traps, depending on the size of a bai, were deployed on distinct trails. The main criterion for the selection of trails was separation from other trails by approximately 300 m, or 150 m at small bais. Care was taken to use equal numbers of large (>30 cm) and small ($\leq$ 30 cm) trails at each bai, unless only large animal trails could be reliably identified. To record both small and large animals, cameras were positioned at 30–50 cm height and a distance of at least 2 m from the trail. Camera traps worked 24 h a day and were set to no delay, that is, to be triggered by all motion events without a quiet period. Information on the date and time was automatically imprinted on each photo. Entirely swampy bais were avoided in this study as animal trails are difficult to distinguish in such habitats.

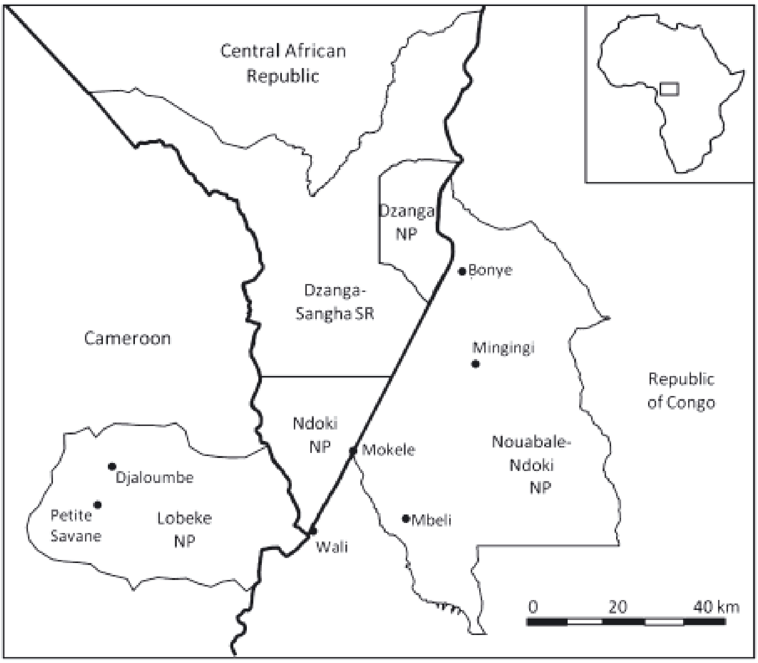

Fig 1 Map showing the study area in Central Africa. The seven bais surveyed are located in the Lobeke (Cameroon) and Nouabale-Ndoki (Republic of Congo) National parks as well as the latter's surrounding area. Both National parks together with the Dzanga and Ndoki National Parks as well as the Dzanga-Sangha Special Reserve (Central African Republic) constitute the Trinational de la Sangha protected area

In total, 47 camera trap sessions of approximately 2 weeks were conducted across seasons and bais, with five cameras being taken down by elephants and a leopard within a few days of set-up. Two of these cameras worked for 3 days and were included; the other three failed cameras were excluded from analysis. We further excluded failed images, where the camera was either triggered by sunlight or the flash was blocked by a leaf or branch resulting in a dark picture.

Data collation and analysis

For all pictures, the animal species captured was identified. Any fleeing behaviour was noted as well as the direction of each animal (walking to or coming from the bai) and whether an animal was walking alone or in a group; a group was defined as animals of the same species walking in the same direction with a maximum interval of 10 min between individuals. When an individual or group of the same species passed a camera trap twice within 30 min (see also O'Brien, Kinnaird & Wibisono, 2003), distinct features of the animals (e.g. notches and holes in the ears of elephants) were studied on the pictures to assess whether it was the same individual or group. Double counts identified in this manner were excluded from analysis.

To investigate diurnal and nocturnal activity patterns, the time interval from 6:00 to 17:59 was considered as daylight hours and the night from 18:00 to 05:59 according to dawn and dusk in the equatorial forest. Elephant diurnal visiting rates were compared with nocturnal rates at different bais (excluding Petite Savane due to its small sample size). Regarding activity patterns of the remaining species, data from all bais were combined due to low sample sizes. Seasonal differences in species presence and activity were compared where camera trap stations functioned during both seasons (excluding Mbeli bai). As the number of recording days in both seasons varied slightly, station-specific data collected were compared for the period of fewest collection days. We further examined the use of small versus large trails by different mammal species. To account for differences in sampling effort across trail size classes, trapping rates (i.e. the numbers of records divided by the respective number of recording hours) were compared.

Statistical analyses of daily activity patterns of different mammal species were conducted using circular statistics in the program Oriana version 4.01 (Kovach, 2011). Data were plotted on a circular scale with 24 hourly sections, and the total length of the circular axis representing 1 day. The Rayleigh's uniformity test was used to evaluate the probability that the data (e.g. records of different mammal species) were distributed uniformly on the circular axis. To compare more than two samples, for example, differences in the distributions of elephants at different bais, the Watson–Williams F-test was used (Kovach, 2011).

Differences between the numbers of elephants visiting each bai during the day versus the night were investigated using Wilcoxon tests. Nonparametric tests were used for all analysis because normality was not reached after data transformation. The Spearman correlation coefficient was calculated to test for correlations between the numbers of elephants during the night versus the day at each bai. The Mann–Whitney *U*-test was applied to examine differences regarding the number of elephants between the rainy and the dry season as well as large versus small trails. All noncircular statistics were performed in SPSS version 20 (IBM, Armonk, NY, USA). Statistical significance was set at $\alpha \leq 0.05$.

Results

Camera trap data summary

In 697 camera trap days (15282 h), 5772 photo events were recorded, 280 of which could not be identified and were excluded from further analysis. In total, 25 mammal species were identified (listed in Table 1) besides mice, squirrels, a giant pouched rat (*Cricetomys* sp.), birds and humans.

For each bai, species captured by camera traps were compared with species lists provided by long-term studies conducting direct observations (of at least 1 year) at the respective bai (Nzooh Dongmo, 2003; Mowawa, 2006; Dieudonne, 2010; K. Greenway, pers. comm.), with the exception of Mokele bai where no such observational data were available (Table 1). At Bonye, Mingingi and Wali,

Table 1 Mammal species recorded at different bais. The total number of species recorded at each bai by camera traps, direct observations (Nzooh Dongmo, 2003; Mowawa, 2006; Dieudonne, 2010; K. Greenway, pers. comm.) and in combination

Species	Bonye	Mbeli	Mingingi	Mokele	Wali	Djaloumbe	Petite Savane
Brush-tailed porcupine *Atherurus africanus*	+		+			+	+
Marsh mongoose *Atilax paludinosus*	+	1	+			1	1
Peter's duiker *Cephalophus callipygus*	1	1	1	+	*	1	1
Bay duiker Cephalophus dorsalis	+	*			+	+	*
Blue duiker *Cephalophus monticola*	1	1	+	+	+	1	1
Black-fronted duiker *Cephalophus nigrifrons*	1		1	+			
Yellow-backed duiker *Cephalophus silvicultor*	+	+		+	1	1	1
Agile mangabey *Cercocebus agilis*	+	*		+		+	+
Moustached monkey *Cercopithecus cephus*		*				*	1
De Brazza's monkey *Cercopithecus neglectus*	+	*				*	*
African civet *Civettictis civetta*		1			+	1	
Spotted hyaena *Crocuta crocuta*	+						
Genet *Genetta* sp.	+		+	+		1	1
Western lowland gorilla *Gorilla g. gorilla*	*	1	1	+		1	1
Guereza colobus *Guereza colobus*	*	*	*			1	1
Water chevrotain *Hyemoschus aquaticus*	*	+	+	+	1	1	1
Giant hog *Hylochoerus meinertzhageni*	+	1				1	1
African forest elephant *Loxodonta a. cyclotis*	1	1	1	+	1	1	1
Chimpanzee *Pan troglodytes*		*	1			1	*
Leopard *Panthera pardus*	1	1	+		+	1	*
Red river hog *Potamochoerus porcus*	1	1	1			1	1
Pangolin *Smutsia* sp.						1	1
African forest buffalo *Syncerus caffer nanus*	1	1	1	+	1	1	1
Bongo *Tragelaphus euryceros*	1	1	1	+	+	1	1
Sitatunga *Tragelaphus spekei*	1	*	1		+	*	1
Camera traps	18	13	15	11	10	20	18
Direct observations	12	18	9	–	5	20	20
Total	21	20	16	11	11	23	22

Species only recorded by camera traps (+) or direct observations (*) as well as by both (1) are indicated.

camera traps yielded higher numbers of species than direct observations recording 86%, 94% and 91%, respectively, of the total number of species detected by both methods (Table 1). In contrast, at Mbeli and Petite Savane, camera traps recorded fewer species than those recorded during long-term direct observations, detecting 65% and 82%, respectively, of the total number of species provided by both methods. At Djaloumbe, each method detected 87% of the total known species.

Semi-aquatic bai living species of the subfamily *Lutrinae* only recorded by direct observations were excluded as it is assumed that they would not be detected by camera traps on forest trails. At Bonye bai, first evidence was provided for the occurrence of the spotted hyaena in the north of Nouabale-Ndoki NP.

Temporal patterns of use

Mammal species recorded by camera traps solely during the day include the agile mangabey, the guereza colobus and the marsh mongoose. Records of the civet, the spotted hyaena, the genet, the pangolin and the brush-tailed porcupine were only made during the night. Leopard captures were predominantly at night (nine of eleven). Information on capture time of different species visiting the bais is presented (Table 2).

Activity patterns of forest elephants revealed by camera traps showed evidence of preference for nocturnal bai visits (Fig. 2 and Table 2). Distributions differed significantly across bais (Watson–Williams F-test: $F = 4.917$, $df = 6$, $df_2 = 3898$, $P < 0.05$). Significantly more elephants were recorded during the night in all bais, with the exception of Petite Savane where few (34) elephants were captured (Table 3). Altogether, 86% of elephants visited the bais during the night (95% at Mokele, 93% at Djaloumbe, 91% at Mbeli, 88% at Petite Savane, 87% at Mingingi, 84% at Wali and 74% at Bonye). Bonye demonstrated the greatest diurnal elephant use among the studied bais. High numbers of elephants (more than 50) were recorded between 14:00 and 18:00, while at other bais, more than 50 elephants were only recorded after 18:00. Only for Mokele bai, a significant correlation was found between the numbers of elephants recorded during the day and the night (Table 3).

Data collected for approximately 9800 recording hours at six bais were used for the investigation of differences between months of the rainy and the dry season. No significant differences regarding the number of elephants between both seasons were detected except at Djaloumbe bai (Table 3). At Wali, more (although not significant) buffaloes were recorded in the rainy season (33 individuals) than in the dry season (eight) (Mann–Whitney *U*-test: $U = 87.5$, $n = 16$, $P > 0.05$); at Mokele (39 individuals) and Petite Savane (nine), buffaloes were recorded solely in the rainy season. More bongos (although not significant) were recorded during the dry season in comparison with the rainy season (111 and 56 animals, respectively; Mann–Whitney *U*-test: $U = 110$, $n = 16$, $P > 0.05$) at Djaloumbe. At Mokele, bai bongos were filmed only in the rainy season (41 records). At the remaining bais and for other species, not enough records were available for the investigation of seasonal patterns.

Table 2 Time of mean activity for different mammal species recorded by camera traps combining data from all bais

Species	Time of mean activity	Rayleigh test
Tragelaphus spekei	06:22 ± 03:32 circstdev	$r = 0.649$, $z = 5.1$, $n = 12$, $P < 0.05$
Cephalophus nigrifrons	10:15 ± 03:25 circstdev	$r = 0.669$, $z = 9.9$, $n = 22$, $P < 0.05$
Cephalophus callipygus	11:23 ± 03:35 circstdev	$r = 0.642$, $z = 41.6$, $n = 101$, $P < 0.05$
Cephalophus monticola	11:31 ± 05:14 circstdev	$r = 0.39$, $z = 39.7$, $n = 261$, $P < 0.05$
Gorilla gorilla gorilla	14:14 ± 03:02 circstdev	$r = 0.729$, $z = 26.1$, $n = 49$, $P < 0.05$
Hylochoerus meinertzhageni	16:44 ± 03:32 circstdev	$r = 0.729$, $z = 26.1$, $n = 49$, $P < 0.05$
Potamochoerus porcus	19:23 ± 05:28 circstdev	$r = 0.359$, $z = 14.9$, $n = 116$, $P < 0.05$
Cephalophus silvicultor	21:04 ± 02:29 circstdev	$r = 0.808$, $z = 14.4$, $n = 22$, $P < 0.05$
Loxodonta africana cyclotis	22:44 ± 04:07 circstdev	$r = 0.557$, $z = 1212.4$, $n = 3905$, $P < 0.05$
Hyemoschus aquaticus	23:14 ± 03:04 circstdev	$r = 0.724$, $z = 27.2$, $n = 52$, $P < 0.05$
Cephalophus dorsalis	23:59 ± 02:46 circstdev	$r = 0.769$, $z = 17.1$, $n = 29$, $P < 0.05$
Syncerus caffer nanus	01:05 ± 03:53 circstdev	$r = 0.595$, $z = 51.1$, $n = 144$, $P < 0.05$
Tragelaphus euryceros	01:58 ± 05:12 circstdev	$r = 0.395$, $z = 55.4$, $n = 355$, $P < 0.05$

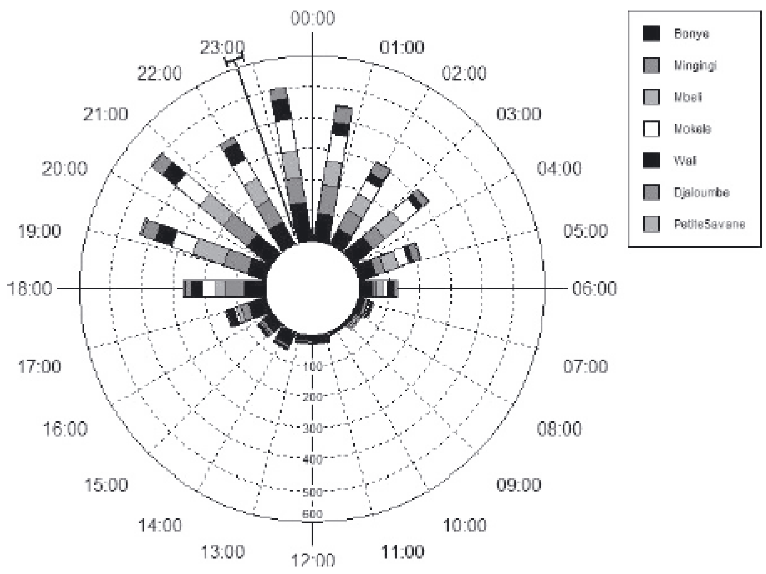

Fig 2 Circular histogram illustrating the distribution and mean of elephant numbers recorded by camera traps throughout the day across all bais. The numbers of elephants differs significantly from a random distribution ($r = 0.556$, $z = 1212.4$, $n = 3905$, $P < 0.05$) with 22:44 being the mean time of elephant activity

