The Ecology of Forest Elephant Distribution and its Implications for Conservation

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PREFACE

This thesis was written by myself and is the result of my own work, unless otherwise acknowledged at the end of appropriate chapters.

ABSTRACT

Genetic evidence suggests that extant African elephants, currently recognised as two sub-species in the genus *Loxodonta*, should be divided into distinct species; savannah elephants (*L. africana*) and forest elephants (*L. cyclotis*). Forest elephants are most abundant in the equatorial forest of the Congo Basin, and account for a considerable portion of Africa's elephants. Despite their key role in forest ecosystems, few data on forest elephant ecology are available, at a time when intense hunting and widespread habitat fragmentation and conversion pose an increasingly severe extinction threat. A study of forest elephant ecology was initiated in the remote Ndoki Forest of northern Congo. The goal was to identify the ecological determinants of elephant distribution and ranging, and to determine the impact of human activity, at a relatively intact site. Data from a local, intensively surveyed site, and repeated extensive foot surveys over a 253km swathe of the Ndoki Forest, which traversed the northwest-southeast drainage gradient, revealed a spatial and temporal partitioning in the availability of resources important to elephants on several scales. Dicotyledon browse was most abundant in open canopy *terra firma* forest, light gaps, and swamps, while monocotyledon food was most concentrated in *terra firma* forest to the southeast, and was super-abundant in localised swamp patches. Mature and old leaf abundance was correlated with rainfall, but new leaves were not. During low rainfall periods, new leaf production was highest in the southeast, becoming widespread as rainfall increased. Forest clearings, clumped in the northwest, contained high mineral abundance in seep-hole water, most concentrated during dry periods. Fruit availability was negligible in swamps, high in closed canopy *terra firma* forest, and while correlated with rainfall, its temporal and spatial distribution was highly irregular. Drinking water, confined to rivers, was widespread and abundant. Elephants ate leaves, bark, wood, stems, roots, and fruit from over 350 plant species. Leaves dominated food selection, and browsing rates were highest in open canopy forests, particularly swamps. Fruit consumption increased dramatically as its availability increased. Elephants constructed trail systems that allowed efficient exploitation of high payback resources, notably water, minerals, and fruit.

Elephant distribution and ranging was investigated using data from dung counts and GPS telemetry. Dung data showed that elephant abundance was consistently high in the northwest, most likely due to the influence of forest clearings and high quality swamp habitat, about which elephants were permanently aggregated. During dry periods, elephant abundance increased in the northwest and in proximity to rivers. As rainfall increased, elephants dispersed out of the northwest, they selected upland forest, and their distribution tracked the patchy distribution of fruit across the landscape. Telemetry data revealed that individual elephants ranged over large areas (up to nearly 2000km^2), and travelled up to 57km in 48 hours, which allowed them to exploit resources over large areas. The widespread distribution of browse and drinking water, and the large body size of elephants, meant that quasi-nomadic ranging in search of fruit patches, was a low-risk strategy with a potentially high nutritional payback. The ecological determinants of elephant distribution and ranging were outweighed by human activity, including forestry prospection, and elephants avoided areas of high human impact.

Their large-scale ranging patterns, and the widespread distribution of their resources, means that forest elephants are particularly vulnerable to habitat fragmentation. Road building to facilitate logging in remote forest blocks was identified as a major threat to the conservation of elephants. Immediate conservation actions were proposed, which include: the establishment and maintenance of large core areas of integrally protected habitat in remaining isolated forest blocks; planning for ecologically and socially optimal road construction; and reduced impact logging to conserve critical fruit trees. Applied research is required to identify potential conservation sites, improve survey methods, quantify the impact of logging on elephant ecology, ranging and demographics, and to understand the role of elephants in ecosystem function, and how it is disrupted by range restriction, population reduction, and logging.

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Two people shaped my life in the Ndoki Forest. Mike Fay introduced me to the forest and its elephants. Many of the ideas developed in this thesis originated from our early wanderings together deep in the Ndoki. In the early years at Ndoki, Richard Ruggiero created an environment in which my only responsibility was to explore and learn. I did not appreciate the extent of his contribution until years later. Many members of staff of the Nouabalé-Ndoki National Park (NNNP) worked hard toward the success of this project. The Director, Bryan Curran, mobilised aeroplanes, boats, trucks, money, and personnel, often at the last minute, to help this project run smoothly. I also thank Jerome Mokoko-Ikonga, Paul Elkan, Sarah Elkan, Dos-Santos Domingos, Mahammet Abdouyale, Richard Parnell, Mark Gately, Emma Stokes, Dave Morgan, Steve Gulick, and Gaston Gobolo. From The Dzanga-Sangha Project in CAR, I thank Allard Blom, Guy Rondou, Urbain Agatoua, Lisa Steel, Nigel Orbell, and especially Cloe Cipolletta.

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LIST OF VEGETATION TYPE ACRONYMS

Vegetation types of the Ndoki Forest used in this thesis (descriptions are provided in Chapter 2)

Bai	Generic local name given to forest clearings
CF	*Cleistanthus* sp. forest
FF	Flooded forest
GDF	*Gilbertiodendron dewevrei* forest
GDFF	*Gilbertiodendron dewevrei* flooded forest
GDFH	*Gilbertiodendron dewevrei* with *Haumania dankelmaniana* forest
LAF	*Lophira alata* forest
LCS	Low closed scrub
LG	Light gap
MCF	Mixed closed forest
MF	Marantaceae forest
MMCF	Mokala riverine mixed closed forest
MMOF	Mokala river mixed open forest
MOF	Mixed open forest
PAF	*Plageostyles africana* forest
PAKA	*Guibourtia demeusei* flooded forest
PF	*Parinari* sp. forest
RF	*Rinorea* sp. forest
STREAM	Stream
SWP	Swamp
TF	*Terminalia superba* forest
VF	Vine forest
VLF	Vine / *Laccosperma* sp. forest
VLS	Vine/L*accosperma* sp. swamp
VS	Vine swamp

CHAPTER 1. INTRODUCTION

In his treatment of extinct Proboscideans published in 1991 Gary Haynes wrote:

> *'Very soon, perhaps within 20 years, no more studies of free-roaming animals will be possible as elephant populations disappear, shot for ivory and meat, and become more and more closely managed to guarantee that the species will live on, severely limited in their behaviour and movement. Soon, in a last attempt to save some of them, no more elephants will be allowed to die natural deaths in regions uninhabited and unvisited by human beings. Before long, the last remaining wilderness areas of Africa and Asia will be developed, manicured, and managed, and wild elephants, like cattle on ranches, will be carefully herded and supervised to ensure their survival…. If we thoughtfully record these last remaining decades in the existence of free-roaming modern elephants, perhaps we shall be enabled to see how the end came also to mammoths and mastodons'.*

I hope that in 'thoughtfully recording' my observations on the ecology of forest elephants and their habitat, this thesis may help us to better understand extant elephants, avoid the final extermination, and keep 'manicuring, herding, and supervision' to a minimum in Africa's last forest wildernesses.

This study had two ultimate goals. The first was to identify the ecological determinants of distribution and ranging of forest elephants (*Loxodonta africana cyclotis*) at a relatively intact site in Africa's equatorial forest, and determine how these may be modified by human activity. The second was, from these data and from previous studies, to develop a set of management principles to promote successful forest elephant conservation. This chapter describes the context of the study in terms of both the regional and local conservation status of forest elephants, and the scientific basis on which ecological research questions were developed and posed. A brief overview of the ecology of forest elephants is given here, and each subject area is presented in greater detail as an introduction to each chapter. This chapter ends with a brief introduction to each chapter and a general description of the study site.

THE CONSERVATION CONTEXT

The 1980s saw Africa's elephants massacred from an estimated continental population of 1.3 million in 1979 to just 609,000 ten years later (Douglas-Hamilton 1989), killed mostly for their teeth. During that decade wildlife managers, conservationists, and some politicians battled to stem the slaughter in east and southern Africa (Douglas-Hamilton and Douglas-

Hamilton 1982; Douglas-Hamilton 1988; Cobb 1989; Western 1989b) which culminated, among other things, in a ban on the international trade in ivory (Sharp 1997). During this time of visible slaughter of savannah elephants (*Loxodonta africana africana*), there was a general feeling that the 'invisible' elephants (*L. a. cyclotis*) of the vast equatorial forests, largely uninhabited and unknown, were relatively free from poaching and that large numbers of elephants remained (Anon. 1984a; Owen-Smith 1988). A decade previously, however, Parker (1979) had demonstrated that 60% of ivory exports from Africa came from central Africa.

Between 1979 and 1988 (Luxmoore *et al.* 1989) estimated that 2822 tonnes of ivory left central Africa, though they were unable to determine how much was from savannah or forest elephants, nor the number of dead elephants that this ivory represented. At the same time as their vulnerability was acknowledged, biologists also recognised that almost nothing was known of the basic biology, abundance, distribution, or conservation status of forest elephants (Barnes *et al.* 1995a). Status reports were either speculative and from models based on unrealistic assumptions (Anon. 1984b; Martin 1986), or from extrapolations from limited datasets (Burrill and Douglas-Hamilton 1987). Preliminary studies of forest elephant ecology had been completed in human-dominated landscapes in West Africa (Alexandre 1978; Merz 1981; Short 1981, 1983; Merz 1986a,b,c), but ecological information from central Africa was largely anecdotal (Carroll 1988a). In response, a regional survey across six central African countries (Democratic Republic of Congo [DRC, former Zaire], Congo, Cameroon, Gabon, Central African Republic [CAR], and Equatorial Guinea) was implemented in the late 1980s. The goal of this research was to provide baseline data on the distribution and abundance of forest elephants in central Africa, and to assess the impact of the ivory trade (Barnes 1989b).

Despite logistical difficulties and safety issues (Barnes and Jensen 1987; Alers *et al.* 1992), minimal sampling coverage (Alers *et al.* 1992), and technical problems of counting elephants in forests using dung (Wing and Buss 1970; Barnes and Jensen 1987; Barnes 1989a; Barnes and Barnes 1992; Barnes *et al.* 1994, 1997a; White 1995; Barnes 1996b, 2001), a number of important conclusions were forthcoming. An estimated 172,400 forest elephants (230,400 if savannah elephants were included), remained in central Africa (Michelmore *et al.* 1994; Barnes *et al.* 1995a). The DRC contained an estimated 72000 elephants, the highest of any country surveyed (Michelmore *et al.* 1994), though low sampling coverage meant that extrapolations were unreliable and confidence in this estimate was low (Barnes *et al.* 1995a). Using a more conservative estimation method, Alers *et al.* (1992) suggested there were 64,000 elephants left in DRC. In Gabon, where sampling coverage had been more widespread, the total elephant population was estimated at 61,800±20,200 by Barnes *et al.* (1995b) and 55,000 by Michelmore *et al.* (1994) using the same data. In 1989 Central Africa probably contained close to one third of Africa's elephants (Barnes *et al.* 1995a).

Survey data consistently showed a strong positive correlation between elephant density and perpendicular distance from roads or villages – 'man determined the distribution of elephants' (Barnes *et al.* 1991; Fay 1991; Fay and Agnagna 1991b; Alers *et al.* 1992; Michelmore *et al.* 1994). The gradient of this relationship was significantly changed by habitat type and poaching levels. Elephant density was high in secondary compared to primary forest, presumably since elephants prefer the more abundant understorey browse offered in secondary vegetation (Barnes *et al.* 1991; 1995a,b). Ironically, past human disturbance of the forest created excellent habitat for elephants, which became accessible when no longer occupied by people. Poaching was widespread throughout the central African forest, particularly in DRC (Alers *et al.* 1992; Michelmore *et al.* 1994). In areas of high poaching pressure elephant density with distance from roads and rivers increased more slowly than where poaching pressure was low (Michelmore *et al.* 1994; Barnes *et al.* 1995a). Even in the most remote areas, human activity was the major determinant of elephant distribution (Barnes *et al.* 1991).

The main stimulants of poaching identified were the price of ivory, poverty, corruption, and the widespread availability of firearms (Barnes 1993; Barnes *et al.* 1995a). Other threats to elephants included logging and development projects such as road building, mining and oil exploration, all of which increase human population density, stimulate market economies and may lead to commercial hunting and over-exploitation of wildlife, including elephants (Fay and Agnagna 1991a, 1993; Wilkie *et al.* 1992; Barnes *et al.* 1995a). The over-riding conclusion from the survey was that human activity, particularly poaching, was the major determinant of forest elephant distribution and abundance in central African forests.

The 1989 survey and the cascade of scientific literature it provoked had far-reaching and tangible benefits for forest elephant conservation. The vulnerability of forest elephants to poaching was exposed, and a number of constraints to effective forest elephant conservation were identified. These included ignorance of basic forest elephant biology, ineffectiveness of wildlife departments in central Africa, corruption, and the difficulty of working in remote forests (Barnes *et al.* 1995a). A number of large forest blocks where elephant densities were high and human disturbance was low were identified, in which conservation appeared to have the highest chance of success. Management recommendations from the survey included the development of a network of national parks in the largest, most remote forest blocks that remained, particularly in northeast Gabon, northern Congo, southeastern CAR, and southwestern Cameroon (Barnes *et al.* 1995a). By the mid-1990's national parks had been created in two of these areas (Nouabalé-Ndoki in Congo and Dzanga-Ndoki in CAR) and wildlife reserves set up in the other two (Minkébé in Gabon and Lac Lobéké in Cameroon, which subsequently also became a national park).

The early 1990's also saw the rejuvenation of 6 central African protected areas through the European Union-funded ECOFAC project, including three particularly important areas for elephant conservation. The Lopé Reserve in Gabon contained the highest recorded densities of elephants anywhere in central Africa (White 1994c). Salonga National Park in DRC was the biggest protected area in central Africa and once a stronghold for elephants (Alers *et al.* 1992), while Odzala National Park, Congo, still contained high elephant densities (Hecketsweiler 1990, 1991; Fay and Agnagna 1991b). By the mid-1990s then, the capacity to do effective conservation was building across the region.

The 1989 moratorium on international ivory trading reduced the demand and the price of ivory, which reduced the motivation for elephant poaching and lowered the rate of killing (Fay and Agnagna 1993). In the early 1990s, the governments of central African nations had shown a commitment to conservation through the support for and creation of a number of new protected areas and as participants in the Convention of the International Trade in Endangered Species (CITES). The international donor community appeared to be increasingly willing to pay for conservation in central Africa. Furthermore, the problems of deforestation, development, and rapidly expanding human populations were lower than elsewhere in Africa (Barnes 1990; Barnes 1997). The early 1990's also saw instability in the price of central African timber, which resulted in temporary stagnation of the logging industry (GEF 1992a, b). The combination of these factors indicated that the practices and politics of forest elephant conservation had swung from an 'out of sight out of mind' ignorance in the 1980's to a high profile and active international agenda several years later.

Despite these advances, elephant conservation remained fragile. Fay and Agnagna (1993) suggested the ivory ban had only a limited effect in reducing poaching, blaming a combination of economic and law enforcement issues. Widespread poverty meant that illegal, marginally profitable activities were worthwhile if the risks of capture and punishment were negligible (Leader-Williams *et al.* 1990), which, outside of heavily subsidised protected areas was the case in much of central Africa. Elephant poaching and ivory trafficking was therefore still an attractive source of income for rural people. Furthermore, many traders assumed that the ivory ban was a temporary measure, thus they were prepared to keep buying on a limited scale, stockpile, and wait for a resumption of trading (Fay and Agnagna 1993). Control of poaching required both effective continuation of the ivory ban (uncertain given the pro-ivory trade lobby), and effective law enforcement (unrealistic given the capacity of national wildlife departments) both in and out of protected areas. Growing political instability throughout central Africa was also a concern. Large numbers of displaced refugees from Rwanda and Burundi in the early 1990's, and the armed conflict that swept through DRC, put enormous pressure on wildlife outside of protected areas. Regional stability also risked compromising international funding for conservation, and national government capacity and interest in conservation when they had more immediate and pressing issues of national security to manage, which also reduced management ability inside protected areas. In the Republic of Congo, armed conflict in 1997 almost brought an end to international conservation funding (Blake, pers. obs.) at exactly the time a huge proliferation of firearms (Demetriou *et al.* 2001), a dysfunctional government, and an increasingly desperate population had a dramatic impact on elephants and other wildlife.

In the face of these mounting threats, one realistic strategy for elephant conservation was protected areas management where financial resources and efforts could be focussed, and stable funding secured. Among sites identified across central Africa, the Nouabalé-Ndoki National Park, with its high international profile, national government and donor commitment, low human population density, and good relations between park managers, local people, and foresters had relatively high potential for success.

THE ECOLOGICAL CONTEXT

A pre-requisite to species conservation and protected areas management is an understanding of the biology of target species, landscapes, or ecosystems (Soulé 1986; Feidler and Jain

1992; Cox 1993). The savannah elephant is perhaps the most widely studied large mammal in Africa (Kingdon 1997), while the forest elephant remains poorly known (White *et al.* 1993). There has been much debate on the taxonomic distinction between the two sub-species (Eltringham 1982) since considerable morphological, genetic, ecological and social differences exist. Morphologically, forest elephants are smaller, have rounded, lobeless ears, straighter and thinner downward pointing tusks compared to savannah elephants (Sikes 1971). Recent genetic evidence (large genetic distance, multiple genetically fixed nucleotide site differences, and extremely limited hybridisation) suggest that African elephants should be divided into two distinct species, *Loxodonta africana* (bush elephants) and *Loxodonta cyclotis* (forest elephants) (Roca *et al.* 2001). There has been speculation on the existence of a second distinct species of forest elephant, the pygmy elephant (*Loxodonta africana pumilio*) (Blancou 1951, 1962; Edmond-Blanc 1955; Western 1986). However morphological studies (Pfeffer 1960), genetic analysis (Georgiadis 1994; Roca *et al.* 2001), and considerably more detailed and widespread ecological studies involving observations of forest elephants from several sites (Turkalo and Fay, 1995, 2001; Short, 1981, 1983; Merz, 1986a,b,c; White *et al.*, 1993; Powell, 1997), suggest the notion of pygmy elephants comes from mis-identification of precocious juvenile and sub-adult elephants as adults.

Obviously, forest and savannah elephants evolved in very different habitat conditions, that is reflected in their morphology, ecology, and social organisation. Savannah and woodland habitats of east and southern Africa tend to be more homogeneous and contain lower plant species diversity compared to the highly diverse, temporally and spatially heterogeneous rainforest environment of central Africa (White 1983; Whitmore 1990; Richards 1996). Permanent water tends to be sparse in savannahs during dry periods, which limits the ranging of elephants. The onset of the rains replenishes seasonal water sources, which allows elephants to expand out of their dry season range and exploit nutritious new grass (Western 1975; Western and Lindsay 1984). In forests, water remains clumped into rivers and streams but these are frequent, permanent, and never more than a few kilometres apart (Powell 1997).

Savannah elephants are generalist grazers/browsers, with grass making up 60-95% of the diet depending on habitat and season (Owen-Smith 1988). Forest elephants eat a highly diverse selection of species and plant parts made up of leafy browse (both dicotyledons and monocotyledons), roots, pith, and bark, and grass usually makes up a minimal part of the diet (Merz 1981; Short 1981; White *et al.* 1993), though grass may be eaten when available

(Tchamba and Seme 1993). Unlike savannah elephants which live in a habitat where fruit is generally rare, forest elephants are highly frugivorous (above references).

The ranging patterns of savannah elephants vary from tens of square kilometres up to over 10,000km^2 in the arid deserts of Namibia (Douglas-Hamilton 1972; Viljoen 1989b; Lindeque and Lindeque 1991; Thouless 1995, 1996). When rainfall in savannahs is plentiful during the wet season, elephant movements track the productivity gradient of grasslands but they are obliged to return near to permanent water and swamps during low rainfall periods (Western 1975). Prior to this study, limited telemetry data suggested that forest elephants had home ranges of up to ca. 600km^2 (Powell 1997), and that humans, secondary forest, and fruit availability may drive seasonal movements and distribution (Short 1983; White 1994d; Powell 1997).

The social organisation of forest elephants has been studied at the ‘Dzanga Bai’ in CAR, to the northwest of the Ndoki Forests for over a decade (Turkalo and Fay, 1995, 2001). Andrea Turkalo, who directs the study, has collected an enormous dataset over this period on social dynamics, group composition, social behaviour, reproductive rates, and also has individual identifications for over 2500 elephants that visit the bai (Turkalo and Fay, 2001). Group size tends to be small in forest elephants compared to the large herds of tens or even hundreds of individuals often seen in savannah elephants (White *et al.* 1993; Querouil *et al.* 1999; Turkalo and Fay 2001). The most common social unit in forests appears to be a single female, occasionally two, with associated offspring, though larger groups may form. Turkalo (pers. comm.) suggests that a higher order social organisation similar to that in savannah elephants described by Moss (1988) may exist in forest elephants, since greeting ceremonies and affiliative behaviour between smaller social units is frequently observed among elephants at Dzanga. Differences in feeding ecology, the distribution of resources, and the lower predation pressure in forests compared to savannahs may all influence the grouping patterns between sub-species (White *et al.* 1993).

STUDY SITE

Congo background

This study was conducted in the Ndoki Forest of northern Republic of Congo (Congo) (Figure 1.1). Congo straddles the equator (3° 41'N-5° 2'S, 11° 9'E-18° 39'E), and covers a surface area of 342,000km^2. It is bordered by the Democratic Republic of Congo (DRC) and Angola (enclave of Cabinda) to the east, the Central African Republic (CAR) to the north, Cameroon to the northwest, and Gabon to the west. The southwestern boundary of Congo is an Atlantic coastline of ca. 170km (Figure 1.1). The human population of Congo is low, with 2,590,000 inhabitants according to a national census in 1995, or a mean density of 8 humans km^{-2}, with an estimated growth rate of ca. 2.2% per year in 2001 (http://www.cia.gov/cia/publications/factbook/geos/cf.html). The population is highly urbanised, with over 50% of inhabitants living in the nation's two major cities of Brazzaville and Pointe Noire, both in the south of the country (Figure 1.1). In much of the north, the human population is below 1 inhabitant km^{-2}, concentrated along major rivers, and large tracts of land contain few or no people.

Following independence from France in 1960, the political system of Congo rapidly turned to Marxism, which continued until political reforms in 1991, and the nation's first democratically elected president in 1992. Civil unrest quickly followed in 1993, and a full-scale civil war erupted in 1997, which ended with the reinstatement of the former Marxist President, Denis Sassou-Nguesso. Democratic elections have yet to be hosted following the end of the war. During the war at least 10,000 people and probably considerably more, were killed, and over 200,000 inhabitants displaced from Brazzaville and elsewhere (http://news.bbc.co.uk/hi/english/world/africa/country_profiles/newsid_1076000/1076794.stm.).

The economy of Congo is based primarily on the exploitation of natural resources, dominated by oil (offshore production) and timber, with natural gas, lead, copper, and a number of other minerals of lesser economic importance (www.cia.gov/cia/publications/factbook/geos/cf.html). Following elections and before the civil war, the World Bank and the International Monetary Fund (IMF) supported economic reforms. The reform programme ended in June 1997 with the onset of civil war. Following the war, economic progress was badly hurt by slumping oil prices and the resumption of armed conflict in December 1998. In 1999, Congo had an estimated international debt of $US5 billion.

Subsistence agriculture and the exploitation of wildlife are the basis of the rural economy. Manioc (cassava) is the major subsistence crop, with bananas, maize, and peanuts also cultivated. Cash crops include sugarcane, palm oil, cacao, and coffee. Instability in the markets coupled with political unrest and degradation of national transport infrastructure has reduced production and export value of these crops in recent years.

Sixty-five percent of the surface area of Congo, or 220,060km^2 is natural forest, which accounts for 9.6% of the central African total (including Rwanda and Burundi), estimated to be 2,2801,100km^2 (FAO 2000). Approximately 147,740km^2 (69%) of this is relatively closed canopy forest on *terra firma* and 65,660km^2 is swamp forest (Hecketsweiler 1990; Sayer 1992). Forest conversion through deforestation for agricultural development and habitat degradation through commercial timber exploitation has reduced the extent of forest cover, and affected the ecological character of much of the Central African forest. In Congo, the rate of forest loss is low and over 62% of the original forest cover of the country still remains. However of this total, only 29% was undisturbed and ecologically intact 'frontier' forest in 1997 (Bryant 1997). Forests through most of southern Congo have been selectively logged at least once, and often several times since the late nineteenth century. Logging was slow to develop in the remote north of the country, due primarily to its isolation and the logistical difficulties of infrastructure development, but has gained considerable momentum in recent years.

Following forest inventory and management planning in the 1970s, the forests of northern Congo were divided into management blocks called *Unités Forestières d'Amanagément* (UFA's, or forestry management units) which were designated as production forest. The surface area of this potential production forest was an enormous 8,984,750ha divided into 21 UFA's, which covered all but the extreme west, the non-exploitable swamp forests of the north-east, and the central savannahs (Figure 1.1). Due to extremely high transport and operating costs, only high-grade timber species are currently logged in the northern forests, restricted largely to two species of African mahogany (*Entandrophragma cylindricum* and *E. utile,* Meliaceae).

Conservation has become an increasingly important land use in Congo in the last decade. Two national parks in the north, Odzala and Nouabalé-Ndoki, with a combined area of 1,746,836ha, are legally protected from logging and all other forms of consumptive use. The Nouabalé-Ndoki National Park is part of a tri-national conservation initiative involving Cameroon and CAR, described below. A third National Park in the south, the Conkouati-Douli, of 345,183ha completes the nation's National Park system, which accounts for a total of 6.6% of Congo's surface area (Figure 1.1). National financial and technical capacity to manage these areas is limited, and at present the national parks rely heavily on support from the international community, particularly the European Union (EU), the United States Agency for International Development (USAID), and international NGOs.

THE NDOKI FOREST

The Ndoki Forest, with the Nouabalé-Ndoki National Park at its core (Figures 1.1, 1.6), is found between 1.5° to 3°N, and 16° to 17°E. The climate is transitional between the Congolo-Equatorial and sub-equatorial zones with a mean rainfall of 1422mm per annum (NNNP records). Rainfall is bimodal, with peaks usually in June and October, and a main dry season from December to March (Figure 1.2) with between 100 and 120 rainy days per year (ORSTOM 1969). The average daily temperature is 26°C (mean annual minimum = 21.5° and mean annual maximum = 26.6°) with little seasonal variation (Figure 1.3).

Topography varies considerably across the Ndoki Forest. To the northwest *terra firma* uplands and flat plateaux rise on gentle slopes from usually wide flooded valleys to reach altitudes of ca. 600m above sea level (MSL). Slopes near the headwaters of the major rivers to the north of the NNNP are occasionally moderate and rarely steep. To the southeast, the study area descends to ca. 330m MSL into the extensive floodplain of the Likouala aux Herbes River - the *Cuvette Congolaise* or Congo swamp basin. There are three major intact watersheds originating in the NNNP, the Ndoki which runs southwest into the Sangha River and the Motaba and Likouala aux Herbes which drain east and south into the Oubangui River (Figure 1.4). Soils throughout the study region are of generally sandy texture and poor quality of three main types: arenosols to the north and west, ferrasols to the southeast in the Likouala aux Herbes basin on *terra firma*, and gleysols in the swamps further southeast (ORSTOM 1969, 1983; FAO/UNESCO 1988).

Figure 1.1. Location of Congo in Africa, protected areas, production forests, and national infrastructure

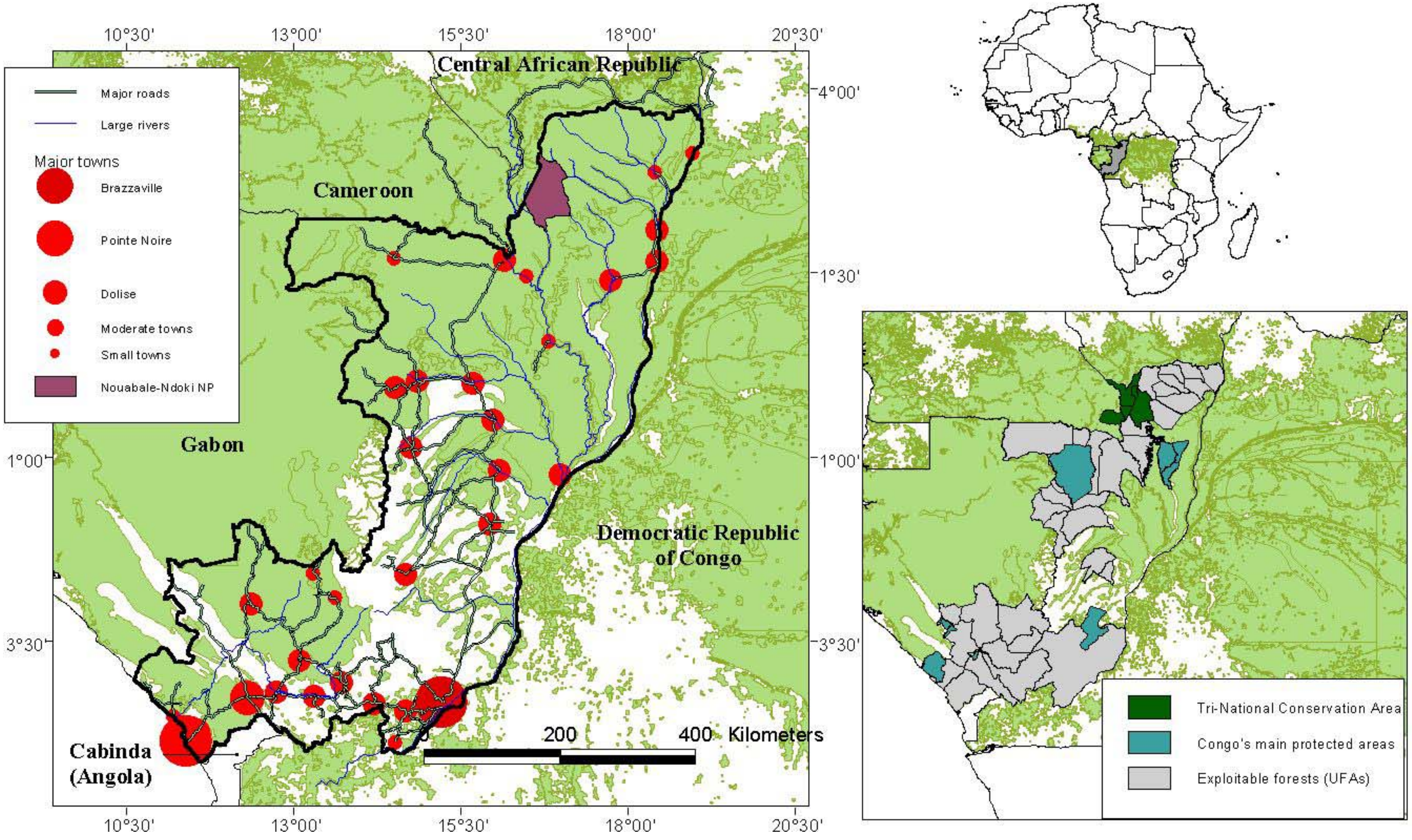


Figure 1.2. Mean monthly rainfall recorded in the NNNP from 1998-2000

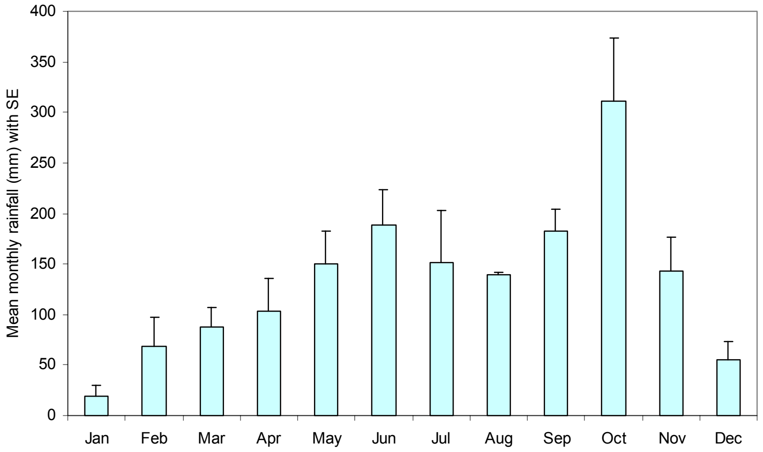


Figure 1.3. Mean monthly maximum and minimum temperature in the NNNP from 1998-2000

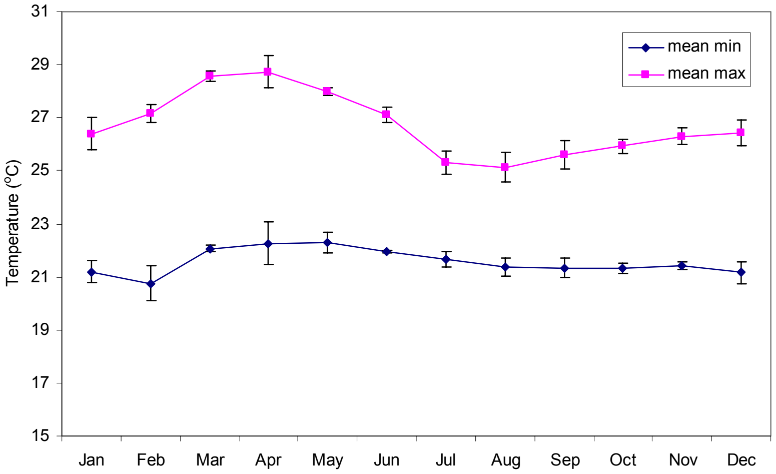
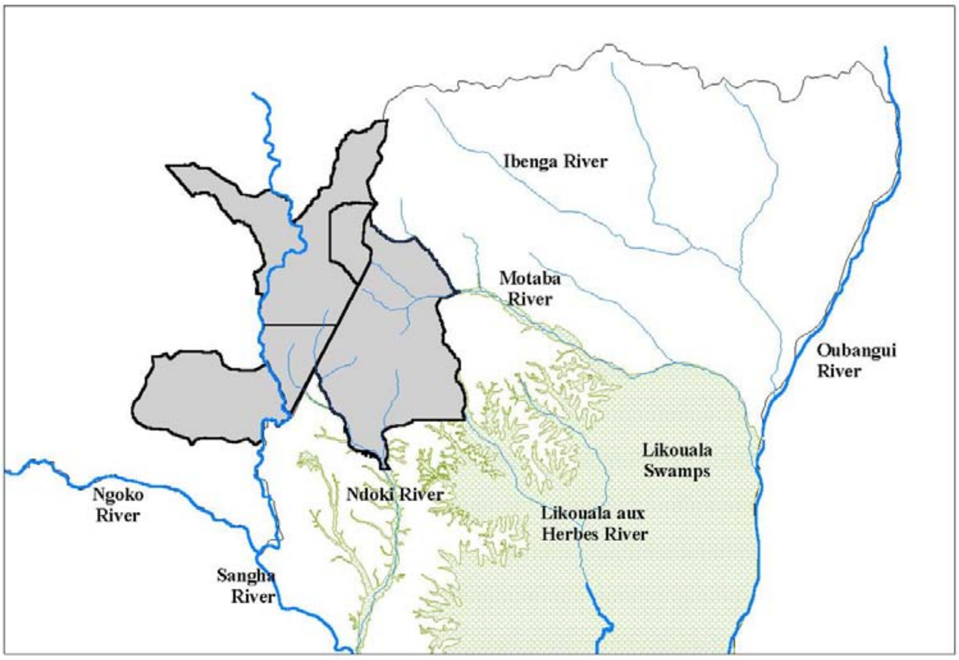


Figure 1.4. The Tri-National Conservation Area and major rivers and swamps of the northern Congo



The Ndoki Forest is embedded in wet Guineo-Congolian lowland rainforest, transitioning to the north into dry Guineo-Congolian lowland rainforest, and into swamp forests to the south (White 1983). Within this broad classification, *terra firma* is dominated by Sterculiaceae-Ulmaceae semi-deciduous forest described by (Rollet 1964; Letouzey 1968), with large patches of mono-dominant *Gilbertiodendron dewevrei* forest along watercourses and upland plateaux (Blake and Fay 1997), and swamp forests. Swamps consist of several vegetation formations, often dominated by *Raphia* spp. and *Guibourtia demeusei* (Letouzey 1968; Moutsamboté *et al.* 1994). Forest clearings, often called *bais* by local Bayaka people, are a characteristic feature of landscape, and are thought to be created and maintained by elephants and other large mammals (Klaus *et al.* 1998). These clearings, which are often dominated by sedges and grasses, may contain abundant mineral deposits in the soil, which attract a wide variety of animals, including elephants (Klaus *et al.* 1998; Turkalo and Fay 2001). The Ndoki forest retains a diverse fauna including several large, charismatic species such as forest elephants, gorillas (*Gorilla gorilla gorilla*), chimpanzees (*Pan troglodytes troglodytes*), forest buffalo (*Syncerus caffer nanus*), bongo (*Tragelaphus euryceros*), and leopards (*Panthera pardus*), often found in high densities (Carroll 1986, 1988a, 1996; Fay and Agnagna 1992; Nishihara 1994; Blake *et al.* 1995; Kuroda 1996; Ruggiero 1998; Klaus-Hugi *et al.* 1999, 2000; Turkalo 1999; Blake In press). The verified large mammal fauna is presented in Table 1.1.

The human population, traditionally Bantu agriculturist-fishermen and Bayaka (pygmies) semi-nomadic hunter-gatherers, is one of the lowest in Africa, with a mean density in the study area of <1 km^{-2} (Hecketsweiler 1990; Eves and Ruggiero 2000). Archaeological evidence (Fay 1997) indicates that Bantu people were widespread throughout the Ndoki forest between ca. 2300 and 900 BP, after which they apparently and inexplicably disappeared from the forest interior. Throughout Congo, the colonial period saw a concentration of human settlement on navigable rivers, and extant villages are now concentrated along major rivers and roads. Over the last 30 years, commercial forestry practices have caused high levels of immigration into logging towns developing on the margins of the study area.