Table 3 Mean time of elephant activity at different bais revealed by circular statistics

	Elephant activity pattern		Day versus night	Dry versus wet season
	Time of mean activity ± circstdev	Wilcoxon test	Spearman's correlation	Mann–Whitney *U*-test
Bonye	22:27 ± 05:07	$z = 4.706$, $n = 31$, $P < 0.05$	$r = 0.223$, $n = 31$, $P > 0.05$	$U = 88$, $n = 15$, $P > 0.05$
Mokele	23:07 ± 03:27	$z = 4.541$, $n = 29$, $P < 0.05$	$r = 0.388$, $n = 29$, $P < 0.05$	$U = 57$, $n = 14$, $P > 0.05$
Djaloumbe	23:10 ± 03:51	$z = 5.175$, $n = 40$, $P < 0.05$	$r = 0.013$, $n = 40$, $P > 0.05$	$U = 68.5$, $n = 14$, $P > 0.05$
Mingingi	22:29 ± 03:56	$z = 4.920$, $n = 32$, $P < 0.05$	$r = 0.134$, $n = 32$, $P > 0.05$	$U = 91$, $n = 15$, $P > 0.05$
Petite Savane	21:43 ± 04:53	$z = 1.872$, $n = 34$, $P > 0.05$	$r = 0.071$, $n = 34$, $P > 0.05$	$U = 86.5$, $n = 15$, $P > 0.05$
Wali	22:08 ± 03:58	$z = 4.865$, $n = 32$, $P < 0.05$	$r = 0.024$, $n = 32$, $P > 0.05$	$U = 115$, $n = 16$, $P > 0.05$
Mbeli	23:00 ± 03:46	$z = 3.921$, $n = 20$, $P < 0.05$	$r = 0.195$, $n = 20$, $P > 0.05$	–

Significant differences between numbers of elephants recorded during the day versus the night (Wilcoxon test) as well as correlations between numbers recorded during the day and the night (Spearman's correlation) are indicated. Significant differences between the number of elephants recorded in the rainy versus the dry season (Mann–Whitney *U*-test) are provided for each bai (excluding Mbeli where camera traps were set-up only during the rainy season).

Impact of trail size

Camera traps at large trails yielded significantly more photos than those set-up at small trails and higher numbers of records per observation hour for elephants (Mann–Whitney *U*-test: $n_L = 18$, $n_S = 10$; $U_{Total} = 30$, $P < 0.05$; $U_{Elephants} = 36$, $P < 0.05$). In total, more bongos were recorded on large trails than on small trails (3.45 and 0.24 records per 10 h of observation, respectively), although this was not significant (Mann–Whitney *U*-test: $U = 73.5$, $n_L = 18$, $n_S = 10$, $P > 0.05$). Certain species were more often recorded on small trails, such as the water chevrotain, the marsh mongoose and some duiker species (Fig. 3).

Discussion

In the present study, camera traps were employed at each bai for a relatively short period of three to four weeks. Yet, they recorded most (65–94%) of the mammal species known to visit the respective bai (as derived from both

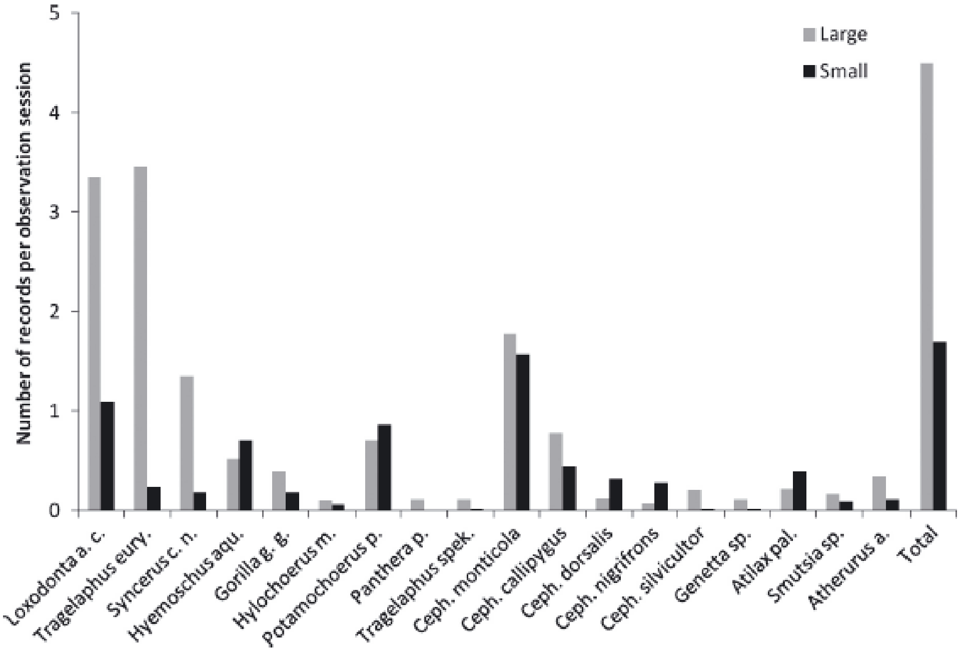

Fig 3 Usage of small (black bars; n = 10) versus large (grey bars; n = 18) trails by different mammal species. Observation rates are presented as numbers of observations per 100 h for all species except elephants, which are presented as number per 10 h. Observation rates of total species are also presented as number per 10 h. Species with <10 records have been excluded from the graph although they are represented in the 'total' category

camera traps and long-term studies using direct observations). These results confirm that camera trapping is an effective method for species inventories as it has been shown in other studies on medium to large-sized mammals (Rovero, Tobler & Sanderson, 2010). While a two-week time frame per season appeared to capture most species (see also Gompper *et al.*, 2006), capture effectiveness was greater at some bais than others. This might be due to the sampling design, species density or differences in bai-specific characteristics (mineral resources, feeding plants, human activity, etc.). Probably because of the 24-h sampling, a number of (primarily nocturnal) species were observed with the camera survey approach that were not seen during direct observations. Consequently, camera traps provide high-quality species occupancy data in the forest setting (see also Matsubayashi *et al.*, 2007) with much lower man-hour requirements than direct observations.

Species not detected by camera traps were mainly arboreal monkeys that, as part of their antipredator behaviour, do not typically enter bais on trails (Janson, 1998; Blake *et al.*, 2010; Link *et al.*, 2011). Only the guereza colobus is known to regularly visit bais for longer durations searching for food. Camera traps appear highly applicable for the detection of species using permanent trails to enter clearings such as forest elephants, bongos and forest buffaloes (Klaus-Hügi, Klaus & Schmid, 2000; Blake, 2002). Results show that large trails were more frequently used and captured significantly higher numbers of elephants than small trails, although small trails were of importance to capture smaller species such as the water chevrotain, the marsh mongoose and duiker species. In general, results indicate that camera traps have a very low impact on forest mammals because among the 467 captures that showed animal reaction, only twelve depicted fleeing. The feasibility of identifying age and sex classes and even individual forest elephants found in the present study confirms findings from Varma, Pittet & Jamadagni (2006) that camera traps have potential for the study of the population structure of elephants.

As expected, diurnal species such as the western lowland gorilla, the chimpanzee, the agile mangabey, the guereza colobus and the marsh mongoose were recorded by camera traps solely during the day (Estes, 1992; Djagoun *et al.*, 2003; Kingdon, 2003), while the bongo visited the bais preferentially in the night (Klaus-Hügi, Klaus & Schmid, 2000; Elkan, 2003). Large numbers of buffalo have been recorded at clearings during the day by several studies (Magliocca, 2000; Melletti *et al.*, 2007; Gessner, 2008), yet camera traps recorded significantly higher numbers of buffaloes during the night at all bais except Djaloumbe. Camera traps showed a clear distinction between diurnal (blue duiker, Peter's duiker and black-fronted duiker) and nocturnal (bay duiker) duiker species (Estes, 1992; Kingdon, 2003). Although the yellow-backed duiker is thought to be active both during day and night (Kranz & Lumpkin, 1982; Newig, 2001), this species was recorded by camera traps only during the night.

Applying acoustic monitoring tools at six forest clearings in Gabon, Wrege *et al.* (2012) found that 79% of all elephant visitation occurred at night. Similar results were found in the present study with 74–95% of the elephants visiting the seven bais during the night. At Bonye, higher percentages of elephants (23.3%) were recorded during the day than at the remaining bais (6.3–15.7%) with increasing numbers from 14:00 on (Fig. 2). Bonye is located very close to Dzanga bai, C.A.R. (23 km), and many individually identified elephants are known to frequent both clearings (Inkamba-Nkulu, 2007). A long-term, individually based monitoring project at Dzanga has recorded high densities of elephants throughout the day with increasing numbers in the afternoon (Turkalo & Fay, 1995). Consequently, it is possible that elephants show a similar activity pattern at these clearings as they share the same elephant population and are both rarely frequented by poachers. As forest clearings represent easy hunting grounds, it is generally assumed that higher visitation rates of elephants during the night reflect the elephants' reaction to poaching pressure (see Ruggiero, 1999). Our sample of human captures was too small to investigate any such relationship, but indicates camera traps may be a useful metric to identify levels of human pressure.

At each bai, a significant difference between the number of elephants recorded during the day and the night was detected (except Petite Savane). No significant correlation between day and night numbers of elephants was found for any of the bais except Mokele. This confirms findings from Wrege *et al.* (2012) who recorded large changes in nocturnal elephant numbers without proportional changes in daytime numbers. Although our data are limited by the short-study period and the fact that camera traps only faced selected trails (not providing total numbers of animals visiting a bai), our results indicate that care has to be taken by inferring demographic trends when monitoring changes in elephant numbers only during the day.

Seasonal differences in the number of elephants recorded were not significant, with the exception of Djaloumbe bai. In contrast, camera trap data suggest that overall more buffalo visited the bais during the rainy season. While insights drawn are from a relatively short period and may not allow understanding of seasonal use, results show that camera traps are presumably able to provide necessary data for greater insight to seasonal use patterns given more thorough sampling.

In conclusion, the present study demonstrates that camera traps are valuable tools for species inventories and monitoring of certain mammal species, especially African forest elephants, at bais. Camera traps allow simultaneous monitoring of multiple bais, allowing direct comparison, and are especially time and cost-effective in remote areas. As such, camera trap data are likely to be the best means to conduct species distribution modelling and implement a large-scale monitoring programme. Camera traps cannot replace direct observations that provide more precise individual-based demographic and behavioural data. Yet, camera traps provide important data on mammal species activity patterns day and night, with the latter being a time of high mammal activity which is missed by direct observations. Further, long-term studies are needed combining direct observations and camera traps at bais to investigate the relation of data provided by camera traps and numbers of individual animals visiting a bai.

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7 Differentiation in mineral constituents in elephant selected versus unselected water and soil resources at Central African bais (forest clearings)

Julia Metsio Sienne, Rainer Buchwald, George Wittemyer

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SHORT COMMUNICATION

Differentiation in mineral constituents in elephant selected versus unselected water and soil resources at Central African bais (forest clearings)

**Julia Metsio Sienne · Rainer Buchwald ·
George Wittemyer**

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Abstract Natural forest clearings (bais) in the Central African rain forest attract large numbers of mammals. Little is known about the factors influencing bai use by forest species, though geophagy and hydro-mineral resources are assumed to be important attractants. In the present study, clay and mineral concentrations in water and soil were examined at 15 bais. Water samples from elephant excavated pits showed significantly higher concentrations of most minerals sampled relative to surface waters. But mineral portfolios varied markedly between bais. Geophagy sites were less differentiated from control soil samples, leading to the interpretation that geophagy may not structure bai visitation. Monthly sampling of pit water at one bai suggested higher dry season mineral concentrations, which may relate to seasonal wildlife visitation patterns. The complexity and variability in bai-specific mineral resources suggest there is not a single determining factor (or mineral) driving bai use. The protection of bai mosaics should be a conservation priority in order to ensure access to the portfolio of minerals likely required by endangered species such as the African forest elephant *Loxodonta africana cyclotis*.

Keywords African forest elephant · Geophagy · Limiting factors · Nutrition · Spatial heterogeneity

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J. Metsio Sienne (✉) · R. Buchwald
Vegetation Science and Nature Conservation Group,
Carl von Ossietzky University, 26111 Oldenburg, Germany
e-mail: metsio.sienne@gmx.de

G. Wittemyer
Department of Fish, Wildlife and Conservation Biology,
Colorado State University, Fort Collins, CO 80523, USA

Introduction

Mineral availability is thought to strongly shape wildlife distributions and densities (Milewski 2000). Geophagy is critical for the nutritional (mineral) budgets of numerous species in a variety of environments worldwide (Klaus 1998). It is also thought to be driven by gastro-intestinal disorders alleviated through clay ingestion (Ayotte et al. 2006).

The Central African rain forest natural clearings, locally known as bais, are considered to be mineral-rich sites attracting large numbers of African forest mammals, including elephant *Loxodonta africana cyclotis* (Turkalo and Fay 1995; Gessner et al. 2013). Relatively few studies have been conducted on the mineral properties of these features (see Klaus 1998). Mineral concentration in water holes at Central African bais has received even less attention, though elephants spend most of their time (60–90 %) at bais consuming water (J. MS, pers. observation). Consumed water resources are acquired from upwelling water (springs) in the bottom of holes that they dig in or nearby streams in contrast to geophagy where soils are the target of consumption. Magliocca (2000) reported high mineral concentrations in pit water at three bais, though sampling was limited.

Here, we compared mineral concentrations and clay content of soil and water consumed by elephants with those of random locations at 15 bais in Central Africa. In addition to comparison between used and available sites, our design provides insight to the relative nutritional importance of soil versus water resources. Furthermore, seasonal changes of mineral concentrations in three water holes at Dzanga bai are investigated.

Material and methods

Soil and water samples were collected from April 2011 to March 2012 at a forest stream and 15 clearings, five in the Lobeke National Park (Cameroon), nine in the Nouabale-Ndoki National

Park (Republic of Congo), and its surrounding area as well as the clearing Dzanga (Central African Republic) (Fig. 1).

Water samples were taken once in the rainy and again in the dry season from upwelling sources at the bottom of at least three holes dug by elephants (elephant holes) and one surface source at 11 bais and a forest stream. At Dzanga bai samples were taken once a month from April 2011 to February 2012 in three pits that were identified in collaboration with Andrea Turkalo and one surface water sample. A total of 100 samples from water upwelling at the bottom of elephant holes and 35 surface water samples were taken and analyzed.

Geophagical sites in bais were identified by recent feeding traces of elephants. Soil samples (of approximately 300 g dry weight) were collected at geophagy sites (n=20) within bais that had been used by elephants over longer periods (0–70 cm deep), at randomly selected non-geophagy control sites (n=27) within the bai (0–10 cm deep) and at three randomly selected non-geophagy sites (n=27) in the surrounding forest (5–10 cm deep). Samples were air-dried in the field and stored in plastic bags until analysis.

In the laboratory of the University of Oldenburg, sand, silt, and clay fractions were determined according to the method described by Schlichting et al. (1995). The pH was measured in a 0.01 M $CaCl_2$ suspension. The chloride concentration was determined with an electrode sonde (Mettler Toledo DX235-Cl, reference electrode inLab302) in a volumetric 1:10 soil/distilled water suspension. Mineral concentrations of Al, Ca, Cu, Fe, K, Mg, Mn, Na, P, S, Sr, and Zn in soil samples were analyzed by inductively coupled plasma optical emission spectrometry (ICP-OES) after extraction following the method of Ayotte et al. (2006). The iodine concentration of soil samples was analyzed in the laboratory of the Institute of Geoecology, Technical University Braunschweig, according to the method applied by Gilfedder et al. (2007).

The pH, conductivity, and the chloride concentration of water samples were measured by the respective electrode sonde. Due to logistic constraints samples had not been acidified and filtered (0.45 µm) in the field and consequently were pre-treated previous to further mineral analysis as follows: to a

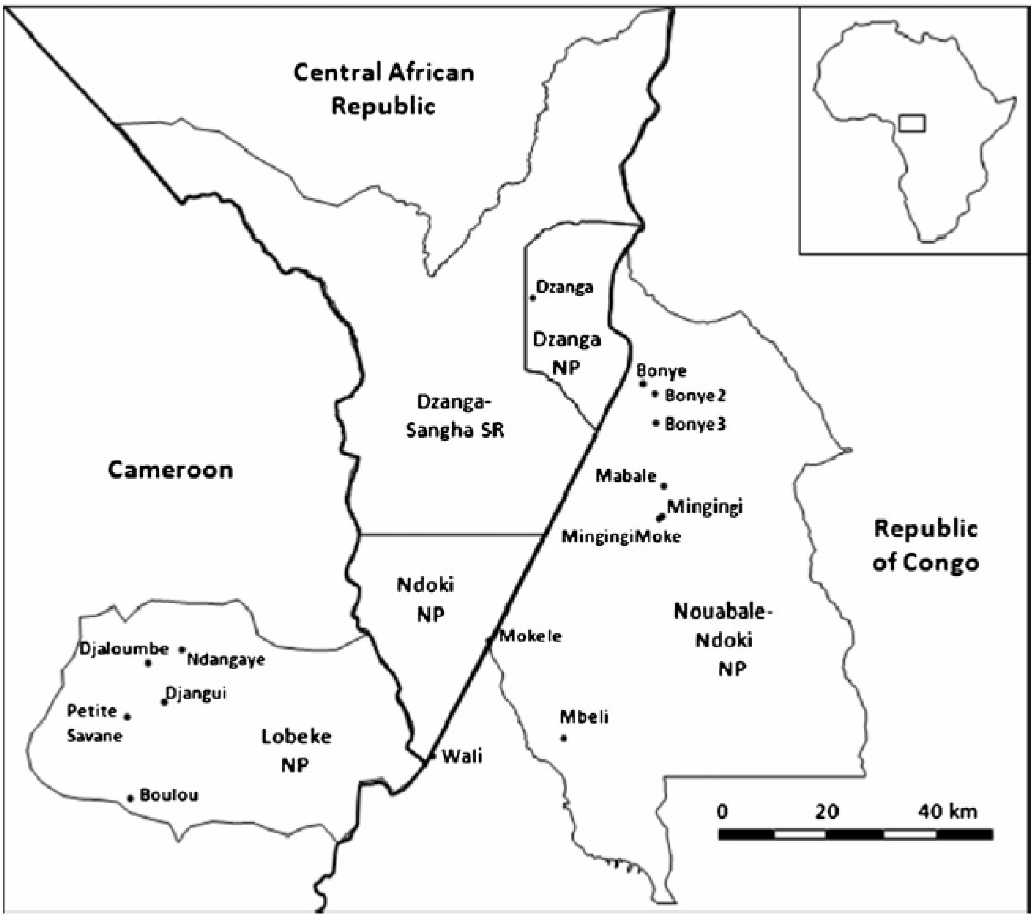

Fig. 1 Map showing the 15 bais surveyed in the Lobeke National Park (Cameroon), Nouabale-Ndoki National Park (Republic of Congo), and Dzanga National Park (Central African Republic). The three National Parks together with the Ndoki National Park and the Dzanga-Sangha Special Reserve constitute the Trinational de la Sangha area

25 ml aliquot of each sample, 32 % HCl was added until a pH of 2.0–2.5 was reached. This was left for 24 h, then sonicated for 1 h and passed through a 0.45-µm filter. Afterward, cations were determined by ICP-OES, and the iodine concentration was analyzed photometrically.

The average mineral (and clay) concentrations of bai-specific geophagical samples and control samples within and on the periphery (forest) of each bai were compared using paired Wilcoxon tests. Samples from each site associated with each bai were averaged to avoid problems with pseudo-replication. Similarly, mineral concentrations from bai-specific elephant hole and surface water samples were averaged and examined using paired Wilcoxon tests, where seasonal effects were also examined by comparing within and between seasons. Correlations between conductivity and concentrations of different minerals (except I) as well as between monthly mean conductivity and precipitation (data provided by A. Turkalo) were assessed using non-parametric methods. Non-parametric tests in SPSS version 20 were performed since normality was not reached after data transformation. Monthly conductivity data from Dzanga were log transformed and analyzed by univariate ANOVA and subsequent post hoc Tukey-B test. Statistical significance was set at $\alpha \leq 0.05$ for all analysis.

Results

The mean concentrations of minerals measured were higher in elephant hole water relative to surface water across all 11 bais and the forest stream (Fig. 2). Pair-wise comparison from averaged elephant hole water samples and surface samples in the respective bais collected during two seasons showed significantly higher concentrations in water samples from the bottom of elephant holes for all minerals except Al, Cu, and I (Table 1).

Significantly positive correlations were found between conductivity and all mineral concentrations (Table 1). The conductivity measured in elephant hole water samples at Dzanga bai varied significantly from April 2011 to February 2012 with a major peak from November to January and a minor peak in July (ANOVA and post hoc Tukey-B, d.f. = 10, $F = 9.00$, $P < 0.05$; Fig. 3). Both peaks coincide with a decrease in rainfall, though there was no significant correlation between conductivity and rain (Spearman correlation, $n = 11$, $R_s = -0.273$, $P > 0.05$).

The highest concentrations of minerals were found at bais in Cameroon where higher concentrations than the mean of elephant hole water were found for 15 (Djaloumbe) and 11 (Djangui) minerals, and mean conductivity of elephant hole water samples was more than 20 times higher than at the other bais (Fig. 4). Geophagical samples at all Cameroonian bais showed higher concentrations in 5–12 minerals relative to the mean concentration from geophagical and control samples. In the remaining bais, no more than four minerals with high concentrations were found.

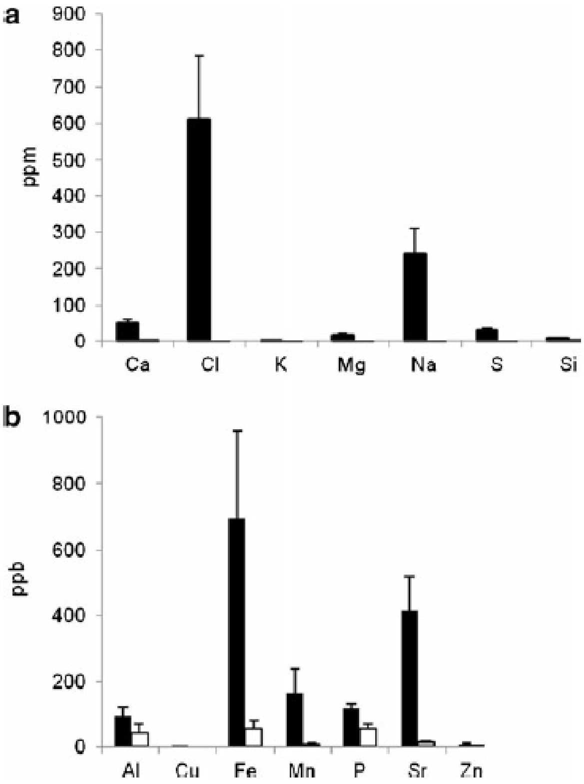

Fig. 2 Mean concentrations (with standard errors) of **a** Ca, Cl, K, Mg, Na, S, and Si; **b** Al, Cu, Fe, Mn, P, Sr, and Zn in elephant hole water samples (*black bars*) and surface water samples (*white bars*) collected in 11 bais and a forest stream

Significantly higher concentrations of Na and S were found in geophagical samples in comparison to control forest samples, while higher concentrations of I were found in control forest samples relative to geophagical samples. Comparing geophagical samples and control samples within bais, significant differences were only found for S (Tables 1 and 2).

Discussion

Mineral access and geophagy have long been assumed to be the driver of bai visitation, yet our knowledge of what attractants bring elephants to a bai has not been adequately addressed. In view of the high effort and large amount of time elephants spend acquiring water from the bottom of deep water holes while in bais, we assumed these water sources would be richer in nutritionally important minerals relative to surface water. Supporting this prediction, elephant hole water showed significantly higher concentrations of most minerals analyzed in comparison to surface water. The largest differences found were for Cl, Na, S, and Zn, though Ca, Mg, Mn,

Table 1 Pair-wise comparison (Wilcoxon test) of mineral and clay concentrations between geophagical and control soil samples within bais (*n*=10), between geophagical and control forest samples (*n*=10), and bai-based pair-wise comparison of mineral concentrations in water hole (*n*=70) and average control surface water (*n*=22) samples from 11 bais

	Geophagical–control bai		Geophagical–control forest		Water surface–ground		Conductivity–minerals	
	Wilcoxon test		Wilcoxon test		Wilcoxon test		Spearman correlation	
	Z value	*P* value	*Z* value	*P* value	*Z* value	*P* value	*R* value	*P* value
Al	1.78	0.074	0.66	0.508	0.438	0.661	*0.224*	*0.009*
Ca	0.76	0.445	1.07	0.285	*3.847*	*0.000*	*0.969*	*0.000*
Cl	1.78	0.074	1.78	0.074	*3.847*	*0.000*	*0.763*	*0.000*
Cu	1.48	0.139	0.26	0.799	0.674	0.500	*0.326*	*0.000*
Fe	1.07	0.285	0.15	0.878	*2.419*	*0.016*	*0.384*	*0.000*
I	0.15	0.878	1.89	0.059				
K	0.87	0.386	0.26	0.799	*3.393*	*0.001*	*0.739*	*0.000*
Mg	0.15	0.878	0.663	0.508	*3.815*	*0.000*	*0.958*	*0.000*
Mn	1.27	0.203	1.58	0.114	*2.711*	*0.007*	*0.356*	*0.000*
Na	0.66	0.508	*2.29*	*0.022*	*4.042*	*0.000*	*0.875*	*0.000*
P	0.56	0.575	1.38	0.169	*2.127*	*0.033*	*0.465*	*0.000*
S	*2.37*	*0.018*	*2.37*	*0.018*	*3.718*	*0.000*	*0.876*	*0.000*
Si					*3.652*	*0.000*	*0.752*	*0.000*
Sr	0.46	0.646	1.68	0.093	*3.815*	*0.000*	*0.937*	*0.000*
Zn	1.26	0.208	1.07	0.285	*2.482*	*0.013*	*0.314*	*0.000*
Clay	1.58	0.114	0.66	0.508				

Spearman rank correlations between conductivity and measured mineral concentrations in 135 ground and surface water samples are also listed. Significant findings are noted by *italics*

Fe, and Sr demonstrated tenfold higher concentration in the water from the bottom of elephant holes. Sodium as well as Cl is critical to regulatory functions in the body such as the transmission of nerve impulses and gastric acid. Rode et al. (2006) assumed that Na may be a cause for crop raiding by elephants due to low availability of alternative sources. Dietary recommendations of sodium for savannah elephants (forest elephant specific recommendations are not available) are 1, 000 ppm (Ullrey et al. 1997) or approximately 45 g day^{-1} for a 5,000-kg elephant (Holdo et al. 2002). This could easily be met by the consumption of elephant hole water or alternatively bai soil, but not surface water or forest topsoil.

High concentrations of Na, Cl, and S in lick water have also been reported by Riesenhoover and Peterson (1986) and Clayton and MacDonald (1999) in North America and Indonesia. Like Na, S may function as an indicator of mineral rich sites for elephants due to its strong odor. As a potential parasiticide and fungicide (Mattson et al. 1999) and as an important element in rumen microbial communities (Ayotte et al. 2006), S may be an important mineral attractant. Regarding daily requirements of sulfur for elephants (1,500 ppm; Ullrey et al. 1997) the mean concentrations found in sampled substrates during the present study appear rather low, yet daily needs could be met in certain bais such as Djaloumbe (up to 346 ppm in elephant hole water), Djangui (up to 148 ppm in elephant hole water), and Ndangaye (up to 2,120 ppm in geophagical soil).

Further underlining the differences in mineral concentrations between bais, I concentrations at Djaloumbe (up to 172 µg l^{-1}) were higher than the mean of all bais (5.6 µg l^{-1}) and surpassed the range of 0.01-70 µg l^{-1} for drinking water reported by Edmunds and Smedley (1996). The fundamental role of iodine especially for the brain and reproduction of elephants has been emphasized by Milewski (2000).