Table 1.1. Large mammal fauna of the Ndoki forest

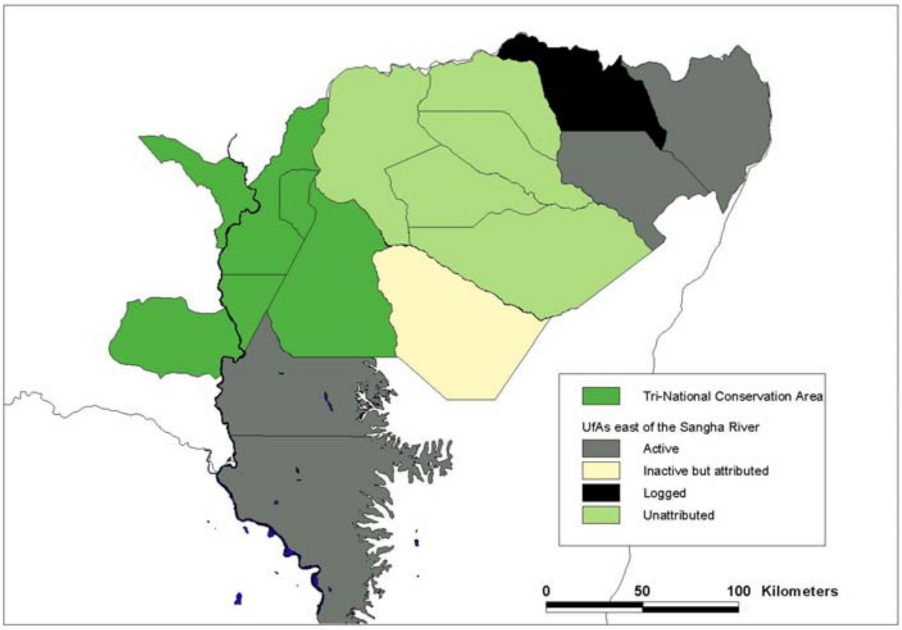
Order	Scientific name	English name
Carnivora	*Lutra (Hydrictis) maculicollis*	Spot-necked otter
	Aonyx congica	Swamp otter, Congo clawless otter
	Mellivora capensis	Ratel
	Atilax paludinosus	Marsh mongoose
	Civettictis civetta	Civet
	Panthera pardus	Leopard
	Profelis aurata	Golden cat
	Crocuta crocuta	Spotted hyaena
Proboscidea	*Loxodonta africana cyclotis*	Forest elephant
Artiodactyla	*Potamochoerus porcus*	Red river hog
	Hylochoerus meinertzhageni	Giant forest hog
	Hippopotamus amphibius	Hippopotamus
	Hymenoschus aquaticus	Water chevrotain
	Syncerus caffer nanus	Forest buffalo
	Tragelaphus spekei	Sitatunga
	T. euryceros	Bongo
	Cephalophus callipygus	Peters duiker
	C. dorsalis	Bay duiker
	C. leucogaster	Gabon duiker, white-bellied duiker
	C. nigrifrons	Black fronted duiker
	C. sylvicultor	Yellow-backed duiker
	C. monticola	Blue duiker
Edentata	*Manis gigantea*	Giant pangolin
Tubulidentata	*Orycteropus afer*	Aardvark
Primates	*Allenopithecus nigroviridis*	Allen's swamp monkey
	Cercopithecus nictitans	Spot-nosed guenon
	C. cephus	Moustached guenon
	C. pogonias	Crowned guenon
	C. neglectus	De Brazza's monkey
	Colobus (Procolobus) badius	Red colobus
	Colobus guereza	Black & white colobus, guereza
	Lophocebus albigena	Grey cheeked mangabey
	Cercocebus agilis	Agile mangabey
	Pan troglodytes troglodytes	Common chimpanzee
	Gorilla gorilla gorilla	Western lowland gorilla

LAND USE MANAGEMENT

Commercial timber exploitation is the region's major economic activity and land use. At the beginning of this study, only four companies were active in the Congo east of the Sangha River (Figure 1.5), with a fifth UFA previously exploited but no longer active. The major producer of timber during the 1980's and 1990's was a German-owned, French-managed company, *Congolaise Industrielle du Bois* (CIB) operating in the Pokola concession some 43km south of the park. In 1997, following a civil war in Congo, the CIB was granted the Kabo UFA, immediately south of the park (Figure 1.5), which had been poorly managed for some years and had fallen into stagnation. CIB rapidly increased production in Kabo and soon thereafter were also awarded the Loundougou UFA, a concession of 390,816ha to the east of the national park. This gave the company a total area of exploitable forest of 1,430,816ha.

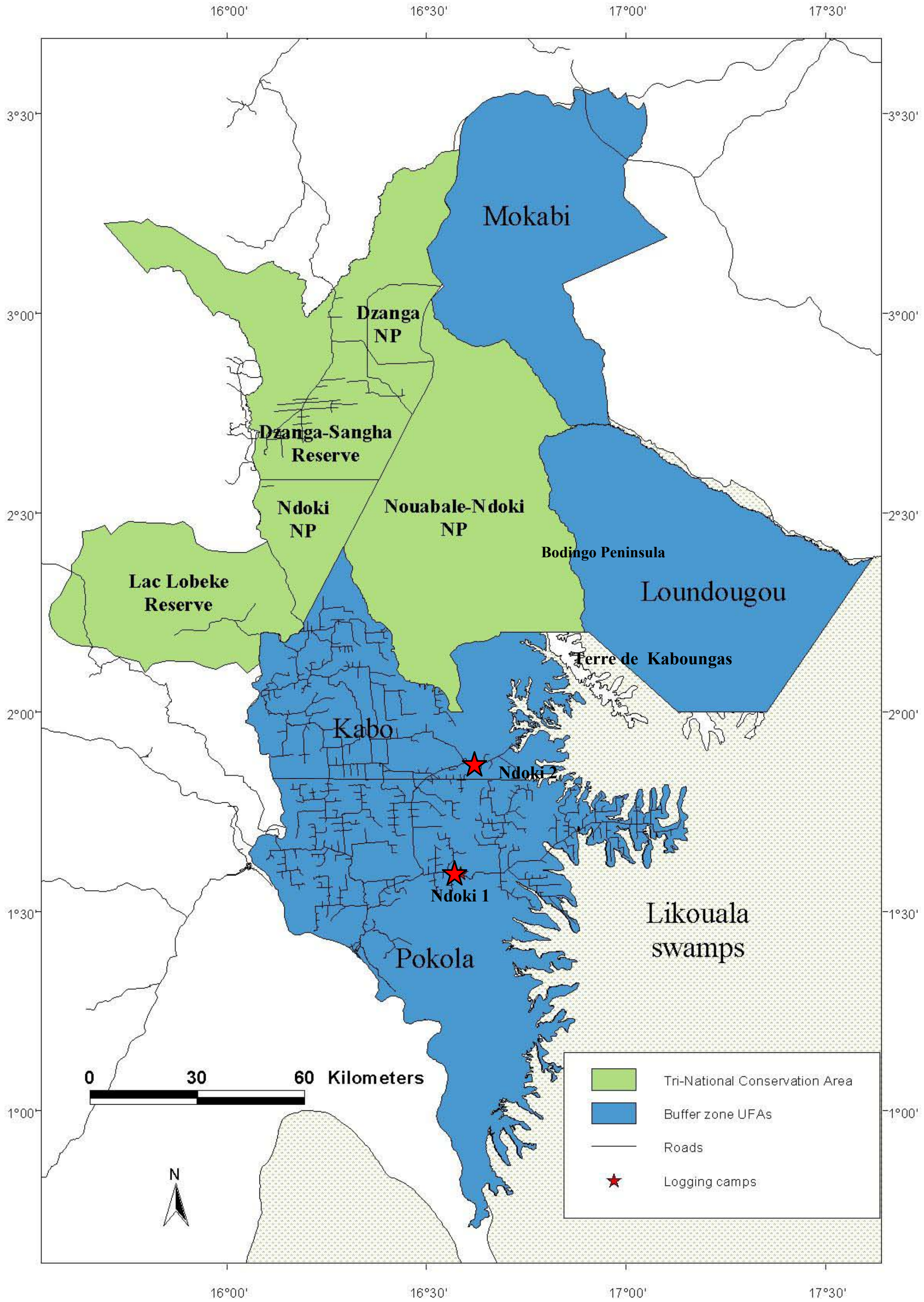
The logging industry is responsible for most economic development of the northern Congo, including job creation, revenue generation, and road, bridge, and logging camp construction. Almost exclusively, the road infrastructure east of the Sangha River has been built by logging companies. From their bases on the Sangha River, the CIB in the Pokola concession and SNBS in Kabo rapidly expanded east. In 1991, the CIB built a dike across the Ndoki River and within two years a logging camp, called Ndoki 1, for 120 workers and their families had been constructed at the site (Figure 1.5). The road quickly opened up a new trade route directly from a formerly isolated group of villages on the *Terre de Kaboungas* (a spit of land near the Likouala swamps) to Pokola, and beyond to destinations as far away as Douala. By late 1997, a second dike had been constructed across the Ndoki River (Figure 1.6) with a second logging camp, Ndoki 2, for 100 families on the east side of the river completed shortly afterwards. These camps opened up the entire forest between the Ndoki and Likouala swamps to logging, road infrastructure development, and human encroachment. They also provided the logging company with the means to push further east into the 4230km^2 Loundougou concession (Figure 1.6). Road construction associated with forestry over the last 25 years has dramatically changed the land use options for northern Congo. Since the end of the civil war in 1997, it has been a preoccupation of the current Congolese government to develop the road infrastructure as a first step toward bringing economic development to the north. To this end logging companies are being encouraged to develop their road infrastructure as fast as possible.

Figure 1.5 Status of forestry concessions in northern Congo, east of the Sangha River, in early 1998



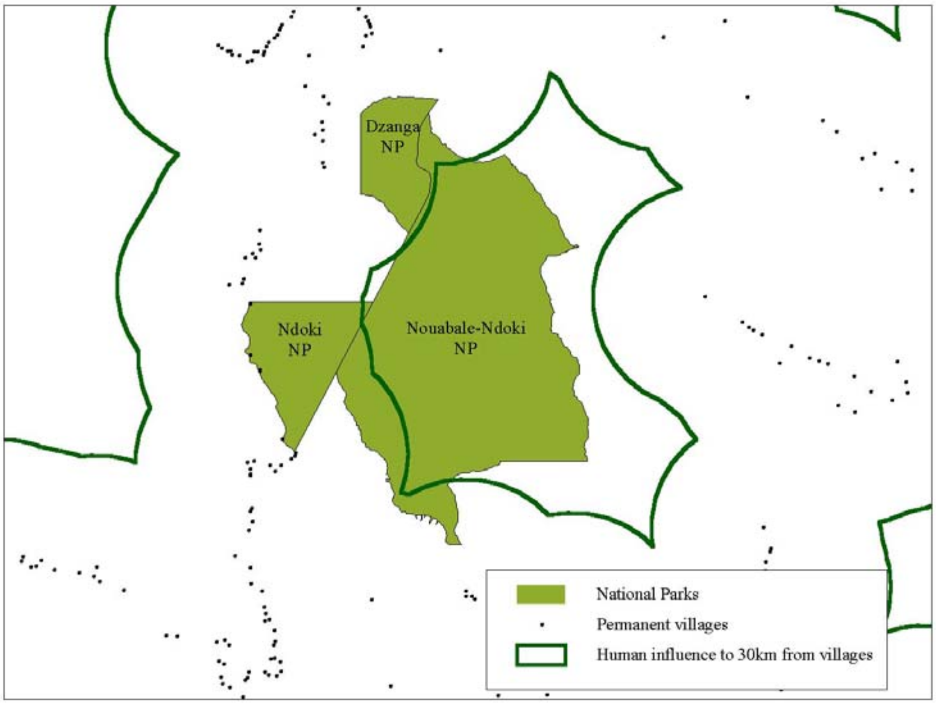
Due to the low human population density and distribution along major rivers, much of the Ndoki forest has experienced low pressure for consumptive use by local people. When this study began, the landmass beyond 30km (a long days walk) from the nearest village (Figure 1.7) included most of the NNNP and its peripheries. This area was almost never accessed for subsistence hunting (WCS 2001). Elephant hunting had been a major activity on the northern sector of the park and also to the southeast, but was dramatically reduced with the arrival of the Congo Forest Conservation Project in 1991. Further from the park boundaries, elephant poaching and commercial bushmeat hunting in the region were practically uncontrolled.

Figure 1.6. Land use context of the Ndoki Forest



Seemingly at odds with the desire for logging, road development and employment, conservation represents the last major land use in the Ndoki Forest. In the immediate study area, the NNNP dominates the landscape, covering 392,169ha of intact forest. The Park is contiguous with and is part of a wider Tri-National Conservation Area, involving the Dzanga-Sangha Dense Forest Reserve, which includes the Dzanga and Ndoki NPs in CAR, and the Lac Lobéké NP in south-west Cameroon (Figure 1.6). Conservation management in the Ndoki forest involves a matrix of land uses from complete protection within the Nouabalé-Ndoki National Park, to an evolving system of buffer zone management which includes logging zones, traditional and subsistence hunting zones, safari hunting areas, and no hunting areas. The legal framework for these activities now exists in all of the logging concessions in Congo which border the NNNP, and the Pokola concession, a total landmass of ca. 1,908,000ha. Thus while logging and road construction have proceeded at a formidable rate, the legal mandate of the government/NGO partnership to be involved in land use and wildlife management decision making had increased from zero in 1989 (the first forest elephant status report was published (Barnes 1989b), to nearly 20,000km^2 ten years on.

Figure 1.7. Known villages in 1998, showing a 30km human influence zone around them



GOALS OF THIS THESIS

Set against the backdrop of limited data and understanding of forest elephant ecology, the worsening conservation status of the sub-species, and the specific management issues at the Ndoki site, this thesis had both scientific and conservation goals. The first was to determine the patterns of geographical and temporal distribution and ranging of forest elephants at a single, relatively undisturbed, study site (the Ndoki Forest of northern Congo). The second was to explain these patterns in relation to the heterogeneity of resource distribution, the large body size of elephants, and to determine how the ecology of elephant distribution was influenced by human activity. The third was to describe the implications of ecology and human disturbance for forest elephant conservation, and develop a suite of management guidelines to improve conservation efforts at Ndoki and throughout central Africa.

The objectives of this thesis were to:

1. Quantify, on a landscape scale, the spatial and temporal distribution and relative abundance of food and mineral resources available to forest elephants;
2. Quantitatively describe the feeding ecology of forest elephants and identify resources of particular importance;
3. Describe the permanent elephant trail system of the Ndoki forest and identify those ecological factors that influenced their formation;
4. Quantify the seasonal distribution patterns of forest elephants at Ndoki, identify the ecological factors that most strongly influence elephant distribution, and quantify their relative effects;
5. Quantify the impact of human activity on forest elephant distribution;
6. Describe the movements of individual forest elephants at a relatively undisturbed site (the Ndoki Forest), in particular to quantify home range size and the scale over which forest elephants may range;
7. Generate a suite of recommendations to improve forest elephant conservation at Ndoki and across the range in central Africa, based on existing information and the new contribution to the understanding of forest elephant ecology made by this thesis.

The thesis has been organised in a logical sequence of largely self-contained chapters, each addressing specific parts of the puzzle. A detailed description of the specific objectives of each chapter is given at the end of each introduction. Chapter 2 describes some of the spatial and temporal habitat variability across a large swathe of the Ndoki Forest, particularly the availability of important food and mineral resources. In Chapter 3, the feeding ecology of elephants is described, including an analysis of foraging success rate in different habitats. In Chapter 4, it is argued that the distribution and abundance of resources and their importance for elephants results in the formation of a complex trail network through the forest which increases foraging efficiency. Chapter 5 quantifies the seasonal change in the distribution of elephants, and explains the patterns observed in relation to a number of environmental variables. Specifically, these are food (fruit, and both monocotyledon and dicotyledon browse), minerals, rivers, swamps, rainfall, elephant trails, and human activity, particularly logging prospection. In Chapter 6, a GPS telemetry study of forest elephants is described which provided the first high quality data on the movements of individuals. Individual movement patterns are used to verify the conclusions drawn in Chapter 5. In Chapter 7, the conclusions from this research are drawn together and their conservation implications are discussed. To conclude Chapter 7, a number of conservation recommendations are proposed within the context of this research. Chapter 8 ends the thesis with an overview of the study and a summary of its most important conclusions.

CHAPTER 2. VEGETATION OF THE NDOKI FOREST

INTRODUCTION

Among the important determinants of the density and distribution of elephants in African forests are vegetation characteristics and the distribution of important resources (Wing and Buss 1970; Short 1983; Merz 1986b; Carroll 1988a; Barnes *et al.* 1991, 1995b; Fay and Agnagna 1991b; White 1994b). Wing and Buss (1970) found that savannah elephants in Kibale Forest, Uganda, preferred colonising and scrub forest over more closed canopy vegetation types and were most abundant in open canopy forest with a dense herbaceous understorey and high densities of trees in small size classes. This conclusion was confirmed by Kasenene (1987), Nummelin (1990), and Struhsaker *et al.* (1996) who found that elephants in Kibale used heavily logged forest more than lightly logged, and preferred large light gaps over small ones, and all gaps over closed canopy forest.

In Central Africa, forest elephants also occur at high density in open canopy, including secondary, forests (Barnes *et al.* 1995a, b; Powell 1997), where the abundance of understorey browse may be high compared to more closed canopy forest types (Short 1983; Barnes *et al.* 1991). The highest consistent density of forest elephants yet recorded (ca. 3 individuals ha^{-1}) was in the Marantaceae forest of the Lopé Reserve, Gabon (White 1994b), where Terrestrial Herbaceous Vegetation (THV) (Rogers and Williamson 1987) dominates the herb layer. Like the scrub forests of Kibale, the Lopé Marantaceae forest is also a late stage in forest succession toward closed canopy, mature forest (White 2001). Swamp forests may also offer an abundant source of herbaceous browse (Barnes *et al.* 1991), as they do for savannah elephants in east Africa (Western and Lindsay 1984). In addition to browse, fruit availability may also influence the density and distribution of forest elephants (Short 1983; Merz 1986b; White 1994d; Powell 1997).

While gross trends in food availability are qualitatively apparent, few studies attempting to explain the seasonal distribution of forest elephants have quantified forest structure, composition, and the spatial and temporal distribution of elephant foods concurrently with data on feeding ecology and spatial distribution of elephants, particularly over large spatial scales. Examples do exist from forests further east in Africa. In their classic study, Wing and Buss (1970) collected an enormous dataset on the vegetation characteristics and ecology of elephants in the Kibale Forest. In the same forest, Struhsaker *et al.* (1996)

quantified some elements of elephant food resource availability with data on the relative abundance of elephants. However, Kibale Forest is inhabited by savannah elephants which are ecologically (Short 1981) and genetically (Roca *et al.* 2001) distinct from forest elephants. In west Africa, Short (1983) and Dudley *et al.* (1992) explained the seasonal distribution of elephants in relation to food availability, but provided no data on either the spatial or seasonal distribution of foods. In central Africa, Powell (1997) described the density and distribution of trees over 10cm diameter at breast height (dbh) and in some cases 3cm dbh, and the seasonal abundance and distribution of fruits. These data were used to explain elephant distribution and seasonal movements, though the distribution and abundance of herbaceous vegetation was not included in the analysis, nor was vegetation enumerated in swamps or riverine forest. White (1994d) quantified the temporal abundance of favoured elephant fruit species and demonstrated a strong positive correlation between the abundance of *Sacoglottis gabonensis* fruit and elephant density.

The forest of the Ndoki region of northern Congo has been classified as moist semi-deciduous forest (Rollet 1964; Letouzey 1968). Embedded in this gross classification is a finer grained vegetation mosaic of swamps, mono-dominant *Gilbertiodendron dewevrei* forest, Marantaceae forest, sedge and grass dominated clearings, and a number of more subtle vegetation types (Moutsamboté *et al.* 1994; Fay 1997; Blake In press). Quantitative data from the Ndoki Forest on forest structure and composition do exist, but are from two localised somewhat atypical sites [secondarised forest (Fay 1997), and forest close to an extensive mineral lick complex with inflated elephant abundance (Carroll 1996; Goldsmith 1999)], and forest wide resource availability for elephants remains poorly known. The aim of this study was to quantify broad patterns in the spatio-temporal distribution of important food resources for elephants in the Ndoki Forest. Of particular interest was the species composition and abundance of large trees, understorey trees, THV, and fruit. The seasonal change in mineral concentrations in forest clearings, which are known to be nutritionally important for elephants and other large mammals in the region (Klaus *et al.* 1998; Turkalo and Fay 2001) was also measured. This study was conducted simultaneously with research on elephant feeding ecology and distribution over a large swathe of the Ndoki Forest, with the ultimate goal of testing specific hypotheses on the relationship between resource availability, elephant feeding ecology and elephant distribution and abundance.

Specifically, the questions addressed in this study were:

1. What were the major identifiable vegetation types in the Ndoki forest, what was their spatial distribution, their species composition and the abundance of large trees, understorey trees, and THV, particularly as related to elephant foods?
2. What was the spatial and temporal pattern of leaf and fruit production in the Ndoki forest, particularly for important elephant foods?
3. Were there detectable patterns of elephant resource distribution along ecological and geographical gradients?
4. Based on these data, how did different vegetation types in the Ndoki forest rate as elephant habitat?

STUDY SITE AND METHODS

Quantitative data was collected from two sites. The first was an extensive landscape-scale survey which covered a linear distance of 253km, and which traversed the major drainage gradient from uplands in the northwest to the Congo River swamp basin in the southeast. The second site was for a more intensive survey and took place in a localised area to the southwest of the NNNP near the village of Bomassa (Figure 2.1). The extensive survey took 1 month to complete and was repeated every three months over two years. The intensive survey took 5 days to complete and was repeated monthly over one year. At both sites, data on elephant feeding ecology and dung counts were concurrently collected, and are described in later chapters. Rainfall was measured by colleagues daily at two sites; the Mbeli *Bai* gorilla research station in the NNNP, and at Bomassa. Monthly averages were calculated for each site. Mbeli rainfall data were used as a covariate in the analysis of extensive survey data, while Bomassa data were used for the intensive survey analysis.

Extensive survey

In March 1998, the extensive survey track was established (Figure 2.1). The survey team consisted of a single observer, and a varying number of local Bambenzele and Bantu guides and porters. The observer was accompanied by one guide, usually 1-2km ahead of the main group of porters. On the first survey, compass headings were used to maintain the general desired direction of travel along a path of least resistance or 'recce' (Walsh and White 1999; White and Edwards 2000b). The survey track was non-randomly located due to the logistical difficulties of travelling over such a large geographical scale on foot. An attempt was made to pass through a wide variety of vegetation types and ecological and human use gradients located from previous work in the region and from satellite imagery. Continuous data were collected on trail type (human trail, no trail, elephant trail). All biological data collected were geo-referenced with an accuracy of ± 100m (95%CL) with Global Positioning System (GPS) data which were collected every 15 seconds throughout the survey. A running rélévé of vegetation type based on subjective observations of structure and/or species composition was recorded, and for one survey all distances were also measured using topofil.

LARGE TREES

A quantitative inventory of large trees (>50 dbh) was conducted during surveys 2 and 3. Every 20 minutes along the track, a circular vegetation plot of 10m radius was established centred on where the observer was standing. Within the plot all trees over 50cm dbh were identified and recorded. Initially plots were measured using a tape but after the observers became familiar with the radius distance subsequent plots were usually estimated, except when a tree was borderline in which case the plot radius was measured. Tree diameter was usually estimated, but where there was doubt that a tree was >50 dbh it was measured for confirmation. Field identification of trees was made by a Congolese botanist (Mr. G. Kossa-Kossa) and the principal observer. Samples and digital video images of plant characters were made of unknowns for subsequent identification by Dr. D. Harris of the Royal Botanical Garden, Edinburgh, Scotland.

UNDERSTOREY VEGETATION

During the four surveys of year 2, species composition of understorey woody vegetation, THV species composition and abundance, and leaf phenology of both taxa were quantified. Every 20 minutes, a circular plot of 10m radius was established. The closest tree or woody shrub in each of four size classes was identified. Tree size classes were 1-2.5 cm, 2.5-5cm, 5-10cm, and 10-20cm dbh, selected because they included the majority of tree sizes most commonly browsed by elephants (Wing and Buss 1970). For each plant, the relative abundance of new, mature, and old leaves was estimated on a four-point scale (1 = rare, 2 = few, 3 = common, 4 = abundant). Ripe and unripe fruits and flowers were recorded in the same way. Lianas were not included in the sample, despite their importance in the diet of forest elephants (Chapter 3), since their leaves were usually obscured and phenophase was usually impossible to estimate. Terrestrial herbaceous vegetation was identified to species or genus, and the relative abundance of each within the plot was ranked on the same four-point scale. For each species, the abundance of leaves in each phenophase was ranked as for dicotyledons. Terrestrial herbaceous vegetation was defined as all ground-rooted species in the families Arecaceae, Commelinaceae, Costaceae, Marantaceae, Poaceae, and Zingiberaceae.

FRUIT AVAILABILITY

During all surveys, all 'fruitfall events' of succulent fruits and pods over ca. 1cm in diameter observed from the survey track were recorded, identified to species where possible, and relative abundance ranked in the usual way. A fruitfall event was defined as the fruitfall from an individual plant seen from the survey route.

MINERAL AVAILABILITY IN *BAIS*

Mineral composition of ‘salt licks’ is known to strongly influence the distribution of elephants and other large mammals in African ecosystems and elsewhere (Weir 1972). Using laboratory techniques, Klaus *et al.* (1998) found that *bai* soils were rich in a number of minerals including sodium (Na), potassium (K), calcium (Ca), magnesium (Mg), phosphorus (P), and manganese (Mn). Weir (1972) asserted that electrical conductivity was an adequate field method for estimating Na content of water and soil, which was confirmed for Na, K, Ca, and Mg by Ruggiero and Fay (1994). In this study, the electrical conductivity of standing water in drinking holes (both active and inactive) dug by elephants was measured in four *bais* (Bonye1, Bonye 2, Mingingi 1, Mingingi 2) (Figure 2.1). Active holes were defined as those holes with obvious fresh or recent digging (feet, tusks, or trunk) estimated to be less than 1 week old, while inactive holes were those holes where no fresh or recent activity was observed. All holes in either category were assigned a number, and a random sample of five of each type was selected. Fewer than 5 holes were sometimes present in a *bai*, in which case all available holes were sampled. Notes on the substrate surrounding the hole, distance from running water, vegetation, and subjective estimates of elephant activity levels were recorded. A sample of standing water from each hole was taken in a plastic beaker and the probe of a YSI^{R} hand-held conductivity meter inserted, submerged, and shaken to dislodge bubbles in the probe chamber. Values of conductivity, specific conductivity and temperature were recorded after 2 minutes. After each reading, the conductivity meter probe was washed thoroughly in de-ionised water before the next reading was taken.

Intensive survey

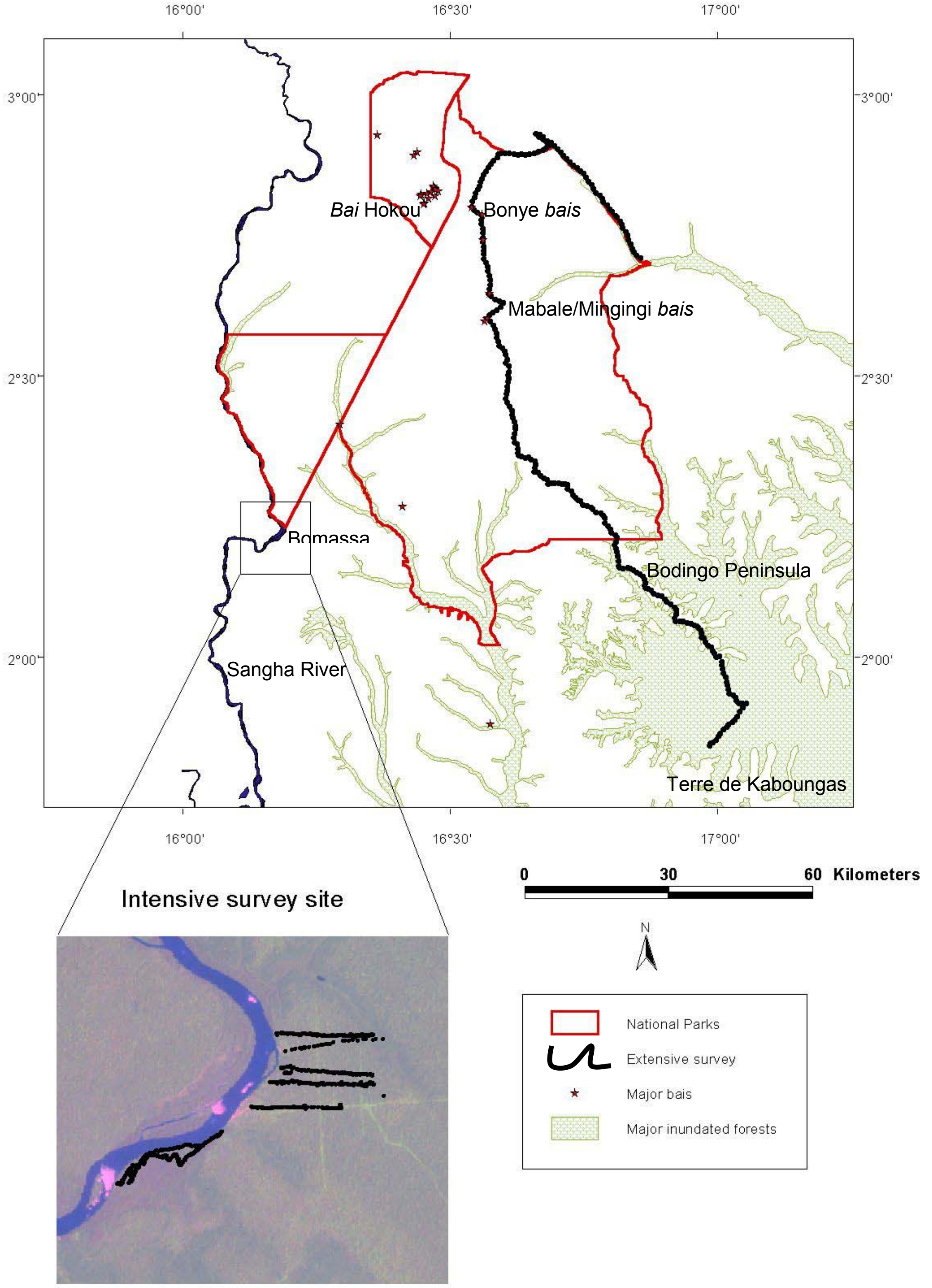
In July 1999, a phenology circuit was established on a series of existing trails in the forest near the village of Bomassa (Figure 2.1). A sample of individuals (in most cases 10) of large tree species whose fruits were important in the diet of forest elephants (Chapter 3) was located and each tree tagged with a unique number. Each month over a full year, the phenophase of leaves and fruit on each tree, and fruitfall under each individual, was quantified following the usual four-point scale. Observations in the canopy were made using 10x40 binoculars. When walking the circuit, fruitfall from all succulent drupes and pods observed from the trail was also quantified following the methods used on extensive surveys. Understorey vegetation plots were established every 250m along the circuit and were enumerated following the extensive survey methodology.

RESULTS

Results are presented by first providing data on species composition by vegetation type for the three plant types on which data were collected (canopy trees, understorey trees, and THV), followed by a description of the geographical distribution of the major vegetation type along the extensive survey track. Temporal and spatial phenology patterns of fruitfall and understorey leaf production are then described for both the extensive and intensive surveys.

A total of 24 general forest vegetation types (Table 2.1) was identified based on structural characteristics and species composition. A 25th vegetation type was forest clearing, divided into 3 sub-types, and which contained few or no trees. Forest vegetation types were divided into three broad classes; *Terra firma*, Inundated, and Transition. *Terra firma* was forest on well-drained soils and was never flooded. Transition vegetation formed the interface between riverine and *terra firma* vegetation, the soils of which were usually well drained or occasionally saturated. Inundated forest was characterised by permanently or seasonally saturated soils and/or standing water.

Figure 2.1. Landscape context of vegetation surveys



Forest structure and composition

TREES OVER 50 DBH

A total of 1361 large tree plots (surface area = 42.8 ha) was inventoried for trees over 50 cm dbh. The mean tree density was 44.6 individuals ha^{-1} (Table 2.1). Several vegetation types, which were poorly represented in the Ndoki Forest did not contain a sufficient number of plots (a subjective cut off sample size was set at 15 plots or 2000m^2) to quantify structure or species composition (labelled non-applicable (na) in Table 2.1). The codes shown in Table 2.1 are used to identify vegetation types throughout this thesis.

Table 2.1: Summary canopy tree data for the main vegetation types identified (excluding *bais*), ranked by elephant fruit tree density

Vegetation type	Acronym *	km	% distance	N large tree plots	Ha	N trees	Trees ha^{-1}	Elephant fruit trees ha^{-1}	Shannon-weiner index
T. superba forest	TF	4.7	1.9	25	0.8	60	76.4	33.1	4.2
Mixed closed forest	MCF	25.3	10.0	96	3.0	151	50.1	18.2	5.1
Marantaceae forest	MF	9.9	3.9	45	1.4	60	42.4	17	4.1
Mixed open forest	MOF	73.4	29.0	448	14.1	701	49.8	15.6	5.5
G. dewevrei with *H. dankelmaniana* forest	GDFH	5.8	2.3	16	0.5	35	69.6	13.9	1.6
P. africana forest	PAF	3.2	1.3	20	0.6	46	73.2	10.9	2.4
Mokala river mixed open forest	MMOF	21.4	8.4	139	4.4	173	39.6	10.5	4.5
G. dewevrei forest	GDF	37.7	14.9	171	5.4	332	61.8	9.7	2.2
G. dewevrei flooded forest	GDFF	7.5	3.0	40	1.3	84	66.8	8	1.8
Vine swamp	VS	8.8	3.5	80	2.5	34	13.5	8	1.8
Vine forest	VF	11.8	4.7	64	2.0	60	29.8	5.5	3.8
Cleistanthus sp. forest	CF	5.8	2.3	38	1.2	44	36.9	3.4	3
Vine L*accosperma* sp. swamp	VLS	6.3	2.5	44	1.4	19	13.7	3.3	1.3
Flooded forest	FF	8.8	3.5	69	2.2	63	29.1	2.3	3.5
Lophira alata forest	LAF	2.0	0.8	14	0.4	10	na	na	na
Low closed scrub	LCS	0.2	0.1	1	0.0	0	na	na	na
Light gap	LG	11.5	4.5	13	0.4	16	na	na	na
Mokala riverine mixed closed forest	MMCF	1.3	0.5	5	0.2	11	na	na	na
G. demeusei flooded forest	PAKA	1.0	0.4	6	0.2	13	na	na	na
Parinari sp. forest	PF	0.1	0.0	1	0.0	1	na	na	na
Rinorea sp. forest	RF	1.4	0.6	6	0.2	4	na	na	na
Stream	STREAM	2.4	0.9	4	0.1	2	na	na	na
Swamp	SWP	0.9	0.3	11	0.3	12	na	na	na
Vine / *Laccosperma* sp. forest	VLF	1.9	0.7	6	0.2	3	na	na	na
Total		253.1		1361	42.8	1946			
Mean							44.6	11.4	

*Acronyms are also given at the beginning of this thesis, and should be referred to throughout this and subsequent chapters.

A total of 1946 trees of 139 species in 38 families was recorded in the 1361 plots. Tree density varied considerably between vegetation types with a maximum of 76.4 trees ha^{-1} in TF to a minimum of 13.5 trees ha^{-1} in VS (Kruskal-Wallis Test: $P < 0.0001$, df = 13). Highest tree densities occurred in mono-dominant forests (GDF, GDFF, GDFH) or those in which a single species made up a large majority of individuals (PAF and TF) (Table 2.1), while the lowest were found in inundated vegetation types (with the exception of the mono-dominant GDFF). Mixed species t*erra firma* forests had the highest tree diversity (estimated by the Shannon-weiner index) followed by transition vegetation and inundated forests. Mono-dominant *terra firma* and vine swamp forests were the least diverse (Table 2.1).

Species composition varied considerably by vegetation (Table 2.2). In mixed species *terra firma* forests no single species dominated, with the top species in MOF (*Anonidium mannii*) and MCF (*Duboscia* spp.) accounting for 6.1% and 9.3% of individuals respectively. The top 10 species accounted for 42.4% and 49.7% of individuals (Table 2.2). In GDF, *G. dewevrei*, alone accounting for 71.7% of all stems, while the second most common species, *Manilkara mabokeensis* comprised just 4.8% of stems. The other forms of *G. dewevrei* forest showed a similar dominance of this species. In TF, *Terminalia superba*, accounted for 20.0% of individuals, with the second most important species, *Myrianthus arboreus*, little more than half as common (11.7% of stems). No single species or group of species was dominant in VF with the most abundant species comprising only 8.3% of all trees, and 55.0% for the top 10. In VS however a single species, *G. demeusei*, dominated the large tree component of vegetation representing 32.1% of all trees. This species was the most abundant large tree in most inundated vegetation types and often formed near mono-dominant stands.

The distribution of large trees varied systematically across drainage gradients on both small and large scales. The abundance of elephant fruit trees increased significantly with distance from rivers (Spearman's rank correlation: rho = 0.359, N = 226, $p < 0.001$), though the abundance of non-elephant fruit trees did not (rho = 0.129, N = 226, ns). Likewise there was a significant increase in elephant fruit tree abundance with increasing distance from the southeast terminus of sampling (the beginning of the Likouala swamps) (rho = -0.176, N = 171, $p < 0.05$), but not for non-elephant trees (rho = 0.072, N = 171, ns). Thus on moving up both localised and landscape-scale drainage gradients, the abundance of elephant fruit tree increased, while for non-elephant trees there was no change.