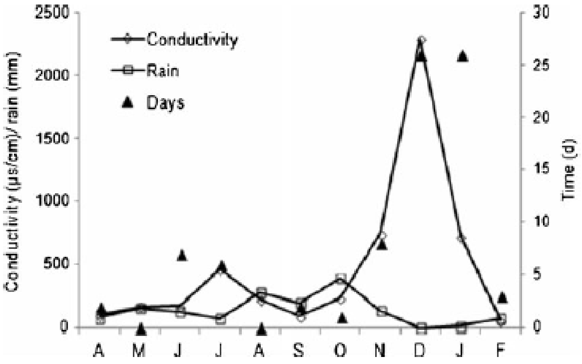

Fig. 3 Mean monthly conductivity measured in three water holes at Dzanga bai and the respective monthly precipitation measured at Dzanga camp from April 2011 to February 2012. On the secondary axis, the number of days between sample collection and the last rain is displayed

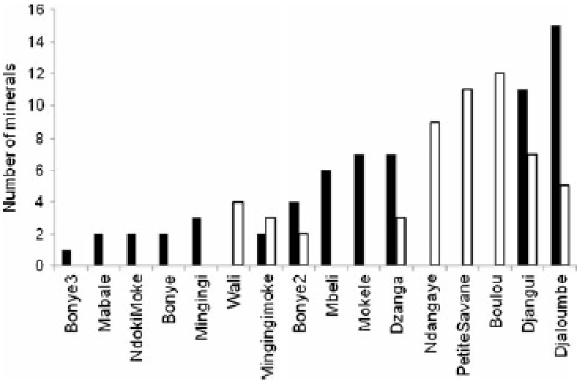

Fig. 4 Number of minerals in bai-specific ground water samples with higher concentrations than the mean of all ground water (*black bars*) and the mean of geophagical soil samples (*white bars*) at different bais. At Mabale, no minerals showed higher concentrations than the mean of geophagical soil samples; for the remaining bais, zero indicates that no heavily used geophagical sites were found. Bais in Lobeke National Park (Ndangaye, Boulou, PetiteSavane, Djangui, and Djaloumbe) show highest concentrations of minerals

The role of Mg and Ca in terms of bai use is unclear as Holdo et al. (2002) suggested that maintenance requirements of these two minerals might be met by elephants through forage alone. Concentrations of Zn, Fe, and Mn measured in water sources were negligible in comparison to dietary recommendations for elephants (40 ppm; Ullrey et al. 1997).

Blake (2002) suggested that an increased requirement for minerals in the dry season might drive aggregations around bais during this time. In potential support for this hypothesis, our results demonstrated that mineral concentrations were seasonal, with a major peak of mineral concentrations in the dry season at Dzanga bai. The driver of this seasonal fluctuation was speculated to relate to seasonal ebbing of spring water flow.

Mineral rich soil has also been hypothesized to be an attractant for elephants to bais and, in particular, clay or Na may be major drivers for geophagy. Tropical rain forests are in general rich in digestion impeding secondary plant compounds such as tannins that may be absorbed by clay minerals (Klaus 1998). Yet, clay is not likely driving bai use since no significant differences in clay concentrations were found between used and unselected elephant sites. Significantly higher concentrations of Na were found in geophagical soil compared to random forest soils, yet not in comparison to random non-geophagy bai soil, suggesting this as well is not an attractant to bais. In contrast, significantly higher concentrations of S were found in geophagical soil samples relative to control samples both within and around bais. Another important driver of geophagy may be I since its retention in the soil is correlated to organic matter and clay (Hu and Moran 2010). Findings of elephant feeding traces at the roots of trees that may reduce leaching of I may support the importance of this micronutrient for elephants as suggested by Milewski (2000).

Altogether, mineral consistencies varied markedly across sites, rendering the interpretation of factors driving geophagy difficult. The presence of elephant geophagical sites (licks of several square meters) throughout the forest in the study area and the lack of heavily used geophagical sites at several bais frequented by elephants suggest that geophagical reasons may not be the predominant driver of visitation. Geophagy, however, certainly seems a reasonable driver of elephant visitation to bais like Petite Savane and Boulou where

Table 2 Mean concentrations of clay and minerals in geophagical soil (20 sites), non-geophagical soil within bais (27 sites, control), and forest soil (27 sites) at ten bais

Element (ppm), clay (%)	Geophagical soil within bai Mean ± S.E.	Control non-geophagical bai Mean ± S.E.	Control non-geophagical forest Mean ± S.E.
Clay	16.59±2.24	10.45±1.63 ^{c}	15.61±1.56 ^{c}
Al	245.27±36.07	139.39±15.84 ^{c}	240.46±21.01 ^{c}
Ca	456.29±107.84	458.08±111.92	324.75±137.90
Cl	596.26±225.88	441.36±201.31	37.77±6.53
Cu	2.57±0.66	2.56±0.61	1.84±0.44
Fe	237.21±45.64	155.77±20.38	167.00±31.28
I	1.63±0.30	1.93±0.40	3.16±0.37
K	35.30±7.33	29.00±5.77	40.94±11.63
Mg	98.32±18.87	116.93±27.09	81.96±19.26
Mn	23.55±5.19	14.07±4.27	11.59±4.35
Na	435.34±142.23 ^{b}	345.99±144.6	31.26±12.54^{b}
P	9.95±2.20	8.20±0.87 ^{c}	12.84±3.15 ^{c}
S	313.19±123.08 ^{ab}	50.13±18.21 ^{a}	5.75±1.84^{b}
Sr	2.48±0.48	2.17±0.54	1.49±0.69
Zn	2.95±0.58	1.66±0.34	1.35±0.43

The respective samples from each site (*n*=20 or 27) associated with each bai (*n*=10) were averaged for pair-wise comparison

[a] Significant differences (Wilcoxon) between geophagical and control bai samples

[b] Significant differences (Wilcoxon) between geophagical and control forest samples

[c] Significant differences (Wilcoxon) between control bai and forest samples

no water holes were found. And, in support of this bai-specific mechanism, these bais showed the highest numbers of above average mineral concentrations (11 and 12, respectively, out of 14) among geophagical samples (Fig. 4).

In conclusion, water from the bottom of elephant holes appeared to represent an important source of minerals for elephants while geophagy was interpreted as playing a minor role at most bais surveyed. Sodium, S, Cl, and I are suggested as important attractants. Other large mammal species such as forest buffalo and bongo antelope regularly visit bais and use elephant excavated sites, likely attracted to the same resources. Results emphasized differences between bais and seasons regarding concentrations of various minerals in water and soil. Differences in mineral concentrations between and within sites (Magliocca 2000; Ayotte et al. 2006) and seasons (Kreulen 1985) might explain the 'failure' to define a single mineral driving geophagy and bai use by forest elephants and other mammal species (though methodological differences between studies is also a hindrance). In fact, these differences between sites indicate that the heterogeneity in bai systems as well as other mineral sites worldwide, e.g., licks in other tropical systems, may be critical to the survival and wellbeing of forest species. Consequently, the protection of multiple bais should be a conservation priority in order to avoid the exclusion of important or unique sites from protection planning. Studies on the mineral availability and concentrations at bais are needed over a broader region of Central Africa and in respect to the diversity of species using bais in order to provide insight regarding reliance on these features by at risk forest species.

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8 Plant mineral concentrations related to foraging preferences of western lowland gorilla in Central African forest clearings

Julia Metsio Sienne, Rainer Buchwald, George Wittemyer

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Plant mineral concentrations related to foraging preferences of western lowland gorilla in Central African forest clearings

Short title: Minerals in gorilla bai feeding plants

Abstract

In the Central African rain forest, mineral resources essential to organisms are distributed heterogeneously. Forest clearings, locally known as bais, attract numerous species presumably due to the mineral richness of these sites, though understanding of the factors drawing species to bais remains speculative. Western lowland gorillas (*Gorilla g. gorilla*) selectively feed on particular plant species and parts within bais, but studies of such feeding preferences have focused on one site. Here, we compared concentrations of minerals and macronutrients from plants gorillas consumed and those they did not in 16 bais to gain inference regarding drivers of resource selection within bais and bai use. The availability of gorilla feeding plants varied between surveyed bais, with some consumed species occurring only at a few bais. Regardless of bai specific species composition, significantly higher concentrations of Na, K and Ca were found in consumed plants, and other trace minerals were more common in consumed plants. In contrast, macronutrients appeared to play no major role in feeding plant selectivity with consumed species often having lower concentrations than non-consumed species. We found evidence for seasonal differences in Mg and Na concentrations, but the concentrations of other minerals in consumed plants were consistent across time. These findings provide insight to the drivers of bai visitation by gorillas. The high variation in species across bais may elicit use of multiple bais, but the general increased mineral composition of consumed species across bais suggests metabolic requirements may be met through consumption of a variety of species.

Key words: Western lowland gorilla, minerals, forest clearings, feeding selectivity

Introduction

Minerals are essential dietary components that can influence multiple aspects of population biology including food selection, home range patterns and animal health [Rode et al., 2003]. As a result, mineral availability and heterogeneity are important determinants of the distribution and density of animal populations [Janson & Chapman, 2000]. The importance of spatial heterogeneity in minerals can be especially pronounced in ecosystems where ecological factors cause mineral limitations, such as mineral leaching in tropical rain forest. In Central African forests, minerals are limited and high mineral concentrations in natural forest clearings (bais) appear to be major attractants to the biota of these systems [Magliocca & Gautier-Hion, 2002; Klaus, 1998; Metsio Sienne et al., 2013]. As such, studying dietary aspects of forest species in bais has the potential to shed light on mineral budgeting and mineral driven behaviors in these systems.

Western lowland gorillas are one of the better studied species in relation to dietary needs. Studies of the nutritional concentrations in gorilla food items have focused on forest plant species and on macronutrients such as fiber and protein. Gorilla diets include a wide range of differing food items [230 items, 180 species reported by Rogers et al., 2004], yet they are highly selective feeders [Remis et al., 2001; Magliocca & Gautier-Hion, 2002; Levrero, 2005]. Findings from Calvert [1985] indicated lignin (avoided), digestibility and crude protein (preferred) were major factors influencing food selectivity by western lowland gorillas in Cameroon. In contrast to Magliocca & Gautier-Hion [2002] who report avoidance of fibrous foods within bais, Remis et al. [2001] suggest that in general gorillas are able to consume relatively high amounts of fiber and secondary plant compounds due to their body size and digestive anatomy and meet their nutritional needs through a balance of fruit and foliage consumption. A study by Nishihara [1995] in swamp and terra firma forests showed fibrous parts of plants to constitute the major diet of western lowland gorillas in Northern Congo. Doran-Sheehy et al. [2009] reported western lowland gorillas in the Northern Republic of Congo to be highly selective on ripe fruits rich in energy while leaves represented major fallback food. Fruits consumed by lowland gorillas at Bai Hokou (Central African Republic) had relatively low concentrations of minerals such as Ca, Mg, P, Na and Fe and gorillas were not able to achieve Ca requirements through fruit consumption [Remis et al. 2001]. In order to meet mineral requirements, gorillas in general are suspected to choose food selectively in relation to its nutrient content [Remis et al., 2001; Rode et al., 2003]. Accordingly, multiple studies state that the mineral contributions of foliage to the diet of western lowland gorillas need further examination.

Gorilla foraging within bais is thought to be focused on mineral acquisition, possibly because primary foraging species are poorly presented in bais, and because bais also present predation risks to gorillas. In relation to these constraints, gorillas only spend an estimated 1% of their daytime at bais [Parnell, 2002]. As such, bai feeding behavior in this species potentially affords the unique opportunity to investigate mineral related dietary preferences in isolation from energetic dietary drivers. Magliocca & Gautier-Hion [2002] report that gorillas consumed only four out of 45 recorded plant species at Maya Nord bai (Republic of Congo). They found higher concentrations of minerals (especially Na and Ca) in clearing feeding plants compared to *Haumania liebrechtsiana* (an important forest food plant for gorillas) and concluded that these minerals as well as K might determine feeding selectivity of gorillas at Maya Nord [Magliocca & Gautier-Hion, 2002]. According to Rodes et al. [2006], Na and P are amongst the most limiting nutrients for herbivores. Nishihara [1995] analyzed the protein, lipid, Fe and Na concentration of *Haumania danckelmania* and *Hydrocharis* spec. and reported high mineral concentrations for the latter which is one of the predominant plants gorillas eat in bais. However, information on the nutritional content of western lowland gorilla bai feeding plants is limited to single bai studies and, therefore, potentially subject to the nuances of the limited number of sites studied. The plant species and their nutritional content that are selectively eaten by gorillas likely vary between sites, but studies assessing drivers of resource selection across sites are lacking. Collection and analysis of a greater diversity of species across different bais can improve current knowledge on the nutritional needs of western lowland gorillas and drivers of bai use in addition to documenting feeding plant availability across bais.

The present study focused on mineral and macronutrient concentrations in feeding plants at 16 bais in Central Africa with the goal of understanding factors driving bai use and plant consumption by gorillas. To do this, we compared mineral and macronutrient concentrations in plants consumed by gorillas to those parts not consumed [Nishihara, 1995; Magliocca & Gautier-Hion, 2002; Nowell & Fletcher, 2006; present study], and contrasted mineral concentrations within the same species across different bais. Samples were collected in the wet and dry season in order to control for potential seasonal effects as well as to test for seasonal differences that might influence bai visitation patterns by gorillas. Assuming particular minerals are the main factor determining feeding plant selection by gorillas at bais, we expected (1) consumed plants to be richer in selected minerals, (2) protein and fiber content to show little differentiation across consumed and not consumed species (in contrast to findings of Magliocca & Gautier-Hion [2002] but in line with Remis et al. [2001]), and (3) the plant species consumed by gorillas to not necessarily be the most abundant species across different bais. By contrasting plant and mineral properties of plants across different bais, our study provides insight regarding differences in gorilla feeding plant characteristics, availability and abundance between bais that are important for conservation management. As such, this study provides broader scale inference of lowland gorilla dietary components when within mineral rich bai sites, offering insight to dietary requirements of this threatened species.

Methods

Study site

The study area is located in the Sangha Trinational Protected Area Complex (TNS), Central Africa. We collected data from April 2011 to March 2012 at 16 clearings (bais), five in the Lobeke National Park (Cameroon) and eleven in the Nouabale-Ndoki National Park (Republic of Congo) and its surrounding area (Fig 1). These bais were chosen based on accessibility, the presence of large mammals and a low degree of human disturbance/activity. In addition, the bais studied were selected to cover a broad range of vegetative, size and soil moisture characteristics. Permissions to conduct research were granted by wildlife management authorities in the respective countries. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates. Most of the TNS area is covered by primary forest belonging to the 'Guineo-Congolian regional centre of endemism' [Harris, 2002], though part of Lobeke (20%) had been selectively logged before its declaration as National Park [Stromayer & Ekobo, 1992]. The climate is equatorial with mean annual rainfall around 1600 mm and an average annual temperature of about 25°C. The major dry season (<100 mm rainfall/month) lasts from December to February, and the major rainy season from September to November [MINEF, 2004; Doran-Sheehy et al., 2009]. The area hosts important populations of the western lowland gorilla and other large mammals such as the African forest elephant (*Loxodonta africana cyclotis*) [Stokes et al., 2010].

Data collection

For nutrient analysis, plant samples were taken once in the dry and once in the rainy season in order to control for possible seasonal differences. Since nutrient content may change with the time of day [Ortmann et al., 2006] all samples were taken in the morning. In order to account for possible differences in nutrient contents between bais, we collected each of the 14 targeted species in at least three bais (collection being dependent on presence) with the exception of *Spirogyra* spec. and *Cyrtosperma* spec. that were found only in one and two bais, respectively. Within a bai, several samples (N=5-50) of each species were collected with differing sampling locations being chosen in respect of the species' availability and accessibility.

Among the plant species identified in the surveyed bais, the five major plant species known to be consumed by gorillas [Nishihara, 1995; Magliocca & Gautier-Hion, 2002; Nowell & Fletcher, 2006] were collected: *Cyrtosperma* spec., *Hydrocharis chevalieri*, *Ludwigia* spp., *Pycreus mundtii*, *Rhynchospora corymbosa*. A further nine plant species not consumed by gorillas, but known to be consumed by other large mammals (i.e. elephants and buffalo), were also collected. Specific plant parts (leaves, stem, rhizome, roots) of *Rhynchospora corymbosa* and *Ludwigia* spp. were examined separately since, according to published literature and direct observations, gorillas feed only on certain parts of these species. *Hydrocharis chevalieri* parts were also examined separately since Nowell & Fletcher [2006] report differences in selectivity across different age classes of gorillas. Finally, only the roots of *Cyrtosperma* spec., that are the only part of this plant known to be consumed by gorillas [Nishihara, 1995], were analyzed due to limited weight of collected leaves and stems. Altogether, nine plant parts from five species that have been reported as feeding species by western lowland gorilla studies [including the present study; Nishihara, 1995; Magliocca & Gautier-Hion, 2002; Nowell & Fletcher, 2006] were classified as consumed feeding items and the remaining 13 plant parts from 11 species that have not been reported in the literature as feeding targets of gorillas as non-consumed items.

After collection samples were immediately weighed to 0.1g and then air-dried in the sun and weighed following the method described in Ortmann et al. [2006]. Total dry matter was then assessed by drying an aliquot of 0.5g from each sample in the laboratory for 24 hours at 105 °C [Ortmann et al., 2006].

The content of crude protein as well as neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL) was analyzed by LUFA Nord-west according to the methods described in VDLUFA Volume 3. Due to logistic constraints these analyses were restricted to one sample each of 18 plant parts. The roots of *Cyrtosperma* spec. and *Ludwigia* spp. were excluded from this analysis due to limited sample weight as well as leaves and stems from the non-consumed species *Eriocaulon* spec*.* Following the Kjeldahl procedure, crude protein was determined based on the nitrogen content with the standard conversion factor of 6.25.

Mineral analyses were conducted for all samples in the laboratory of the Carl von Ossietzky University Oldenburg. Samples were ground to fine powder in a zirconia mill (Retsch MM200). An aliquot of 10mg was dissolved with 400µl HNO_3 in a digestion unit during 6 hours at 95°C. Afterwards the sample was treated with 60µl 32%-H_2O_2 for 2 hours at 56°C and replenished to 2ml with Aqua dest. Subsequently, Na, Ca, Mg, K and Fe concentrations were determined in an atomic absorption spectrometer (AAS), and the P concentration with a photometer.

The abundance of feeding plants was investigated at 14 bais, excluding Wali and Mbeli bai where no vegetation surveys were possible due to the high water level and swampy character, respectively, of these bais. Initially, different vegetation types within a bai were identified by their floristic homogeneity. Within each vegetation type one plot (4x6m^2) was then delimited in a randomly chosen location. Additionally, four plots were surveyed at a bai within a vegetation type that covered more than 10ha. Following the method of Braun-Blanquet [Dierschke, 1994] vegetation species were classified into four categories: dominant (26-100% of cover), medium (6-25%), rare (1-5%) and sporadic (<1%). At each bai, the percentage of vegetation cover was generated for each species calculating the average of the abundance class of a certain species within a vegetation type (e.g. dominant: 63%) and multiplying it by the total area of the respective vegetation type. Then, the total area covered by this species in the bai was calculated by summing up the areas covered across all vegetation types. Based on this, the percentage of the bais total vegetation cover was derived for each species.

Data analysis

In order to compare nutrient concentrations between consumed and non-consumed plant species, we used generalized linear mixed model (GLMM, fit by the Laplace approximation) with a logit link function where a binary response variable designated consumed species (assigned 1) and non-consumed (assigned zero). In our models, season was incorporated as a fixed effect and bai as random effect. In cases where several plant parts of a particular species were collected from the same bai during the same season, their nutritional values were averaged to avoid pseudoreplication. Due to differences in samples sizes and bai representation, mineral concentrations of P, K, Ca, Mg, Na and Fe in samples species were included as predictor variable in one multivariate model, while macronutrients (crude protein, NDF, ADF and ADL) were analyzed in a separate multivariate model. For all multivariate models, the presented model was identified using model selection [Burnham & Anderson, 2002]. Thereby covariates not offering additional explanatory power (i.e. that covary with an included variable) were excluded. In addition to the most parsimonious multivariate model, we present results from univariate analysis of each mineral and macronutrient metric. While we acknowledge the potential for type I error in such an analysis, we present these results to ensure an exhaustive examination of the minerals and macronutrients assessed here (co-varying minerals or macronutrients may lead to exclusion of one or more since additional explanatory power is not gained through their inclusion, but that does not necessarily mean they are not driving aspects of the behavior of interest).

Separately, GLMMs were run on consumed and non-consumed plant parts of *Rhynchospora corymbosa, Hydrocharis chevalieri* as well as of *Ludwigia* spp. to assess differences in mineral constituents between parts. Since sample size of plant parts did not allow resolution of a multivariate model, univariate models were run for each species with different minerals as predictive variables. However, the sample set of Mg measurements were limited, precluding analysis. In the case of *Hydrocharis chevalieri*, the binary response variable designated roots and rhizomes (preferred by adults; assigned 1) as well as leaves and stems (preferred by infants; assigned zero).

Nutrient concentrations between the dry and rainy season from the same species were compared using t-tests for paired samples. In order to compare the abundance of consumed versus non-consumed plant species, a Wilcoxon test was performed on the mean vegetation cover (percentage) of each species across bais. All analyses were performed in the program R version 2.15.2 [R Foundation for Statistical Computing 2012].

Results

Consumed versus non-consumed

The best fit model designated using model selection indicated Na, Ca and K concentrations were the primary differences between consumed and non-consumed plant species in our multivariate analysis (Table 1). In univariate models of minerals, all minerals analyzed showed significantly higher concentrations in consumed versus non-consumed plant species (Table 2, Fig 2a-f), though we note these results must be interpreted with caution given the high degree of covariation between minerals. No significant differences were found between consumed and non-consumed plant species for crude protein, NDF, ADF and ADL in univariate or multivariate models (Table 2, Fig 3a-d). In addition, we found no evidence for a seasonal effect on mineral availability in species analyzed.

The pith of *Rhynchospora corymbosa* showed significantly higher concentrations of P, K, Ca and Mg in comparison to the leaves and roots (reported as not being consumed by gorillas) (Table 2). Only slight differences were detected between plant parts regarding crude protein, NDF, ADF and ADL (Table 3). Consumed plant parts of *Ludwigia* spp. (stem, roots) showed significantly higher concentrations of K in comparison to leaves (discarded by gorillas), and showed no significant differences for the other minerals examined (Table 2). Higher concentrations of crude protein were found in non-consumed plant parts as well as lower concentrations of NDF and ADF (Table 3). The mean concentration of Fe (4.27mg/g and 0.69mg/g, respectively; GLMM: N=26, Z=2.324, P=0.0201) and Na (3.12mg/g and 2.17mg/g, respectively; GLMM: N=26, Z=2.373, P=0.0176) were significantly higher in roots and rhizomes (preferred by adults) compared to leaves and stems (preferred by infants) from *Hydrocharis chevalieri*. In contrast, leaves and stems of *Hydrocharis chevalieri* showed higher mean concentrations of Ca (15.02mg/g and 7.61mg/g, respectively; GLMM: N=26, Z=-2.456, P=0.0140) and Mg (6.74mg/g and 1.98mg/g, respectively; GLMM was not feasible) than its roots and rhizomes.

Seasonal differences

Significantly higher concentrations of Mg were found in the rainy season (t-test for paired samples: T=-2.7605, P<0.01, df=55) while Na concentrations were significantly higher during the dry season (t-test for paired samples: T=4.2169, P<0.01, df=55) (Fig 4a-b). For the remaining minerals no seasonal differences were detected (t-test for paired samples: P: T=-0.6606, P=0.5116, df = 55; K: T=0.0503, P=0.9601, df=55; Ca: T=-1.4382, P=0.1561, df=55; Fe: T=-0.1852, P=0.8537, df=55).

Availability

The abundance and frequency of the examined plant species at the surveyed bais are shown in Table 4. The consumed plant *Rhynchospora corymbosa* occured at 71% of the surveyed bais and typically was in relatively high abundance. *Pycreus mundtii* and *Hydrocharis chevalieri* were reported only at three bais. *Hydrocharis chevalieri*, however, was found with relatively high vegetation cover at two of these bais and also at Mbeli bai that was not subject to a vegetation inventory. *Ludwigia* spp. was detected at most bais, though generally at low abundance. Only a few individuals of *Cyrtosperma spec.* were found at Guga and Bakussa bais. Non-consumed species represented up to 48% of vegetation cover and were present at 7-71% of the surveyed bais. No significant difference was found regarding the percentage of vegetation cover of consumed versus non-consumed species across bais (Wilcoxon test: W=19, P>0.05, N=13).

Comparison with other studies

Mineral concentrations reported here for the sampled species are comparable to those reported in the literature, with the exception of slightly higher concentrations of Na to those reported by Nishihara [1995] and Magliocca & Gautier-Hion [2002] (Table 5). Concentrations of all minerals measured in bai plants were high in comparison to mean concentrations from western lowland gorilla forest feeding plant species reported by Remis et al. [2001] and Calvert [1985]. Mean concentrations of crude protein, NDF, ADF and ADL measured in bai plants lay within the range of those reported by other studies on western lowland gorillas foraging, with the exception of lignin that was relatively low in the present study [Calvert, 1985; Rogers et al., 1990; Remis et al., 2001].

Discussion

Western lowland gorillas are selective feeders and visit bais in order to feed on particular plant species [Magliocca & Gautier-Hion, 2002]. Since bais represent mineral rich sites, minerals presumably are important factors driving this behavior. Mean concentrations of Ca, Mg, P, Na and Fe measured in this study were high relative to those reported in gorilla forest feeding plants [Remis et al., 2001]. In this study, even the lowest Na concentration measured in a bai feeding plant (2.0 mg/g) surpassed the highest reported concentration in western lowland gorilla forest feeding plants in Cameroon [0.8mg/g; Calvert, 1985]. Most plants analyzed by Calvert [1985] showed lower Fe concentrations than the minimum concentration measured in consumed plants in this study. The median concentrations of Ca, K, Mg and P in bai feeding plants were several times higher than those reported among forest feeding plants [Calvert, 1985], though it is notable that Ca and K concentrations in specific forest plants exceeded the maximum concentrations found in this study. Though it is possible that methodological differences caused slight differences in measured concentrations between studies, it is unlikely that the scale of differences reported here was due to methodology. As such, these results provide further evidence of the importance of bai plants as mineral sources (particularly, for Na) and indicate that findings from Magliocca & Gautier-Hion [2002], showing higher mineral concentrations in feeding plants from one bai versus forest feeding plants, can be transferred to a large number of bais.

In addition, our results demonstrate that crude protein, ADF and NDF were in markedly lower concentrations in consumed bai foods relative to levels reported in species consumed in the forest. Gorilla diets in the forest [Calvert, 1985; Popovich & Dierenfeld, 1997] and other primates [Fashing et al., 2007] are, however, reported to focus on such resources. Our findings corroborate those of Magliocca & Gautier-Hion [2002] indicating that bai resource selection was aimed at mineral acquisition and likely differs from food selectivity in forest feeding sites outside bais. This might further explain why gorillas spend only a small amount of time in bais and feed very selectively on plant species and parts presumably depending on their current physiological and reproductive status.

It has been suggested that the role of protein in primate food selection may be overestimated since a proportion of the protein measured may be fiber-bound and thus indigestible [Rothman et al., 2008]. Indeed, mountain gorillas (*Gorilla beringei*) have modest protein requirements for growth and protein consumption exceeds requirements [Rothman et al., 2008]. The concentration of ADF, in particular, was above the recommended minimum concentration of 25% for captive gorillas [Popovich & Dierenfeld, 1997].