Table 2.2. Composition and abundance of the 'top' 30 species for selected vegetation types

Rank	Trees over 50 cm dbh	MOF	% total		Trees over 50 cm dbh	MCF	% Total
1	*Anonidium mannii**	43	6.1	1	*Duboscia spp.**	14	9.3
2	*Petersianthus macrocarpus*	40	5.7	2	*Petersianthus macrocarpus*	11	7.3
3	*Celtis* sp.	37	5.3	3	*Anonidium mannii**	10	6.6
4	*Duboscia* spp.*	31	4.4	4	*Manilkara mabokeensis**	7	4.6
5	*Terminalia superba*	31	4.4	5	*Pentaclethra macrophylla*	7	4.6
6	*Entandrophragma cylindricum*	26	3.7	6	*Entandrophragma cylindricum*	7	4.6
7	*Strombosiopsis tetrandra*	25	3.6	7	*Pterocarpus soyauxii*	6	4.0
8	*Pentaclethra macrophylla*	24	3.4	8	*Celtis* sp.	5	3.3
9	*Manilkara mabokeensis**	23	3.3	9	*Oxystigma oxyphyllum*	5	3.3
10	*Strombosia pustulata*	17	2.4	10	*Erythrophleum suaveolens*	3	2.0
	1-10		**42.4**		**1-10**		**49.7**
11	*Panda oleosa**	16	2.3	11	*Blighia welwitchii*	3	2.0
12	*Pterocarpus soyauxii*	14	2.0	12	*Staudtia* sp.	3	2.0
13	*Blighia welwitchii*	14	2.0	13	*Polyalthea suaveolens*	3	2.0
14	*Gilbertiodendron dewevrei*	13	1.9	14	*Diospyros crassiflora**	3	2.0
15	*Celtis adolphi-frederici*	12	1.7	15	*Angylocalyx pinaertii*	3	2.0
16	*Myrianthus arboreus**	12	1.7	16	*Gilbertiodendron dewevrei*	2	1.3
17	*Cleistanthus* sp.	11	1.6	17	*Irvingia excelsa**	2	1.3
18	*Staudtia* sp.	11	1.6	18	*Klainedoxa gabonensis**	2	1.3
19	*Nesogordonia papaverifera*	10	1.4	19	*Terminalia superba*	2	1.3
20	*Polyalthea suaveolens*	9	1.3	20	*Xylopia aethiopica*	2	1.3
	11-20		**17.4**		**11-20**		**16.6**
21	*Angylocalyx pinaertii*	9	1.3	21	*Strombosia pustulata*	2	1.3
22	*Oxystigma oxyphyllum*	9	1.3	22	*Gambeya lacourtiana**	2	1.3
23	*Lophira alata*	8	1.1	23	*Alstonia boonei*	2	1.3
24	*Eribroma oblongum*	8	1.1	24	*Pausinistalia macroceras*	2	1.3
25	*Gambeya lacourtiana**	8	1.1	25	*Ongokea gore*	2	1.3
26	*Autranella congoensis**	8	1.1	26	*Piptediniastrum africana*	2	1.3
27	*Anopyxis klaineana*	7	1.0	27	*Amphimas* sp.	2	1.3
28	*Erythrophleum suaveolens*	7	1.0	28	*Plagiostyles africana*	2	1.3
29	*Entandrophragma utile*	7	1.0	29	*Gambeya beguei**	2	1.3
30	*Mansonia* sp.	7	1.0	30	*Antaris africana*	2	1.3
	21-30		**11.1**		**21-30**		**13.2**
	Top 30 as % of total trees		**70.9**		**Top 30 as % of total trees**		**79.5**

Table 2.2 contd.

	Trees over 50 cm dbh	GDF	% total		Trees over 50 cm dbh	TF	% Total
1	*Gilbertiodendron dewevrei*	238	71.7	1	*Terminalia superba*	12	20.0
2	*Manilkara mabokeensis**	16	4.8	2	*Myrianthus arboreus**	7	11.7
3	*Anonidium mannii**	7	2.1	3	*Duboscia* spp.*	6	10.0
4	*Duboscia* spp.*	6	1.8	4	*Anonidium mannii**	3	5.0
5	*Pachyelasma tessmannii*	4	1.2	5	*Petersianthus macrocarpus*	2	3.3
6	*Pterocarpus soyauxii*	3	0.9	6	*Celtis* sp.	2	3.3
7	*Celtis adolphi-frederici*	3	0.9	7	*Klainedoxa gabonensis**	2	3.3
8	*Dialium* sp.	3	0.9	8	*Celtis adolphi-frederici*	2	3.3
9	*Irvingia grandifolia**	3	0.9	9	*Diospyros crassiflora**	2	3.3
10	*Irvingia excelsa**	3	0.9	10	*Gambeya beguei**	2	3.3
	1-10		86.1		1-10		66.7
11	*Petersianthus macrocarpus*	2	0.6	11	*Ceiba pentandra*	2	3.3
12	*Strombosiopsis tetrandra*	2	0.6	12	*Pentaclethra macrophylla*	1	1.7
13	*Pentaclethra macrophylla*	2	0.6	13	*Sterculia gigantea*	1	1.7
14	*Panda oleosa**	2	0.6	14	*Pteliopsis hylodendron*	1	1.7
15	*Blighia welwitchii*	2	0.6	15	*Angylocalyx pinaertii*	1	1.7
16	*Cleistanthus* sp.	2	0.6	16	*Tridesmostemon omphalocarpoides**	1	1.7
17	*Staudtia* sp.	2	0.6	17	*Eribroma oblongum*	1	1.7
18	*Tessmannia africana*	2	0.6	18	*Santeria trimera*	1	1.7
19	*Klainedoxa gabonensis**	2	0.6	19	*Ganophyllum giganteum*	1	1.7
20	*Mammea africana**	2	0.6	20	*Milicia excelsa*	1	1.7
	11-20		6.0		11-20		18.3
21	*Balanites wilsoniana**	2	0.6	21	*Markhamia sp.*	1	1.7
22	*Millettia laurentii*	2	0.6	22	*Triplochiton scleroxylon*	1	1.7
23	*Copaifera mildbraedii*	2	0.6	23	*Burseraceae sp.*	1	1.7
24	*Celtis* sp.	1	0.3	24	*Lannea welwitchii*	1	1.7
25	*Terminalia superba*	1	0.3	25	*Albizia adianthifolia*	1	1.7
26	*Entandrophragma cylindricum*	1	0.3	26	*Donella pentagonocarpa*	1	1.7
27	*Nesogordonia papaverifera*	1	0.3	27	*Ficus* sp.	1	1.7
28	*Polyalthea suaveolens*	1	0.3	28	*Pancovia* sp.*	1	1.7
29	*Lophira alata*	1	0.3	29	*Trichilia* sp.	1	1.7
30	*Eribroma oblongum*	1	0.3	30			
	21-20		3.9		21-20		15.0
	Top 30 as % of total trees		96.1		Top 30 as % of total trees		100.0

Table 2.2 contd.

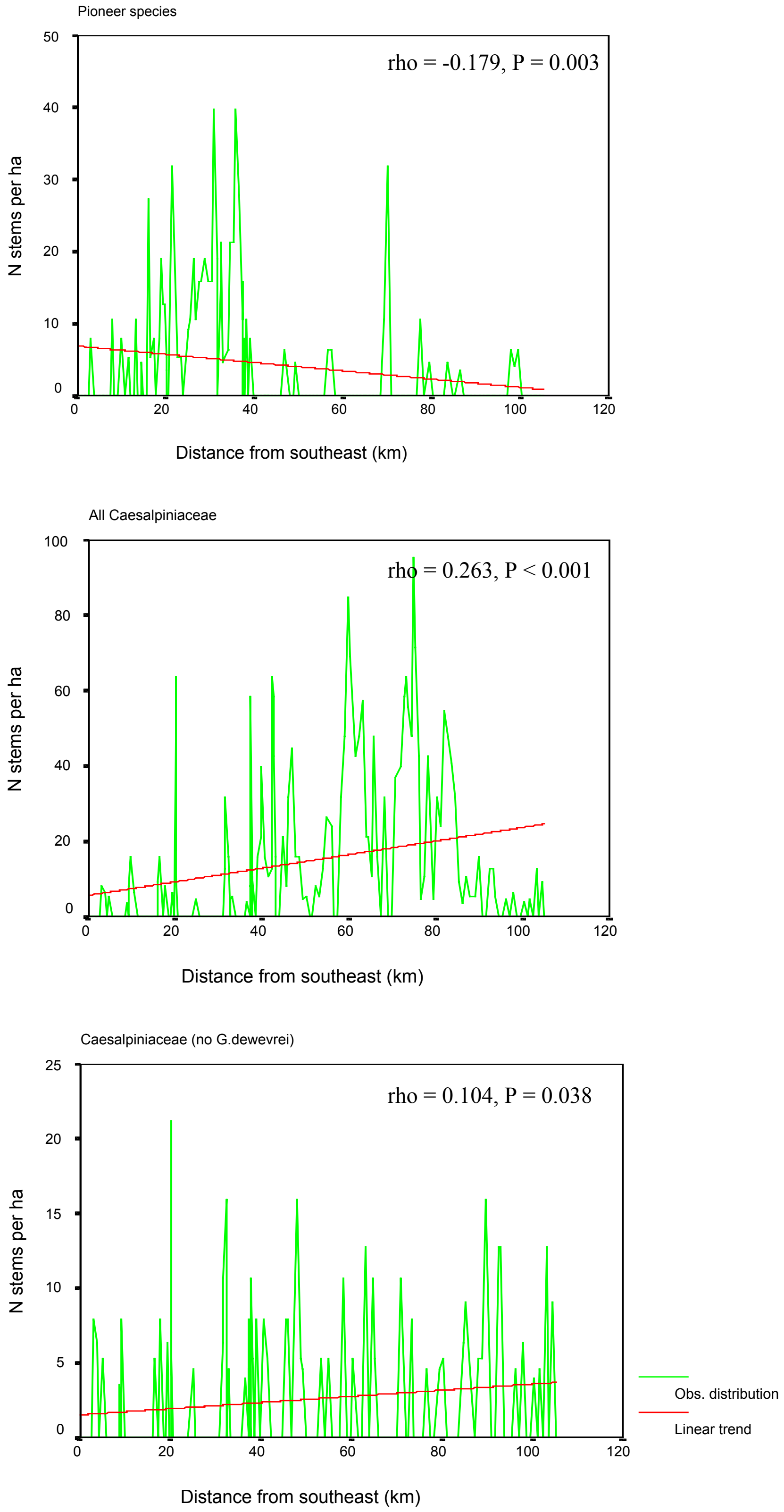
	Trees over 50 cm dbh	VF	% Total		Trees over 50 cm dbh	VS	% Total
1	*Petersianthus macrocarpus*	5	8.3	1	*Guibourtia demeusei*	17	32.1
2	*Lophira alata*	5	8.3	2	*Gilbertiodendron dewevrei*	7	13.2
3	*Mitragyna stipulosa*	5	8.3	3	*Cleistanthus* sp.	4	7.5
4	*Cleistanthus* sp.	4	6.7	4	*Daniella klaineana*	4	7.5
5	*Erythrophleum suaveolens*	3	5.0	5	*Klainedoxa sp.**	3	5.7
6	*Piptediniastrum africana*	3	5.0	6	*Lophira alata*	2	3.8
7	*Manilkara mabokeensis**	2	3.3	7	*Erythrophleum suaveolens*	2	3.8
8	*Pterocarpus soyauxii*	2	3.3	8	*Macaranga* sp.	2	3.8
9	*Staudtia* sp.	2	3.3	9	*Grewia* sp.	2	3.8
10	*Gilbertiodendron dewevrei*	2	3.3	10	*Mitragyna stipulosa*	2	3.8
	1-10		55.0				84.9
11	*Myrianthus arboreus**	2	3.3	11	*Pycnanthus marchalianus**	2	3.8
12	*Macaranga sp.*	2	3.3	12	*Pterocarpus soyauxii*	1	1.9
13	*Irvingia grandifolia**	2	3.3	13	*Parinari excelsa*	1	1.9
14	*Strombosiopsis tetrandra*	2	3.3	14	*Symphonia globulifera*	1	1.9
15	*Pentaclethra macrophylla*	1	1.7	15	*Xylopia staudtii*	1	1.9
16	*Entandrophragma cylindricum*	1	1.7	16	*Lasiodiscus* sp.	1	1.9
17	*Celtis* sp.	1	1.7	17	*Pseudospondias* sp.	1	1.9
18	*Oxystigma oxyphyllum*	1	1.7				
19	Klainedoxa gabonensis*	1	1.7				
20	*Terminalia superba*	1	1.7				
	11-20		23.3				15.1
21	*Gambeya lacourtiana**	1	1.7				
22	*Ongokea gore*	1	1.7				
23	*Panda oleosa**	1	1.7				
24	*Detarium macrocarpum**	1	1.7				
25	*Sterculia gigantea*	1	1.7				
26	*Pycnanthus marchalianus*	1	1.7				
27	*Celtis adolphi-frederici*	1	1.7				
28	*Dialium* sp.	1	1.7				
29	*Tetrapleura tetraptera**	1	1.7				
30	*Pteliopsis hylodendron*	1	1.7				
	21-30		16.7				
	Top 30 as % of total trees		95.0				

* = 'important elephant fruit species' (see text for definition)

Distribution of Caesalpiniaceae and pioneer species

On traversing the northwest-southeast gradient, there appeared to be a qualitative increase in the abundance of pioneer species and a decrease in species of Caesalpiniaceae in *terra firma* forest. The most obvious of the Caesalpiniaceae was *G. deweveri*, which was found predominantly in the north and centre portions of the survey (Figure 2.2) though other species appeared to decline on traversing from northwest to southeast. Pioneers were defined as those species found in the Ndoki which were listed as such by (Powell 1997), based on the classifications of a number of previous authors (references in Powell, 1997). In the extreme southeast of the NNNP and onto the Bodingo Peninsula these species appeared to become conspicuous in the canopy, particularly *Terminalia superba, Ceiba pentandra, Triplochiton scleroxylon*, and *Milicia excelsa*. *Terminalia superba* forest contained the highest proportion of pioneer species of any vegetation type and was found only in the southeast of the study area. Gross distribution of the number of stems ha^{-1} for each taxon in *terra firma* forest only, with distance from the southeast terminus of sampling, is shown in Figure 2.2. The trends in the distribution of three taxa, pioneer species, Caesalpiniaceae, and Caesalpiniaceae excluding *G. dewevrei*, were tested using Spearman's correlation coefficient. All three taxa showed significant relationships in the predicted direction (i.e. Caesalpiniaceae increasing with distance from the southeast, and pioneer species decreasing) (Figure 2.2)

Figure 2.2. Distribution of pioneer species and Caesalpiniaceae with distance from the southeast terminus of sampling in *terra firma*



UNDERSTOREY VEGETATION

Dicotyledons

A total of 1664 understorey plots was enumerated during year 2 of this study, in which 6479 trees and shrubs from at least 239 species were identified (most abundant species shown in Table 2.3). The top 10, 20, and 30 species made up 51.5%, 67.9%, and 76.5% of all stems respectively. The most common species across all vegetation types and all size classes was *Thomandersia laurifolia*, which accounted for 10.9% of stems, followed by *Rinorea welwitchii* (8.6%) and *Diospyros bipindensis* (6.3%). *Thomandersia laurifolia* occurred in the top ten species for all vegetation types including inundated vegetation, and in CF accounted for fully 20% of all stems. In the most widespread *terra firma* mixed vegetation types (MOF and MCF), nine of the top ten species were common to both, the exceptions being *Drypetes chevalieri* found only in the top ten for MCF and *Tabernaemontata penduliflora* in MOF. *Gilbertiodendron dewevrei* comprised 30.7% of all stems in GDF, but was not in the top ten species in any of the mixed species forests. In GDFH the abundance of *G. dewevrei* was low compared to GDF accounting for only 13.2% of stems, while *T. laurifolia* increased from 6.4% of stems in GDF to 16.1% in GDFH. In addition to the often mono-dominant *G. dewevrei*, two additional species were particularly abundant in one or more vegetation types. In FF, the unknown species *Moindja* (local name) comprised 32.2% of all stems, and was never recorded in *terra firma* forests. In VLF *Dichostemma glaucescens* was the dominant species accounting for 30.0% of all individuals. This species was widespread and common in most vegetation types existing in high proportions in both inundated and *terra firma* habitats.

Table 2.3. Top 30 species overall recorded in understorey plots as a percentage of all stems for major vegetation types

Bold = preferred elephant browse species (more than 0.5% of leaf browsing records), Underlined - never browsed

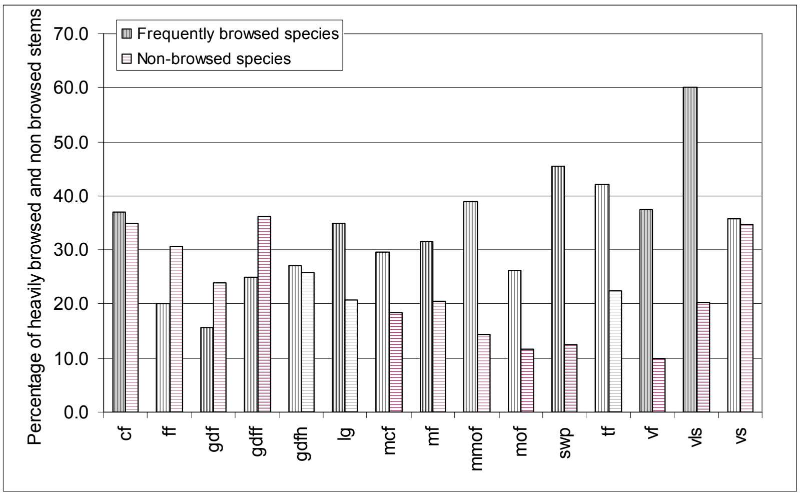
Species	CF	GDF	GDFH	LG	MCF	MF	MOF	MMOF	PAF	TF	VF	SWP	GDFF	FF	VLF	VS	N veg types
Thomandersia laurifolia	20.0	6.4	16.1	8.8	9.2	13.4	9.0	19.2	21.9	5.4	16.5	19.9	8.8	8.7	25.0	8.3	15
Rinorea brachypetala	17.0	7.7	5.7	4.6	13.2	2.8	11.5	11.4	14.6	1.1	10.6	2.6	3.1		5.0	1.2	14
Diospyros bipindensis	16.6	9.8	5.2	3.9	7.0	2.8	5.5	6.8	0.0	2.2	5.9	5.8	13.5	1.7	5.0	3.2	15
Dichostemma glaucescens	8.1	0.7	1.1	8.5	0.6	1.4	0.7	9.1	0.0	2.2	12.6	16.0	2.1	2.6	30.0	18.6	15
Gilbertiodendron dewevrei	0.4	30.7	13.2	0.3	0.8		0.8	0.2	0.0	0.5	0.3		23.3			0.2	11
Polyalthea suaveolens	0.9	2.8	4.0	2.6	7.3	8.8	7.2	1.8	5.2	8.6	3.1	0.6	1.0				12
Lasiodiscus sp.	0.9	0.3		3.6					0.0			12.2	6.7			20.6	6
Millettia sanagana		0.1		4.6	4.2	3.7	4.0	1.8	1.0	22.2	1.1		0.5				9
Moinja unk spp.	0.4			2.9					0.0			2.6	1.0	32.2		15.8	6
Diospyros sp. totolo	0.9	1.7	2.3	3.3	4.3	2.3	4.5	1.1	2.1	5.4	2.2						10
Pleiocarpa pycnantha		1.4	0.6	2.6	4.3	4.6	5.0		0.0	1.6	1.4						8
Tabernaemontana penduliflora	0.9	1.2	1.1	3.3	2.2	5.1	4.4	0.9	5.2	1.1	1.4				5.0		11
Cleistanthus mildbraedii	3.8	1.0	2.9	1.3	1.4		0.8	1.1	9.4		0.3	3.2	7.8			3.2	11
Drypetes chevalieri		3.3	2.3	2.0	2.6	0.5	2.3	1.6	0.0		0.8		3.1				9
Pancovia cf. pedicellaris		0.8	1.1	2.3	2.3	1.9	3.1		1.0	4.3	0.3					0.8	9
Strombosia pustulata	0.9	0.7	2.3	0.7	3.7	2.3	2.8	0.5	2.1	2.7	0.8						10
Rinorea sp. episa	0.4	0.7	1.7	0.3	1.7	0.5	2.2	2.5	0.0	0.5	3.9	3.2				0.4	12
Isolona hexaloba	0.9	3.2	2.9	1.0	0.8	0.5	0.7	3.0	1.0	0.5	1.4		2.6	1.7			12
Garcinia cf. ovalifolia	2.1	1.4	1.1	0.7	1.9		0.5	2.7	0.0	0.0	1.1	3.2	2.1		5.0	1.0	13
Garcinia punctata		0.4		1.3	1.7	3.2	1.9	0.5	0.0	1.6	1.1		1.6				9
Manilkara mabokeensis	0.9	2.9	1.7	0.3	1.9		1.0	1.6	6.3		0.3	0.6	0.5			0.4	11
Dialium sp.	0.9	0.8	2.9		1.2	0.5	0.8	0.7	0.0	0.5	2.2	1.3	3.1	1.7	5.0	0.4	14
Macaranga sp.				6.5		0.5	0.1		0.0		0.3		0.5	7.8		2.6	7
Drypetes sp. Gbaya	1.3	0.6	0.6	0.7	2.3	0.9	0.9	1.8	0.0	0.5	0.8	0.6		0.9			12
Rinorea illicifolia	1.3			0.3	1.4	0.5	1.0	0.9	0.0	2.2	1.1	1.9		0.9		1.6	11
Trichilia monadelpha		0.1		0.3	0.3	3.2	1.6		0.0	6.5	0.3		0.5				8
Ritchea aprevaliana		1.4	1.7	0.7	1.1	0.5	1.0	1.1	1.0	1.6	0.6						9
Crotonogyne pogei	0.4	2.1	1.7		0.2		0.4	0.5	2.1	1.1	0.8	1.9	2.1	2.6		0.6	12
Carapa procera		0.8	1.7	1.0	1.6	1.4	1.1	0.2	0.0	1.1	0.6						9
Caloncoba mannii	1.7			0.3	0.3	1.9	0.9	1.1	0.0	0.5	2.2						8

Important elephant browse species

Of the top 30 species for all vegetation types, 7 were frequently (>0.5% of all feeding records, Chapter 3) browsed by elephants, while 3 were never recorded as browsed. The most commonly browsed species, *T. laurifolia*, was also the most abundant dicotyledon species recorded in the forest, while the second and third most common species (*R.*

brachypetala and D. bipendensis) were never eaten. Vine/*Laccosperma sp.* forest contained the highest relative abundance of heavily browsed species at 60.0% of all stems (Table 2.3), followed by SWP with 45.5% and TF at 42.2% of the top 30 species (Figure 2.3). The lowest relative frequency of browse species was found in GDF where they accounted for 15.6% of all stems, followed by FF (20.0%) and GDFF (24.9%). Overall, among the top 30 species, 33.4% of all stems were frequently eaten species, with a total of 59.8% of stems of known food species. Over the entire dataset, 54.6% of all stems (excluding unknowns) were of elephant food species, thus among all stems encountered by a foraging elephant a little over half would, on average, be potentially a browse stem.

Figure 2.3: Proportion of heavily browsed and non-browsed understorey trees in the top 30 trees by vegetation type



Across vegetation types highly significant differences were detected in the number of stems of browsed species per plot between vegetation types (Kruskal-Wallis Test: P < 0.001, df = 15). *Terminalia superba* forest contained the highest number of browse stems per plot with a mean of 2.52, followed by PAF with a mean of 2.48 browse stems per plot. The three *G. dewevrei* forest types contained the lowest number of browse stems. When gross habitat types were compared (light gaps, *terra firma*, transition, inundated and *G. deweveri*) the browse stem frequency per plot was significant different (Kruskal-Wallis Test: P < 0.001, df = 4). Plots in *G. dewevrei* had a browse stem frequency less than half that in all other habitat types, and the highest overall frequency was in inundated vegetation types (Figure 2.4). Thus, at a given location in TF, an elephant should expect 5 of the nearest 8 stems to be edible, and by contrast in GDF, less than 2 of the nearest 8 stems should be suitable browse. Almost identical patterns were observed for the mean number of species per plot by vegetation type (Figure 2.5).

The differences in elephant browse species frequency by vegetation type were negatively correlated with canopy tree density (Spearman's rank correlation coefficient: rho = -0.506, N = 15, P <0.05) across all vegetation types (figure 2.6), though there was no significant relationship between the density of elephant fruit trees and browse frequency. In two cases, a generally rare species eaten by elephants dominated the understorey. In TF, *Millettia sanagana* made up 22.2% of stems and was commonly browsed, though this species never exceeded 4.6% of stems in any other vegetation type. *Lasiodiscus* sp., also frequently browsed, was only found in inundated vegetation, whereas in VS, it comprised 20.6% of all stems.

Figure 2.4. Mean frequency of dicotyledon browse species per plot by vegetation type

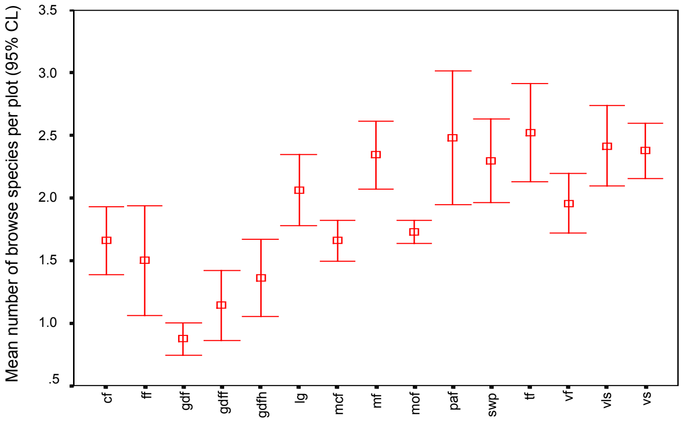


Figure 2.5. Mean frequency of dicotyledon browse stems per plot by vegetation type

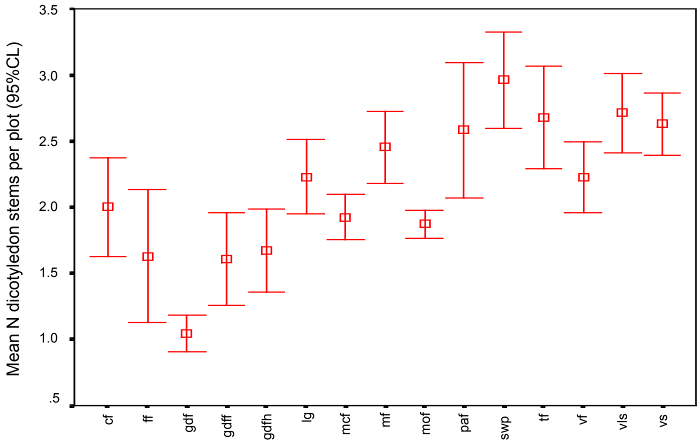
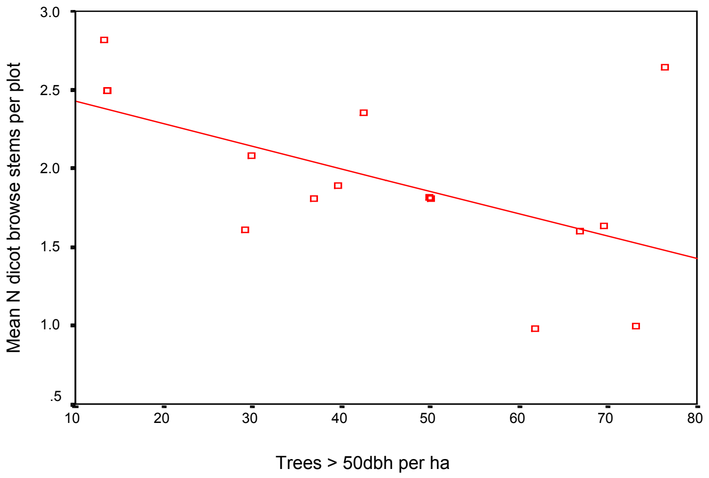


Figure 2.6. Relationship between canopy tree density and frequency of elephant browse stems in the understorey



Terrestrial herbaceous vegetation

At least 26 species from the 6 families included in the study were recorded in understorey plots (Table 2.4). The highest number of species recorded by vegetation type was 20 recorded in LG and the lowest was 6 species in FF (Figure 2.7). The maximum number of THV species recorded in a single plot was 8, recorded only once. Seven species were recorded in plots 3 times, and 6 species 8 times. The modal class was 2 species per plot across all habitat types and the mean was 2.27 species per plot (SD = 1.13). In 290 plots (17.0% of total) no THV were recorded (Figure 2.8).

The number of THV species per plot varied significantly by vegetation types (Kruskal Wallis Test: $P < 0.0001$, df = 15). The highest mean number of species per plot was in GDFH at 3.3, followed by TF and MF (2.9 and 2.6 respectively) (Figure 2.9). The number of species per plot and the mean abundance per species were positively correlated, indicating that where conditions were favourable for a high number of species the abundance of each species was also high (Spearman's rank correlation coefficient: rho = 0.126, $P < 0.01$, n = 1337). An index of overall abundance of THV was calculated as the sum of ranks for each species per plot for each vegetation type (Figure 2.10). Abundance was highly significantly different across vegetation types (Kruskal Wallis Test; $P < 0.0001$, df = 15), and was highest in GDFH followed by MF, TF and LG. In LG, which was ranked only eighth in terms of mean number of species per plot (Figure 2.9), THV species diversity overall was ranked highest (Figure 2.7) and THV abundance was ranked fourth overall (Figure 2.10). In light gaps then, a relatively small number of species dominate the vegetation, but these species were abundant. The abundance of THV in *terra firma* forests varied across drainage gradients both locally (distance from nearest river) and across the landscape (distance from Likouala swamps), however the local scale was the inverse of the regional scale. Abundance increased significantly, though weakly, with increasing distance from the nearest river (Spearman's rank correlation coefficient: rho = 0.222, N = 226, P < 0.01), but with increasing distance from the Likouala swamp basin abundance decreased (Spearman's rank correlation: rho = 0.411, n = 226, P < 0.001).

Table 2.4. Monocotyledon species recorded from all understorey plots

Family	Species	N plots recorded	% of total plots
Marantaceae	*Haumania dankelmaniana*	993	59.8
Commelinaceae	*Palisota brachythyrsa*	385	23.2
Marantaceae	*Sarcophrynium sp.*	326	19.6
Commelinaceae	*Palisota ambigua*	313	18.8
Poaceae	*Leptaspis coshleata*	287	17.3
Commelinaceae	*Palisota sp.*	169	10.2
Zingiberaceae	*Aframomum sp.*	125	7.5
Marantaceae	*Ataenidia conferta*	120	7.2
Arecaceae	*Laccosperma sp.*	109	6.6
Marantaceae	*Marantochloa filipes*	101	6.1
Marantaceae	*Megaphrynium macrostachyum*	36	2.2
Marantaceae	*Trachyphrynium braunianum*	34	2
Commelinaceae	*Rhyncospora corymbosa*	27	1.6
Zingiberaceae	*Renealmia sp.*	22	1.3
Arecaceae	*Raffia sp.*	16	1
Commelinaceae	*Commelinaceae sp.*	14	0.8
Cyperaceae	*Cyperaceae sp.*	13	0.8
Marantaceae	*Halopegia azurea*	13	0.8
Arecaceae	*Eremospatha sp.*	12	0.7
Marantaceae	*Marantochloa sp.*	11	0.7
Commelinaceae	*Commelina sp.*	8	0.5
Marantaceae	*Hypselodelphys sp.*	8	0.5
Arecaceae	*Arecaceae sp.*	5	0.3
Custaceae	*Costus sp.*	4	0.2
Marantaceae	*Haumania liebrechtsiana*	1	0.1
Marantaceae	*Marantochloa cordifolia*	1	0.1

Figure 2.7. Total number of monocotyledon species recorded by vegetation type

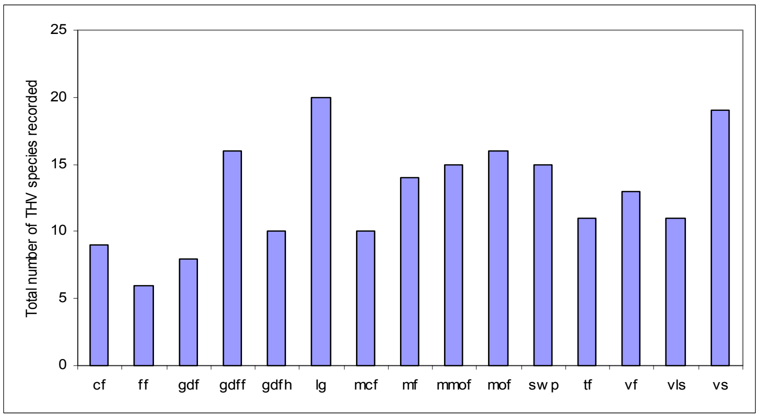


Figure 2.8. Frequency of number of monocotyledon species recorded per plot

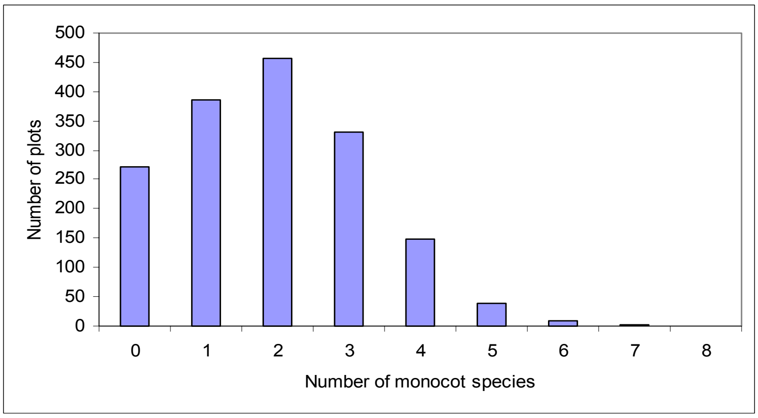


Figure 2.9. Mean number of THV species per plot by vegetation type.

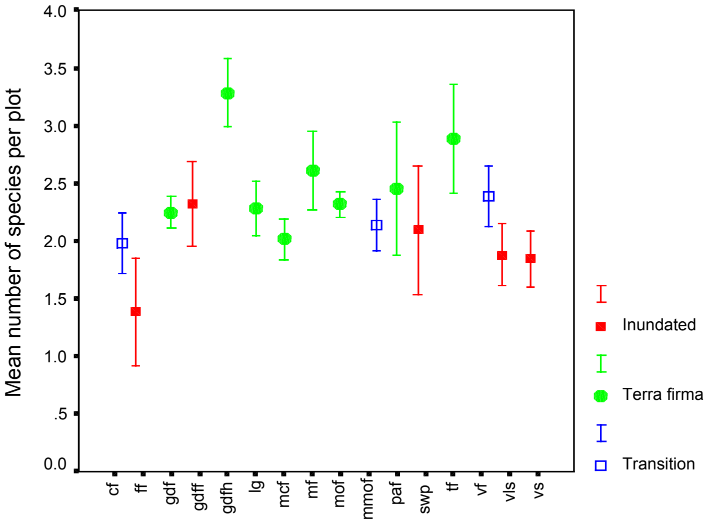
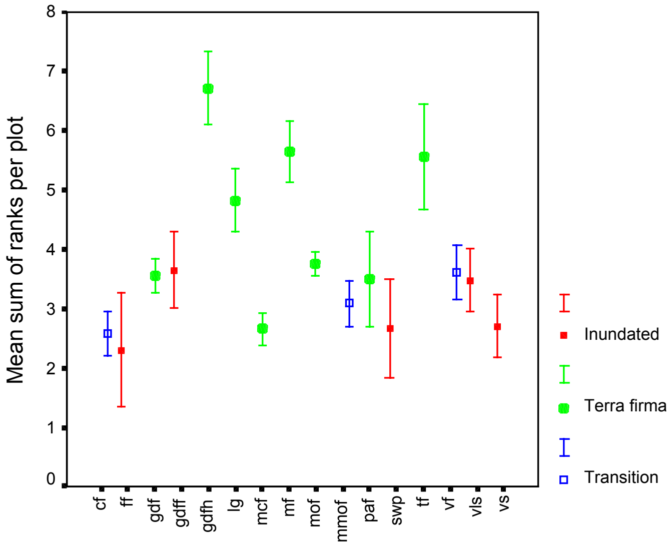


Figure 2.10. Relative abundance score of THV by vegetation type



The most abundant species overall was *Haumania dankelmaniana*, found in 993 or 59.8% of all plots, followed by *Palisota ambigua and Palisota* sp., *Palisota brachythrysa* and *Sarcophrynium* spp. The grass species, *Leptaspis cochleata*, was rarely abundant but was widespread in *terra firma,* occurring in 17.3% of all plots. Abundance and dominance of THV species varied considerably by vegetation type (Table 2.5). *Haumania dankelmaniana* made up over 20% of records in all but three vegetation types, all three of which were in swamp habitats. In only one vegetation type, FF, was *H. dankelmaniana* not recorded, nor was it seen casually (Table 2.5). Seven taxa (*A. conferta, H. dankelmaniana, M. filipes, P. ambigua, P. brachythyrsa, Palisota* sp., *L. cochleata.*, and *Sarcophrynium* spp.) were dominant in *terra firma* vegetation types, while four taxa were dominant in inundated vegetation types (*Aframomum* spp.*, Laccosperma* sp. *Raffia* spp. and *Sarcophrynium* spp.). Only a single taxon, *Sarcophrynium* spp., was present in all habitats and reached a maximum abundance in GDFH where it was found in 97.7% of plots

Table 2.5. Percentage of plots in which each species was recorded by vegetation type

species	CF	GDF	GDFH	MOF	MCF	MF	MMOF	PAF	TF	LG	SWP	VF	VLS	VS	FF	GDFF
Aframomum sp.*	0.0	1.6	6.8	2.9	0.7	13.0	2.5	4.2	12.8	23.4	4.4	2.2	30.0	18.8	0.0	4.1
Arecaceae sp.	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	2.1	0.0	2.2	1.1	0.0	0.0	0.0	0.0
*Ataenidia conferta**	0.0	0.0	18.2	10.4	10.4	11.1	1.7	4.2	57.4	14.3	0.0	4.4	0.0	0.0	0.0	2.0
Commelina sp.*	0.0	0.0	0.0	0.2	0.0	0.0	0.8	0.0	0.0	5.2	0.0	0.0	0.0	0.0	3.3	0.0
Commelinaceae sp.	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	3.9	0.0	1.1	0.0	4.7	3.3	0.0
Costus sp.	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.8	0.0	2.0
Cyperaceae sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	3.9	0.0	0.0	1.7	3.1	0.0	0.0
Eichornea sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0
Eremospatha sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.9	0.0	0.0	5.0	1.6	0.0	0.0
Halopegia azurea	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	1.3	4.4	0.0	5.0	2.3	0.0	2.0
Haumania dankelmaniana	49.2	73.2	97.7	81.4	58.5	96.3	69.5	83.3	93.6	55.8	24.4	69.2	1.7	1.6	0.0	32.7
Huamania liebrechtsiana	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hypselodelphys sp.	0.0	0.0	0.0	0.5	0.0	1.9	0.0	0.0	4.3	0.0	2.2	0.0	0.0	1.6	0.0	0.0
Laccosperma sp.	0.0	0.0	0.0	0.7	0.0	0.0	2.5	0.0	0.0	11.7	4.4	2.2	83.3	9.4	0.0	14.3
Marantochloa cordifolia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
*Marantochloa filipes**	9.5	11.5	6.8	5.6	4.9	5.6	6.8	8.3	4.3	2.6	6.7	7.7	1.7	0.8	0.0	16.3
Marantocloa sp.	3.2	0.0	0.0	0.0	0.6	0.0	0.8	0.0	0.0	0.0	4.4	0.0	0.0	0.8	0.0	6.1
*Megaphrynium macrostachyum**	0.0	0.0	0.0	4.3	0.0	9.3	0.0	0.0	19.1	3.9	0.0	0.0	0.0	0.0	0.0	2.0
*Palisota ambigua**	7.9	35.0	56.8	23.4	13.4	31.5	14.4	20.8	14.9	18.2	4.4	25.3	3.3	0.0	0.0	24.5
*Palisota brachythyrsa**	19.0	47.5	68.2	23.7	17.1	33.3	30.5	33.3	0.0	13.0	11.1	31.9	0.0	0.0	0.0	16.3
Palisota sp.	9.5	19.7	22.7	11.1	7.9	18.5	11.0	12.5	6.4	6.5	2.2	6.6	0.0	0.8	3.3	14.3
Leptaspis cochleata	17.5	15.3	18.2	23.4	23.8	24.1	28.8	37.5	12.8	20.8	4.4	18.7	0.0	1.6	0.0	8.2
Raffia sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	3.9	33.3	0.0
Renealmia sp.	4.8	0.0	2.3	1.2	0.0	5.6	2.5	0.0	0.0	1.3	2.2	3.3	0.0	0.8	0.0	2.0
Rhyncospora corymbosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.0	2.2	0.0	0.0	7.0	0.0	0.0
Sarcophrynium spp.*	20.6	7.1	22.7	22.9	14.0	7.4	12.7	20.8	42.6	16.9	15.6	15.4	38.3	25.8	6.7	51.0
Trachyphrynium braunianum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.2	0.0	0.0	10.0	7.8	10.0	6.1

* = species accounting for more than 0.5% of all elephant feeding records (Chapter 3).