In the present study Ca, K and especially Na occurred in significantly higher concentrations in consumed bai plants in comparison to non-consumed plants. Results from univariate analysis indicate that the remaining minerals (Fe, Mg and P) show higher concentrations in consumed versus non-consumed plant species as well. Within species and even within individual plants, certain parts differed significantly in their mineral concentration. The pith of *Rhynchospora corymbosa*, which is specifically extracted and eaten by gorillas, contained significantly higher concentrations of P, K, Ca and Mg in comparison to the remaining, discarded plant parts. In the case of *Ludwigia* spp., the consumed stems and roots showed significantly higher concentrations of K in comparison to the leaves. Similarly, significantly higher K concentrations in eaten versus non-eaten bai species in Maya Nord bai were reported by Magliocca & Gautier-Hion [2002]. Concentrations of K measured in some forest feeding plants, however, surpassed those measured in bai feeding plants in this study indicating that K may not be a driver for bai visitation. It is also important to consider that K can be antagonistic to Na and Ca, which are important dietary nutrients [Kreulen, 1985]. Sodium is an essential mineral that is often deficient in herbivorous diets and has been reported to influence the behavior of mammals [Fashing et al., 2007; Metsio Sienne et al., 2013]. The consumption of decaying wood by gorillas has been related to the need of meeting their sodium requirements [Rothman et al. 2006]. Na and Ca were hypothesized to determine feeding selectivity by Magliocca & Gautier-Hion [2002] who found highest concentrations of these minerals in the most actively selected species, which surpassed concentrations in the important gorilla staple *Haumania liebrechtsiana* [Magliocca & Gautier-Hion, 2002]. Our results reinforce these findings, providing support from a larger number of species and bais.

In interpreting the results of this study, it is important to consider the complexity of interactions between minerals in respect to specific metabolic requirements. The effect of K was mentioned above, likewise Na is an antagonist to Ca, i.e. more Ca is needed when Na is consumed, and Ca is known as inhibitor to Fe. Finally, the nutrient and mineral demand of each individual depends on its current status and food consumption. Nowell & Fletcher [2006] report the roots and rhizome of *Hydrocharis chevalieri* to be generally preferred by gorillas, but infants feed more on leaves and stems than other age classes. Combined with our results, this indicates that infants may select for parts rich in Mg and Ca that are important for bones and the nervous system while other age classes select for parts rich in Fe and Na. Studies on mineral concentrations of different plant species and parts combined with observations on selectivity of individuals from different ages and sex classes are needed to shed more light on western lowland gorilla nutritional needs.

Altogether, our results indicated that Ca, K and especially Na were likely candidates for selection though no mineral was clearly responsible for driving bai use by western lowland gorillas. Generally, studies on geophagy and water resources used by large mammals show that animals are attempting to access a variety of compounds, with single target minerals being rare. The mineral rich soil and water resources of Central African bais are used by numerous mammals such as elephants, buffalo and bongo antelopes [Turkalo & Fay, 1995; Klaus et al., 1998; Metsio Sienne et al., 2013]. Oates [1978] suggested that guereza colobus (*Colobus guereza*) fulfill their requirements of Na and other minerals by consumption of aquatic plants. As such, the results here may reflect drivers of bai selective feeding in other species.

Temporal and spatial differences

The vegetation community differed across the studied bais, therefore our sampling design did not allow for detailed assessment of species specific differences across bais. However, differences between mineral concentrations measured in the present study and those reported for the same species by Nishihara [1995] and Magliocca & Gautier-Hion [2002] provide evidence for heterogeneity across sites and seasons. These differences presumably are related to differing mineral concentrations in soil and water resources across bais [Metsio Sienne et al., 2013].

Seasonal variation in mineral concentrations in plants was only found for Mg and Na, with other minerals remaining constant across seasons. However, seasonal differences were rather small, thus they may not influence bai visitation patterns.

Availability

Assuming that gorillas fed selectively on nutrient rich plant species, we expected that the bai species consumed would not be the most abundant species. This was not necessarily the case, with consumed species abundance being variable depending on species. *Hydrocharis chevalieri*, reported as major bai feeding plant by several studies, was present at 21% of the surveyed bais. *Ludwigia* spp. and *Rhynchospora corymbosa* were present at most bais, yet gorillas feed only on particular parts of these species. Altogether, abundance did not appear to determine consumed plants since consumed plants belonged neither to the most abundant species nor to the rarest species. This indicates that findings from Magliocca & Gautier-Hion [2002], who report that some feeding species were rare at Maya Nord while others were abundant, can be transferred to a large number of bais.

In conclusion, the present study confirmed the findings of earlier, single site studies, expanding the scope of their results by investigating drivers across multiple bais with diverse geophysical and biotic properties. This study also highlighted differences in feeding plant availability between bais. The protection of a mosaic of bais providing gorilla feeding plants may therefore be essential to their survival and should be a conservation priority.

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Tables

Table 1 Model selection: Overview on the multivariate models performed with different minerals as explanatory variables and a binary response variable designating consumed (assigned 1) and non-consumed (assigned zero) plants. Beside the Akaike's information criteria (AIC) and the Akaike weights (w) are presented for each model.

Rank	P	K	Mg	Ca	Fe	Na	AIC	Δ AIC	w
1		√		√		√	67.35	0.00	0.38
2		√	√			√	69.16	1.81	0.15
3		√	√	√		√	69.34	1.99	0.14
4		√				√	71.20	3.85	0.06
5	√	√	√	√		√	71.28	3.93	0.05
6	√	√		√	√	√	71.29	3.94	0.05
7		√	√	√	√	√	71.31	3.96	0.05
8		√			√	√	72.51	5.16	0.03
9	√	√	√		√	√	72.60	5.25	0.03
10	√	√				√	72.94	5.59	0.02
11	√	√	√	√	√	√	73.25	5.90	0.02
12	√		√	√	√	√	75.09	7.74	0.01
13	√	√	√	√	√		79.55	12.20	0.00
14		√					84.53	17.18	0.00
15						√	86.57	19.22	0.00
16							91.79	24.44	0.00

Table 2 Results from GLMMs of mineral concentrations and macronutrients between consumed and non-consumed plant species and plant parts (the latter for *Rhynchospora corymbosa* and *Ludwigia* spp.). Models were run for each mineral/macronutrient separately (univariate models), and including all minerals and macronutrients (multivariate model); a binary response variable designated consumed (assigned 1) and non-consumed (assigned zero) species and plant parts, respectively.

		All species				**Plant parts**					
		Multivariate		**Univariate**		***Rhynchospora cor.***			***Ludwigia* spp.**		
	N	**Z**	**P**	**Z**	**P**	**N**	**Z**	**P**	**N**	**Z**	**P**
P	74			2.469	0.014	18	2.467	0.014	16	0.163	0.870
K	74	2.238	0.025	2.913	0.004	18	2.308	0.021	16	1.923	0.055
Mg	74			3.905	<0.001	18	2.275	0.023	16	0.068	0.945
Ca	74	2.396	0.017	3.913	<0.001	18	2.309	0.021	16	-1.279	0.201
Na	74	2.612	0.009	2.310	0.021	18	-0.091	0.928	16	1.165	0.244
Fe	74			2.330	0.020	18	-0.557	0.578	16	0.632	0.527
CP	12	-1.508	0.131	-0.947	0.344						
NDF	12	-1.389	0.165	-0.440	0.660						
ADF	12			-0.188	0.851						
ADL	12	-0.441	0.659	-0.339	0.735						

Table 3 Concentrations of crude protein, NDF, ADF and ADL (reported in % dry matter) for consumed (1) and non-consumed (0) parts of three bai feeding plant species.

	CP	**NDF**	**ADF**	**ADL**	**Consumed**
Rhynchospora corymbosa					
Leaves	9	68.6	40.1	4.6	0
Pith	10.1	63.2	39	2.8	1
Roots	5.5	68	44.2	10.2	0
Hydrocharis chevalieri					
Leaves	14.1	37.4	33	7.1	1
Stem	6.7	49	46.3	4.4	1
Rhizom	4.6	31.7	35.9	2.9	1
Roots	8.4	30.9	27.2	3.6	1
Ludwigia spp.					
Leaves	17.5	10.4	9	5.3	0
Stem	4.9	25.5	29.3	6.4	1

Table 4 The plant species collected are listed with an indication of their preference by gorillas coded as consumed=1 and non-consumed=0. The frequency represents the proportion of surveyed bais where the respective species was recorded. The abundance of the analyzed plant species at the surveyed bais is illustrated as species rank (e.g. 5/36 denotes the fifth species with highest vegetation cover out of 36) as well as the percentage of vegetation cover of the examined plant species.

Species	*Acmella caul.*	*Bacopa cren.*	*Eleocharis actu.*	*Kyllinga erec.*	*Eriocaulon* spec.	*Paspalum* spec.	*Pycreus pect.*	*Pycreus lanc.*	*Hydroch. chev.*	*Ludwigia* spp.	*Rhyncho. cory.*	*Pycreus mund.*
Consumed	0	0	0	0	0	0	0	0	1	1	1	1
Frequency	50%	71%	29%	43%	7%	71%	7%	57%	21%	86%	71%	21%
Djangui	0	7/36	0	0	0	5/36	0	28/36	0	8/36	1/36	22/36
	0	3.69%	0	0	0	8.27%	0	0.12%	0	3.73%	24.61%	0.75%
Mabale	14/25	6/25	5/25	2/25	0	11/25	0	9/25	8/25	22/25	1/25	0
	0.25%	1.77%	2.42%	31.83%	0	1.50%	0	1.61%	1.61%	0.16%	33.99%	0
Ndangaye	26/36	5/36	0	0	0	29/36	0	19/36	0	10/36	1/36	10/36
	0.02%	5.54%	0	0	0	0.02%	0	0.16%	0	2.55%	42.92%	4.13%
Petite	0	0	0	0	0	11/38	0	31/38	0	16/38	1/38	17/38
Savane	0	0	0	0	0	0.29%	0	0.01%	0	0.12%	47.76%	0.09%
Bonye	18/32	4/32	15/32	7/32	0	12/32	0	22/32	0	9/32	0	0
	0.32%	14.36%	0.60%	6.51%	0	1.04%	0	0.15%	0	2.24	0	0
Bonye2	27/31	7/31	0	6/31	0	28/31	0	17/31	0	9/31	13/31	0
	0.02%	1.98	0	5.31%	0	0.02%	0	0.47%	0	2.34%	0.65%	0
Bonye3	14/15	7/15	0	0	0	0	0	0	0	6/15	0	0
	0.03%	2.27%	0	0	0	0	0	0	0	2.66%	0	0
Mingingi	0	3/25	20/25	9/25	0	25/25	0	15/25	0	8/25	13/25	0
Moke	0	12,20%	0.09	1.40%	0	0.02%	0	0.21%	0	1.48%	13.62%	0
Mokele	9/25	0	0	1/25	0	3/25	0	0	0	11/25	2/25	0
	1.07%	0	0	47.84%	0	4.33%	0	0	0	0.74%	30.46%	0
Mingingi	0	12/31	5/31	8/31	6/31	18/31	0	29/31	0	3/31	7/31	0
	0	1.56	4.92%	4.62%	4.82%	0.40%	0	0.02%	0	8.86%	9.00%	0
Guga	0	8/11	0	0	0	0	1/11	0	2/11	3/11	0	0
	0	0.22%	0	0	0	0	59.77%	0	15.52%	15,22%	0	0
Boulou	0	8/13	0	0	0	0	0	0	0	0	0	0
	0	1.14%	0	0	0	0	0	0	0	0	0	0
Djaloumbe	4/20	0	0	0	0	2/20	0	0	0	9/20	14/20	0
	6.57%	0	0	0	0	29.84%	0	0	0	0.80%	0.16%	0
Bakussa	0	0	0	0	0	0	0	0	1/5	0	4/5	0
	0	0	0	0	0	0	0	0	75.68%	0	0.30%	0

Table 5 Comparison of mineral concentrations (mg/g dry matter) and crude protein (CP) measured in plant samples during the present study and other studies reported in the literature. Mean concentrations reported by Remis et al. [2001] and Calvert [1985] for western lowland gorilla feeding plants in the forest are listed besides studies on bai plants.

Species	CP (%)	Fe	Na	Ca	K	Mg	P	Reference
Hydrocharis c.								
stem	6.7	1.2 ± 0.7	2.0 ± 0.7	11.4 ± 1.7	59.9 ± 10.4	4.5 ± 1.1	4.5 ± 2.2	present study
	9.7	0.7	0.3					Nishihara 1995
leaves	14.1	0.2 ± 0.1	2.3 ± 0.9	18.1 ± 1.8	34.3 ± 2.7	8.7 ± 1.3	3.5 ± 1.2	present study
	19.5	0.5	0.4					Nishihara 1995
roots	8.4	5.1 ± 2.4	3.3 ± 0.8	8.5 ± 2.5	57.1 ± 14.1	2.0 ± 0.6	2.9 ± 1.0	present study
		7.3	1.1					Nishihara 1995
Ludwigia spp.								
leaves	17.5	0.7 ± 0.4	2.4 ± 1.0	12.3 ± 4.4	12.8 ± 3.7	4.2 ± 1.7	3.1 ± 1.3	present study
stem	4.9	0.6 ± 0.2	4.6 ± 4.0	11.0 ± 2.9	37.4 ± 17.2	4.3 ± 1.9	3.7 ± 2.4	present study
roots		5.2 ± 6.8	8.9 ± 10.3	4.5 ± 0.5	15.4 ± 2.1	4.2 ± 2.4	1.8 ± 0.8	present study
mean			5.3	9.4	21.9	4.2	2.9	present study
whole plant			3.6	16.1	29.8	7	10.6	Magliocca & Gautier-Hion 2002
Pycreus m.								
	6.0	0.6 ± 0.4	5.3 ± 3.6	5.4 ± 0.8	28.7 ± 7	4.7 ± 1.7	2.4 ± 1.0	present study
			1.5	11.5	44.6	7.7	8.0	Magliocca & Gautier-Hion 2002
Rhynchospora c.								
pith	10.1	0.2 ± 0.1	3.2 ± 1.6	3.8 ± 0.4	34.8 ± 4.8	3.2 ± 0.6	4.1 ± 0.6	present study
shoot, leaf base			0.6	5	42.2	4.1	7.8	Magliocca & Gautier-Hion 2002
Bacopa c.								
	12.4	0.8 ± 0.5	6.2 ± 7.3	9.8 ± 1.6	27.6 ± 9.3	4.9 ± 0.6	2.4 ± 0.4	present study
			12.5	15.3	23.8	7.6	8.1	Magliocca & Gautier-Hion 2002
Kyllinga e.								
	4.5	0.2 ± 0.1	1.7 ± 0.6	3.4 ± 0.4	14.9 ± 2.9	2.1 ± 0.5	1.2 ± 0.4	present study
			0.3	3.0	15.7	3.0	3.8	Magliocca & Gautier-Hion 2002
Food plants	12.68	0.1	0.1	1.8	12.1	1.4	1.3	Remis et al. 2001
Food plants	9.2	0.2 ± 0.2	0.2 ± 0.2	8.4 ± 9.1	28.2 ± 21.2	2.4 ± 1.8	1.5 ± 0.9	Calvert 1985

Figures

Fig 1 Map showing the 16 bais surveyed in the Lobeke National Park (Cameroon) and the Nouabale-Ndoki National Park (Republic of Congo). The two National Parks together with the Ndoki National Park, the Dzanga National Park and the Dzanga-Sangha Special Reserve constitute the Trinational de la Sangha area.