Important elephant THV species

Of the THV species listed in Table 2.5, seven were considered 'important' forest elephants foods (account for over 0.5% of all feeding records, Chapter 3) and which are marked with asterisks in Table 2.5 The number of species per plot across vegetation types were significantly different (Kruskal-Wallis Test: $P < 0.0001$, df = 15), and also between habitat classifications (*Terra firma*, Transition, and Inundated habitat types, Kruskal-Wallis Test: $P < 0.001$, df = 2). The mean number of species per plot was highest in GDFH at 2.0 species, followed by TF and MF, all of which were *terra firma* vegetation types. Within *terra firma*, MCF contained the lowest mean number of species per plot. With the exception of GDFF, inundated forest types contained the lowest mean numbers of species. The relative abundance of important THV foods was also significantly different between vegetation types (Kruskal-Wallis Test: P = 0.0001, df = 15), with GDFH and TF having mean rank scores per plot of 3.4 and 3.1 respectively (Figure 2.12). Whereas LG vegetation was ranked only seventh in terms of the mean number of species per plot (Figure 2.13), THV relative abundance was ranked third.

Figure 2.12. Mean number of 'important' elephant THV food species per plot by vegetation type

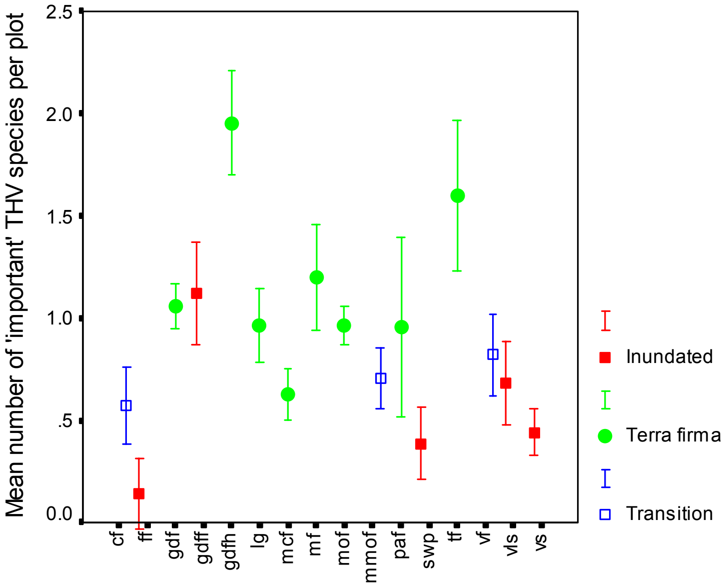
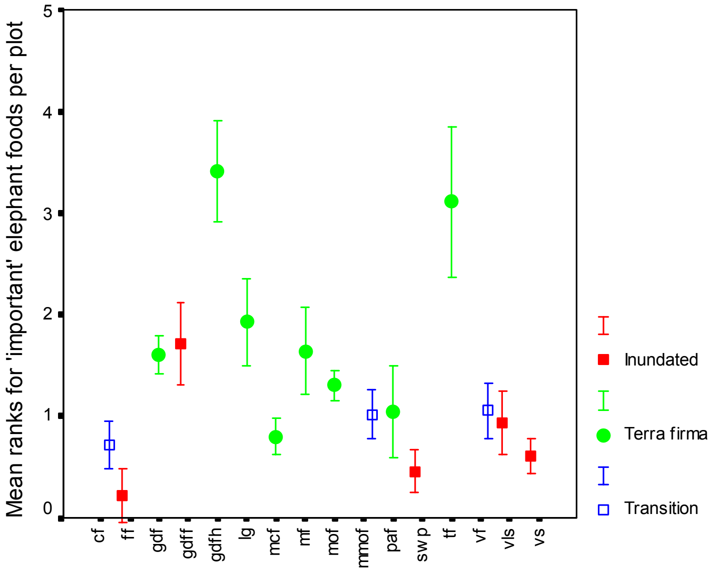


Figure 2.13. Mean ranks of 'important' elephant THV food species per plot by vegetation type



Distribution of major vegetation types

TERRA FIRMA

Mixed Open Forest (MOF) dominated *terra firma* vegetation, covering 94.7km (37.4%) of the survey route (Figure 2.14). Mokala mixed open forest (MMOF) was simply mixed open riverine forest adjacent to the Mokala River (Figure 2.14). *Gilbertiodendron deweveri* forest (GDF) was the second most abundant vegetation type accounting for 37.6 km (14.9%) of the route. *Gilbertiodendron dewevrei* forest occurred in discrete patches and was considerably more abundant to the north and northwest of the Ndoki Forest. This forest type was frequently dominant along watercourses, though was also present on uplands. *G. dewevrei* with *Haumania dankelmaniana* (GDFH) occurred in discrete blocks in upland areas, and comprised 5.77km (2.3%) of the survey route. Mixed closed forest (MCF) accounted for 26.6km (10.5%) of the survey. This forest type was most common on uplands, and was largely absent from riverine areas. Marantaceae forest (MF) was uncommon, and accounted for 9.86 km or 3.9% of the total survey length. The abundance of this forest type increased from northwest to southeast, and it was most common outside the NNNP on the Bodingo Peninsula. There was a highly significant correlation between the abundance of MF and distance from water (Spearman's rank correlation: rho = 0.279. N = 226, $P < 0.001$). *Terminalia superba forest* (TF) made up 4.7 km or 1.9% of the survey route. This vegetation type was found exclusively to the southeast of the region primarily in the Likouala Aux Herbes watershed. It was usually associated with mature closed canopy forest. *Plageostyles africana* forest (PAF) was found in a single discrete patch of forest on the Bodingo Peninsula. Usually a rare tree in the northern Congo, this is the only area where this forest type has been encountered anywhere in the Ndoki region.

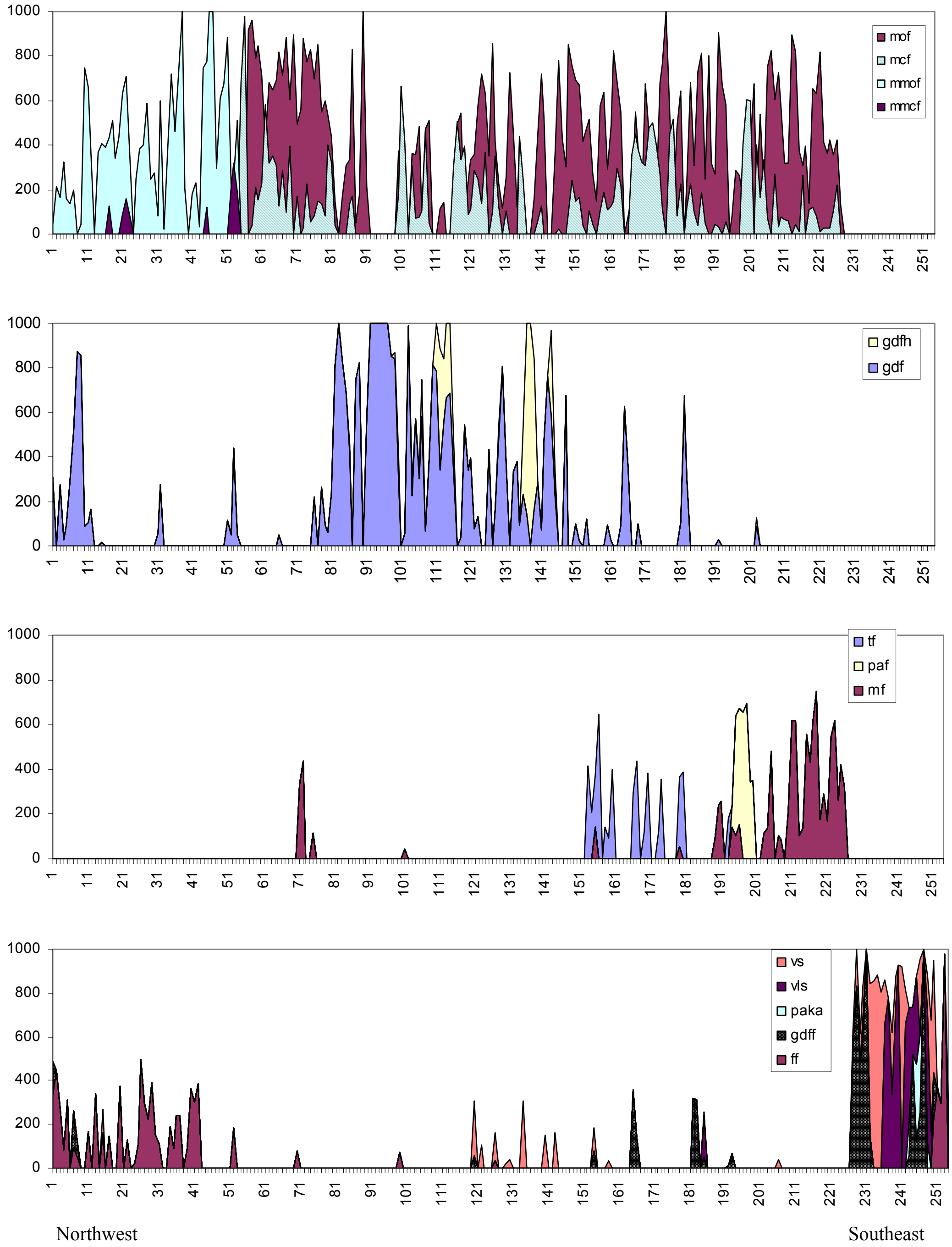
TRANSITION

Vine forest (VF) was present over 11.8 km or 4.7% of the survey route, where it was patchily distributed usually in close proximity to riverine areas. The presence of VF was strongly negatively correlated with distance from water (Spearman's rank correlation coefficient: rho = -0.330, N = 226, $P < 0.001$). *Cleistanthus* sp. forest (CF) was found patchily through the survey and was most abundant along the Mokala River. It was a common riverine vegetation type throughout the area, and is found in seasonally inundated areas but never in permanent swamp. Other transition vegetation types, including *Lophira alata* forest (LAF) were found only along the Mokala River.

INUNDATED

Five vegetation types dominated swamp; flooded forest (FF), vine swamp (VS), vine swamp with *Laccosperma* sp. (VLS) *Gilbertiodendron deweveri* flooded forest (GDFF), and *Guibourtia demeusei* flooded forest (PAKA).

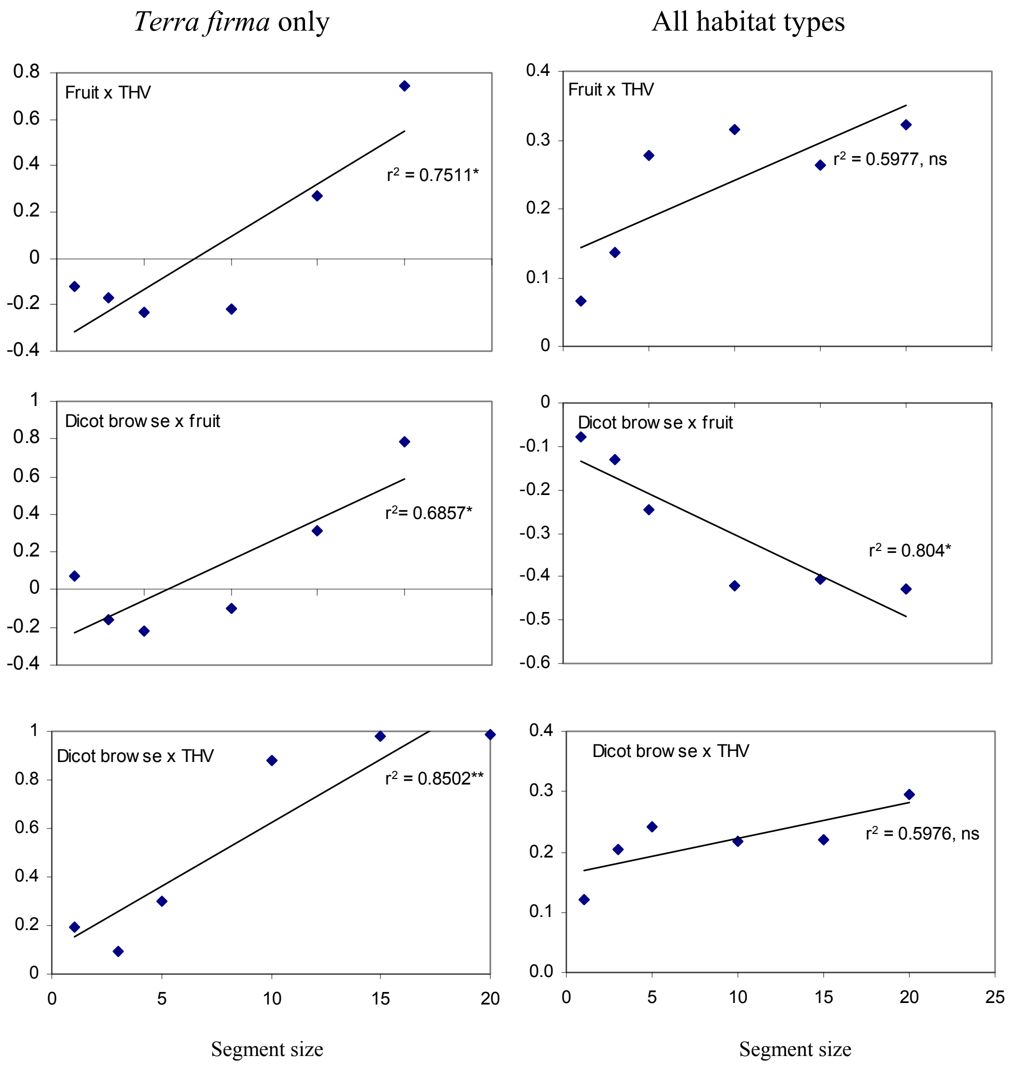
Figure 2.14. Distribution of major vegetation types along survey route



Patchiness of food sources

The scale of patchiness of three food sources, THV, browse:non browse ratio, and fruit was compared across all habitat types, and also within *terra firma* only, irrespective of vegetation type. Figure 2.15 shows the Pearson's correlation coefficients between combinations of variables for different segment sizes along the survey track. In *terra firma* forests, as segment size increased there was an increasing correlation between fruit and THV, dicot browse and fruit, and dicot browse and THV. When swamp segments were included patterns of correlation changed considerably. The trend was similar for both THV and fruit and dicot browse and THV, but they were no longer significant. The relationship between dicot browse and fruit reversed compared to that in *terra firma* segments only, and the negative correlation increased significantly as segment size increased. These results suggest that at small scales in *terra firma* forest there was little pattern in distribution of fruit or THV and dicot browse, and the negative correlation coefficients suggest there may have been some segregation at these scales, which was smoothed as segment size increased. Dicot browse and THV followed a similar trend, though none of the calculated correlation coefficients remained positive even at small scales. The addition of inundated habitats revealed that the habitat dichotomy in fruit and browse distribution between inundated and *terra firma* overcame the pattern of aggregation at large scales in *terra firma* alone.

Figure 2.15. Aggregation between major food classes across different spatial scales



(Y axis in all cases is Pearson's r, note differing scales).

BAIS

There are several different types of clearing found in the Ndoki forest ranging in surface area from hundreds of square metres to tens of hectares, and a number were encountered during the survey. Bambenzele pygmies of the region have a taxonomy for clearings and recognise three major types, all of which are important sources of resources for forest elephants (Figure 2.16). *Endambas* are clearings found in permanent swamps along watercourses. They are usually very deep (sometimes several metres) muddy meadows, with a covering of semi-aquatic herbs, and may support a small number of swamp trees.

Bais are drier forest clearings on or close to watercourses, usually circular or oval depressions, which are usually dominated by species of Cyperaceae and Poaceae. *Yangas* are the third clearing type, which are found in the absence of flowing water, but which may be seasonally or permanently flooded. They support a wide diversity of vegetation types in concentric circles from the centre and up through the drainage gradient. Quantitative data on species composition and abundance of foods in clearings were not collected during this study. Blake *et al*. (unpub. data) conducted quantitative floristic surveys in the three clearing types in 1996, which indicated that *endambas* offer a high abundance of aquatic herbaceous foods, whereas *yangas* often provide a high abundance of sedges in their centre, and palatable browse species near their peripheries. *Bais* also offer both sedges and grasses which are frequently eaten, but the main resource elephants exploit in *bais* are minerals either in solution from seep holes and deep in the underlying substrate of riverbeds, or in soils. *Bais* were concentrated in the northern part of the Ndoki Forest, though also occur in the Kabo and Pokola concessions. *Endambas* occurred frequently in the wide swamps associated with larger rivers such as the Ndoki, Mokala, and Mabale. *Yangas*, which were not directly encountered during this survey, were heavily concentrated to the south of the NNNP, distributed in a wide swathe, initially between the Sangha and Ndoki Rivers, which expanded to low lying areas both west and east of the Ndoki further to the south.

Specific conductivity of *bai* drinking holes

Electrical conductivity of standing water in *bais* varied between *bais*, seasons, and activity level. The mean specific conductivity in active holes was up to 4 times higher than for inactive holes (figure 2.17) and a paired t-test revealed highly significant differences ($t = 5.66$, $df = 19$, $P < 0.0001$). The conductivity of water in Mingingi 1 was consistently higher than the other *bais*, with the mean of active holes in Mingingi 1 twice that of any other *bai*. Figures 2.18a and b show that there was a general trend toward decreasing electrical conductivity of standing water with increasing rainfall for both active and inactive holes across all *bais*. When data were normalised within each *bai* and each hole type by dividing the conductivity values by the highest value in each category, there was no significant relationship for each of the active or inactive holes. However when the normalised data were pooled for both active and inactive holes the relationship, while weak, reached significance ($r = 0.157$, $F_{(1,166)} = 4.2$, $P = 0.042$). In summary, mineral concentrations in *bai* water holes, as indicated by electrical conductivity, were higher during the dry periods than wet, and higher in active compared to inactive holes.

Figure 2.16. Major clearing types of the Ndoki Forest

Yanga

Endamba

Bai

Figure 2.17. Specific conductivity of active and inactive holes pooled across seasons

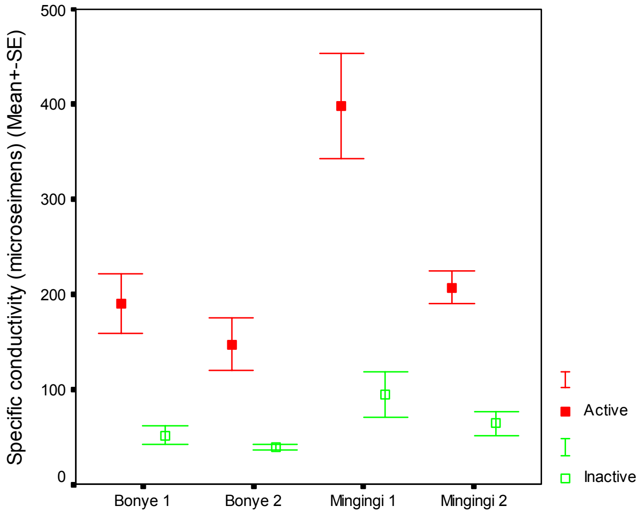
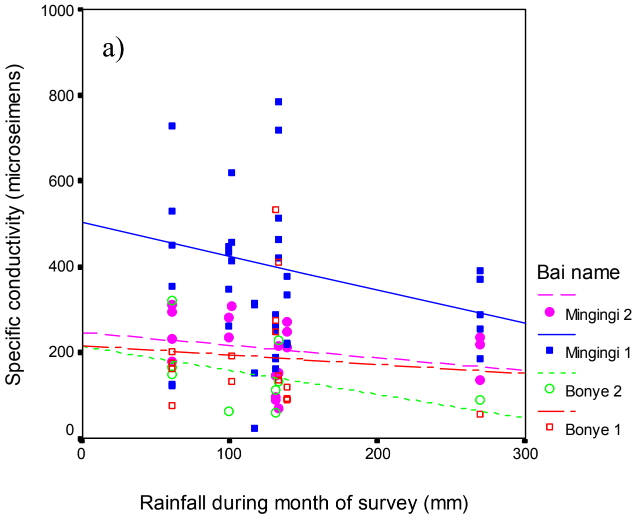
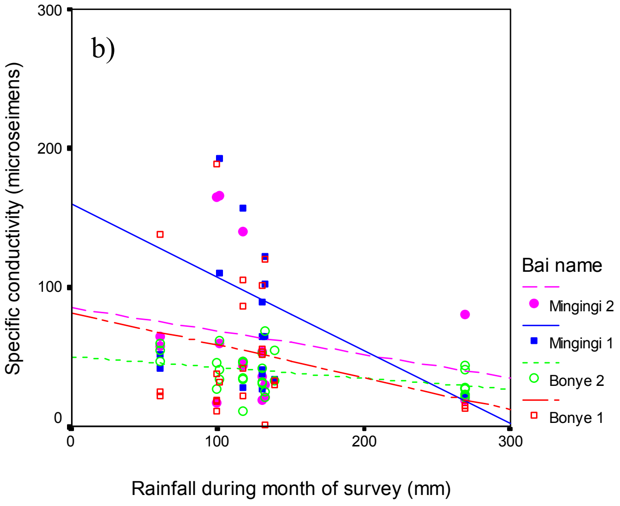


Figure 2.18. Specific conductivity of a) active, b) inactive *bai* holes by rainfall





Phenology patterns in the Ndoki Forest

UNDERSTOREY LEAF PHENOLOGY

Dicotyledons

The intensive understorey phenology survey spanned a year at the Bomassa site. A total of 294 individual small trees from at least 94 species were included in the circuit and observed monthly. Mature leaves were consistently the most abundant phase, followed by old and finally new leaves (Figure 2.19). There were two peaks in production of new leaves, in March and November, with a qualitative decrease during the wettest months of the year (Figure 2.19). Mature and old leaf abundance increased as rainfall increased at the end of the dry season, and both remained high before diminishing when rainfall dropped in October. New leaf production showed no relationship with rainfall (Spearman's rank correlation: rho = -0.175, N = 12, ns), nor was new leaf abundance correlated with the abundance of either mature or old leaves. By contrast, the abundance of both mature and old leaves was positively correlated with rainfall (Spearmans rank correlation: $\text{rho}_{(\text{mature})} = 0.706$, N = 12, P = 0.01; $\text{rho}_{(\text{old})} = 0.692$, N = 12, $P < 0.05$), and were positively correlated (Spearman's rank correlation: rho = 0.755, N = 12, $P < 0.01$) with each other. Change in rainfall from the previous month had no effect on abundance of new leaves, and while qualitatively the abundance of mature and old leaves tracked change in rainfall, the effect was not significant.

'Important' understorey tree elephant foods

The trend in leaf phenophase abundance with rainfall was not significantly difference between important browse and non-browse species. However, the mean monthly leaf scores for important browse and non-browse species were significantly different (Figure 2.20). New leaves were significantly more abundant for important browse than for non-browse species (Wilcoxon signed ranks test: z = -3.059, N = 12, P = 0.002), there was no difference between the abundance of mature leaves for the two classes (z = -0.078, N = 12, P = 0.9), and old leaves were significantly less abundant for important browse than non-browse species (z = 3.059, N = 12, P = 0.002). Thus elephant browse species had, on average, consistently more new leaves and less old leaves per plant.

Figure 2.19: Leaf abundance scores for all dicotyledon species

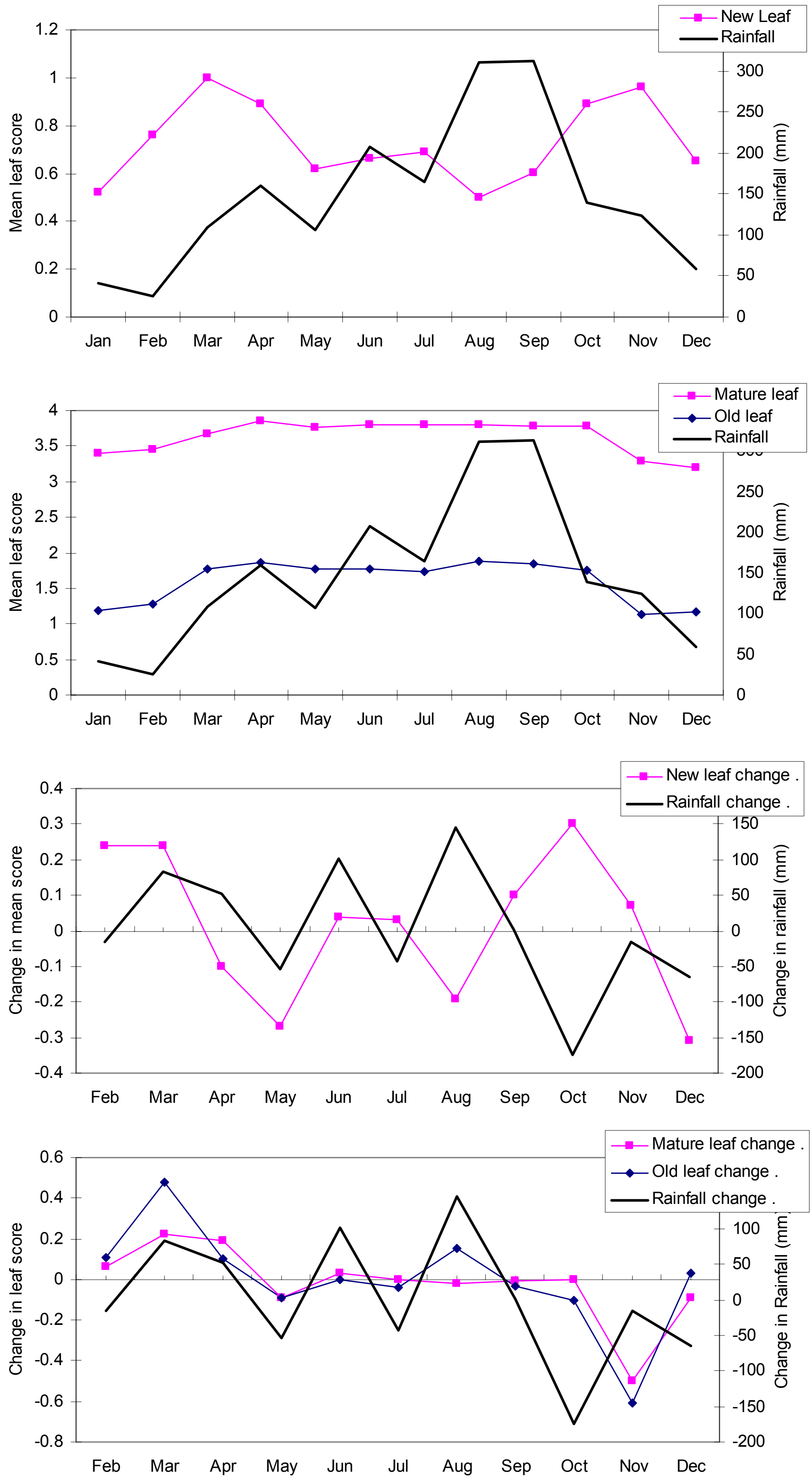
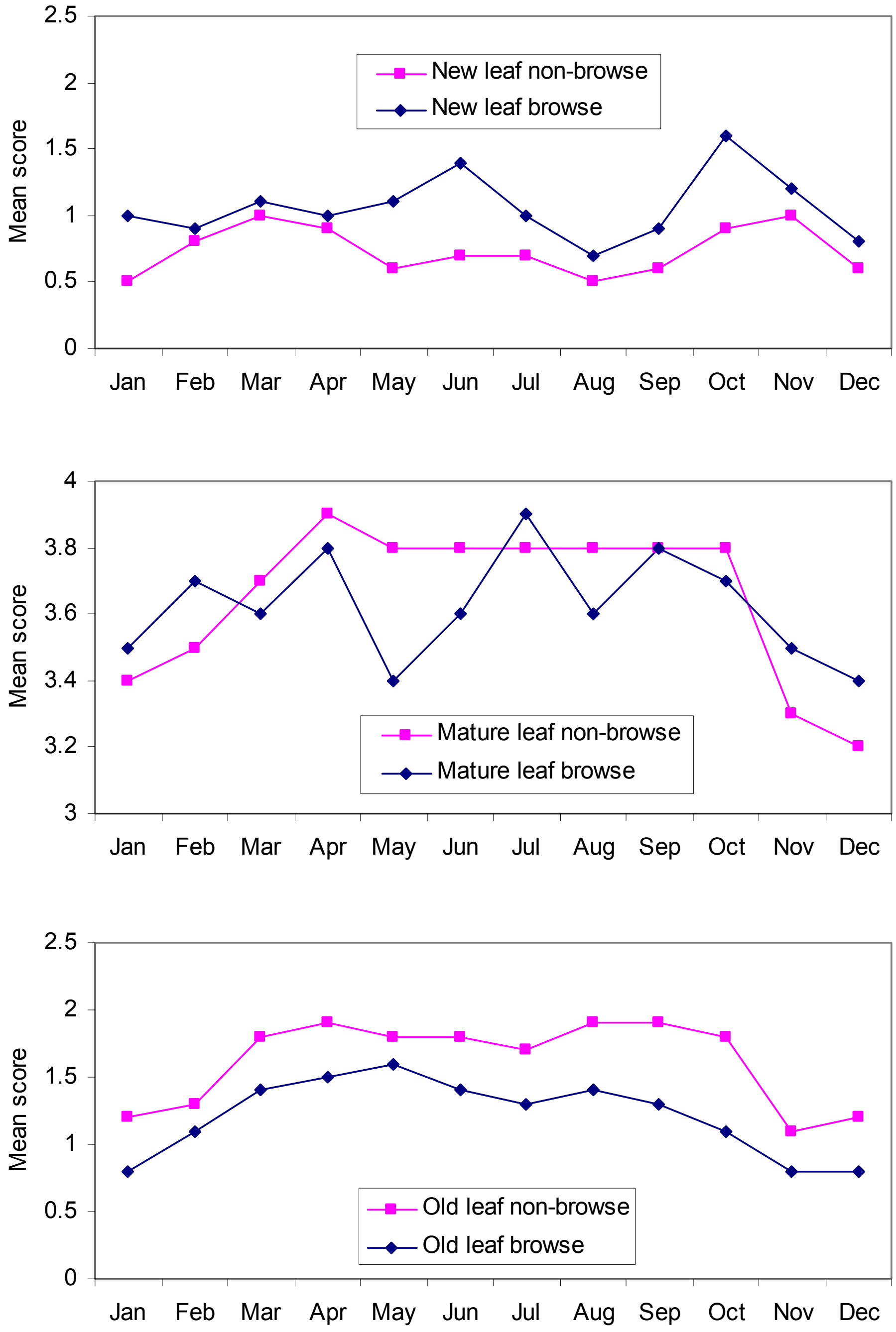


Figure 2.20. Differences in leaf phenophase abundance for browse and non-browse understorey dicotyledon species



Monocotyledons

The leaf phenophase was recorded for 19 taxa of THV. Mature leaves were consistently the most abundant in all months. There was a moderate increase in new leaf score with increasing rainfall (Figure 2.21), though the trend just failed to reach significance (Spearman's rank correlation: rho = 0.56, N = 12, P = 0.059), while mature and old leaf scores were both significantly positively correlated with rainfall (Spearman's rank correlation: $\text{rho}_{(\text{mature})} = 0.775$, N = 12, P < 0.01; $\text{rho}_{(\text{old})} = 0.811$, N = 12, P =0.001). New leaf scores were not correlated with the other phenophases, but mature and old leaf scores were significantly positively correlated (Spearman's rank correlation: rho = 0.678, N = 12, P <0.05). The change in monthly rainfall also has no effect on either new or mature leaf scores (Figure 2.21), while there was a significant positive correlation between change in rainfall and change in old leaf scores (Spearman's rank correlation: $\text{rho}_{(\text{old})} = 0.609$, N = 12, P < 0.05).

Important THV elephant foods

There were no significant differences in the trends in abundance of leaf phenophase with rainfall between important browse and non-browse species. However the monthly leaf scores did reveal significant differences between the two classes (Figure 2.22). Both new and mature leaves were significantly more abundant for non-browse than for browse species (Wilcoxon Signed Ranks Test: $z_{(\text{new})} = -2.118$, P = 0.034; $z_{(\text{mature})} = -3.059$, P = 0.002). By contrast, old leaves were significantly less abundant per month for non-browse than for browse species (Wilcoxon Signed Ranks test: z = -2.133, n = 12, P <0.05). For any time period therefore, THV elephant food species tended to have less new and mature, but more old leaves than non-food species.

Figure 2.21. Forest wide leaf phenology for Monocotyledons, intensive survey

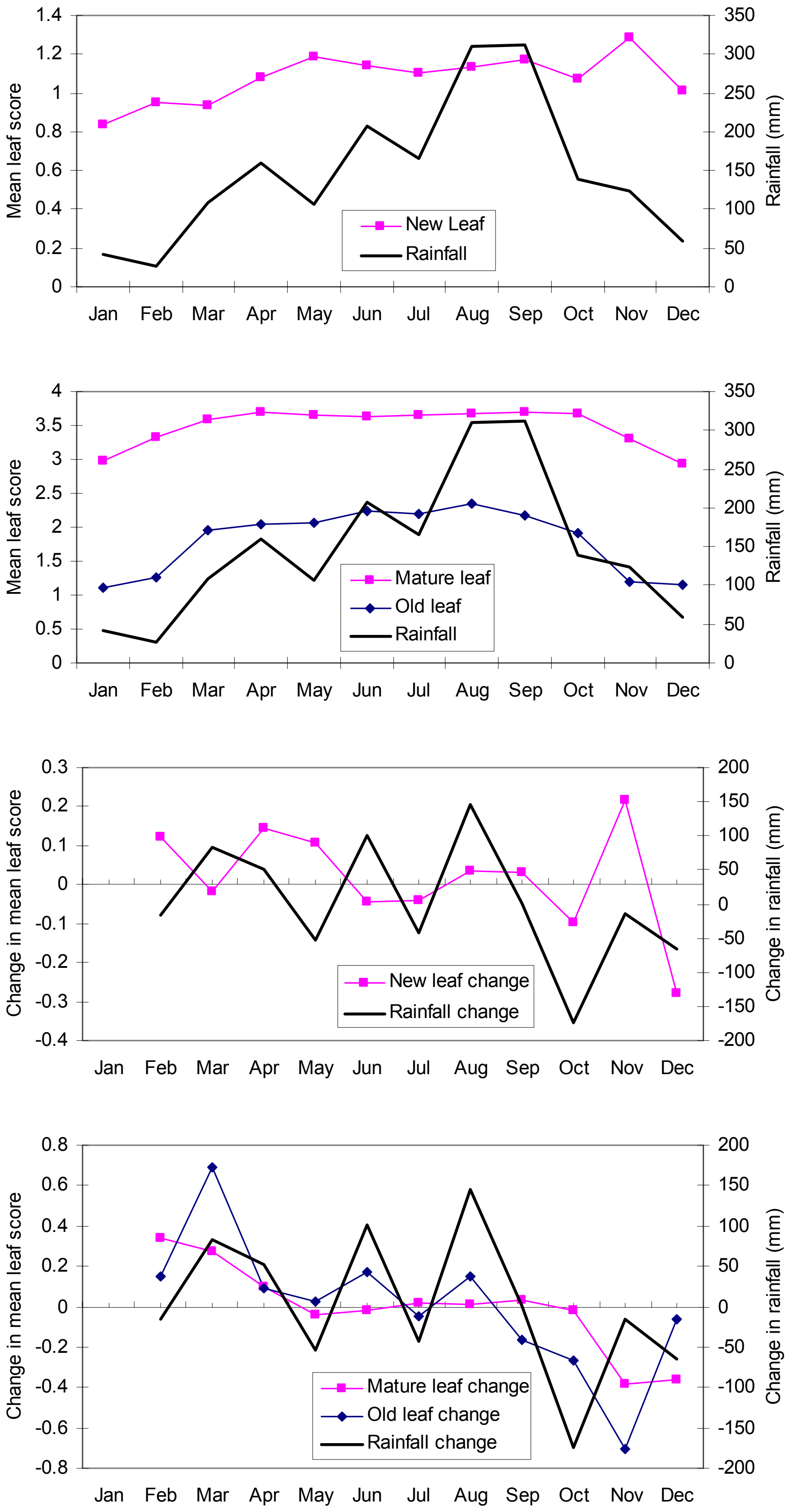
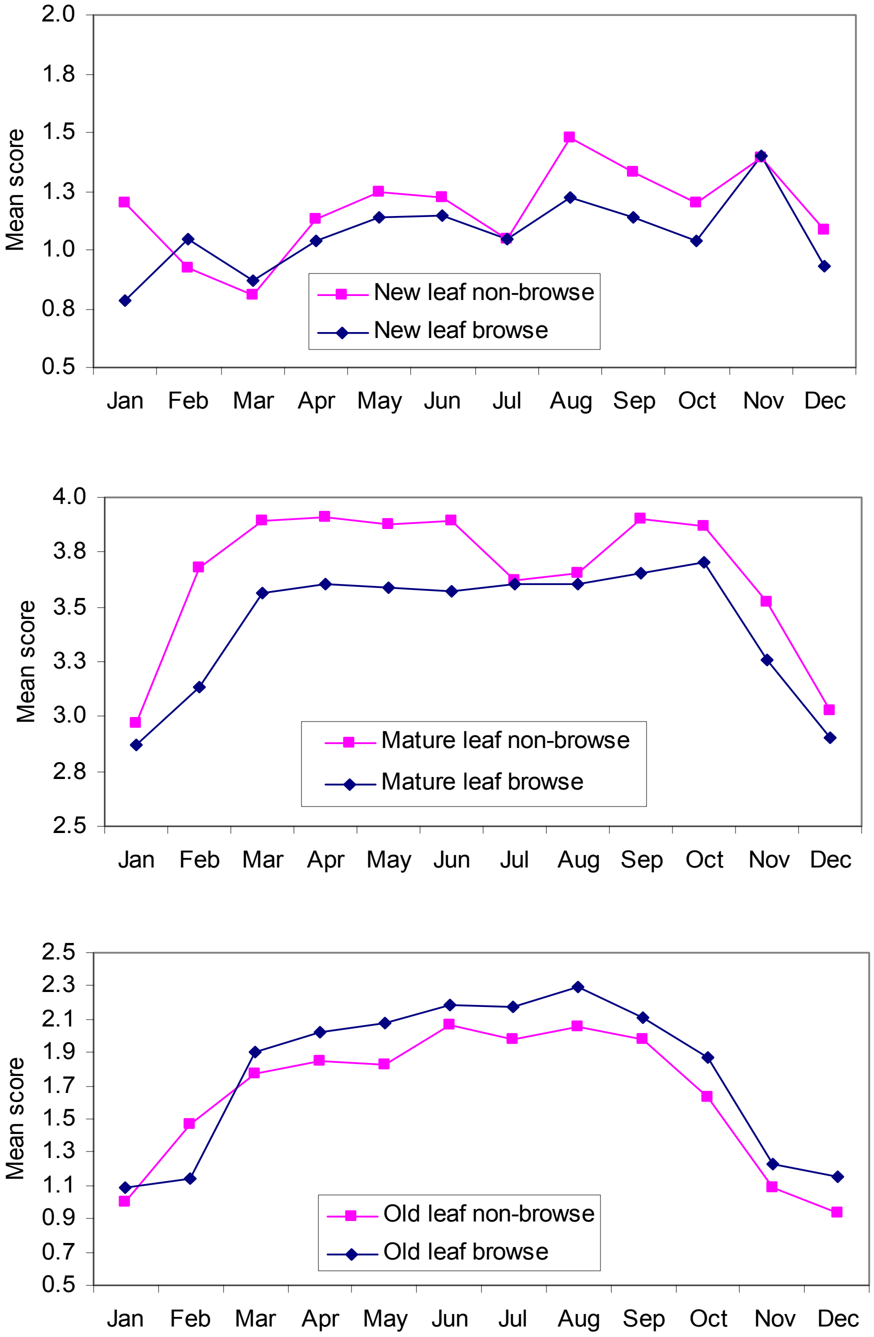


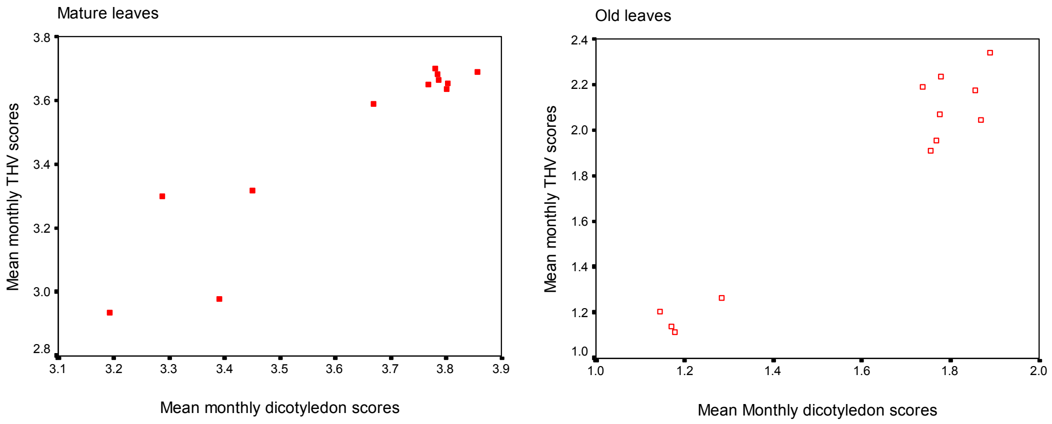
Figure 2.22. Differences in leaf phenophase abundance for browse and non-browse THV species



Comparison of dicotyledon and monocotyledon leaf production

There was no correlation between the monthly new leaf scores between new leaves of THV and dicotyledons (Spearman's rank correlation: rho = -0.105, N = 12, ns), however both mature and old leaf scores were positively correlated (Spearman's rank correlation: $\text{rho}_{(\text{mature})}$ = 0.797, N = 12, P <0.005, $\text{rho}_{(\text{old})}$ = 0.804, N = 12, P <0.005) (Figure 2.23).

Figure 2.23. Relationship between THV and dicotyledon scores for mature and old leaves



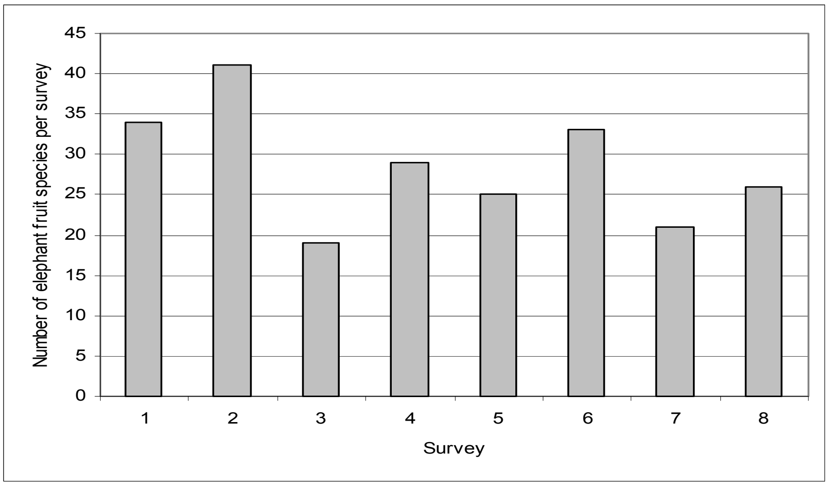
FRUIT ABUNDANCE

In this section temporal patterns of availability of elephant fruit foods from both the extensive and intensive survey sites are quantitatively described. More detailed patterns of temporal and geographical trends in fruit abundance are described in Chapter 5, in which availability is quantified as a covariate for the analysis of seasonal distribution patterns of elephants.

Extensive survey

One hundred and ten fruit species were recorded from the 8 seasonal surveys, of which 53 were eaten by elephants (Chapter 3). The mean number of species present per survey was 28.5 (median = 28), which varied between surveys from a maximum of 41 in the second survey to 19 in the third (Figure 2.24), though the difference was not statistically significant (Chi-square test: $\chi^2 = 13.4$, df = 1, P = 0.0603).

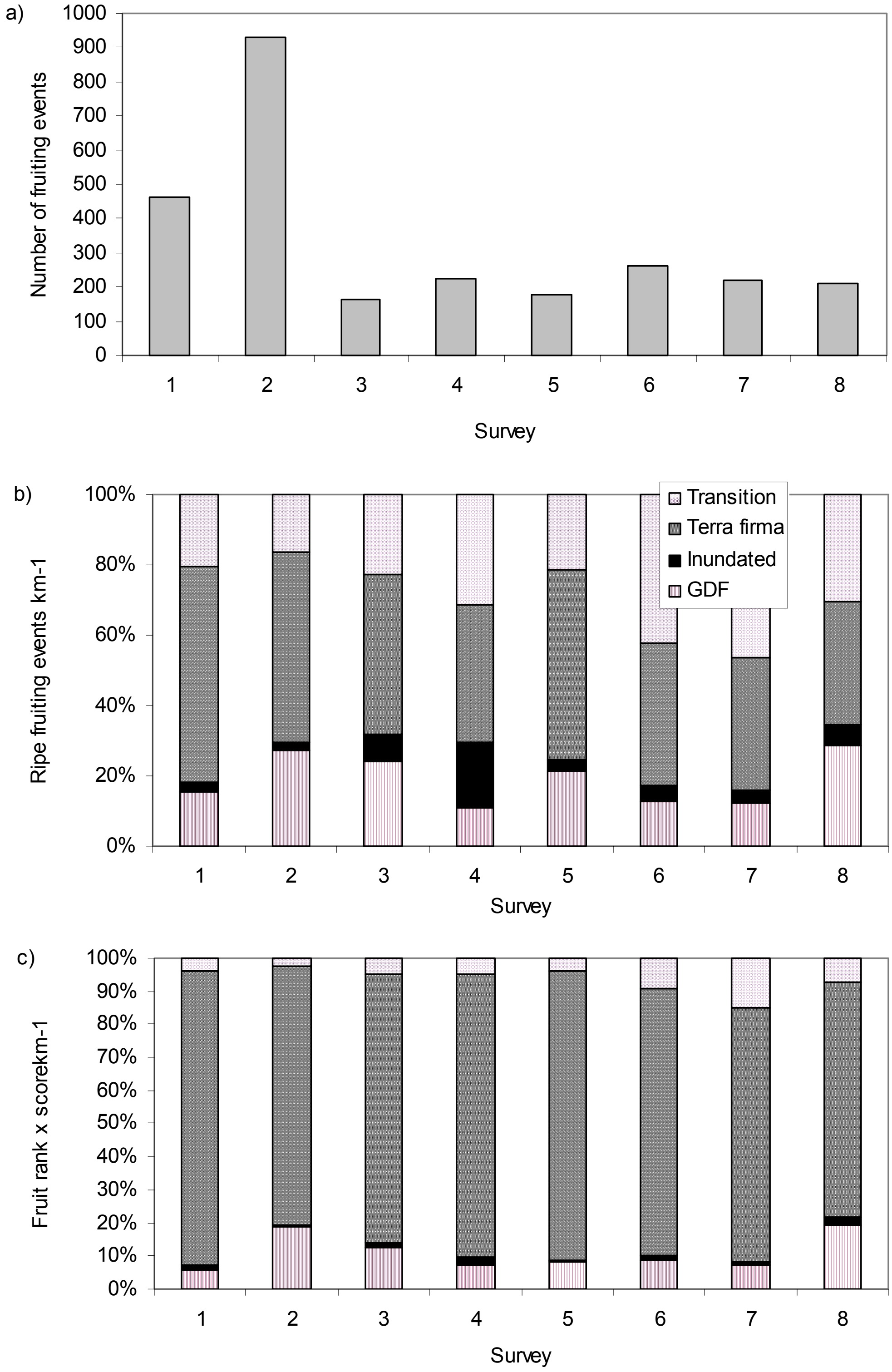
Figure 2.24. Number of elephant fruit species recorded on seasonal surveys over 2 years



Elephant fruit availability by vegetation type and season

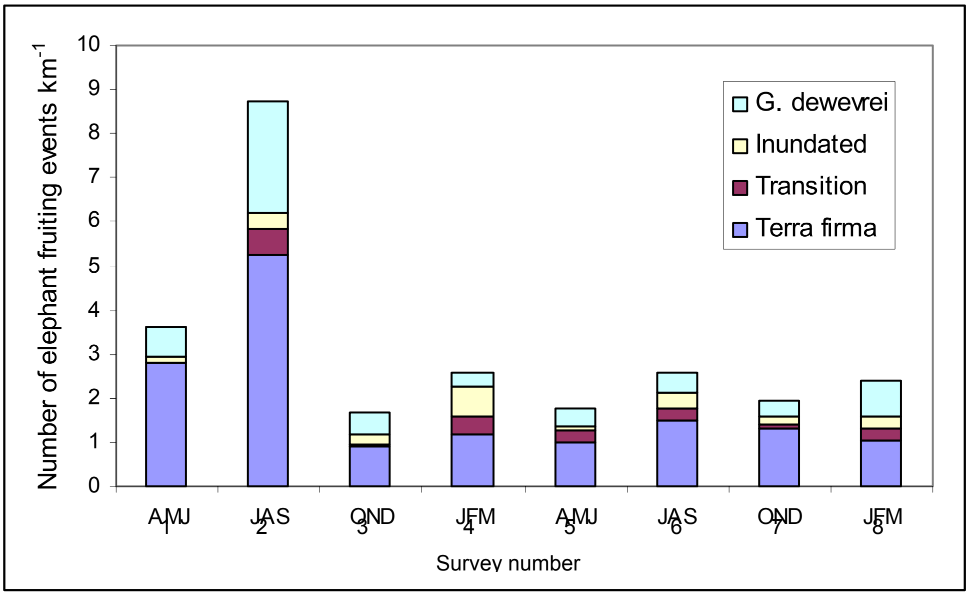
The frequency of fruitfall of elephant food species varied significantly by vegetation type, season, and year (Chi square: $\chi^2_{\text{vegetation}}$, = 2233.65, df = 39, P < 0.0001, χ^2_{season}, = 892.8, df = 31, P < 0.0001, χ^2_{year} = 99.67, df = 12, P < 0.0001). The clearest pattern to emerge from the fruit count data was the uneven distribution of fruit availability between surveys (Figure 2.25a), with the first two surveys accounting for more than half the fruitfall events out of all 8 surveys, and survey 2 alone making up 35% of all fruitfall. Across all surveys the mean number of fruiting events km^{-1} in *terra firma* forest was 1.8, or 2.5 times higher than in GDF, 8.0 times higher than in transition vegetation, and 6.3 times higher than in inundated forest (Figure 2.25b). Fruit availability was low in inundated forests even during peak fruiting seasons, and reached a maximum frequency of just 0.5 events km^{-1} in survey 4, primarily caused by two fruit species, *Grewia* sp. and *Klainedoxa* sp. When fruit availability (rank x score) was compared between vegetation types, the importance of *terra firma* forests over any other vegetation type in terms of fruit availability is striking (Figure 2.25c). The mean fruit abundance value for *terra firma* across all surveys was 71.2km^{-1} compared to 11.0 in GDF, 4.4 in transition forest, and just 0.9 in inundated vegetation. Thus, not only was the number of fruiting events low, but there were almost no preferred species in inundated or transition vegetation.

Figure 2.25. Gross patterns of fruit availability by survey and vegetation type



Among *terra firma* forest types, MCF offered the greatest availability of elephant fruit compared with other vegetation types, and light gaps contained the least (Figure 2.26). The maximum frequency of fruitfall events for any season in any vegetation type was 8.5 events km^{-1} in MCF during the peak fruiting episode of survey 2. Three months later the fruit availability in the same vegetation type was an order of magnitude lower at 0.8 events km^{-1}. During survey 2 then, an elephant would have encountered edible fruitfall every 120m in MCF during September 1998, and only once every 1200m in the same vegetation type three months later.

Figure 2.26. Mean elephant fruitfall frequency km^{-1} by vegetation type pooled for all seasons and years.



Fruit availability by species

Table 2.6 below shows the number of surveys on which fruits of different species were recorded. Four species (6.5% of the total) were seen in all 8 surveys and 12 species (19.4%) were present for only one survey. *Duboscia* spp. dominated fruit production across surveys in terms of the number of fruiting events. Several species showed particularly pronounced peaks in fruit abundance, most commonly those species which fruited in few surveys. *M. mabokeensis* was recorded in 3 surveys during one of which (survey 2) it produced a maximum fruit crop of 168 events. This was the second highest crop recorded for any species, the maximum being 177 events recorded for *S. pustulata,* also an infrequently fruiting species, during the same survey. *Polyalthea suaveolens* was recorded in four surveys, and in one (survey 1) fruited with an order of magnitude more events than in any other survey. *Stromboisopsis tetrandra* fruited during two surveys, with a difference in frequency of two orders of magnitude between them. Most species exhibiting this pattern were usually non-preferred by elephants (Chapter 3). For example, despite their occasional almost super-abundance as furitfall, *S. pustulata, S. tetrandra* and *P. suaveolens* were found in less than 1% of dung piles even in those months (Chapter 3). The major fruit components of elephant diet had consistent but relatively regular fruiting patterns, the clear exception to this being *M. mabokeensis,* which fruited in three seasons, though 98% of all fruiting events were recorded in a single season.

Table 2.6. Fruit species availability by survey period

	Number of fruiting events								
	Survey number								
Fruit species	1	2	3	4	5	6	7	8	N surveys
Brenania brieyi	3	6	1	3	1	10	5	2	8
Drypetes gossweileri	1	5	12	3	2	10	5	3	8
Duboscia spp.	46	73	62	43	40	51	53	30	8
Massularia acuminata	20	48	20	5	14	12	10	5	8
Autranella congolensis	20	9	3	13	4	4		10	7
Klainedoxa gabonensis	36	11	12	10		3	58	41	7
Myrianthus arboreus	30	12		5	9	3	1	3	7
Panda oleosa	25	87	25	3		38	28	14	7
Strychnos aculeata	4	19	5	4		5	1	11	7
Tridesmostemon omphalocarpoides	3	2	2	7	4		1	6	7
Detarium macrocarpum	6	4		7	9	2		3	6
Gambeya lacourtiana	19	1	5	27	15	2			6
Irvingia excelsa	22	6		12	1		7	39	6
Mammea africana		1	1	3		2	1	3	6
Omphalocarpum elatum	4	4		2		4	2	3	6
Balanites wilsoniana	1		1	2			2	3	5
Desplatsia sp.	3	7				7	3	1	5
Gambeya begei	6	2		1		3		2	5
Landolphia sp.	1	8		3	1	1			5
Parinari excelsa		2		1		1	7	4	5
Strombosia pustulata	1	177			12	11	23		5
Tetrapleura tetraptera		1	4		2	19	1		5
Vitex sp.		18	1			10	4	8	5
Antrocaryon micraster	1	1	1					2	4
Ficus sp.				1	2	1		1	4
Gambeya perpulcrum	12		2	13				2	4
Irvingia grandifolia	3	27			3	5			4
Polyalthea suaveolens	158			10	9	2			4
Strombosia grandifolia	1	4				30		2	4
Treculia africana	6	3		1	1				4
Annonidium mannii	1	22			37				3
Irvingia robur	1	7				1			3
Manilkara mabokeensis	3	160				1			3
Pachyelasma tessmannii			2		3	17			3
Pachypodanthium sp.		3		1		1			3
Pycnanthus marchalianus				12	1			12	3

Table 2.6 contd.

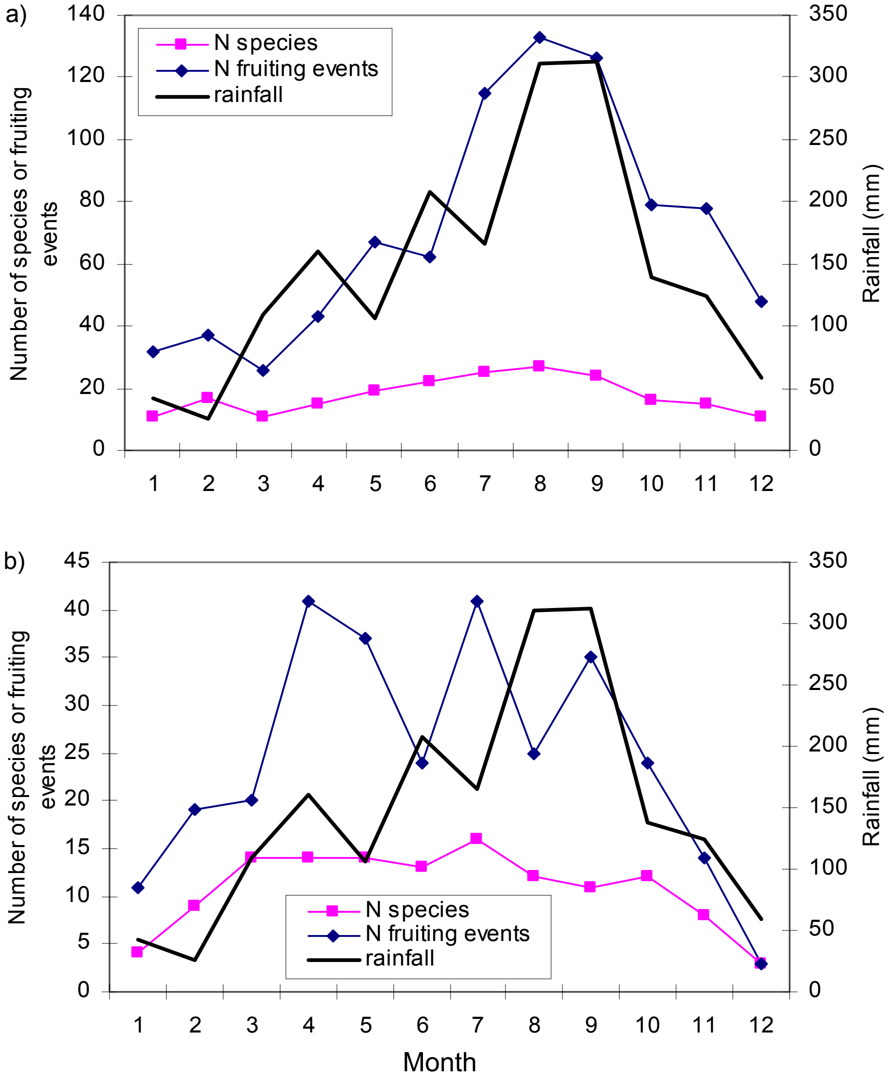
Fruit species	1	2	3	4	5	6	7	8	N surveys
Uvariastrum pierreanum	14	2				2			3
Antrocaryon klaineanum						1		1	2
Chytranthus sp.	2				1				2
Diospyros crassiflora		4			1				2
Gambeya boukokoensis	2	7							2
Grewia sp.			5	30					2
Haumania dankelmaniana		69	1						2
Hexalobus crispiflorus		8			2				2
Cola chlamydantha		2				1			2
Strombosiopsis tetrandra		106				3			2
Swartzia fistuloides		1						1	2
Brevia leptospermum	3								1
Cucurbitaceae spp.		1							1
Donella pentagonocarpa				2					1
Donella pruniformis							1		1
Gilbertiodendron dewevrei					2				1
Omphalocarpum procera		1							1
Pancovia sp.							1		1
Picralima nitida				1					1
Pseudospondias macrocarpus				1					1
Raffia sp.		1							1
Ricinodendron heudelotii							3		1
Strychnos sp.					1				1
Synsepalum stipitatum	2								1
Thomandersia laurifolia	3								1
Grand Total	463	932	165	226	177	264	217	212	

Intensive fruit survey

Fruitfall on transects

A total of 78 species of fruit was recorded during the year of monthly fruitfall surveys at the Bomassa site, including 30 elephant foods. In the case of elephant foods, rainfall in the month of the survey was a significant predictor of both the total number of fruit species recorded (Linear regression: $r = 0.625$, $F_{(1,10)} = 16.642$, $P < 0.01$), and the number of fruiting events ($r = 0.670$, $F_{(1,10)} = 20.308$, $P < 0.001$) (Figure 2.28a). A similar qualitative trend was apparent for non-elephant fruits (Figure 2.28b) though it did not reach statistical significance either for the number of species per month or the number of fruiting events.

Figure 2.28: Number of ripe fruit species and number of fruiting events for a) elephant foods and b) non-elephant foods



Fruitfall under monitored individual trees

Up to 12 individuals of 21 tree species were monitored each month. The number of species with ripe fruit varied from a maximum of 16 in August (one of the wettest 2 months) to a minimum of 3 in March and April at the end of the dry season. (Figure 2.29). The mean size of the fruit crop for a given species increased with the number of species fruiting (monthly fruit scores were positively correlated with the number of species producing ripe fruits, Spearman's Correlation Coefficient; rho = 0.833, $P < 0.0001$, n = 12).

Fruit production was highly variable both between individuals and species. In March and April, only 1.7% of all individuals in the survey produced fruit, increasing to a maximum of nearly one-quarter of all stems (24.7%) in August (Figure 2.29). The proportion of all species fruiting in a given month varied from a low of 17.6% to 88.2%, both maximum and minimum occurring in the same months as those for numbers of individuals (March, April, and August). Both were significantly correlated with rainfall by month (Pearsons correlation coefficient: $r_{(individuals)} = 0.708$, $N = 12$, $P < 0.01$; $r_{(species)} = 0.784$, $N = 12$, $P < 0.05$).

In only 4 of 17 species did more than 50% of individuals produce fruit in a given month (Table 2.7) only doing so between July and October around the peak rainfall period. In August, over 70% of *S. tetrandra* individuals were in fruit, and indeed for the 3 months during which it fruited, more than half the individuals produced fruit. *Breniana brieyi* had the most extended period of high production among individuals, with over 50% fruiting over a 4 month period. Fruit production in the driest months of December, January, and February was limited to 8 of the 17 species (Table 2.7), only one of which, *D. macrocarpa*, fruited in all three months.

Figure 2.29. Rainfall and the percentage of the total number of individual trees and species producing fruit in each month

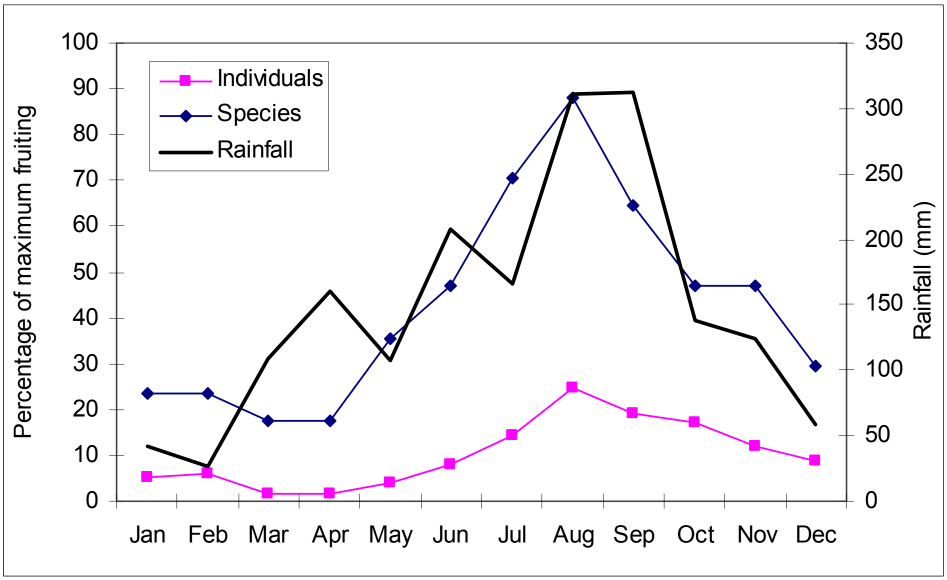


Table 2.7. Percentage of stems with ripe fruitfall per month

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
Rainfall (mm)	41.9	26	108.8	160.6	106.7	208	165.4	310.9	312.6	138.6	123.9	58.45	N months	Low rainfall months (DJF)
Tree species														
Duboscia macrocarpa	40.0	20.0			10.0	10.0	10.0	20.0	10.0	14.3	30.0	44.4	10	3
Klainedoxa gabonensis	18.2	45.5	9.1		9.1			18.2	27.3	54.5	9.1		9	2
Brenania brieyi	25.0					25.0	50.0	50.0	50.0	62.5	37.5	25.0	8	2
Drypetes gossweileri		20.0		10.0	10.0	10.0	10.0	20.0	30.0				7	1
Tetrapleura tetraptera						41.7	25.0	16.7	8.3	8.3	41.7	50.0	7	1
Antrocaryon klaineanum						11.1	11.1	33.3	33.3	33.3	11.1		6	0
Mammea africana	9.1							18.2	9.1		27.3	9.1	5	2
Manilkara pellegriniana							9.1	63.6	54.5	45.5	18.2		5	0
Panda oleosa								16.7	33.3	25.0	25.0	16.7	5	1
Chrysophyllum beguei			10.0	10.0		10.0		10.0					4	0
Detarium macrocarpum				20.0	20.0		20.0	20.0					4	0
Elaeis guineensis		9.1	9.1		18.2	9.1							4	1
Myrianthus arboreus					9.1		18.2	18.2	18.2				4	0
Chrysophyllum africana						20.0	20.0	10.0					3	0
Strombosiopsis tetrandra							54.5	72.7	45.5				3	0
Anonidium mannii							8.3	33.3					2	0
Irvingia grandifolia							20.0						1	0

DISCUSSION

This study has shown that across the Ndoki landscape there is small scale heterogeneity, large scale structure, and also temporal variation in the pattern of resource distribution across the Ndoki Forest, all of which may influence the patterns of foraging and spatial distribution of forest elephants.

Several results were noteworthy concerning fruit tree distribution. Fruit tree abundance varied consistently across drainage gradients on both local and landscape scales. Locally, fruit tree density increased with distance from the nearest river, while across the landscape density also increased, though weakly, with distance from the Likouala swamp basin. There was an order of magnitude difference in the density of fruit trees between the 'best' vegetation type in *terra firma*, and the 'worst' in inundated forest. Only 6 species were recorded in all inundated plots (*T. africana, Klainedoxa* sp. *I. grandifolia, A. mannii, Duboscia* sp. and *P. oleosa*), and of these 5 were represented by just 1 individual. *Klainedoxa* sp. accounting for 75% of all elephant fruit trees in these vegetation types. *Klainedoxa* sp. was seen to fruit heavily in the Likouala swamps in January 2000. It was eaten heavily by elephants and may have provided an important source of dry season fruit. *Treculia africana* was widespread but rare in the swamps. In parts of the Likouala swamps including south of the *Terre de Kaboungas*, *Uapaca* spp. frequently occur in near mono-dominant stands (Blake *et al.* 1995) which may cover many square kilometres (Blake, pers. obs.). The fruits of *Uapaca* spp. are an important food source for elephants in some areas (White *et al.* 1993) and probably represent the only other major source of fruit for elephants in Ndoki Forest swamp habitats. The only other obvious possibility is *Nauclea* sp. a mast fruiting species in the Ndoki, which may be locally common in riverine swamps. This species has never been recorded in elephant dung piles, but the small soft fruits and tiny seeds would be exceptionally difficult to detect.

Elephant fruit tree abundance in mixed *terra firma* forests was high compared with other vegetation types, but reached exceptional density in TF. Particularly impressive in this forest type were the enormous individual trees of *Duboscia* spp. and several species of Sapotaceae, particularly *A. congolensis*, both of which produced a super-abundance of fruit during the first survey. Mono-dominant *G. dewevrei* forests were intermediate between mixed *terra firma* and transition/inundated forests, and unlikely to produce high quantities of fruit foods for elephants. Occasionally however this mast fruiting species produced an enormous crop of seeds (up to 4+ tonnes per hectare (Blake and Fay 1997)), which may be heavily exploited by elephants and other animals. In summary then, there was clear spatial separation of fruit trees – low or none in inundated vegetation with increasing abundance moving up drainage gradients at all spatial scales.

Contrary to fruit tree abundance, the ratio of non-browse:browse dicotyledons by both species and number of individuals was generally highest in inundated forest types, with three notable exceptions in *terra firma*. These were TF, PAF, and MF, all of which had restricted range in the southeastern section of the study area. The lowest frequencies of browse were in the mono-dominant *G. dewevrei* forests. Mixed closed forest contained the lowest frequency of food stems of all *terra firma* vegetation types, while CF and FF, which also have relatively closed canopies, were ranked lowest for inundated and transition forest respectively. Given the favourable conditions for growth of elephant food species in gaps (Wing and Buss 1970; Short 1983; Struhsaker *et al.* 1996), it was surprising that LG was ranked only seventh by proportion of browsed dicotyledon individuals. This may have been because the density of both herbs and lianas were also high in light gaps which may have out-competed small trees and shrubs (Struhsaker *et al.*

1996), and there is little doubt that the total amount of browse was extremely high in light gaps.

The negative correlation between canopy tree density and understorey elephant browse availability is consistent with data collected elsewhere in Africa (Wing and Buss 1970; Struhsaker *et al.* 1996). In the Ndoki, it was the proportion of edible species and individuals which was quantified and not absolute stem density. Most herbivores (Coley, 1983), including savannah (Wing and Buss, 1970) and forest (Short 1983) elephants, are known to prefer the leaves of pioneer species over shade tolerant species. Fast growing gap specialists, are generally less lignified, contain lower levels of fibre and chemical defences, and higher levels of nitrogen and water than do shade-tolerant species (Coley 1983), which makes them less toxic, more palatable, and easier to digest. The relatively strong (and significant) correlation between canopy tree and elephant fruit tree density would suggest that vegetation structure may encourage elephants to partition their habitat use according to foraging preferences. When foraging for fruit they would have greater success in closed canopy *terra firma* forests, and while browsing for understorey dicotyledons they would find a greater availability in open canopy vegetation, particularly inundated habitats.

Many studies of African forest vegetation in relation to large mammal ecology (Williamson 1988; White 1992; Fay 1997) including forest elephants (Short 1981; Powell 1997), have not quantified understorey dicotyledon browse abundance or phenology. Most have been concerned with trees over 10cm dbh, THV, and fruit, often with good reason since these resources are likely to be critical to large generalist herbivores. Surprisingly, the majority of plants eaten by elephants in forests are in the range not quantified by these and other studies. Wing and Buss (1970) showed that in Kibale Forest, 75% of browsed stems were under 2.5cm dbh and 97.5% were under 10.2cm dbh. Chapter 3 of this study confirmed a similar size class selection in forest elephants, finding that 91.5% of browsed stems were 10cm dbh or less. Even Struhsaker *et al.* (1996), who enumerated woody stems down to 2.0 cm dbh, still did not include the majority of browse size classes, though in the same forest, Lwanga (1994) enumerated stems down to 1cm dbh. In Kibale Forest, stem densities in heavily browsed size classes were usually significantly lower in logged (relatively open canopy) forest than in un-logged forest (relatively closed canopy) (Struhsaker *et al.* 1996), yet elephants preferred the open canopy for foraging where they were found in higher densities than un-logged forests. It was concluded that it was the herbaceous and semi-woody undergrowth rather than woody stems that provided abundant and high nutritional value food resources in open forest patches. In the Ndoki, while stem densities were not quantified, qualitative observations indicate that, there too, stem densities of small trees were low but foliage abundance from other dicotyledon plant forms (lianas and dicotyledon herbs) was high, and of all woody stems that were present in gaps, the majority were palatable for elephants.

Numerous authors have described the structure, composition, and ecology of open canopy forests with an abundance of Marantaceae in the understorey (Aubreville 1962; Guillaumet 1967; Letouzey 1968; Maley 1991). White (2001) described Marantaceae forest from Gabon as a successional stage following savannah colonisation, before the development of mature forest. In the Lopé Reserve, this forest type supported the highest densities of large mammals yet recorded in any tropical forest, mainly due to the high elephant biomass (White 1994a). Fay (1997) described a small patch of Marantaceae forest in the Ndoki, characterised by low to moderate large tree density, a relatively open canopy, and a dense understorey of THV. In an extensive review of its distribution in Africa, Fay (1997) concluded that Marantaceae forests were usually associated with areas of past human disturbance. The distribution and abundance of THV and its importance as a determinant of the distribution of terrestrial forest mammals in Africa, particularly elephants and gorillas, has been discussed widely (Rogers and Williamson 1987; Carroll 1988a; Malenky and Stiles 1991; Wrangham *et al.* 1993; Malenky *et al.* 1994; White *et al.* 1995; Fay 1997).

While ubiquitous in its distribution, THV abundance was highest in the southeastern *terra firma* in the Likouala watershed, particularly in TF and MF. Interestingly this geographic trend was contrary to that of elephant fruit trees. Increasing abundance of THV with distance from water on *terra firma* has not previously been reported. The upland distribution of GDFH with its exceptional THV abundance may have had a strong impact on the strength of this correlation. THV is known to reach high abundance in some swamp habitats. Rogers and Williamson (1987) and Wrangham *et al.* (1993) hypothesised that THV stands may require an association with permanent water, which is true of several species. In this study, *Marantochloa cordifolia, M. purpurea, Trachyphrynium braunianum, Halopegia azurea*, *Thalia geniculata,* and at least two species of *Aframomum* were found only in aquatic or semi-aquatic habitats. These species had a very patchy distribution in swamps, and often reached extremely high local densities, most often in very open canopy permanently flooded areas.

The dominant THV family throughout *terra firma* was the Marantaceae, which was represented in 98.9% of understorey plots, followed by the Commelinaceae (53% of plots) and the Poaceae (17% of plots). Species of Zingiberaceae was scarce, in *terra firma*, and were only found commonly in light gaps and swamps. The family Zingiberaceae has been described as a major component of Marantaceae forest (Rogers and Williamson 1987; Malenky and Stiles 1991; Swaine 1992; Hawthorne 1994; White *et al.* 1995). In this study, species of Commelinaceae were more abundant, as was also shown by Fay (1997), who found Marantaceae stems were ca. 29 times more abundant than those of Zingiberaceae, but were only10 times more common than the Commelinaceae in the same region.

The grasses have usually been ignored in studies of the Central African forests, since most studies focus on species of nutritional importance for terrestrial primates in which grass is not a major component (Rogers and Williamson 1987; Malenky and Stiles 1991; White *et al.* 1995). In this study a single species, *Leptaspis cochleata*, was found throughout the forest in 17.3% of plots but was rarely common. Fay (1997) did not census grasses at the Ndakan study site, but did find *L. cochleata,* and speculated that grasses might reach high densities and provide an important food resource for mammals adapted to eat them, such as buffalo and elephants. Grasses were occasionally very abundant in restricted locations and habitats. Indeed, along the edges of large rivers such as the Ndoki and Motaba, and in light conditions in smaller rivers, dense floating mats of tall grasses (unidentified) often covered large areas and provided an enormous local food source frequently heavily grazed by elephants.

The Arecaceae was represented in 8% of plots. Again this family is not usually included in descriptions of the understorey of central African forests and it is difficult to judge its importance at other sites. Fay (1997) found it to be a poorly represented family at Ndakan with stems being more than 400 times less well represented than stems of Marantaceae. In the Ndoki Forest, palms of two types occur in super-abundance in restricted patches in swamps, the rattans and raffias. In the Likouala swamps traversed in this study, rattans (*Laccosperma* spp.) were locally abundant, and aerial surveys suggest that they are common throughout the swamps north of the *Terre de Kaboungas*. These stands often form impenetrable thickets and may be associated with Zingiberaceae. *Raphia* species may dominate vast areas of swamps in the northern Congo, including Ndoki, usually where soils are permanently flooded (Letouzey 1968; Blake *et al.* 1995). This genus was poorly represented in survey plots only being found in the extreme southeast. Aerial surveys (Blake, pers. obs.), and foot surveys (Blake *et al.* 1995) show that further south and east in the heart of the Likouala swamp basin large patches of mono-dominant *Raphia* spp. cover many square kilometres, and offer a huge quantity of potential elephant food.