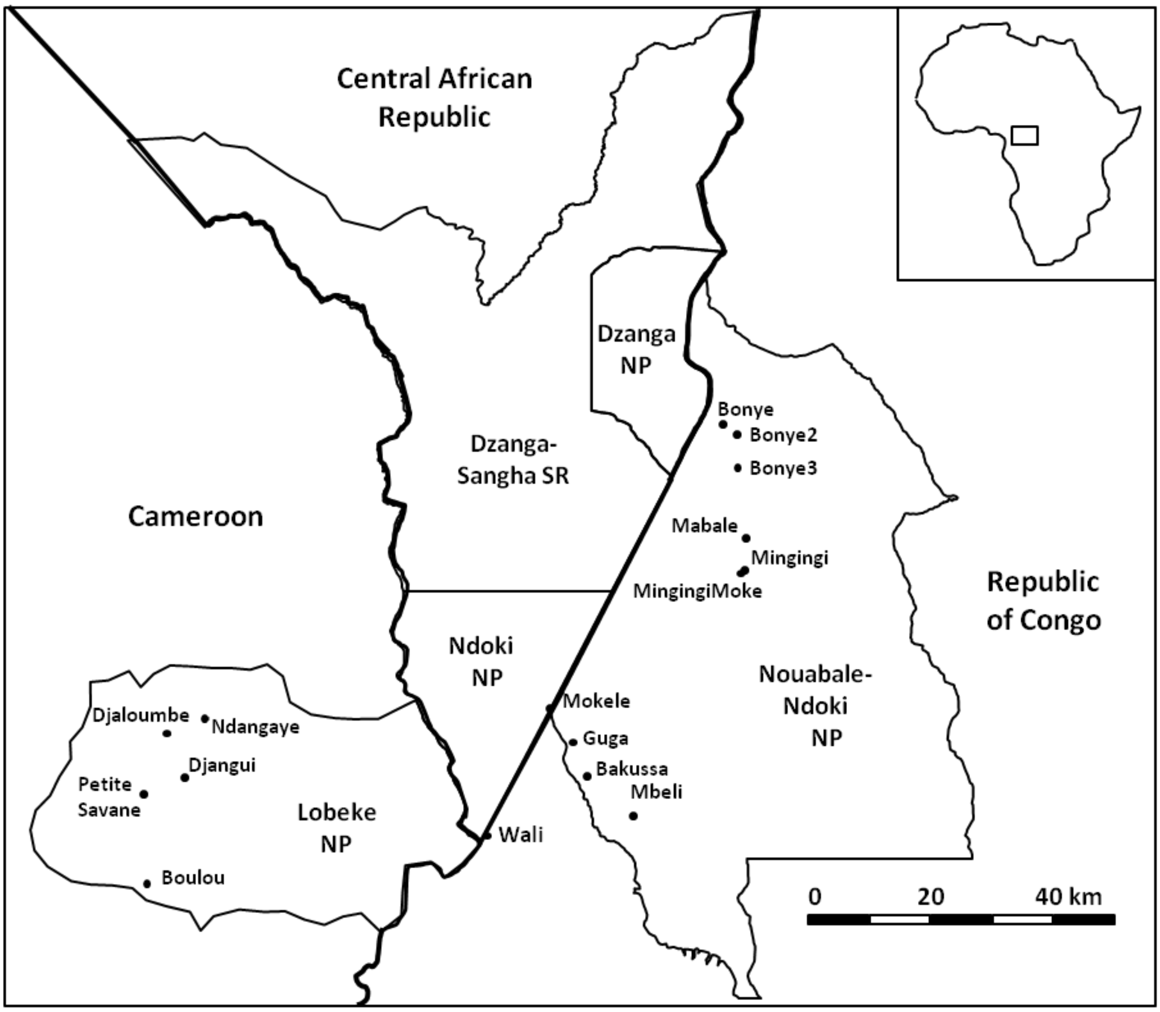


Fig 2a-f Mean mineral concentrations (in mg/g dry matter for P, K, Mg, Ca, Na, Fe) of non-consumed (0) versus consumed (1) bai plants (N=74).

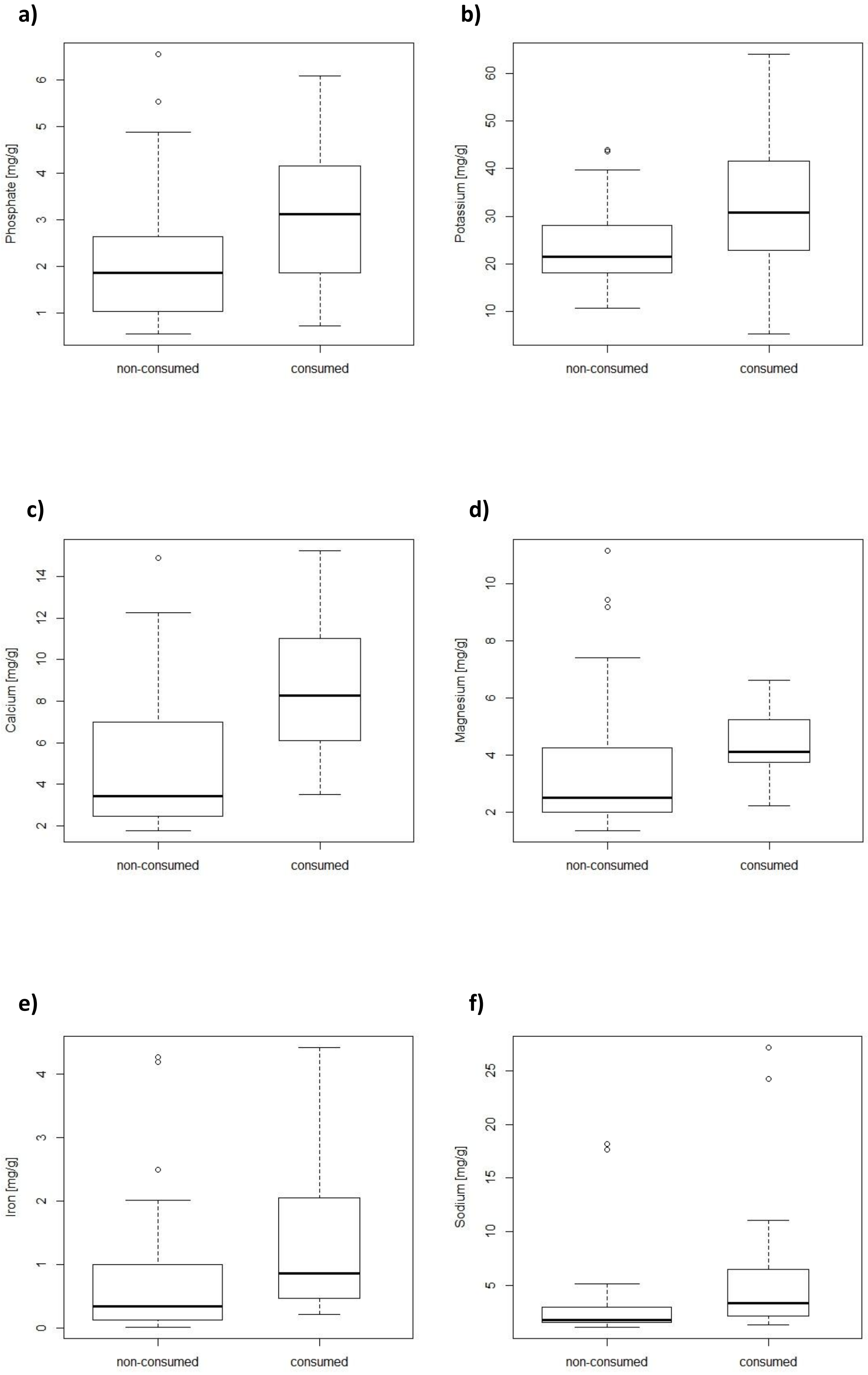


Fig 3a-d Mean concentrations (in % dry matter) of crude protein, NDF, ADF and ADL for non-consumed (0) versus consumed (1) bai plants (N=18).

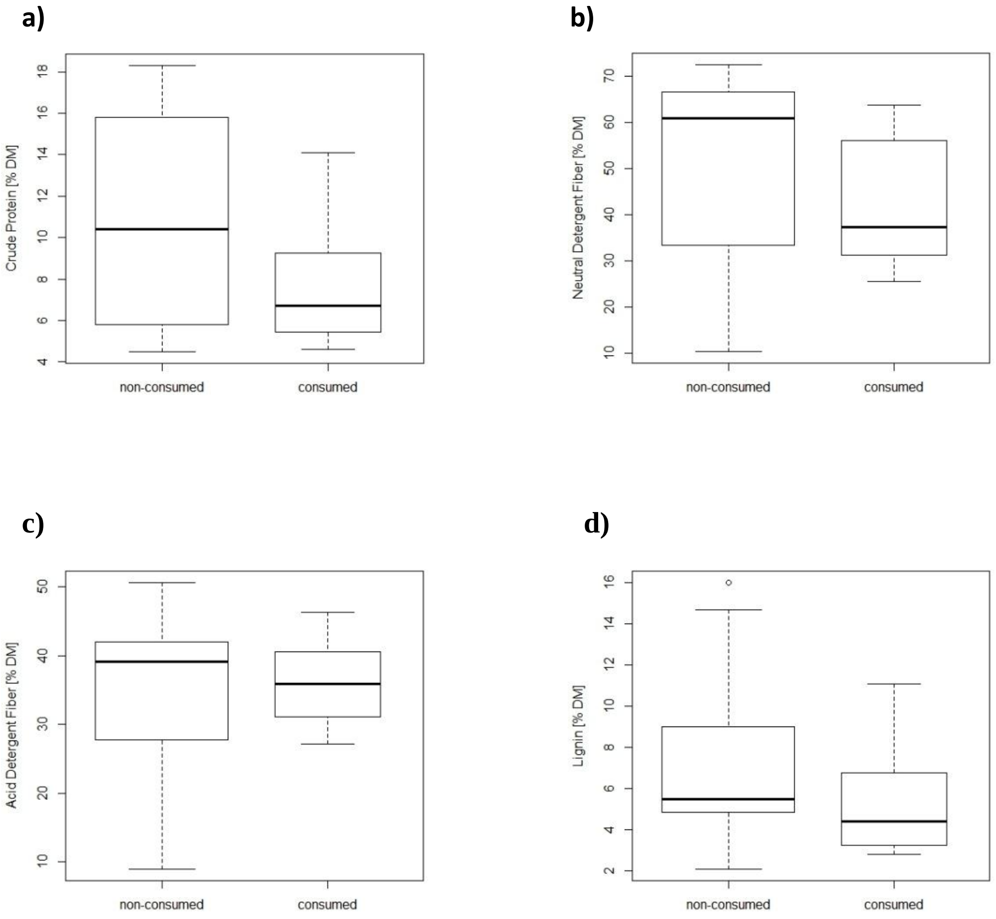
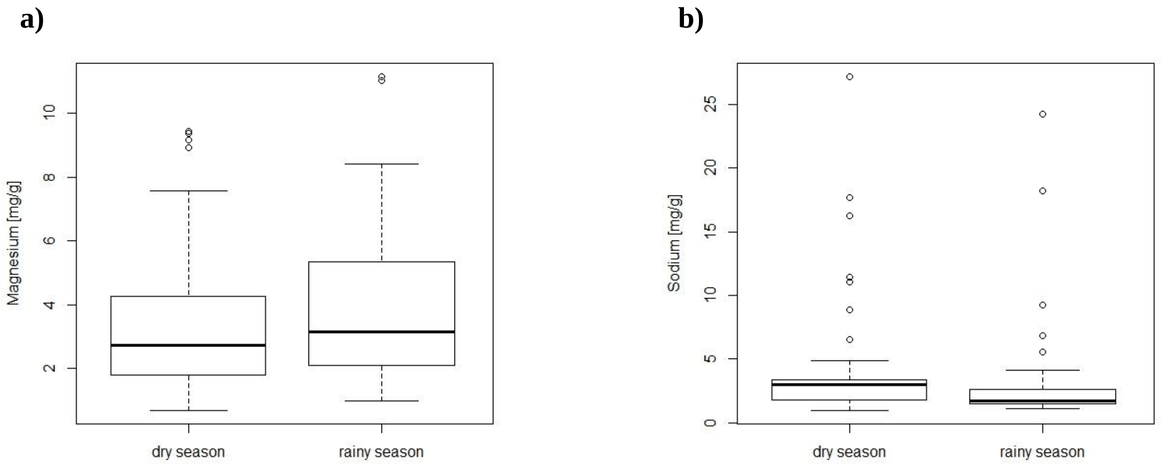


Fig 4a-b Mean concentrations of Mg and Na (in mg/g dry matter) measured in plant samples from the dry (1) versus the rainy (2) season.



9 Synthesis

The present thesis contributes important knowledge on bais that represent key habitats in the Central African rain forest. Here, a résumé on the principal findings of the thesis is given with a focus on the bais' diversity in respect of plants, animals and mineral resources as well as on potential factors influencing bai visitation patterns of large mammals. Recommendations for wildlife management and conservation are provided based on the findings presented in the preceding chapters.

Diversity of bais

The high heterogeneity found between bais in the Sangha Trinational Protected Area Complex indicates that bais across a broad area differ considerably. First of all, the differences between bais in respect of size and soil moisture are conspicuous. A closer look at the bai vegetation further reveals the species richness between as well as within bais. Differences in respect of the plant species composition were found across bais on the regional scale (within the Sangha Trinational area) as well as on the local scale (within a national park) with the latter showing higher similarities. The number of bai plant species identified in the present study, as well as that reported by Boupoya-Mapikou (2010), confirm that bais add considerably to the Central African rain forest's species diversity.

Likewise, the availability and abundance of medium-sized to large mammals' feeding plants varied across bais. The percentage of plant species known to be consumed by mammals was high at all bais. Yet, the vegetation cover of known feeding plants from a particular mammal species varied, being low at several bais. Moreover, the lack of information on bai feeding plants especially for medium-sized mammals limits inference on forage availability. Beside the feeding plant species reported in the literature, numerous consumed plant species could be identified by feeding traces and direct observations of plant consumption. This allowed existing bai feeding plant lists to be expanded and at the same time indicated the need for further studies on feeding plants.