The spatial aggregation between different food types varied depending on scale. Fruit trees were largely absent from swamps, and increased in density with distance from all permanent watercourses and with increasing canopy closure. On the contrary, dicot stem browse to non-browse ratio was higher in swamps than in *terra firma* and decreased with canopy closure. Terrestrial herbaceous vegetation was present in swamps but most abundant in *terra firma* forests to the southeast. These data suggest that vegetation structure would tend to partition elephants in space depending on which resources they were exploiting. When feeding on fruit they should be found in upland closed canopy *terra firma*; when browsing for dicotyledons they should be in light gaps and open canopy vegetation, and when feeding on THV they should tend to aggregate in uplands to the southeast. Spatial pattern also existed in vegetation structure at levels below that of the landscape, with a fine-grained partitioning of browse-rich and fruit-rich patches, presumably due to the mosaic of canopy types, watersheds, and other gross changes in vegetation structure. Why browse and THV correlated positively with fruit at larger spatial scales in *terra firma* is less clear, since it implies some higher forest structure of patches in which these resources vary together. In the case of browse and fruit, this may have been due to the patchiness of *G. deweveri* forests, which occurred at a scale in the range of 10km in which both fruit and browse abundance was low. An obvious pattern of spatial aggregation of THV and fruit trees was not evident.

Forest clearings

Two obvious flaws in the data collected on food availability are that ranks did not adequately quantify the actual amounts of food present, and that no data, even on relative food abundance, were collected from *bais*. Adequate quantitative comparison between diverse plant types such as trees, THV, and the sedges and aquatic herbs in clearings, would only be possible with detailed food biomass estimates, impossible in the context of this study. All three types of clearing provide high food availability for elephants, though yangas and endambas are probably the richest. Yangas were not present in the immediate study area being found most commonly to the southwest of the Ndoki forest. Endambas, which were usually between ca. 0.5-2ha, were a common feature in the swamps of larger rivers, and often contained a superabundance of edible herbs, particularly *Hydrocharis chevalieri* (Hydrocharitaceae).

Bais, which were aggregated in the northern part of the Ndoki forest, provided highly localised access to minerals, the importance of which will be discussed in Chapter 5 in relation to elephant feeding ecology and seasonal distribution. The largest of the monitored *bais*, Mingingi 1, which qualitatively also attracted the highest numbers of elephants, had significantly higher mineral concentrations in seep hole water than the smaller, apparently less frequented *bais*. Mineral concentration of standing water in *bais*, as measured by electrical conductivity, increased during low rainfall periods, which presumably increased mineral available to elephants.

Temporal phenology patterns in the Ndoki forest

PHENOPHASE OF LEAVES

Important in the interpretation of leaf phenology data in terms of the temporal change in leaf food quality for elephants was the difference in abundance of leaf classes of elephant versus non-elephant foods, which was different between monocotyledons and dicotyledons. Elephants selected dicotyledon species that had greater year round abundance of new and mature leaves and lower abundance of old leaves. By contrast, monocotyledon foods had lower abundance of new leaves no difference in mature leaves, and a lower abundance of old leaves. This was interpreted to be due to the difference in plant part selection between the two groups. Elephants usually ate leaves and terminal twigs of dicotyledon species, and stems, tuberous roots, and pith of most monocotyledon species (Chapter 3). New and presumably young mature leaves tend to be more nutritious and easy to digest than late mature and old leaves (above). New leaf production is however energetically expensive, and plants may draw on stored protein contained in tuberous root systems (Chapin *et al.* 1990), which may render roots less nutritious (Warembourg and Estelrich 2001).

At the intensive survey site, rainfall had no significant effect on the production of new leaves for either dicotyledons or monocotyledons, while mature and old leaves were positively correlated with rainfall for both plant types. Rainfall and its associated effects (humidity and soil moisture) are highly seasonal in many tropical forests and may have significant effects on leaf phenology. Alvim (1960) and Alvim and Alvim (1978) found that a minimum water stress level was required before increasing soil moisture resulted in flowering of coffee and leaf bud break in cocoa, thus promoting dry season new leaf production. By contrast, Reich and Borchert (1984) suggested that water stress in the wet tropics should inhibit new leaf production and enhance leaf senescence and leaf fall. In a study of two genera of understorey shrubs on Barro Colorado Island (BCI), Panama, Wright (1991), showed that irrigation advanced the timing of leaf production, providing contrary evidence to the water stress hypothesis. On BCI, the dry season is prolonged and intense relative to the Ndoki Forest, water stress is generally greater, and plant adaptations to it are presumably more advanced. In the Ndoki, all months experience some rainfall and even the lowest rainfall period (Dec-Feb) still maintains a mean of ca. 50mm per month.

There is apparently no published literature on the leaf phenology of understorey trees in Central Africa. Further east in Kibale Forest, Struhsaker (1997) studied phenological patterns in 14 species, though these were canopy trees. He found no consistent pattern in leaf production across all species, with some flushing during the wet season while others flushed at the height of the dry season. Within individual species there were consistent seasonal trends in leaf flush. In the Budongo Forest (geographically close to Kibale) (Fawcett 2000) found a bimodal pattern of forest wide new leaf flush in canopy trees at the beginning of the dry and wet seasons. Seasonal trends in phenology patterns in the tropics are more marked in canopy species than the understorey, where micro-climatic factors are usually more uniform (Richards 1996), and in temperate climates the two differ in their phenological response to environmental variables (Wittaker 1977).

Vegetative growth, as well as flower and fruit production, often occurs in short periods of high productivity, even if environmental conditions appear to be favourable for longer times during the year (Hopkins 1970; Wright 1991). Synchrony in leaf productivity may have evolved not only in response to maximising growth rates at favourable times of the year, but also as a response to herbivory (Aide 1988, 1993). Synchronous leaf production may occur at times when herbivore abundance is low, for instance during the dry season when insects are comparatively rare (Woldka 1978; Lowman 1992), or the strategy may be predator satiation at other times of year (Clark and Clark 1991; Leigh and Windsor 1996). That there was no marked peak in new leaf productivity in the Ndoki *terra firma* forest may indicate that understorey plants do not suffer greatly from water stress and/or herbivore pressure is either low or irregular. Long-term data show that variability between years and between species makes it almost impossible to generalise phenological patterns in tropical forests. Struhsaker (1997) characterised data from Kibale Forest along with those of Newstrom *et al.* (1994) from La Selva, Costa Rica, as highly diverse, complex, and unpredictable. His 14 year study showed that patterns of leaf production (in common with all other phenological characters) were 'neither uniform nor strictly seasonal', and leaf production was particularly irregular both across and within sites. The single year study from the Ndoki is a single datum in a highly variable system and should be interpreted accordingly.

FRUITFALL

This study showed high variability in the availability of fruit within and between years, which has now been demonstrated from a wide variety of sites from Asia, south America, and Africa (Alexandre 1980; Lieberman 1982; Leighton and Leighton 1983; Gautier-Hion *et al.* 1985a; Terborgh 1986; White 1994c; Powell 1997; Tutin and White 1998). The two-year extensive survey revealed that the number of fruiting events in the first two surveys was higher than that in the remaining 6 surveys combined. Both the extensive and intensive surveys showed a clear increase in fruit abundance with increasing rainfall. In the Lopé Reserve, Gabon, White (1994c) found a unimodal pattern of overall fruit production for both unripe and ripe fruits, but did not find a clear relationship with climatological factors, though a correlation did exist between insolation in the month preceding data collection and fruitfall abundance. There was also a correlation between rainfall three months preceding the month of the survey.

Powell (1997) concluded that there was large variation in fruit productivity across years in Cameroon, and suggested that pattern may exist over multiple year cycles. Struhsaker (1997) discussed the problem of trend detection in fruiting patterns in the Kibale Forest, and concluded that most species could produce fruit at any time of the year and under any rainfall regime. In analysing data collected over a minimum of 9 and a maximum of 13 years for 10 species, he claimed to have found four different patterns of fruit production in relation to rainfall but suggested that the determinants of fruiting in tropical forests were still largely unknown.

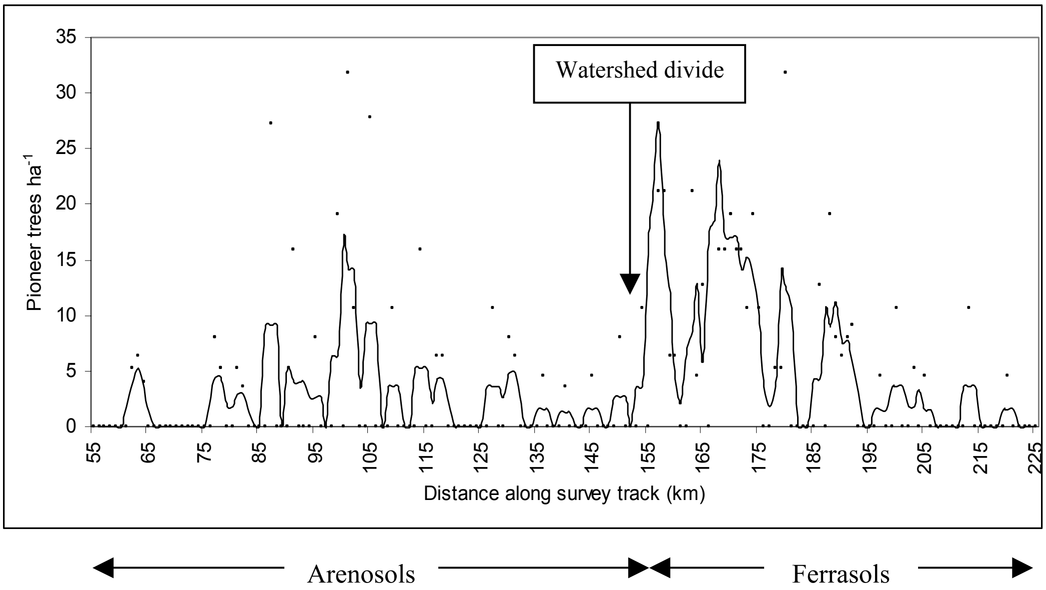
Despite these variable observations, studies do suggest that forest-wide fruit abundance is highest during high rainfall periods (Alexandre 1980; Lieberman 1982; Sourd and Gautier-Hion 1986; Van Schaik 1986; Gentry and Terborgh 1990; Powell 1997). Increases in fruit production also appear to occur during periods of increasing rainfall (Foster 1982; Terborgh 1983). Van Schaik *et al.* (1993) demonstrated that this relationship may be disrupted if the onset of the rainy season is too hard or too early, which prevents pollination and therefore reduces subsequent fruit production.

The El Niño Southern Oscillation (ENSO) is a major cause of inter-annual climate variation, and is known to influence phenological patterns in tropical forests. Wright (1999) found that on BCI, fruit followed a 2 year cycle of extremely high fruit production in response to ENSO, followed by extremely low productivity the following year, which may lead to periods of famine for frugivorous mammals (Foster 1982). In southeast Asia, patterns of mast fruiting in the Dipterocarpaceae, and forest-wide community fruit production peaks markedly during ENSO years (Curran *et al.* 1999; Wich and Van Schaik 2000). By contrast, in Kibale, the production of flowers, fruit, and young leaves of over 70% of species studied were negatively affected by the 1983 ENSO, while those of 1973 and 1976 apparently had no effect (Struhsaker 1997). The remarkably high level of fruit production seen in year 1 of this study was probably due to the ENSO event during that year, though long-term supportive data are unavailable.

Caesalpiniaceae, pioneers, Marantaceae, and forest composition across the Ndoki landscape

The respective distributions of Caesalpiniaceae, pioneer tree species and Marantaceae, and the association between *Terminalia superba* forest and high abundance of elephant fruit trees provokes discussion of forest history in the Ndoki as it relates to past human distribution and elephant abundance. Evidence from the Ituri forest of DRC suggests *G. deweveri* forests are less recently disturbed than other forest types (Hart *et al.* 1996; Hart 2001); and in general increasing abundance of the Caesalpiniaceae is thought to indicate increasing forest maturity (Germain and Evrard 1956; Gerard 1960). To the contrary, pioneer canopy species and heavy Marantaceae understorey forest indicate more recent disturbance. There was a clear spatial segregation of these taxa across the northwest-southeast gradient through the Ndoki Forest. The Caesalpiniaceae were more abundant in the north, with pioneer species and Marantaceae forest becoming most abundant near and to the south of the Sangha – Likouala watershed crest. It is particularly noteworthy that at almost exactly the location where pioneer species increased dramatically, there is a major soil change from poor fertility arenosols to the northwest and higher quality ferrasols to the southeast (FAO/UNESCO 1988) (Figure 2.30).

Figure 2.30. The distribution of pioneer trees on *terra firma* in relation to soil type and the Likouala Sangha watershed crest



Several possible mechanisms may result in Marantaceae forest formation, including fire (Hall and Swaine 1981; Swaine 1992; Hawthorne 1994), permanent water (Rogers and Williamson 1987; Wrangham *et al.* 1993), and natural disturbance such as wind-throw (Letouzey 1968). Anthropogenic factors including forest clearance through past human cultivation, forest colonisation of savannahs of anthropogenic origin, and even logging may be the most widespread determinant, and may over-ride edaphic factors (Aubreville 1967; Letouzey 1968; Carroll 1988a, b; Foresta 1990; White *et al.* 1995; Fay 1997; White 2001). Pioneer canopy species (particularly *T. superba, M. arboreus, M. excelsa, C. pentandra, T. scleroxylon*, *A. adanthifolia*, and *L. welwitchii*) in association with dense Marantaceae to the southeast of Ndoki, compared to the Caesalpiniaceae-rich forest further north, suggest either an underlying adaphic constraint on forest composition or past large scale disturbance to the south.

Fay (1997) found evidence that humans were widespread throughout the Ndoki Forest between ca. 2200 and 900BP from the distribution of oil palm nuts (*Elaeis guineensis*). In this study, Blake (pers. obs.) found living palm trees, an indicator of past human settlement, in open scrub-like forest on ferrasols in the Likouala basin in the heart of a large patch of *Terminalia* forest. Signs of rubber exploitation of *Funtumia elastica* trees during colonial times between the 1920's to the late '50's were also heavy in the Likouala aux Herbes river basin compared to the north. These indicators suggest heavier and more recent human activity in the Likouala basin compared to the north of the Ndoki Forest. Local people further south, on the *Terre de Kaboungas,* confirm that settlements existed in the area before colonial settlement was initiated. There is no oral history of similar human settlement in the deep forest away from major rivers to the north and centre of Ndoki. It is quite possible that these villages were responsible for widespread forest modification for agriculture, which would result in the pioneer/Marantaceae-rich forest mosaic observed.

The relevance of *Terminalia superba* and Marantaceae forests for elephants is clear, since they ranked first and second when elephant resource attributes were compared across vegetation types from this study (Table 2.8). While high browse ranks are easy to explain (open canopy, young forest), the exceptional abundance of fruit trees is more difficult, but a speculative hypothesis seems worth mentioning. In his discussion of pre-colonial human-elephant interactions in central African forests, Barnes (1999) described the forest as an elephant-dominated landscape with semi-permanent, shifting human settlements, creating a mosaic of secondary vegetation in their wake following every shift. This secondary forest which provided high browse availability, was attractive to elephants. Before firearms became widespread, elephants could exploit both human cultivation areas and abandoned fallow. The regeneration of these fallow areas would be dominated by pioneer tree species. However, if elephants were using these areas to forage, they would necessarily be disseminating seeds of fruit foods. If a portion of these seeds germinated and survived, the composition of the resulting forest would be dominated by pioneer and elephant fruit trees, which describes much of the forest to the southeast of Ndoki.

The northwest-southeast drainage gradient and soil change may also influence forest composition. It is recognised that the Caesalpinoid legumes are often associated with poor soils (Jansen 1974; Maisels and Gautier-Hion 1994; Richards 1996) possibly because of competitive advantage through their ability to fix soil nitrogen. While this may help explain their abundance to the north of the study site, it does not account for the dominance of pioneers to the south. The underlying edaphic conditions may, however, explain an underlying human distribution which led to a disturbance gradient from northwest to southeast. Human distribution in Africa, including the equatorial forests, is largely determined by soil fertility (Barnes 1997). In the Ndoki Forest away from the floodplains of major rivers, the poor quality arenosols to the north would make cultivation relatively difficult compared to the richer ferrasols to the southeast, which would favour agriculture and subsequent settlement. Thus, underlying edaphic properties may have led to a human distribution gradient, which resulted in a land use gradient, which led to the broad pattern of forest composition evident today. It is interesting that under this albeit speculative explanation, the richest forest for elephants was also the most recently disturbed by people.

Table 2.8. Vegetation types with ranks for elephant resource attributes quantified in this study (lower numbers mean higher ranks)

	Rank for each measure of resource availability				
Vegetation type	Fruit tree density	Mean fruit-fall	Dicotyledon foods	THV food abundance	Sum of ranks
TF	**1**	**2**	**1**	**2**	**6**
MF	3	4	5	6	18
MCF	2	1	10	10	23
MOF	4	3	9	7	23
GDFH	5	6	13	1	25
PAF	10	8	2	9	29
VF	9	5	8	8	30
LG	12	9	7	3	31
GDF	6	7	15	5	33
VS	8	12	4	13	37
GDFF	7	15	14	4	40
CF	10	10	11	12	43
VLS	14	16	3	11	44
SWP	13	17	6	14	50
FF	12	13	12	15	52

Caveats

The extensive survey route on much of the above data were collected was neither random nor systematic. Rather its location was based on logistical necessity imposed by the scale of the study area, the short time frame in which to collect phenology data under similar climatic conditions, and the hypothesis that elephants were capable of traversing the entire study region rapidly. A time widow of one month was judged to be the maximum period over which each survey could be conducted, so that data collected at the beginning and end of each survey could be compared. Sharp changes in rainfall over the time frame of a single month are infrequent in the Ndoki; thus the one-month survey duration was thought to minimise large-scale temporal fluctuations in climate within a single survey.

The non-random survey may have resulted in two sources of error or bias; failure to include all vegetation types in the sample, and a tendency to select closed canopy - open understorey habitats over open canopy – closed understorey habitats as a consequence of path of least resistance survey methods. The first source of error was minimised in three ways. First, a large number of previous extensive foot surveys throughout the region had failed to find novel vegetation types to those described in this study. Second, aerial surveys in the study area had also not revealed large areas of vegetation obviously different from those through which this survey passed. Third, landsat TM images of the region had been available several years before the survey began, and the final survey route was placed in order to traverse, usually several times, the distinguishable vegetation formations. Furthermore the survey route intentionally traversed a large number of watersheds, and the major drainage gradient across the study region.

The bias toward open understorey forests may have underestimated ground vegetation abundance and over-estimated large tree density. While the magnitude of this potential bias can only be measured through a comparative study using an un-biased random sampling protocol, qualitative observations suggest that errors were low. Nevertheless, extensive survey data are best considered as a quantitative assessment of vegetation characteristics along the 253km-survey route and quantitative extrapolations to the entire Ndoki Forest should be avoided.

When this study began a project to generate a vegetation map of the Ndoki Forest from satellite imagery and ground-based quantitative vegetation data was planned, in collaboration with the University of Maryland. Quantitative vegetation data would provide ground-truthing information for satellite image interpretation. However due to funding difficulties and time commitments of the personnel involved, the final vegetation map was not available for inclusion in this thesis. The project is on-going however, and once completed, the vegetation map will provide a comprehensive quantitative description vegetation distribution and a basis for mapping forest elephant resource relative availability throughout the region.

CONCLUSIONS

1. Within the Sterculiaceae-Ulmaceae forest of the Ndoki landscape was a heterogeneous matrix of vegetation, subjectively classified into over 20 types. The density and species diversity of canopy trees was lowest in swamp vegetation types. In *terra firma* forests, elephant fruit tree density increased with distance from watercourses. In the northeastern portion of the study site, trees in the family Caesalpiniaceae, including mono-dominant stands *of G. dewevrei,* were important components of vegetation. Pioneer species dominated *terra firma* to the southeast, increasing dramatically with a soil change from poor soils in the north, to richer soils in the Likouala aux Herbes basin. The density of important elephant fruit tree species was generally higher in the north compared to the south of the Ndoki Forest, however local densities were highest in patches of *Terminalia superba* forest found to the southeast. The density and diversity of all trees including elephant fruit tree species was particularly low in inundated vegetation types.
2. Among understorey dicotyledons, the ratio of elephant browse:non-browse stems was negatively correlated with canopy tree density. A notable exception to this trend was *Terminalia superba* forest, which contained both high canopy tree density and a high proportion of stems of browse species. The browse:non-browse ratio was also high in inundated forests and *terra firma* light gaps, but was lowest in mono-dominant *G. dewevrei* among *terra firma* forests.
3. A strong increase in the abundance of THV occurred from northwest to southeast, and with distance from the nearest river. However there was no clear relationship between canopy tree density and THV abundance. THV was most abundant in *terra firma forests*, followed by transition, and lowest in inundated vegetation types. In *terra firma* forest, both the number of species and the abundance of THV were highest in *G. deweverei with H. dankelmaniana* forest and *Terminalia superba* forest compared to other forest types.
4. Three types of clearing occurred in the Ndoki Forest, and all were associated with water. Endambas and yangas provided abundant aquatic and secondary browse foods, while *bais* were a source of dietary minerals for elephants. Endambas were found in the swamps of large rivers, and yangas, which were not directly encountered on the

survey route, were most abundant to the south of the NNNP. *Bais* were concentrated on the small headwaters of rivers to the northwest of the Ndoki Forest. Seep hole mineral concentration was highest during periods of lowest rainfall, and was also highest in active elephant drinking sites compared to inactive sites.

5. Monthly phenology data showed no effect of rainfall on the production of new leaves of either understorey dicotyledons or THV. However for both taxa, mature and old leaf abundance was positively correlated with rainfall, and with each other. Patterns of leaf production of elephant versus non-elephant food species in relation to rainfall were similar, however, among dicotyledons, elephant foods had consistently more new and mature leaves, and fewer old leaves than non-food species. Among THV food species, new leaves were consistently less abundant than for non-foods, while old leaves tended to be more abundant. Mature leaf abundance of THV was similar for both food and non-food species.
6. The abundance of elephant fruit foods was highly variable between seasons and between the same season in different years. Fruit abundance was higher during the first two extensive surveys than for the remaining 6 surveys combined. An El Niño Southern Oscillation event occurred during year 1 (1998), which was thought to account for the exceptional fruit production during the first two surveys. The number of elephant fruit species recorded during a single survey ranged from 19 to 42. Fruit was most abundant in *terra firma* forests, was rare in transition vegetation types, and was almost never recorded in inundated vegetation types. However, casual observations suggested that fruit abundance in the Likouala swamps can occasionally be high as a result of heavy fruiting by *Klainedoxa* sp.
7. In summary, fruit availability was generally highest in closed canopy *terra firma* forests during high rainfall periods. Dicotyledon browse was most available in open canopy *terra firma* forest and in swamps, and THV was most abundant in the southeast of the Ndoki Forest, and in locally super-abundant patches in swamps. Finally mineral availability in *bais* was highest to the northwest during low rainfall periods.

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CHAPTER 3. FOREST ELEPHANT FEEDING ECOLOGY

INTRODUCTION

The diet and feeding ecology of elephants (*L. a, africana*) in savannah habitats has been intensively studied for several decades, and is relatively well understood (Buss 1961; Napier-Bax and Sheldrick 1963; Field 1971; Laws *et al.* 1975; Williamson 1975; Field and Ross 1976; Guy 1976; Barnes 1982; Kalemera 1989; Ruggiero 1992; Tchamba 1996). The feeding habits of savannah elephants in forest habitats in eastern Africa have also been studied in some detail (Wing and Buss 1970; Struhsaker *et al.* 1996). These studies generally confirm that grasses dominate the diet during periods of high rainfall, with browse, wood, and bark becoming increasingly important when rainfall is low. Fruit consumption tends to be low since it is scarce in these habitats, though it is readily consumed when available (Wing and Buss 1970; Chapman *et al.* 1992).

The feeding ecology of elephants in forests, particularly in Central Africa, has been less well documented. Studies in west Africa (Alexandre 1978; Merz 1981; Short 1981; Tchamba and Seme 1993) and central Africa (White *et al.* 1993; Powell 1997) show that forest elephants have a highly varied diet of browse, bark, wood, roots, and fruit. Food lists have been produced from several sites, the most extensive being that from the Lopé Reserve, Gabon, where plant parts from 230 species are consumed (White *et al.* 1993). The importance of the vegetative parts of these species has not been quantified since direct evidence is difficult to obtain. Foods which leave tangible evidence such as seeds in dung, enable estimates of relative seasonal consumption of fruit to be made (Merz 1981; Short 1981; White *et al.* 1993; Powell 1997). Despite the lack of quantitative data, secondary woody growth, terrestrial herbaceous vegetation (THV), and fruits all appear to be important components of the diet, at least seasonally, and may influence elephant distribution and abundance (Short 1983; Merz 1986b; White 1994d; Powell 1997).

In Chapter 2, the distribution and availability of some important elephant food resources were described. The goal of this study was to quantify food selection by elephants, and feeding success within the vegetation mosaic of the Ndoki Forest described in Chapter 2, as a basis for determining ecological factors that might influence elephant distribution, ranging, and habitat preferences.

Specific objectives were to:

1. Produce a list of all plant species and plant parts consumed by elephants in the Ndoki forest
2. Quantify differences in food selection by life form and species by habitat type
3. Evaluate the browsing success of elephants in different vegetation types
4. Use these data to construct a set of hypotheses of how habitat attributes may be expected to influence forest elephant distribution, ranging, and habitat selection, which are described and tested in Chapters 5 and 6.

METHODS

Elephant feeding behaviour and food selection was almost impossible to observe directly in the forest even from distances of 5-10m, due to thick foliage and poor light levels. Also, elephants usually fled upon detecting an observer. Attempts to make direct observations were abandoned early in the study in favour of indirect methods. Three methods were used; opportunistic observations of feeding signs, fresh elephant trail follows, and dung analysis.

Opportunistic observations

To provide as comprehensive a food list as possible, throughout the study all feeding sign observed, of any age, which could be positively attributed to elephants, was recorded. For browse this necessarily involved only fresh or recent feeding with associated sign of elephants such as footprints, digging, or broken vegetation. For bark and wood, scarring of trees and chewed wood was usually distinctive, even when months or even years old. During seasonal elephant distribution surveys (Chapter 5), all signs of elephant feeding observed from the survey route and estimated to be fresh or recent were recorded. Positive identification of feeding remains was often difficult for several reasons including 1) elephants frequently pull up or damage plants without feeding on them, 2) gorillas, chimpanzees, and other animals feed on many of the same foods, 3) trampling and feeding often occurred together, particularly in swampy habitats, and it was impossible to tell which species or how much had been eaten. A site was positively identified as an elephant feeding site if fresh prints, dung or other positive indications of elephants such as rubbing or mud deposition were associated with the feeding sign, and of the same estimated age as the sign. Elephant tusk marks or obvious signs of leaf stripping using the trunk also allowed positive identification. Age of feeding sign was estimated based on experience of characteristics such as level of desiccation of leaves and bark, dryness of exudates, and associated sign such as footprints.

In the case of woody species, a single feeding event was defined as all feeding on an individual plant, regardless of plant parts consumed, though all parts consumed were also recorded. For herbs of both dicotyledons and monocotyledons, an event was defined as all the stems of a single species eaten that the elephant could reach without taking a step. The definition was different, since herbs are often found in dense clumps or thickets and 1) there was insufficient time to count every stem fed upon, and 2) many of the apparently separate plants in a clump of herbs are in fact the same individual. Consumption of different species from the same location was recorded as a separate event. The following information was recorded at each feeding site: estimated age (fresh [<24 hrs] or recent [24-48hrs]), plant species, plant part consumed (leaf, stem, bark, wood, roots, etc.), estimated amount consumed on a 1-4 scale (rare, few, moderate, and abundant).

Fresh elephant trail follows

Fresh elephant trails were followed opportunistically throughout the study when time permitted, and at a number of specific sites during the second year. Specific sites were 1) the Likouala swamps north of the *Terre de Kaboungas*, 2) *terra firma*-dominated forest within the NNNP, and 3) both inundated, transition, and *terra firma* vegetation along the Mokala and Lola Rivers to the north of the National Park. Methodology involved searching for fresh elephant tracks at each location and following them once encountered, with the assistance of Bayaka trackers. The number and the age/sex ratios (infants, juveniles, sub-adult and adult females, and bulls) of elephants in the group was estimated by the size of footprints and number of different sets of prints. Time, distance along the feeding trail (either measured using topofil or counting paces calibrated using topofil), vegetation change and all details of food selection and feeding behaviour were recorded as above. For quantitative analysis of inter-feeding site distances, only data from single sets of prints was followed.

Dung analysis

Both systematically and opportunistically throughout the study, the composition of fresh and recent undisturbed elephant dung piles was determined. Dung analysis followed the method described by White (1992), except that the diameter of the largest bolus across its widest axis was measured. The dung was then broken up using two small sticks and the contents examined for fibre, leaf, wood/bark, and fruit remains. The relative abundance of each food type was estimated using a four-point scale (rare, few, common, abundant). All identifiable fruit remains were recorded to species. All seeds were identified in the field where possible, and collections of unknowns were made and subsequently identified by Dr. David Harris of the Royal Botanic Gardens, Edinburgh. All seeds over ca. 1cm were counted, and for smaller seeds the relative abundance was estimated again on a four-point scale. To avoid biasing dung selection during fieldwork, the first two suitable (fresh and intact) dung piles found each day were analysed, and if there was time subsequently during the day, the next pile seen after a certain specified time was selected.

RESULTS

Food species selection by Ndoki elephants

Three hundred and fifty one different plant species from 73 families were consumed, which included 725 plant parts (leaves, bark, wood, stems, roots, and fruits). A further 126 samples of 298 plant parts, mostly clearly of different species, have yet to be identified. Results included here are restricted to known species. Leaf foods were most diverse, with 288 species recorded, followed by wood (small trunks, branches and terminal twigs) with 136 species in the diet (Figure 3.1). One hundred and twenty one species of bark foods were recorded. Elephants most frequently ate one or two plant parts per species, and the maximum of five parts consumed was recorded for six species.

Trees accounted for 45% of food plant species (Figure 3.2), monocotyledons came second with 23% of species, and lianas were ranked third with 16% of species. Ferns and dicotyledon herbs accounted for just 1% and 6% respectively of the total number of food species in the diet.

Figure 3.1. Number of species record for each food type

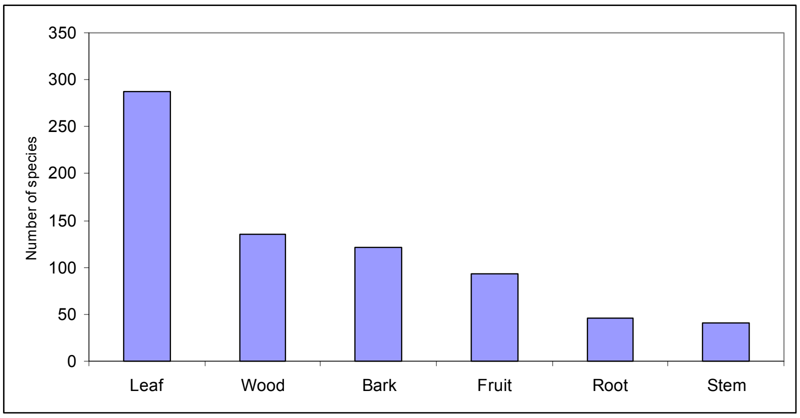
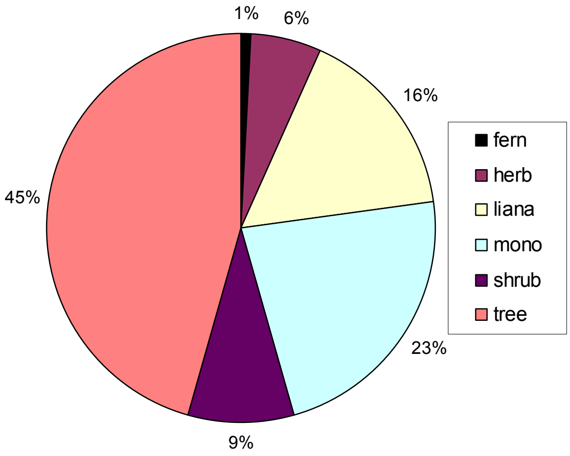


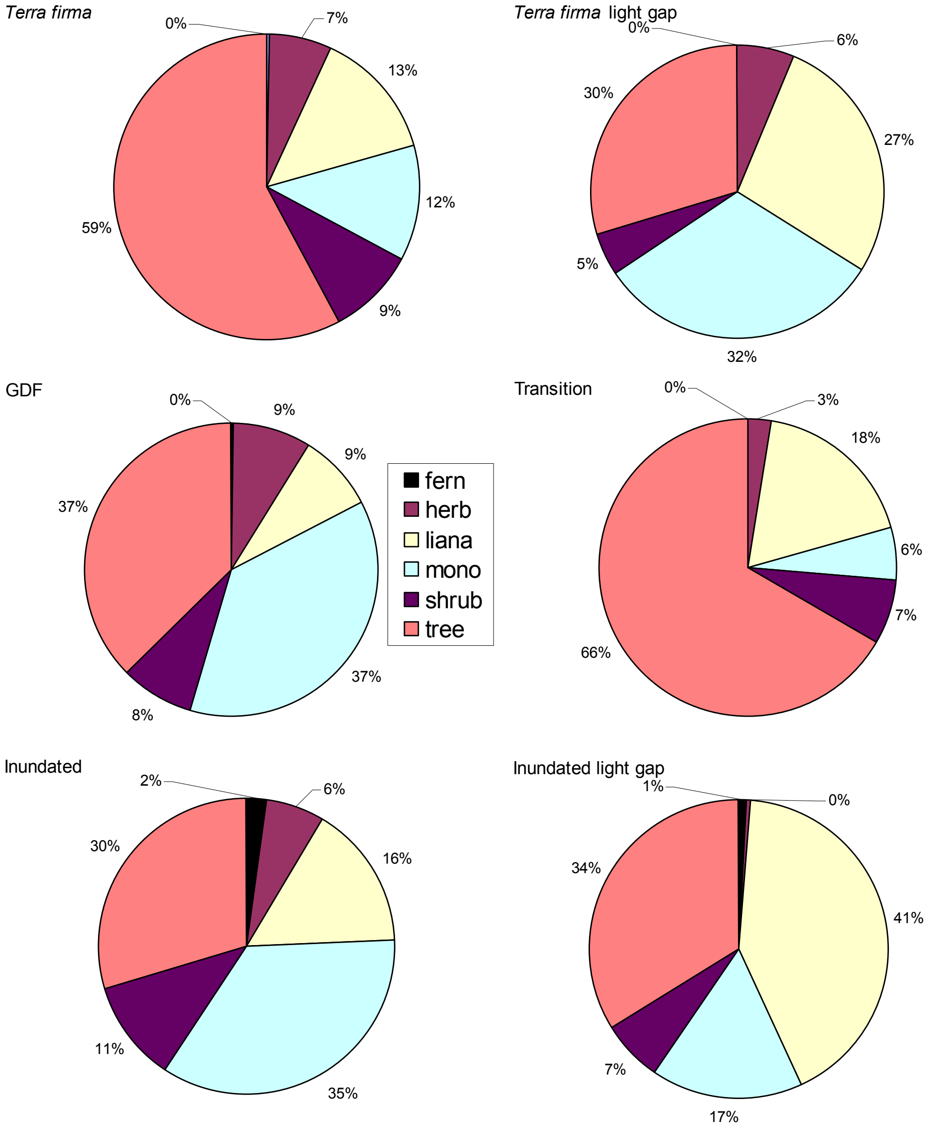
Figure 3.2. Species composition of forest elephant diet by plant life form
(% represents the percentage of each class of total number of SPECIES).



Plant life form selection by vegetation type

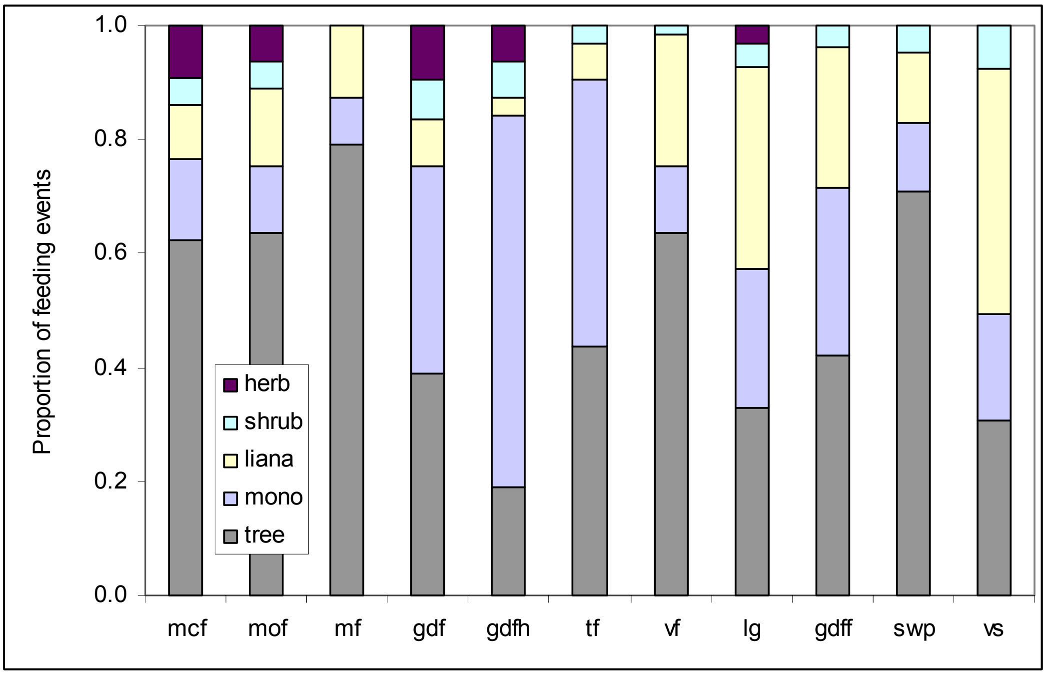
Figure 3.3 shows the relative percentages of each plant life form consumed in the major habitat types of *terra firma*, transition, inundated, *G. dewevrei* forest and light gap vegetation (Chapter 2), though light gaps have been divided into those in inundated and *terra firma* habitats. Trees accounted for the majority of plants selected in *terra firma* and transition habitats, in both of which trees were selected over three times more than any other plant life form. In GDF (for vegetation codes please refer to the list of acronyms at the beginning of this thesis), monocotyledons and trees accounted for equal proportions of feeding events (37%), with the other three main life forms approximately equally selected. In inundated habitats, trees were browsed upon comparatively rarely. Life form selection in light gaps both in *terra firma* and inundated habitats was different to non-light gap. In *terra firma* forest, tree selection in non-light gaps was double that in light gaps, while liana selection doubled in light gaps and monocotyledon feeding tripled. In inundated forest light gaps, the tree selection did not differ markedly from non-light gaps, while liana selection increased over 2.5 fold and monocotyledon selection decreased by half. Both herbs and shrubs were selected considerably less in inundated forest light gaps compared to non-light gaps.