In addition to the diversity in respect of bais' vegetation, the high heterogeneity of mineral concentrations in soil and water resources across bais was revealed by this study. This heterogeneity potentially results from differences at the regional scale, e.g. the parent rock material, given the strong disparities between mineral concentrations at bais in Lobeke National Park and bais in Nouabale-Ndoki National Park. Investigations of parent rock material underlying bais are needed to further our understanding of drivers of differences in mineral availability between sites. They may also contribute important knowledge on the origin of bais.

The particular availability of the above mentioned resources (soil, water and plants) at a bai likely influences its attraction for large mammals. This thesis highlights differences in the occurrence of mammal species between bais. In total, 25 mammal species were shown to use the surveyed bais, though several species were detected only at a few bais (chapter 6). Solely the African forest elephant (*Loxodonta africana cyclotis*), the forest buffalo (*Syncerus caffer nanus*), the bongo antelope (*Tragelaphus spekeii*), the water chevrotain (*Hyemoschus aquaticus*), the Peter's duiker (*Cephalophus callipygus*) and the blue duiker (*Cephalophus monticola*) were reported for all surveyed bais. As a matter of course, the number of mammal species reported here represents only a tiny fraction of the bai fauna. The present study did not investigate the occurrence of small mammals, reptiles, amphibians, birds and other groups visiting or living in bais that certainly add to the bai fauna diversity. In addition, this survey was restricted to a limited number of bais and a relatively short study period. Consequently, the numbers of medium-sized to large mammal species visiting bais in general and the respective bais in particular, are underestimated.

Results indicate clear differences in respect of large mammals' visitation rates between bais though the study design limited by the number of camera traps available did not allow for detailed analysis. The factors influencing the occurrence of large mammals at bais have been in the focus of the present thesis and will be discussed in the following section.

Potential factors influencing bai visitation rates

The potential factors driving bai use by large mammals are numerous. It was beyond the scope of this thesis to cover all these factors. Hence this study focused on bai resources such as soil, water and plants. In the following, bai resources together with further potential factors influencing bai visitation rates of large mammals are discussed.

Bais have important social functions for large mammals (Turkalo & Fay, 1995; Magliocca, 2000; Gessner, 2008). They have been described as social arenas for forest elephants representing meeting points for these large pachyderms (Fishlock, 2010). The open areas of bais provide opportunities for social contacts and facilitate social learning (Fishlock, 2010). Male elephants are thought to use bais also in order to monitor the reproductive status of females (Fishlock, 2010). These observations on forest elephants likely apply as well to other medium-sized to large forest-dwelling mammals. Knowledge on the social behaviour of mammals while within the dense forest is, however, lacking and final conclusions are therefore constrained.

Bai visitation has further been related to the presence of food sources in the surrounding forest. Increased presence of western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli bai was reported for the fruiting season of *Nauclea vanderguchtii* (Parnell, 2002). Fishlock (2010) assumed that elephant ranging patterns are related to high-quality fruit resources in the forest and that elephants visit bais when close to these sites. Fruit trees as well as bais have been reported to influence the formation of permanent elephant trails (Blake & Inkamba-Nkulu, 2004). Evidence that elephant trail density and width increase close to bais (Vanleeuwe & Gautier-Hion, 1998; Blake & Inkamba-Nkulu, 2004) confirms their attraction to elephants. A bai's proper attributes likely impact its use by large mammals, and a higher density will be present when more resources are available in the surrounding forest.

Moreover, given the large amount of time large mammals spend feeding while within bais, it is likely that resources provided in bais represent a major attraction. Results of the present study confirmed that bais are mineral rich sites. Concentrations of the minerals analysed were significantly higher in water from the bottom of holes excavated by elephants in comparison to those in surface water. Differences were most pronounced for nutritional important minerals such as Na, Cl, S, Zn, Ca, Mg, Mn, Fe and also Sr. Sample storage did not allow for accurate measurements of the iodine content in water samples. Nevertheless, results showed high iodine concentrations in elephant water holes at Djaloumbe bai. Iodine potentially plays an important role in bai visitation patterns given its importance for the brain and reproduction of elephants (Milewski, 2000). Studies at multiple bais, applying adequate methods for iodine sampling, storage and analysis are required in order to examine the importance of iodine in the bai context.

Results from the present study indicated that geophagy played no major role at the surveyed bais. Relatively few geophagical sites could be identified at the bais and these sites were less differentiated from control soil samples within the bai and the surrounding forest in respect of mineral concentrations. Higher concentrations of Na and S were, however, measured in bai soil in comparison to forest soil. The high differences between bais indicated that the relevance of geophagical soil at particular bais may have been concealed by soil samples from the majority of bais showing lower mineral concentrations. Finally, in contrast to Klaus (1998), but in accordance with Fishlock (2010), no evidence was found that clay in the soil constitutes an important factor influencing bai visitation of elephants.

Minerals further were confirmed as important factors driving feeding selectivity by western lowland gorillas at bais. Results presented here tend to corroborate that bai feeding plant species possess higher mineral concentrations than forest feeding plants. In contrast to food preferences reported in the forest, within bais gorillas appear not to select plants rich in important macronutrients. This study further demonstrates differences in mineral concentrations in consumed versus non-consumed plant parts of the same species. It underlines the need for detailed nutritional studies combined with direct observations on feeding behaviour of individual gorillas from different age and sex classes in order to shed more light on the western lowland gorilla nutritional requirements. For comparison of the nutrients gorillas gain in the forest with those targeted in bais, these studies should be conducted simultaneously with nutritional analysis of gorilla feeding plants in the forest.

Bai plants represent important dietary components also for other large mammals such as the forest buffalo and the bongo antelope. They may as well constitute important mineral sources for these mammals, though the differences in mineral concentrations between plant species needs to be considered. Similarly, while the present study focused on forest elephants, soil consumption at bais has also been observed for the bongo antelope (Klaus-Hügi et al., 1999), the guereza colobus (*Colobus guereza*; J.M.S., pers. observation) and the western lowland gorilla (Magliocca & Gautier-Hion, 2002; J.M.S., pers. observation).

Altogether, neither in the water and soil nor in consumed bai plants a single mineral could be identified as important factor driving bai use. This is in accordance with numerous studies on soil and water resources used by large mammals worldwide (see chapters 7 and 8). It indicates that the composition of different minerals plays an important role. The particular minerals targeted by an individual may further depend on its current diet and physiological status. Besides, it is essential to consider the antagonistic and synergistic interactions between different minerals when examining mineral concentrations in food sources.

Finally, factors influencing bai use in a negative way, such as poaching, need to be taken into account. In the presence of poachers, elephants are known to avoid bais or to restrict visitation to night time (Ruggiero, 1990). On the other hand, compression, e.g. due to poaching in the region, may lead to an increase in elephant occurrence at a bai (Turkalo et al., 2013).

In conclusion, drivers of bai use are very complex and the high heterogeneity of bais further hampers their identification. Different mammal species are attracted to bais by a differing set of factors. Yet, the mineral rich resources provided at bais play an important role in the bai context.

Management recommendations

The present thesis has underlined the importance of bais for the diversity of the Central African rain forest and for large mammals in particular. In order to protect wildlife in the rain forest, effective management needs to be informed on the occurrence of species as well as on changes in local populations visiting bais. But until today studies have been restricted to single sites due to logistic constraints. In the present study camera traps have been demonstrated as a cost-effective tool for species' surveys and monitoring at bais. Their effectiveness in recording rare and nocturnal species has been highlighted. Results provide further evidence that numerous large mammals such as forest elephants, forest buffaloes and bongo antelopes use clearings preferably in the night. This underlines the importance of monitoring devices running 24 h a day, such as camera traps and autonomous acoustic recordings (Wrege et al., 2012). During daylight, however, camera traps potentially miss animals visiting a bai since they only face certain spots, i.e. trails in this study. Unfortunately, the design of the present study did not allow for comparison of data on visitation rates measured by direct observations and camera traps. Such a comparison may indicate in what way these data are related and whether the actual visitation rate of a particular species can be extrapolated from camera trap data.

Altogether, the use of camera traps is especially recommended at bais where no long-term study conducting direct observations is feasible. Camera traps cannot replace direct observations which allow for more exact identification of individual animals as well as recording of behaviour and resource use at bais. It is suggested to employ camera traps complementary to direct observations in order to provide nocturnal data. Furthermore, camera traps can be set up simultaneously at multiple bais allowing for site comparison. They further may provide evidence for poaching at bais through monitoring changes in visitation patterns of large mammals and providing pictures of poachers.

The high heterogeneity between bais, which has been highlighted by the present study, has important implications for wildlife management. The availability of feeding plants for large mammals varies considerably between bais. Likewise, bais differ strongly in respect of the mineral concentrations (quantitatively and qualitatively) of soil and water resources. Consequently, large mammals likely rely not only on one, but several bais within an area. Furthermore, bais potentially differ in their relevance for particular species in respect of a species feeding ecology. The protection of a bai mosaic is therefore recommended in order to facilitate mammal species the access to a broad supply of important resources.

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Eigenanteil an den Beiträgen

Chapter 5 - Diversity of bais: General features and vegetation

Julia Metsio Sienne

Konzipiert wurde diese Untersuchung von Prof. Dr. Rainer Buchwald und mir. Die bei der vorliegenden Arbeit untersuchten Bais habe ich im Rahmen einer Pilotstudie ausgewählt. Die Datenerhebung im Feld sowie die Auswertung der Daten und die Ausarbeitung wurden von mir durchgeführt. Die Bestimmung der Pflanzenarten erfolgte mit Hilfe von Annemarie Neugebaur, die einen Großteil der Arten im Rahmen ihrer Masterarbeit bestimmte. Bei der Identifizierung von Futterpflanzen wurde ich von lokalen Assistenten unterstützt. Eine Überarbeitung des Manuskripts erfolgte nach Anmerkungen und Anregungen von Prof. Dr. Rainer Buchwald.

Chapter 6 - Assessing species occurrence and species-specific use patterns of bais (forest clearings) in Central Africa with camera traps

Julia Gessner, Rainer Buchwald, George Wittemyer

Online erschienen 2013 in: African Journal of Ecology doi 10.1111/aje.12084

Das Untersuchungsdesign habe ich in Zusammenarbeit mit Dr. George Wittemyer und Prof. Dr. Rainer Buchwald entworfen. Die Feldarbeit habe ich durchgeführt und die Fotos der Kamerafallen ausgewertet. Bei der Analyse der Daten und der Ausarbeitung des Manuskripts hat mich Dr. George Wittemyer unterstützt. Eine Überarbeitung des Manuskripts erfolgte zudem nach Anmerkungen und Anregungen von Prof. Dr. Rainer Buchwald und drei anonymen Gutachtern.

Chapter 7 - Differentiation in mineral constituents in elephant selected versus unselected water and soil resources at Central African bais (forest clearings)

Julia Metsio Sienne, Rainer Buchwald, George Wittemyer

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Das Untersuchungsdesign habe ich in Zusammenarbeit mit Prof. Dr. Rainer Buchwald und Dr. George Wittemyer entworfen. Die Proben in den Lichtungen habe ich mit Hilfe von lokalen Assistenten gesammelt. Wasserproben in Dzanga Bai wurden von lokalen Assistenten und mir genommen.

Niederschlagsdaten in Dzanga wurden von Dr. Andrea Turkalo gesammelt und mir zur Verfügung gestellt. Die Boden- und Wasserproben habe ich mit Hilfe von Melanie Willen aufbereitet. Die Proben wurden im Labor von Eleonore Gruendken, Martina Schulz und mir mit Unterstützung von Adelina Calean und Petra Schmidt analysiert. Die Auswertung der Daten sowie die Ausarbeitung stammen von mir und wurden von Dr. George Wittemyer unterstützt, dessen konstruktive Anmerkungen in das Manuskript eingearbeitet wurden. Die Anmerkungen zweier anonymer Gutachter wurden ebenfalls aufgenommen.

Chapter 8 - Plant mineral concentrations related to foraging preferences of western lowland gorilla in Central African forest clearings

Julia Metsio Sienne, Rainer Buchwald, George Wittemyer

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Das Untersuchungsdesign habe ich in Zusammenarbeit mit Prof. Dr. Rainer Buchwald und Dr. George Wittemyer entworfen. Die Pflanzenproben habe ich mit Hilfe von Assistenten gesammelt und in Deutschland aufbereitet. Die Analyse hinsichtlich von Makronährstoffen erfolgte durch die LUFA Nord-West in Oldenburg. Der Mineraliengehalt wurde von Melanie Willens analysiert. Die Auswertung der Daten sowie die Ausarbeitung stammen von mir und wurden von Dr. George Wittemyer unterstützt. Seine konstruktiven Anmerkungen sowie die zweier anonymer Gutachter wurden in das Manuskript eingearbeitet.

Lebenslauf

Persönliche Daten

Name	Julia Metsio Sienne, geb. Geßner
Geburtsdatum	29.04.1982
Geburtsort	München

Ausbildung

2010 - 2014	Promotionsstudium an der Carl von Ossietzky Universität Oldenburg
2003 - 2008	Diplomstudium der Landschaftsökologie an der Carl von Ossietzky Universität Oldenburg
2002	Abitur am Gymnasium Weilheim i. OB

Beschäftigungsverhältnisse

Seit April 2013	Anstellung im Büro Landschaftsökologie Gessner in Trier
10/2008 - 10/2009	Forschungsassistentin für den World Wide Fund for Nature im Nki Nationalpark, Kamerun

Praktika

03/2010 - 10/2010	Praktikum bei der Wildlife Conservation Society im Nouabale-Ndoki National Park, Republik Kongo
10/2007 - 12/2007	Praktikum beim Max-Planck-Institut für evolutionäre Anthropologie im Salonga Nationalpark, Demokratische Republik Kongo
03/2007 - 07/2007	Praktikum beim World Wide Fund for Nature im Nki Nationalpark, Kamerun
07/2005 - 10/2005	Praktikum beim World Wide Fund for Nature im Lobeke Nationalpark, Kamerun
02/2003 - 04/2003	Praktikum bei der Jatun Sacha Foundation, Ecuador
06/2002 - 12/2002	Praktikum beim Max-Planck-Institut für evolutionäre Anthropologie im Salonga Nationalpark, Demokratische Republik Kongo