Figure 3.3. Food selection by plant life form for general habitat types.



Plant life form selection also varied among more fine-grained vegetation types, and a number of examples are shown below (Figure 3.4). In *G. dewevrei* forests, monocotyledon selection increased from 36% of feeding sites in GDF to 66% in GDFH, while selection of trees and lianas dropped by ca. 50% from GDF to GDFH. Monocotyledon selection by vegetation type was highest in GDFH where they accounted for 66% of all feeding records. Trees dominated food selection in both mixed closed forest (MCF) and mixed open forest (MOF), with minor differences in feeding by plant life form between the two vegetation types. The proportion of trees in the diet was highest in both Marantaceae forest (MF) and swamp (SWP) vegetation (79 and 71% of records respectively), while monocotyledons made up just 8% of feeding events in MF. In *Terminalia superba* forest (TF), the majority of all feeding events recorded (47%) was of monocotyledons. Interestingly in vine forest (VF), the majority of feeding events were of trees (66.2%), with liana feeding accounting for 22.9%. Between SWP and vine swamp (VS) there was a decrease in tree selection from 71% to 31%, and an increase in liana (12% to 42%) and monocotyledon (12% to 19%) feeding, but little change in herb selection. Differences in the proportions of trees, monocotyledons, and lianas selected were highly significant between vegetation type (χ^2_{trees} = 114.19, df = 14, P < 0.0001; χ^2_{mono} = 219.59, df = 14, P < 0.0001; χ^2_{liana} = 119.0, df = 14, P < 0.0001).

Figure 3.4. Plant life from selection by vegetation type



Plant part selection by life form

Elephants selected leaves from trees and lianas in similar proportions (Table 3.1), while woody material was selected more heavily from lianas than trees. It was often apparent that elephants strongly selected liana wood, particularly species with soft, high water content trunks (e.g. *Cissus* spp.). They tended to select trunks for only a few species of tree, notably *Thomandersia laurifolia*, *Chytranthus* sp., *Cola chlamydantha*, and small individuals of *Fagara* spp. Shrub part selection was dominated by leaves, and leaf+wood (usually terminal twigs). Leaf selection was much lower for monocotyledon foods than any of the dicotyledon life forms, representing 25.0% of monocotyledon feeding records. However, leaves with stems were selected on 37.1% of occasions increasing the total for all feeding involving leaves to 62.1%. Roots made up 25.2% of monocotyledon feeding records whereas in woody species roots accounted for a maximum of only 1.7%. Pith from plants of a single family - the Arecaceae - was consumed heavily. While this plant part made up only 4.0% of feeding records, these were often extremely heavy feeding bouts on the pith of large *Raphia* spp. palms or *Elaeis guineensis* (oil palms), and food intake was often exceptionally high (Figure 3.5).

Table 3.1. Plant part selection by plant life form

	Percentage of feeding events			
Plant part	Trees	Lianas	Shrubs	THV
Bark	24.8	7.3		
Leaf	59.9	52.9	82.6	25.0
Leaf+wood/ Leaf+stem	10.9	31.8	14.6	37.1
Root	1.7	1.3	0.7	25.2
Wood	2.7	6.7	2.1	
Stem				3.5
Pith				4.0
Whole plant				5.2
Total	100.0	100.0	100.0	100.0

Figure 3.5. Evidence of elephant feeding on oil palm (*Elaeis guineensis*) pith

Food species selection by vegetation type

The highest recorded food species diversity was in *terra firma* forests with 233 species, and the lowest (78 species) was in *terra firma* light gaps. These values are both a product of the diversity of the diet and habitat type, but also sample size, which varied between habitat types. In *terra firma* light gaps sample size was nearly half that recorded in *terra firma* forest, and thus estimating diversity of food selection between vegetation types is problematic. In several habitat types, food selection was dominated by one or more species. For example, in Transition forest *Thomandersia laurifolia* made up ca. 17.2% of records, 2.3% more than the second most highly recorded species, *Strombosiopsis tetrandra*, which accounted for 14.9% of all feeding signs, while the third highest ranked species made up just 4.5% of records (Table 3.2). A similar pattern occurred in GDF and *Terra firma* LG where the most heavily selected species accounted for 22.6 and 19.9% of sign respectively. In inundated LG, the most commonly eaten species, *Manneophyton fulvum*, was selected twice as frequently as *Palisota ambigua*. Only in *terra firma* mixed forests and inundated habitat types, was there no clear dominance of a single, or pair, of species in elephant food choice.

Several species were common to the 10 most frequently selected species across all habitat types; *Thomandersia laurifolia* was found in all, and was top ranked species in 3 habitats. The monocotyledons, *Palisota brachythyrsa* and *P. ambigua* were found in the top 3 species in 3 habitat types, including both types of light gap, as was *Manneophyton fulvum*, which was top ranked in inundated light gaps. A number of species were also specific to particular habitats, the most obvious being the deep swamp specialists such as *Hydrocharis chevalieri,* the unknown species *Mokoubou*, *Cystosperma senagelensis*, and *Sterculia subviolacea*. Likewise, a number of species frequently selected in *terra firma* habitats were not present in inundated areas including *Whitfieldia elongata*, *Petersianthus macropcarpus*, *Strombosiopsis tetrandra*, *Microdesmis puberula*, and *Funtumia elastica*.

By vegetation type, species dominance in the diet ranged from a maximum of 18.8% (*Ataenidia conferta* in GDFH), 17.2% for *T. laurifolia* in VF, and 17.2% for *A. conferta* in TF, to a low of 5.5% of all records for *T. laurifolia* in VS (Table 3.3). *Thomandersia laurifolia* was the dominant food species in 3 vegetation types, and was recorded in the top 10 in 7 of the 10 vegetation types shown in Table 3.3. *Whitfieldia elongata* was in the top 10 in 7 vegetation types, but absent from inundated habitats. *Garcinia punctata* was in the top 10 food species in 4 of the 10 vegetation types. There was a high degree of consistency in species selection for browse in similar vegetation types. Mixed Open Forest and MCF shared 7 species in the top 10, and in GDF and GDFH 6 species were common to both. *Raphia* spp. swamp was peculiar in that no food species in the top 10 was found in the top 10 of any other vegetation type. This vegetation type is restricted to deep permanently flooded areas with a specialised flora (Chapter 2).

Table 3.2. Top 10 species recorded from fresh feeding signs by major habitat type

M = monocotyledon, D = dicotyledon

Terra firma forest					*Terra firma* LG				
Rank		Species	N	% of total	Rank		Species	N	% of total
1	D	*Thomandersia laurifolia*	94	8.0	1	M	*Palisota ambigua*	18	10.5
2	D	*Whitfieldia elongata*	74	6.3	2	M	*Palisota brachythyrsa*	16	9.4
3	M	*Ataenidia conferta*	59	5.0	3	D	*Whitfieldia elongata*	11	6.4
4	D	*Petersianthus macrocarpus*	53	4.5	4	D	*Manneophyton fulvum*	9	5.3
5	D	*Strombosiopsis tetrandra*	47	4.0	5	M	*Megaphrynium macrostachyum*	9	5.3
6	D	*Microdesmis puberula*	37	3.1	6	D	*Connaraceae sp.*	5	2.9
7	D	*Garcinia punctata*	26	2.2	7	D	*Thomandersia laurifolia*	4	2.3
8	D	*Manilkara mabokeensis*	23	2.0	8	D	*Plaglostyles africana*	4	2.3
9	D	*Landolphia* sp.	21	1.8	9	D	*Cola urceolata*	4	2.3
10	M	*Palisota brachythyrsa*	19	1.6	10	D	*Funtumia elastica*	3	1.8
		Top 10 as % of total species		38.6			Top 10 as % of total species		48.5
		N species		233			N species		78
		N records		1175			N records		171
G. dewevrei (*terra firma*)					Transition				
Rank		Species	N	% of total	Rank		Species	N	% of total
1	M	*Palisota ambigua*	39	11.9	1	D	*Thomandersia laurifolia*	53	17.2
2	M	*Palisota brachythyrsa*	35	10.7	2	D	*Strombosiopsis tetrandra*	46	14.9
3	D	*Whitfieldia elongata*	26	7.9	3	D	*Garcinia ovalifolia*	14	4.5
4	M	*Ataenidia conferta*	15	4.6	4	D	*Cola urceolata*	11	3.6
5	D	*Bartiera sp.*	14	4.3	5	D	*Manniophyton fulvum*	9	2.9
6	D	*Thomandersia laurifolia*	13	4.0	6	D	*Whitfieldia elongata*	7	2.3
7	M	*Sarcophrynium sp.*	12	3.7	7	D	*Landolphia sp.*	6	1.9
8	M	*Marantochloa filipes*	8	2.4	8	D	*Loeseneriella apiculata*	5	1.6
9	D	*Chytranthus* sp.	7	2.1	9	D	*Garcinia punctata*	5	1.6
10	D	*Garcinia punctata*	6	1.8	10	D	*Mitragyna stipulosa*	5	1.6
		Top 10 as % of total species		53.4			Top 10 as % of total species		52.3
		N species		99			N species		113
		N records		328			N records		308
Inundated					Inundated LG				
Rank		Species	N	% of total	Rank		Species	N	% of total
1	D	*Thomandersia laurifolia*	37	4.4	1	D	*Manniophyton fulvum*	22	10.4
2	M	*Commelina sp.*	37	4.4	2	M	*Palisota ambigua*	11	5.2
3	M	*Cystosperma senegalense*	36	4.3	3	M	*Palisota brachythyrsa*	11	5.2
4	D	*Landa na mai*	31	3.7	4	D	*Cola urceolata*	11	5.2
5	M	Poaceae 1	28	3.3	5	D	*Macaranga staudtii*	9	4.2
6	D	*Mokoubou*	26	3.1	6	D	*Thomandersia laurifolia*	6	2.8
7	M	*Hydrocharis chevalieri*	24	2.9	7	D	*Christiana africana*	6	2.8
8	D	*Sterculia subviolacea*	24	2.9	8	D	*Efoua*	4	1.9
9	M	*Rhynchospora corymbosa*	23	2.8	9	D	*Strophanthus* sp.	4	1.9
10	M	Poaceae 2	23	2.8	10	D	*Alchornea cordifolia*	4	1.9
		Top 10 as % of total species		34.6			Top 10 as % of total species		41.5
		N species		159			N species		92
		N records		796			N records		212

Table 3.3. Top 10 most important food species by vegetation type

M = monocotyledon, D = dicotyledon

Mixed open forest					Mixed closed forest				
Rank		Species	N	% of total	Rank		Species	N	% of total
1	D	*Thomandersia laurifolia*	71	10.2	1	D	*Whitfieldia elongata*	29	7.6
2	D	*Whitfieldia elongata*	43	6.2	2	D	*Thomandersia laurifolia*	21	5.5
3	D	*Strombosiopsis tetrandra*	35	5.0	3	M	*Ataenidia conferta*	18	4.7
4	D	*Petersianthus macrocarpus*	34	4.9	4	D	*Landolphia sp.*	15	3.9
5	M	*Ataenidia conferta*	29	4.2	5	D	*Petersianthus macrocarpus*	15	3.9
6	D	*Microdesmis puberula*	20	2.9	6	D	*Microdesmis puberula*	14	3.7
7	D	*Garcinia punctata*	13	1.9	7	D	*Cola urceolata*	13	3.4
8	D	*Manilkara mabokeensis*	13	1.9	8	D	*Autranella congolensis*	11	2.9
9	D	*Garcinia ovalifolia*	12	1.7	9	D	*Garcinia punctata*	10	2.6
10	D	*Dalhouisea africana*	11	1.6	10	D	*Manilkara mabokeensis*	10	2.6
		Top 10 as % of total species		40.4			Top 10 as % of total species		40.9
		N species		182			N species		133
		N records		695			N records		381
G. dewevrei forest					*G. dewevrei* with *H. dankelmaniana*				
Rank		Species	N	% of total	Rank		Species	N	% of total
1	M	*Palisota ambigua*	29	11.0	1	M	*Ataenidia conferta*	12	18.8
2	D	*Palisota brachythyrsa*	25	9.5	2	D	*Palisota ambigua*	10	15.6
3	D	*Whitfieldia elongata*	22	8.3	3	M	*Palisota brachythyrsa*	10	15.6
4	D	*Thomandersia laurifolia*	13	4.9	4	D	*Whitfieldia elongata*	4	6.3
5	D	*Bartiera sp.*	11	4.2	5	D	*Bartiera* sp.	3	4.7
6	M	*Sarcophrynium sp.*	9	3.4	6	D	*Chytranthus sp.*	3	4.7
7	D	*Gilbertiodendron dewevrei*	6	2.3	7	M	*Megaphrynium macrostachyum*	3	4.7
8	D	*Garcinia punctata*	6	2.3	8	M	*Sarcophrynium* sp.	3	4.7
9	M	*Marantochloa filipes*	6	2.27	9	D	*Colletoecema dewevrei*	2	3.1
10	M	*G. punctata*	6	2.3	10	M	*Marantochloa filipes*	2	3.1
		Top 10 as % of total species		50.4			Top 10 as % of total species		81.3
		N species		96			N species		21
		N records		264			N records		62
Terminalia superba forest					Marantaceae forest				
Rank		Species	N	% of total	Rank		Species	N	% of total
1	M	*Ataenidia conferta*	11	17.2	1	M	*Palisota brachythyrsa*	4	8.9
2	M	*Megaphrynium macrostachyum*	4	6.3	2	D	*Garcinia punctata*	3	6.7
3	M	*Sarcophrynium* sp.	4	6.3	3	D	*Thomandersia laurifolia*	2	4.4
4	D	*Strombosiopsis tetrandra*	3	4.7	4	D	*Antrocaryon micraster*	2	4.4
5	D	*Millettia sanagana*	3	4.7	5	D	*Cleistopholis patens*	2	4.4
6	D	*Whitfieldia elongata*	2	3.1	6	D	*Macaranga* sp.	2	4.4
7	D	*Polyalthia suaveolens*	2	3.1	7	D	*Microdesmis puberula*	2	4.4
8	D	*Ceiba pentandra*	2	3.1	8	D	*Brenania brieyi*	2	4.4
9	D	*Cola urceolata*	2	3.1	9	D	*Trichoscypha acuminata*	1	2.2
10	D	*Duboscia macrocarpa*	2	3.1	10	D	*Tabernaemontana penduliflora*	1	2.2
		Top 10 as % of total species		54.7			Top 10 as % of total species		46.7
		N species		23			N species		34
		N records		48			N records		45

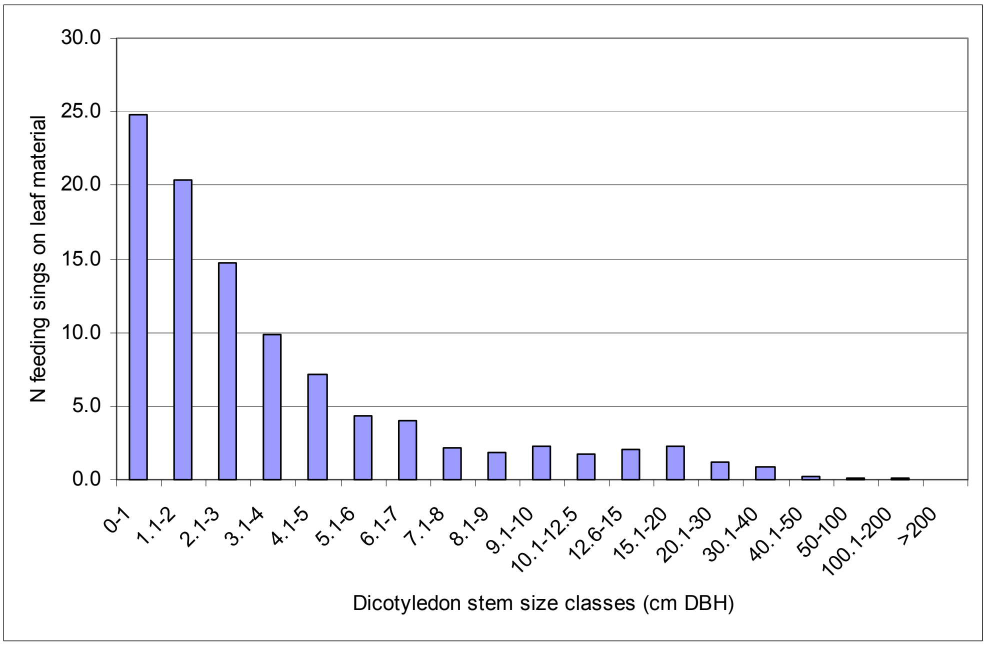
Table 3.3. contd.

Light Gap					Vine forest				
Rank		Species	N	% of total	Rank		Species	N	% of total
1	M	*Palisota ambigua*	18	11.0	1	D	*Thomandersia laurifolia*	27	17.4
2	M	*Palisota brachythyrsa*	16	9.8	2	D	*Landolphia sp.*	6	3.9
3	D	*Whitfieldia elongata*	11	6.7	3	D	*Manniophyton fulvum*	6	3.9
4	D	*Manniophyton fulvum*	9	5.5	4	D	*Strombosiopsis tetrandra*	6	3.9
5	M	*Megaphrynium macrostachyum*	9	5.5	5	D	*Loeseneriella apiculata*	5	3.2
6	D	*Thomandersia laurifolia*	4	2.4	6	D	*Garcinia ovalifolia*	5	3.2
7	M	*Connaraceae* sp.	4	2.4	7	D	*Cola urceolata*	5	3.2
8	D	*Plagiostyles africana*	4	2.4	8	D	*Whitfieldia elongata*	3	1.9
9	D	*Cola urceolata*	4	2.4	9	D	*Leptoderris* sp. 2	3	1.9
10	D	*Funtumia elastica*	3	1.8	10	D	*Mitragyna stipulosa*	3	1.9
		Top 10 as % of total species		50.0			Top 10 as % of total species		44.52
		N species		74			N species		79
		N records		164			N records		155
Vine swamp					*Raphia* spp. swamp				
Rank		Species	N	% of total	Rank		Species	N	% of total
1	D	*Thomandersia laurifolia*	5	5.5	1	M	*Cystosperma senegalense*	23	11.5
2	D	*Leptoderris sp. 1*	5	5.5	2	D	*Mokoubou*	20	10.0
3	D	sb 359	5	5.5	3	M	*Raphia* sp.	16	8.0
4	M	*Halopegia azurea*	4	4.4	4	D	*Olax subscorpioidea*	14	7.0
5	D	*Papilionaceae unk.*	3	3.3	5	D	*Sterculia subviolacea*	13	6.5
6	D	*Cola urceolata*	3	3.3	6	D	*Ina*	10	5.0
7	D	sb 363	3	3.3	7	M	*Commelina* sp.	10	5.0
8	M	*Sarcophrynium sp.*	3	3.3	8	M	*Rhynchospora corymbosa*	7	3.5
9	D	*Efoua*	2	2.2	9	D	*Landa na mai*	6	3.0
10	D	*Manniophyton fulvum*	2	2.2	10	D	*Drypetes* sp.	6	3.0
		Top 10 as % of total species		38.5			Top 10 as % of total species		62.5
		N species		54			N species		49
		N records		91			N records		200

Browse selection by size class for woody trees and shrubs

Data were collected on the size class of browsed trees and shrubs from a total of 2020 stems. The most heavily browsed size class was also the smallest with stems of less than 1cm accounting for 24.8% of all records (Figure 3.6). There was a consistent decrease in browse rates with increasing stem size. Stems of 10cm dbh or less made up 91.5% of records.

Figure 3.6. Browse selection by stem size class (dbh)



Feeding on bark

Elephants fed on at least 121 species of bark from 36 families in the Ndoki Forest. Thirteen species of Sapotaceae, and 11 species of Caesalpiniaceae were consumed with the top 10 families accounting for 63% of all species. The majority of feeding signs were trees, but a number of lianas were also stripped. Elephants usually picked pieces of bark from trees with their tusks though occasionally on smaller trees they would strip it with their teeth. Depending on the species, bark either broke off in plaques (e.g. *Ceiba pentandra*), small granular pieces (Panda oleosa), fibrous tufts (*Petersianthus macrocarpus*) or long strips sometimes up to ca. 10m up the trunk of large trees (e.g. *Pachypodanthium* sp., *Oxystigma oxyphyllum*). Usually bark was eaten in small quantities (e.g. 5 x 5 cm to 10 x 10 cm or smaller); however occasionally an elephant would take huge quantities up to several square metres in a single feeding bout in the case of species such as *Ceiba pentandra*.

Data to quantify bark feeding and rates of species selection on large trees were collected during a study of the distribution of trees >40 dbh in relation to elephant trails (Chapter 6). A total of 435 individual trees over 50cm DBH out of 5689 individuals enumerated (7.65%) showed signs of bark feeding by elephants, representing 56 species out of a total of 166 species identified (34.13% of species) (Table 3.4). The top section of Table 3.4 shows scarring rates for those species in which 10 or more individuals were enumerated. Of this selection, the most commonly barked species was *Autranella congolensis,* for which nearly 65% of individuals were scarred, and in 4 species 50% or more individuals showed signs of bark feeding. Elephants appeared to prefer soft or fibrous barks to hard or siliceous barks. Bark feeding rates were often very different in closely related species. Among *Entandrophragma* species, *E. utile* was frequently fed upon, while *E. cylindricum* was not recorded as food on a single occasion through the study. Similarly, *Strombosiopsis tetrandra* and *Sterculia subviolacea* was heavily exploited, while *Strombosia pustulata* was never recorded and *Sterculia tragecantha* was rarely seen scarred. In these and most other similar examples the non-preferred species had thinner, harder bark than the preferred species.

Table 3.4. Bark scarring rates of trees >40cm dbh

Species	Heavy	Moderate	Few	Rare	N trees enumerated	N trees scarred	% trees scarred
Autranella congolensis	11				17	11	64.7
Pachyelasma tessmannii	9	3	1		21	13	61.9
Panda oleosa	31	10	10		88	51	58.0
Gambeya beguei	4	3	2	1	19	10	52.6
Mammea africana	11	4	3		39	18	46.2
Detarium macrocarpum	7	1	1		20	9	45.0
Pteliopsis hylodendron	9	4	2	1	37	16	43.2
Strombosiopsis tetrandra	25	16	19	5	174	65	37.4
Petersianthus macrocarpus	20	10	15	5	150	50	33.3
Syzygium sp.	1	1	3		15	5	33.3
Treculia africana	1		4		15	5	33.3
Oxystigma oxyphyllum	14	1	6	1	71	22	31.0
Manilkara mabokeensis	5	12	36	9	239	62	25.9
Entandrophragma utile	1	1	1		12	3	25.0
Triplochiton scleroxylon	4				19	4	21.1
Albizia ferruginea	1	1	1		17	3	17.6
Gambeya boukokoensis		3	1		23	4	17.4
Gambeya lacourtiana		1	1	2	24	4	16.7
Pentaclethra macrophylla	4	1	2	1	52	8	15.4
Tessmannia anomala		1	2		20	3	15.0
Entandrophragma angolense	1		2		22	3	13.6
Macaranga barteri		4	2		50	6	12.0
Tetrapleura tetraptera	1			1	17	2	11.8
Amphimas sp.		1	1		26	2	7.7
Drypetes sp.	1				22	1	4.5
Xylopia hypolampra	1	1	1		68	3	4.4
Duboscia spp.	3	1	4	1	275	9	3.3
Nesogordonia sp.	1		1		73	2	2.7
Alstonia boonei		1			39	1	2.6
Drypetes gossweileri			1		39	1	2.6
Tessmannia africana		1			39	1	2.6
Celtis adolphi-frederici		2			84	2	2.4
Synsepalum sp.			1		46	1	2.2
Irvingia grandifolia		1			47	1	2.1
Annonidium mannii			3	3	333	6	1.8
Blighia welwitschii			1		56	1	1.8
Sterculia gigantea	1				59	1	1.7
Irvingia excelsa		1			93	1	1.1
Angylocalyx pinaertii	1				101	1	1.0
Gilbertiodendron dewevrei	3			1	605	4	0.7
Celtis spp.		1			177	1	0.6

(Table 3.4 contd)

Species	Heavy	Moderate	Few	Rare	N trees enumerated	N trees scarred	% scarred
Antrocaryon micraster	1				1		100.0
Donella pruniformis	3				5	3	60.0
Hannoa klaineana		1			2	1	50.0
Parkia bicolor	1				2	1	50.0
Tridesmostemon omphalocarpoides	1	1			6	2	33.3
Guenya unk. sp.	1				3	1	33.3
Xylopia staudtii		1	1		8	2	25.0
Omphalocarpum elatum			1		4	1	25.0
Stemonocoleus micranthus		1			4	1	25.0
Sterculia tragecantha		1			4	1	25.0
Anacardiaceae sp. *boudoundou*			1		5	1	20.0
Meliaceae sp. *Bombondo*			1		5	1	20.0
Cleistopholis sp.			1		5	1	20.0
Allanblackia floribunda	1				6	1	16.7
Antiaris sp.	1				7	1	14.3

Elephant foraging rates in different vegetation types

Three complimentary datasets were collected to estimate elephant foraging rates (number of feeding events per kilometre of linear distance walked by one elephant) in different vegetation types. The effect of permanent elephant trails on foraging rate was also investigated. Three study areas were selected: 1) the Mokala-Lola swamps and adjacent *terra-firma* forest, 2) the Likouala swamps from the Bodingo Peninsula to the *Terre de Kaboungas*, 3) throughout the NNNP but usually within 10km of a *bai*. Foraging included all non-fruit food feeding sites, since it was rarely possible to positively identify a fruit-feeding site from indirect evidence. Table 3.5 summarises data collected from a total of 114km of fresh elephant trail follows.

Table 3.5. Survey effort and summary foraging rates in the three study areas.

Study area	N trail follows	Distance (km)	Mean trail length (km) (SD)	Feeding events	**Feeding events km^{-1}**
Likouala swamps	49	24.425	0.498 (0.820)	375	**15.35**
NNNP	53	71.404	1.347 (1.255)	425	**5.95**
Lola/Mokala River	30	18.2	0.606 (0.633)	742	**40.77**
Total/mean	132	114.029	0.86	1542	**13.52**

In the Likouala swamps, the level of flooding (up to 1.5m) meant it was impossible to distinguish permanent trails from non-trails in most cases, and data below are presented by vegetation type alone.

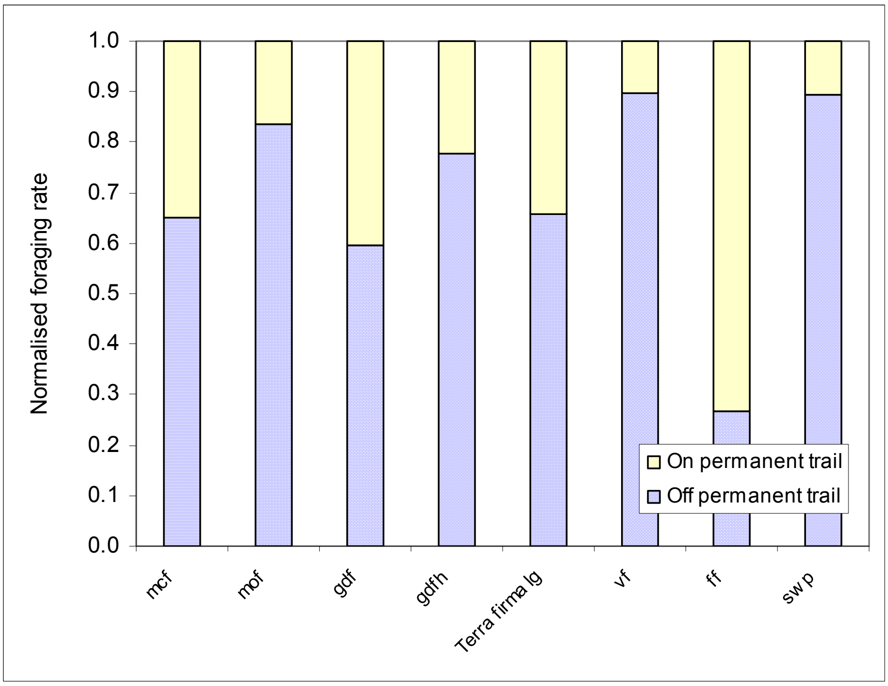
Table 3.6. The influence of vegetation type and permanent elephant trails on foraging rate

	Likouala swamps		National Park				Lola/Mokala River			
Vegetation type			Off trail*		On trail		Off trail		On trail	
	FR	km	FR	km	FR	km	FR	km	FR	km
Mixed Closed Forest			7.0	3.72	3.7	20.47	26.5	3.28	14.3	2.72
Mixed Open Forest			13.6	5.60	4.2	18.32	39.3	1.65	6.2	0.16
G. deweveri Forest	0.0	1.43	14.6	2.67	6.1	13.6	23.7	0.46	20.0	0.85
G. deweveri Forest with *H. dankelmaniana*			22.2	1.17	6.3	1.76				
Terra Firma Light Gap			55.1	1.22	18.2	1.92			10.3	0.10
Vine Forest	9.6	0.52	136.4	0.05	11.2	0.09	27.3	0.74	7.6	1.57
Terminalia superba Forest							49.6	0.27		
Cleistanthus sp. Forest	7.1	0.7								
Low Closed Scrub										
G. dewevrei Flooded Forest	8.8	9.29								
Vine Swamp	11.1	5.75								
Vine/*Laccosperma* sp. Swamp	8.6	0.82								
Flooded Forest	7.7	0.77					28.3	0.71	77.2	0.30
Lophira alata Flooded Forest	0.0	0.42								
Swamp			25.0	0.08			147.0	0.30	20.3	2.46
Raphia sp. Swamp							366.2	0.29		
Stream							193.4	0.77		
Sterculia sp. Flooded Forest							132.8	0.60	0.0	0.18
Inundated Light Gap	44.7	4.29					99.0	0.14		
Vine/*Laccosperma* sp. Forest										
Aframomum sp Light Gap	87	0.06								

* = on or off permanent elephant trails
FR = foraging rate (number of feeding events per kilometre)
Km = number of kilometres of trails followed

Foraging rates varied considerably across sites and between vegetation types (Tables 3.5 and 3.6). Several points are noteworthy. Firstly was the exceptionally high foraging rates in swamp forests of the Mokala/Lola Rivers compared to any other vegetation type, which reached a maximum of 366.2km^{-1} in *Raphia* sp. swamp. The total distance surveyed was low in each of these habitats, but pooling the data and calculating the mean foraging rate in swamp, *Raphia* swamp, *Sterculia* sp. flooded forest, and inundated light gaps gave a mean rate of 193.4 feeding events per km for a sample distance of 1.93km. Secondly, foraging rates off permanent trails in mixed species *terra firma* forests at the Lola/Mokala site were more than double the rates within the NNNP *terra firma*, and 1.6 times higher in *G. dewevrei* forest. Thirdly, in the National Park, the foraging rate in light gaps was over double that in any other vegetation type which has a moderate or large sampled distance (vine forest clearly had the highest observed rate, but only 50m of trails was surveyed). Fourth, foraging rates in the Likouala swamps were an order of magnitude lower than rates in the Lola/Mokala swamps, but were comparable with the rate in *terra firma* forests off trails within the park. A fifth point of particular interest was the significant negative effect of permanent elephant trails on foraging rate when comparisons were made across all sites and vegetation types for which data were available (Sign test: negative differences = 11, positive differences = 1, P = 0.006) (Table 3.6 and Figure 3.7). The most profitable foraging areas identified from this study therefore, were the Lola/Mokala swamps, particularly *Raphia* sp. swamp, inundated and *terra firma* light gaps, and profitability was greatly increased when elephants were not on permanent trails.

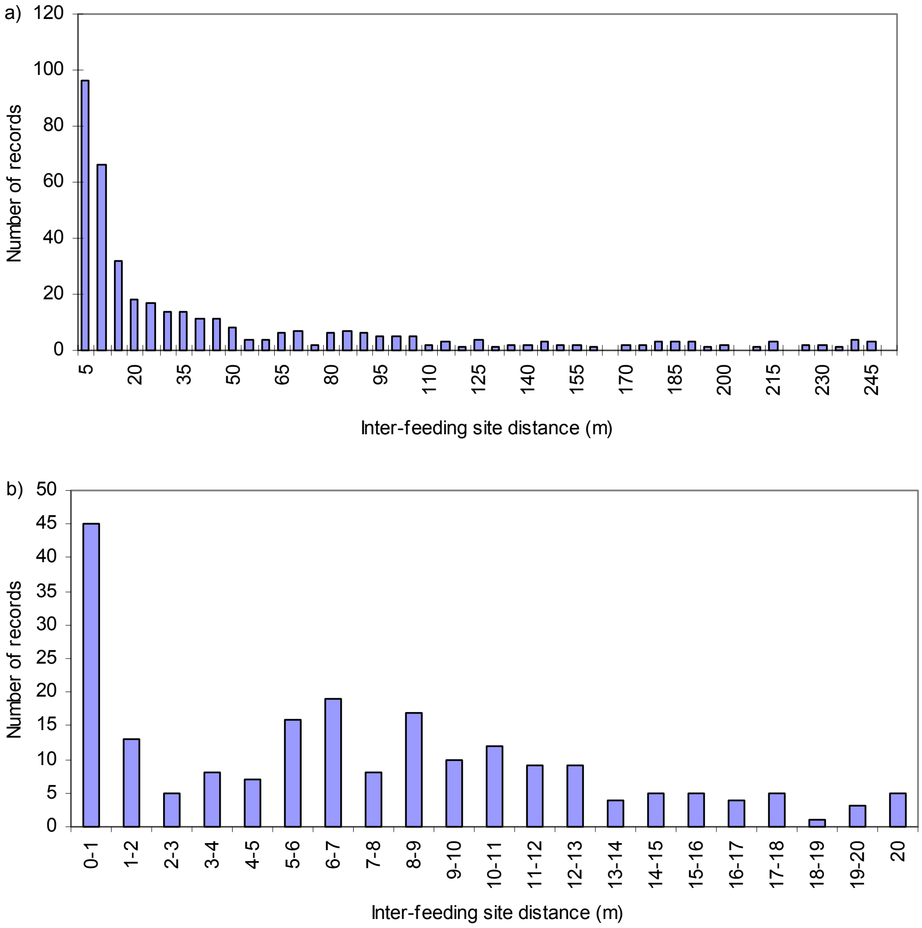
Figure 3.7. Difference in foraging rates on and off permanent elephant trails normalised by vegetation type



Inter-feeding site distance for non-fruit foods

Inter-feeding site distances varied from 0m to 1475m, with a mean of 107m (SD 192). The maximum of 1475m was the furthest an elephant was observed to travel without feeding throughout the study. The frequency distribution of inter-feeding site distances was heavily skewed toward small inter-site distances (Figure 3.8a,b). Whether distances were grouped by 1m or 5m intervals, the smallest distance was always the most frequent. At 1m intervals, the mode was 0-1m with 9.8% of all records, and intervals between 0-20m made up 45.6% of all records. Thus elephants are most likely to feed immediately after having browsed, and as distance after a feeding event increases the likelihood of feeding decreases.

Figure 3.8. Frequency of inter-feeding site distances and coarse and fine-grained scales



Fruit in the diet

A total of 860 dung piles was analysed over a three-year period from January 1998 to December 2000. The composition of dung piles was always dominated by fibrous material from leaves, wood, pith, roots and stems. Fruit remains were recorded in 94.0% of dung piles. At least 96 species of fruit were consumed from 35 families (Table 3.7a). The most commonly represented family both in terms of the number of dung piles containing fruit and also the number of species consumed was the Sapotaceae, which accounted for 19.3% of all fruit records in dung piles and comprised 13 species. The Tiliaceae was next most common, and accounted for 13.3% of fruit records, but was represented by only three species and dominated by *Duboscia* spp. [*D. macrocarpa* and *D. cf. viridiflora*] (Table 3.7b), followed by the Moraceae (4 species). The top ten families accounted for 81.4% of all fruit remains recorded, and 53 species or 55.2% of all identified species.

The most commonly recorded species in dung piles were *Duboscia* spp. found in 53.4% of all dung piles, followed by *Omphalocarpum elatum* and *Strychnos aculeata* (Table 3.7b). It was impossible to tell *D. macrocarpa* and *D. cf. viridiflora* apart from seeds, and seldom from fruit fragments so the two species were lumped. The top 10 fruit species accounted for 6.7% of fruit records, and 12 species were found in more than 10% of dung piles. The maximum number of fruit species identified in a single dung pile was 16 with a mode of 3 and mean of 4.3 (SD = 2.7, n = 860) (Figure 3.9).

Figure 3.9. Number of fruit species per dung pile (N = 860)

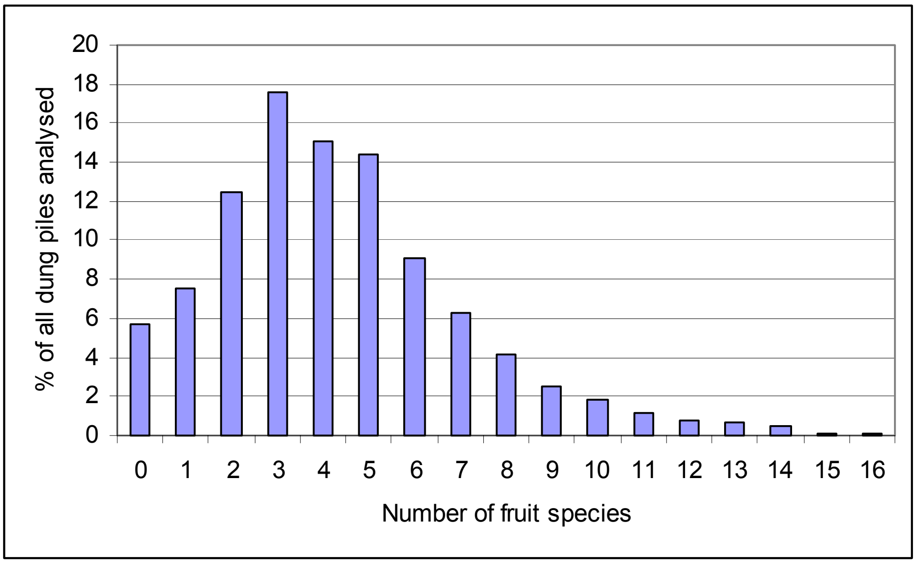


Table 3.7a. Plant families with fruit remains found in dung piles

Family	% of dung piles	% of fruit records	% of identified species
Sapotaceae	86.4	19.3	13.5
Tiliaceae	59.5	13.3	3.1
Moraceae	46.2	10.3	4.2
Loganiaceae	34.7	7.7	2.1
Annonaceae	32.3	7.2	8.3
Irvingiaceae	32.2	7.2	6.3
Mimosaceae	22.5	5.0	2.1
Rubiaceae	17.5	3.9	2.1
Papilionaceae	15.4	3.4	2.1
Euphorbiaceae	14.5	3.2	6.3
Arecaceae	9.0	2.0	4.2
Anarcardiaceae	6.0	1.3	4.2
Caesalpiniaceae	5.8	1.3	4.2
Marantaceae	5.7	1.3	3.1
Cucurbitaceae	5.6	1.3	1.0
Pandaceae	5.6	1.3	1.0
Apocynaceae	5.0	1.1	4.2
Sapindaceae	4.2	0.9	3.1
Clusiaceae	3.2	0.7	2.1
Verbenaceae	2.8	0.6	2.1
Ebenaceae	2.7	0.6	4.2
Balanitaceae	1.4	0.3	1.0
Acanthaceae	1.1	0.2	1.0
Costaceae	0.9	0.2	1.0
Olacaceae	0.9	0.2	2.1
Sterculiaceae	0.9	0.3	2.1
Chrysobalanaceae	0.4	0.1	2.1
Burseraceae	0.2	0.1	1.0
Cyperacaeae	0.2	0.1	1.0
Menispermaceae	0.2	0.1	1.0
Myristicaceae	0.2	0.1	1.0
Violaceae	0.2	0.1	1.0
Caricaceae	0.1	0.0	1.0
Zingiberaceae	0.1	0.0	1.0
Unknown	18.1	4.0	
No fruit	6.0	1.3	

(N = 860 dung piles)

Table 3.7b. Top 30 fruit species recorded in dung piles

	Species	N records	% of dung piles	% of records
1	*Duboscia* spp. (two species)	460	53.4	12.0
2	*Omphalocarpum elatum*	379	44.0	9.9
3	*Strychnos aculeata*	290	33.7	7.6
4	*Myrianthus arboreus*	269	31.2	7.0
5	*Tetrapleura tetraptera*	182	21.1	4.8
6	*Anonidium mannii*	178	20.7	4.6
7	*Swartzia fistuloides*	131	15.2	3.4
8	*Klainedoxa gabonensis*	124	14.4	3.2
9	*Treculia africana*	119	13.8	3.1
10	*Massularia acuminata*	93	10.8	2.4
11	*Gambeya lacourtiana*	90	10.5	2.3
12	*Drypetes gossweileri*	81	9.4	2.1
13	*Irvingia grandifolia*	75	8.7	2.0
14	*Tridesmostemon omphalocarpoides*	73	8.5	1.9
15	*Autranella congolensis*	60	7.0	1.6
16	*Brenania brieyi*	57	6.6	1.5
17	*Cucurbitaceae* sp.	48	5.6	1.3
18	*Panda oleosa*	48	5.6	1.3
19	*Elaeis guineensis*	47	5.5	1.2
20	*Desplatsia dewevrei*	47	5.5	1.2
21	*Uvariastrum pierruanum*	44	5.1	1.1
22	*Megaphrynium macrostachyum*	42	4.9	1.1
23	*Klainedoxa* sp. 2	40	4.6	1.0
24	*Antrocaryon klaineanum*	35	4.1	0.9
25	*Gambeya beguei*	34	3.9	0.9
26	*Manilkara mabokeensis*	32	3.7	0.8
27	*Gambeya perpulchrum*	30	3.5	0.8
28	*Mammea africana*	26	3.0	0.7
29	*Pachypodanthium* sp.	25	2.9	0.7
30	*Irvingia excelsa*	24	2.8	0.6

The mean number of fruit species recorded per dung pile increased significantly though weakly with rainfall (Figure 3.10, Spearman's Rank Correlation: rho = 0.285, N = 850, $P < 0.001$). The total number of fruit species seen in dung each month during extensive surveys was strongly positively correlated with rainfall in the month of the survey (Figure 3.11, Spearman's Rank Correlation: rho = 0.857, N = 8, $P < 0.01$). The number of species of fruit recorded per survey was significantly positively correlated with the number of fruit species recorded in dung, but the relationship was weak for data from extensive surveys ($r = 0.131$, $F_{(1, 370)} = 6.477$, $P < 0.05$), however there was no effect of the number of fruiting events on the number of species recorded in dung ($r = 0.023$, $F_{(1,370)} = 0.203$, ns). Data from the intensive survey was the reverse of the extensive data with the number of fruiting events a strong predictor of fruit in dung, while the number of fruit species available was not (number of fruitfall events, r = 0.804, $F_{(1,9)} = 16.47$, $P < 0.005$: number of fruitfall species, r = 0.049, $F_{(1,9)} = 0.021$, ns)

Figure 3.10. Number of fruit species recorded in dung piles versus rainfall throughout the study

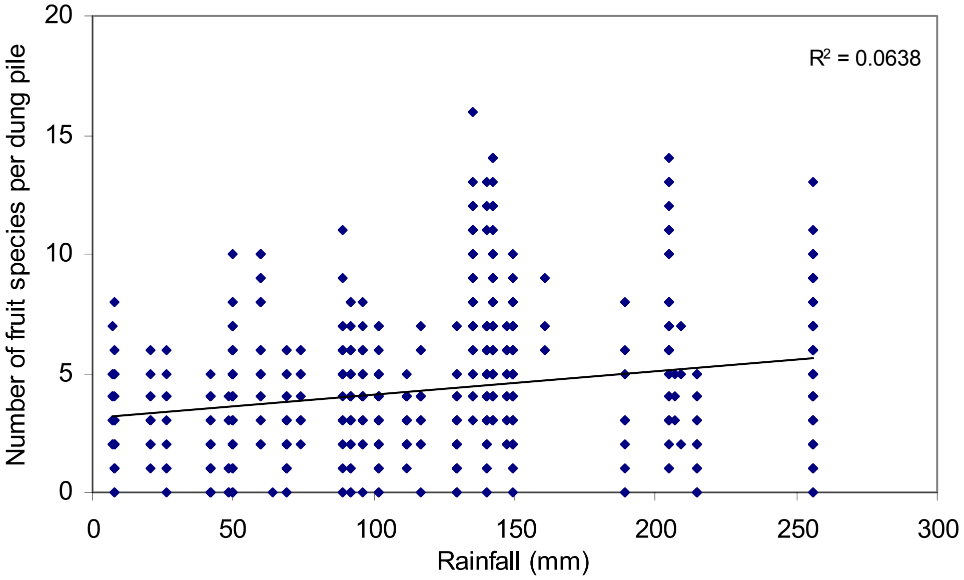
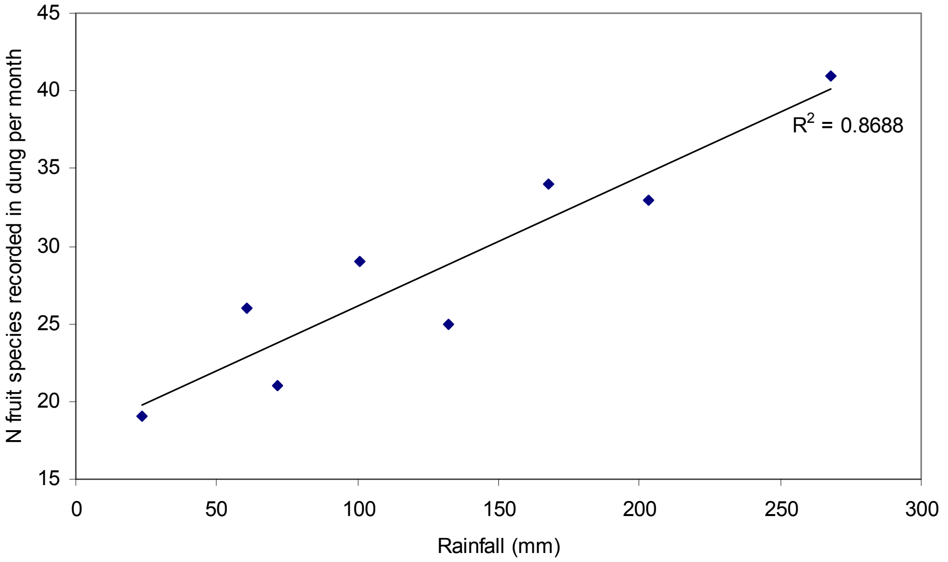


Figure 3.11. Number of fruit species recorded in dung against rainfall for the month of the survey



SEASONAL CONSUMPTION OF FRUIT BY SPECIES

During the 8 extensive surveys, 53 fruit species were identified in dung piles, of which 5 species were recorded in all surveys (Table 3.8). The majority of species were temporally ephemeral in the diet, with nineteen species (35.8%) recorded in only a single survey, and 7 in two surveys (Table 3.8). The availability of some species such as *Manilkara mabokeensis* was temporally clumped, and these species were unavailable as a food resource for much of the year (Chapter 2), while others may have been available but ignored by elephants. To compare the monthly consumption of fruit by species, monthly data in which at least 15 dung piles were analysed were lumped over the three years of the study.

Table 3.8. Fruit species in dung piles from extensive surveys

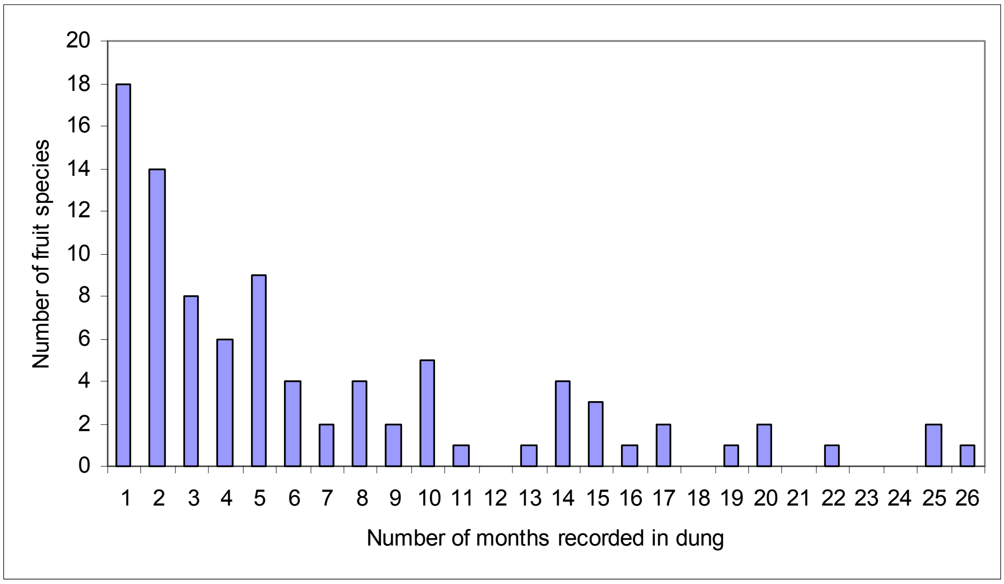
	Percentage of dung piles in which each species occurred								
Species	1	2	3	4	5	6	7	8	N seasons
Brenania brieyi	2.8	4.4	2.2	4.0	10.0	24.4	12.8	10.4	8
Duboscia spp.	38.9	28.9	66.7	56.0	64.0	75.6	61.7	43.8	8
Massularia acuminata	8.3	4.4	24.4	4.0	10.0	19.5	19.1	10.4	8
Omphalocarpum elatum	41.7	33.3	42.2	58.0	44.0	34.1	19.1	64.6	8
Strychnos aculeata	50.0	24.4	53.3	48.0	30.0	65.9	19.1	60.4	8
Klainedoxa gabonensis	30.6		4.4	18.0	6.0	4.9	12.8	33.3	7
Panda oleosa	8.3	6.7	13.3	2.0		9.8	2.1	6.3	7
Swartzia fistuloides	16.7		17.8	46.0	12.0	7.3	8.5	47.9	7
Treculia africana	38.9	8.9		2.0	16.0	2.4	2.1	4.2	7
Tridesmostemon omphalocarpoides	16.7	2.2		28.0	10.0	2.4	2.1	22.9	7
Autranella congolensis	11.1	2.2		4.0	28.0	26.8		4.2	6
Gambeya lacourtiana	22.2	2.2		4.0	68.0	4.9		4.2	6
Myrianthus arboreus	77.8	20.0		4.0	54.0	51.2		2.1	6
Cucurbitaceae sp.			6.7	8.0		2.4	4.3	12.5	5
Drypetes gossweileri			20.0		2.0	43.9	8.5	12.5	5
Elaeis guineensis				4.0	4.0	2.4	4.3	2.1	5
Irvingia excelsa	2.8	2.2			6.0	7.3		6.3	5
Anonidium mannii		55.6	6.7		58.0	12.2			4
Antrocaryon klaineanum	2.8				4.0	7.3		8.3	4
Desplatsia dewevrei	2.8			2.0	2.0	4.9			4
Gambeya beguei	30.6			8.0	20.0			4.2	4
Uvariastrum pierruanum	5.6	48.9			8.0	2.4			4
Hexalobus crispiflorus	2.8	2.2			6.0				3
Irvingia grandifolia		40.0	2.2		6.0				3
Mammea africana		4.4		12.0				4.2	3
Sapotaceae sp.				6.0	4.0	2.4			3
Tetrapleura tetraptera			53.3			75.6	10.6		3
Chytranthus sp.				12.0				2.1	2

Table 3.8 contd.

	Percentage of dung piles in which each species occurred								
Species	1	2	3	4	5	6	7	8	N seasons
Detarium macrocarpum					4.0	7.3			2
Pachyelasma tessmannii				6.0		14.6			2
Pachypodanthium sp.		2.2			12.0				2
Polyalthea suaveolens	8.3	4.4							2
Thomandersia laurifolia					2.0	2.4			2
Vitex doniana		2.2	4.4						2
Angylocalyx pinaertii					2.0				1
Antrocaryon micraster						2.4			1
Balanites wilsoniana					4.0				1
Diospyros crassiflora		2.2							1
Donella pentagonocarpa					2.0				1
Donella pruniformis		2.2							1
Gambeya perpulchrum	13.9								1
Grewia sp.			2.2						1
Irvingia robur			2.2						1
Klainedoxa sp. 2								6.3	1
Manilkara mabokeensis		51.1							1
Picralima nitida						7.3			1
Raphia sp.				2.0					1
Ricinodendron heudelotii							2.1		1
Sterculiaceae sp.						2.4			1
Strychnos sp.								2.1	1
Tabernaemontana crassa			6.7						1
Uapaca sp.							2.1		1
Unk sp. liana				2.0					1
N species	22	24	18	24	30	30	17	24	

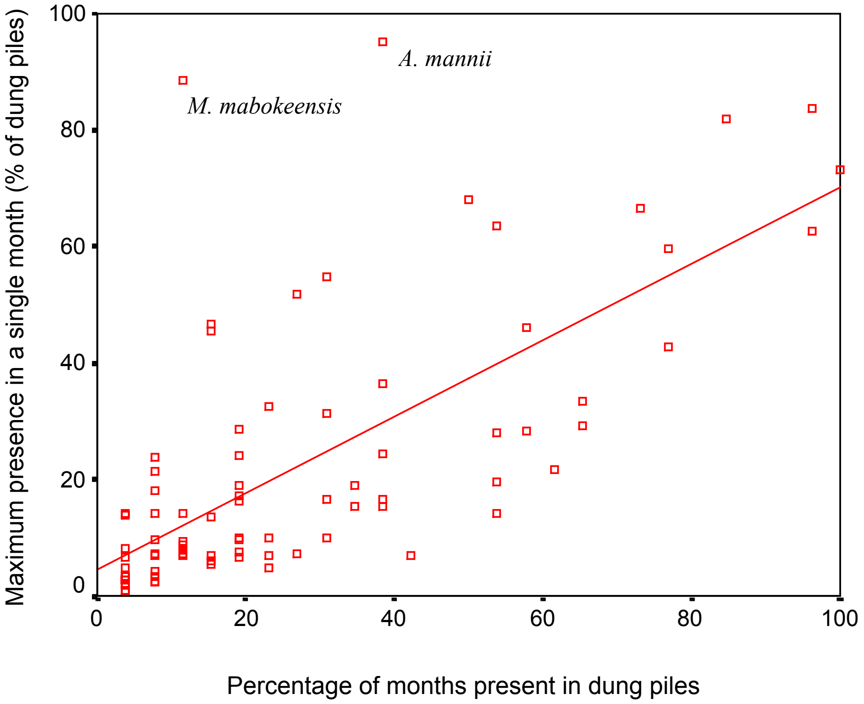
Only one species, *Omphalocarpum elatum,* was present in all 26 months, with *Duboscia spp*., and *Strychnos aculeata* found in 25 months, and *Myrianthus arboreus* in 22 months. The majority of species were present in just one month (19.8%), and 32.5% of species were recorded in 1 or 2 months (Figure 3.12). The number of months in which a species was recorded in dung was positively correlated with its maximum frequency of occurrence in dung piles sampled in a single month (Figure 3.13. Spearman's Rank Correlation: rho = 0.759, N = 89, $P < 0.001$), thus fruit species consistently found in the diet were also consumed in higher quantities in some months than species less consistently eaten. Two clear outliers in this general trend (Figure 3.12) were *Manilkara mabokeensis* and *Anonidium mannii*, both of which were consumed in few months, but for both, the maximum presence in dung piles for a single month was extremely high (88.5% and 95.2% respectively). Both these species had discrete temporal fruiting periods with high forest-wide abundance.

Figure 3.12. Frequency of species by number of months present in dung piles



Note: X axis represents only 26 months of a 36 month dung study, since 10 months in which less than 15 dung piles were analysed have been excluded.

Figure 3.13. Fruit species presence in dung by month and abundance in a single month



ELEPHANT FRUIT PREFERENCES: CONSUMPTION BY AVAILABILITY

Elephants showed strong preferences for some fruit species and avoidance of others. For those species where sufficient data were available for both abundance, Rank Preference Indices were calculated following the methodology described by Johnson (1980) cited by Krebs (1999), which provides an estimate of relative rather than absolute preferences among a suite of resources. The consumption and availability of each species was ranked, and then availability rank was subtracted from consumption rank to estimate relative preference, with the smallest relative rank indicating the most preferred resource. Preference rank indices were calculated for each season, with an overall estimate calculated as the mean of seasonal indices (Table 3.9). The indices in Table 3.9 are a general indication of preference ranks, since in some cases a species appeared in dung but fruitfall was not recorded and therefore a preference index could not be calculated. The extensive coverage of the survey nevertheless suggested that these species were strongly preferred. Seven species (*Anonidium mannii, Antrocaryon klaineanum, Swartzia fistuloides, Treculia africana, Omphalocarpum elatum, Strychnos aculeata, Uvariastrum pierruanum*) were recorded in dung for more seasons than they were recorded as fruitfall, which indicates that their preferences indices may be underestimates. All other species listed in table 3.9 were recorded as fruitfall in more, or the same number of months in which they appeared in dung piles.

Swartzia fistuloides was by far the most preferred species, 6 rank points higher than the next most preferred fruit, *Omphalocarpum elatum*. *Swartzia fistuliodes* was observed in dung during 7 surveys, yet was recorded as fruitfall in just 2 surveys. Fruitfall of this species was so rare that the seed remained unidentified for nearly two years, despite appearing in 131 dung piles. The distribution of this species must be extremely patchy, since it is one of the rarest elephant fruit trees in the Ndoki forest (Chapter 2). *Omphalocarpum elatum* fruits were also rarely seen on the ground, though this tree is considerably more common than *S. fistuloides*. There was no significant relationship between preference index and either the number of surveys a species was recorded in dung, or the number of surveys in which fruitfall of that species (Chapter 2) was recorded.

The sign of preference indices was inconsistent across surveys for nearly half (45%) of species. However, the magnitude of the CV (all signs positive) was negatively correlated with preference index (Spearman's rank correlation: rho = -0.775, N = 24, $P < 0.01$)

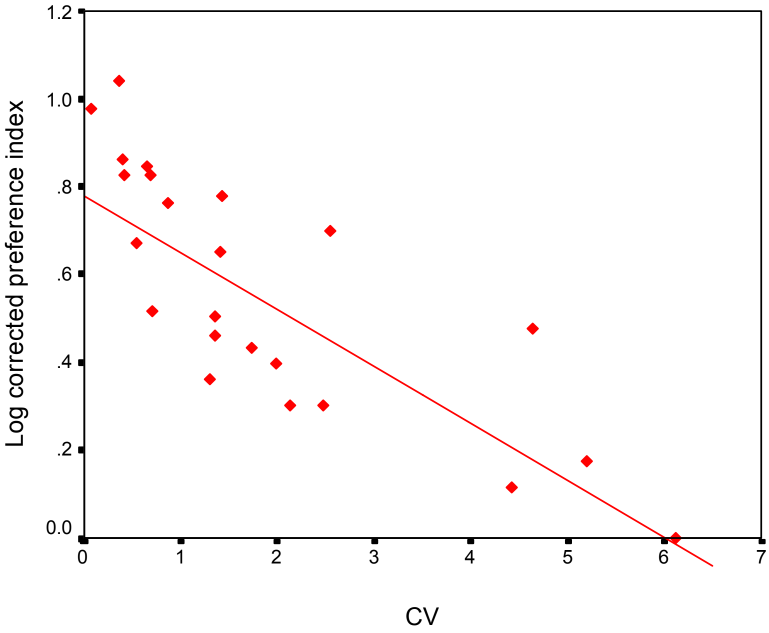
showing that where preference or avoidance for a particular species was strong, it was also consistent across survey periods (Figure 3.14)

Table 3.9. Elephant fruit species preferences

Negative values = preferred, positive values = avoided

	Rank preference index for each extensive survey									
Species	1	2	3	4	5	6	7	8	**Mean**	**CV**
Swartzia fistuloides								-17	**-17**	
Omphalocarpum elatum	-12	-12		-17		-6	-8	-9	**-11**	**0.36**
Antrocaryon klaineanum						-9		-10	**-9.5**	**0.07**
Treculia africana	-8	-11		-5	-5				**-7.3**	**0.39**
Gambeya beguei	-6			-12				-3	**-7**	**0.65**
Strychnos aculeata	-13	0	-4	-10		-7	-10	-3	**-6.7**	**0.69**
Mammea africana		-14		-7				3	**-6**	**1.42**
Pachypodanthium sp.		-5							**-5**	
Tetrapleura tetraptera			-7			-2	-5		**-4.7**	**0.54**
Tridesmostemon omphalocarpoides	-8	-7		-4	4		-2	-2	**-3.2**	**1.35**
Uvariastrum pierruanum	6	-19				4			**-3**	**4.63**
Brenania brieyi	0	-3	-2	-4	-2	2	-1	-8	**-2.3**	**1.29**
Annonidium mannii		-5			1				**-2**	**2.12**
Diospyros crassiflora		-2							**-2**	
Myrianthus arboreus	-3	-1		-1	-1	-10		8	**-1.3**	**4.42**
Gambeya lacourtiana	-1	-10		7	-2	1			**-1**	**6.12**
Gambeya perpulcrum	0								**0**	
Duboscia spp.	2	3	0	1	1	0	-1	1	**0.9**	**1.38**
Manilkara mabokeensis		1							**1**	
Vitex sp.		7	-4						**1.5**	**5.19**
Drypetes gossweileri			2		10	-1	2	-3	**2**	**2.47**
Irvingia grandifolia		-1			6				**2.5**	**1.98**
Autranella congolensis	5	4		6	-1	-5		7	**2.7**	**1.73**
Massularia acuminata	6	7	2	-1	8	4	-2	-1	**2.9**	**1.36**
Klainedoxa gabonensis	3		6	-1		4	4	4	**3.3**	**0.71**
Desplatsia sp.	0					9			**4.5**	**1.41**
Detarium macrocarpum					14	-4			**5**	**2.55**
Irvingia excelsa	11	1			2			9	**5.8**	**0.86**
Grewia sp.			6						**6**	
Pachyelasma tessmannii						6			**6**	
Panda oleosa	8	8	6	1		10	7	7	**6.7**	**0.42**
Polyalthea suaveolens	12								**12**	
N fruiting events per survey (Chapter 2)	463	932	165	226	177	264	217	212		

Figure 3.14. Mean fruit preference index versus the CV of preference indices



DISCUSSION

Diet composition

Among African elephants, the desert dwelling elephants of Namibia have the lowest reported dietary diversity with just 33 species browsed (Viljoen 1989a). In Queen Elizabeth National Park, Uganda, Field (1971) estimated that elephants ate 37 and 28 species in each of the two major vegetation types identified, short grass/thicket and tall grassland respectively, with no fruit recorded. In the Kidepo Valley National Park also in Uganda, Field and Ross (1976) reported 59 species in the diet of elephants, including three species of fruit. In the somewhat more arid Ruaha National Park, Tanzania, Barnes (1982) indicated that elephants browsed on a maximum of 12 species in any one season, occasionally feeding on fruit, though a species list of all foods was not given. Similarly low dietary diversity has been reported elsewhere in savannah habitats (Napier-Bax and Sheldrick 1963; Laws *et al.* 1975; Kalemera 1989; Ruggiero 1989; Kabigumila 1993; Tchamba 1996). This low diversity of foods is probably a reflection of low plant species diversity of grassland habitats, since in a more diverse vegetation mosaic of mangrove, woodland, forest, and grassland in Mozambique, elephant diet comprised at least 95 species identified from dung contents alone (De Boer *et al.* 2000). When savannah elephants have access to rainforest, the habitat with the highest vegetation diversity on earth (Whitmore 1990), dietary diversity increases dramatically. In Kibale Forest, Uganda, Wing and Buss (1970) reported over 200 woody plant species 'utilised' by elephants, though it is unclear how many of these were actually consumed.

In the Bia forest, Ghana, Short (1981) recorded 170 species of food plant, 135 of which were browse species and 35 species were fruits identified from dung. Tchamba and Seme (1993) list only 39 species eaten by forest elephants in the Santchou reserve, Cameroon, 17 of which were fruit, and Merz (1981) recorded 44 fruit species in elephant diet in the Tai forest, Ivory Coast. In the highly diverse forest of the Lopé Reserve, Gabon, forest elephants ate at least 304 food items from 230 plant species in 52 families (White *et al.* 1993). In this study in the Ndoki Forest, elephants ate over 100 more species than in the Lopé, from 73 families.

It is difficult to compare and contrast diet lists across forest sites since the duration and intensity of research has varied between sites. The study by Short (1981) lasted for just 7 months, and that of Merz (1981) was shorter still, while Tchamba and Seme (1993) studied elephants over 16 months in Cameroon. The elephant diet list of White *et al.* (1993) came from 8 years of accumulated data, though observations were made opportunistically during a study focussing on great apes. The reason why the food list from Ndoki is comparatively large may have more to do with the focus and duration of the study, than the absolute diversity of the Ndoki elephant's diet. While the rate of accrual of new food species fell as the study progressed, it had not reached asymptote by the end, suggesting the actual number of food species consumed is higher than the current list indicates.

Plant life form selection

Overall, trees were the most heavily browsed plant life form, though habitat differences were high and the overall ratio is misleading since it is subject to different sampling effort in different habitats. Feeding rates on trees and monocotyledons were not significantly correlated with the abundance scores of these plant types, and liana feeding rate was not significantly correlated with any measured attribute of vegetation structure or composition (Chapter 2), and selection apparently contradicted availability in some cases. The rates of feeding on trees were highest in Marantaceae Forest (MF) (79%) and lowest for monocotyledons (8%) despite the fact that this forest type was ranked only 5th in dicotyledon browse stems:all stems ratio and was ranked second by number of THV food species per plot (Chapter 2). The mean rank of THV food abundance in MF was 1.6 whereas in both TF and GDFH was over 3. Although MF was dominated by THV, the most dominant species was the highly non-preferred species *Haumania dankelmaniana* (Chapter 2). While other THV species were present, they were often difficult to detect in thickets of *H. dankelmaniana*. By contrast, dicotyledon stems were more conspicuous in these Marantaceae thickets, and the ratio of edible species was relatively high. It is probable that elephants usually detected dicotyledon browse before edible THV. In *Terminalia superba* forest (TF), both edible dicotyledon frequency and THV abundance were high but THV foods were selected on 47% of all feeding occasions, 39% more than in MF. The reason for this shift in selection was probably due not just to the increase in overall abundance of THV foods, but also to species composition and forest structure. In TF, there was a high abundance of three THV– *Ataenidia conferta, Megaphrynuim macrostachyum*, and *Sarcophrynium* spp. (Table 2.5, Chapter 2), which all grew in large, dense, and highly conspicuous stands compared to MF. The dominance of THV feeding in *G. dewevrei with H. dankelmaniana* (GDFH) was to be expected given that this vegetation type was ranked first by overall abundance of THV foods. Both VS and SWP had high ratios of tree browse versus non-browse species, and very low abundance of edible THV compared to other vegetation types, which is reflected in the relatively low feeding rates on THV. In VS, with their often astonishingly high abundance of lianas, elephants ate a higher proportion of lianas (42%) than in any other vegetation type, the second highest liana feeding rate being in light gaps (LG) with 35.2%.

Herbs made up a small proportion of diet in all vegetation types, never exceeding 10% of feeding events, and were an insignificant part of the diet in all but mixed *terra firma* forests. Finally ferns (Pteridophytes), which are generally rare in the Ndoki forest (Chapter 2) except in highly localised patches in light gaps in deep swamp, never constituted more than 2% of food selection in any vegetation type.

These data are difficult to compare with those from studies in savannahs because in the latter feeding behaviour is usually studied by direct observation. However, some gross differences are clear. Like elephants in the Ndoki, Tchamba (1996) showed that diet selection of elephants in the savannahs of Cameroon is strongly influenced by habitat type. In vegetation types dominated by browse species, elephants feeding rates on browse were more than 4 times higher than on grasses, while in mixed vegetation they switched to a greater proportion of grass relative to browse, and where grass dominated the vegetation, elephants ate grass 7 times more frequently than browse items. In Lake Manyara, Tanzania, Kalemera (1989) found that browsing versus grazing rates were generally proportional to the availability of these life forms by habitat, with high grazing/low browsing in grass-dominated vegetation, and the reverse in woodlands where browse is plentiful.

Unlike Ndoki elephants, savannah elephants feed primarily on grasses, which may make up more than 60% of the annual diet (Owen-Smith 1988). Field and Ross (1976) found that grass made up 46% of feeding observations, trees accounted for 28%, herbs for 17%, and shrubs for 9%. Field (1971) used time spent feeding on each plant life form as a measure of frequency of selection, and found that annually grasses made up 71% of observations compared to 6.4% for browse, and 22.9% for herbs. However, he found considerable variation with rainfall and habitat. In short grasslands for example, browse feeding decreased from 40% of the diet in the dry season to just 10% in the wet season. In tall grass habitat, herb feeding increased to a maximum of ca. 40% of the diet from low to high rainfall, while a decrease in rainfall meant an increase in grazing to over 90% of the total intake in that habitat. In the Ruaha National Park, there was also a seasonal change in the relative intake of different plant forms, with high dicotyledon browsing rates in the dry season, giving way to heavy grazing in the wet season (Barnes 1982). In northern Cameroon, Tchamba (1996) showed a similar trend with browsing frequency 3.5 times that of grazing during the dry season, which decreased to 1.3 times in the wet season. In studies of savannah elephants, there is almost no mention of any monocotyledon species except grass being eaten. Grass was rarely fed on in the forest of Ndoki, but was readily consumed during the dry season in larger rivers.

There is limited information on food selection of forest elephants based on life form. Tchamba and Seme (1993) reported that the 'bulk of elephant feeding in the Santchou Reserve, Cameroon, was either grazing or stripping off fruit' which accounted for 45% and 38% of records, while only 6% of feeding observations were of elephants eating leaves and twigs. The Santchou Reserve is a matrix of forest, swamp forest, savannah, and farmland, and feeding rates may vary by vegetation type and these data probably do not reflect overall life form selection rates. Other published studies of forest elephant feeding present species lists by life form as an indicator of the importance of each but give no information on the relative frequency with which the different forms are eaten (Merz

1981; Short 1981; White *et al.* 1993). These studies all show that small dicotyledon trees are the most commonly eaten plant type in terms of number of species. This study has highlighted the importance of monocotyledons besides grasses in the diet, which accounted for up to 66% of feeding records depending on vegetation type. White *et al.* (1993) found 'abundant' monocotyledon remains (excluding grasses) in dung samples throughout the year in the Lopé Reserve, though neither Merz (1981) nor Short (1981) listed a single monocotyledon food species in their study sites, though these species were present in the understorey.

Plant parts consumed

Across all plant life forms, leaves constituted over 50% of feeding events, being highest in shrubs, and when leaves and wood (terminal twigs) are combined, these two plant parts accounted for over 90% of feeding signs for trees and shrubs. Considerably more wood from trunks was consumed for lianas than trees, suggesting that liana wood is more palatable. It was usually the case that liana wood was softer, more fibrous, and contained more liquid than the wood of trees. When tree wood was eaten it was usually from small saplings. Lianas of several genera (e.g. *Cissus, Landolphia*) contain copious quantities of water, which are used as a water source by pygmies. Elephants frequently chewed on the stems of these plants, spitting out the fibres when the liquid was spent. Bark feeding was most common on trees, and qualitatively elephants appeared to prefer large size classes over small, consistent with forest elephants elsewhere (White *et al.* 1993). Short (1981) found that bark was relatively infrequently selected by elephants in Ghana, which accounted for just 3% of feeding events and was limited to few species. In the Ndoki Forest, bark made up 25% of feeding events on trees and 7% for lianas, with over 7.5% of all trees from a sample of over 5000 trees showing evidence of bark feeding. Dicotyledon roots were a minor part of the diet, though occasionally an elephant would devour the roots of a single tree. On one occasion, a huge quantity of root from a *Gambeya pentagonocarpa* tree of ca. 100cm dbh was dug up by an elephant, who proceeded to eat the majority of the roots excavated, including some up to ca. 8cm in diametre. Generally, however, both frequency of feeding and quantities of dicotyledon roots consumed was low.

The selection of plant parts from monocotyledons was also dominated by leaf and leaf+stem feeding, though within families there were considerable differences. For the

Marantaceae, roots and the non-photosynthetic stem-bases dominated food choice. Occasionally, large patches of interwoven root masses in dense stands would be dug up and consumed, particularly roots of *Megaphrynium machrostachyum*. More usually, the Marantaceae were not found in these dense clumps, and elephants would pull up a single clump, bite off the root and discard the rest of the plant. By contrast, for species of Commelinaceae, preferred plant parts were almost exclusively upper stems and leaves. In one species of Marantaceae, *Thalia geniculata*, leaf blades and upper stems were eaten abundantly, while stem-bases and roots were never recorded as eaten. This species was always rooted in saturated soil, often in standing water, and had an light cellular structured base and lower stem. The leaf blade was more malleable than other Marantaceae species, with low fibre and silica content and a soft pliable texture more like that of Commelinaceae, whereas other Marantaceae species often had brittle, siliceous leaf blades.

Foraging rate by vegetation type

The data for foraging rates on non-fruit foods were a crude attempt to evaluate elephant foraging success by vegetation type. These estimates were crude for several reasons. The study relied on secondary evidence of feeding rather than direct observations which meant there was no way of knowing what fraction of feeding events went unnoticed, either because the elephant had eaten a whole plant and left no visible sign, or there was a bias toward seeing obvious feeding events versus more subtle evidence. The quantity (biomass) of ingested material from each plant consumed could not be calculated, and the only way to estimate the amount eaten was the 1-4 ranking scale. These problems were particularly evident when comparing consumption among different plant forms or between different vegetation types. For example, the vegetation of swampy *bais* may be dominated by a thick mat of aquatic herbs, which are frequently eaten by elephants. Elephants have to wade through deep mud to reach these patches, trampling and otherwise disturbing large areas often over hundreds of square metres. In such cases, there was no way to tell whether the elephant had fed or whether they had simply wallowed through the deep mud. Furthermore, even if feeding signs could be positively identified, there was no way to tell whether the elephant had eaten 500grams or 50kg of food material. Similarly, an elephant feeding heavily in a grove of Raffia trees (*Raphia* spp.) may eat 5kg of pith from each of five plants over a 50m distance, and further down the trail may have fed on five *Thomandersia laurifolia* stems stripping 5 leaves from each plant also over 50m. While the relative rank of quantity eaten would have been 'abundant' for the *Raphia* sp. and rare for the *T. laurifolia*, the frequency of feeding events would be recorded as 1 event every 10m for both sections. Nevertheless across most *terra firma*, transition, and swamp vegetation types, errors and biases were thought to be consistent enough to provide a rough estimate of foraging success rates, while in some swamp vegetation types feeding rates were probably grossly underestimated.

Most feeding sites involved very small quantities of food. Leaf stripping was usually only several (5-10) leaves from a plant per site, bark feeding was most often an area less than 20 x 20cm, and monocotyledon root feeding was rarely more than a single stem per site. On few occasions did an elephant consume a large quantity of any single plant species or plant part. The main exceptions (except in the swamp vegetation mentioned above) to this were the pith of palm trees (*Elaeis guineensis* and *Raphia* spp.), the bark of *Ceiba pentandra*, occasionally roots of *Megaphrynium machrostachyum* patches, and the leaves of canopy tree falls.

Feeding rate varied enormously between vegetation types for which data were available, ranging off permanent trails from 366 signs km^{-1} in *Raphia* sp. swamp to 7.0 km^{-1} in MCF, and on trails to a minimum of 3.6 km^{-1} also in MCF. In general, the more open the forest canopy, the greater was the feeding frequency. There was a marked decrease in success from swamp light gaps and *Raphia* sp. swamp, through VS and VF to GDFH, to MOF, MCF, and finally GDF. This follows the general pattern of decreasing browse availability indicated in Chapter 2 for both woody stems and THV across these vegetation types. Observations from forests in east and west Africa (Wing and Buss 1970; Short 1981, 1983; Struhsaker *et al.* 1996) are consistent, which is to be expected given the greater density of understorey vegetation as canopies become more open. Foraging success was highest in swampy areas and light gaps, which were vegetation types in which fruit tree abundance and fruit availability was low (Chapter 2). An obvious exception was TF, which was both rich in fruit and understorey browse, but the general pattern was clear. This is further evidence suggesting partitioning of space when elephants are feeding on browse or fruit – for maximum efficiency, elephants should feed in swamps and open habitats for browse, and closed canopy forests for fruit.

The quantitative differences in feeding rates on and off permanent trails support the qualitative notion of Short (1981) that feeding rates are low on trails. Often elephants would follow trails for a considerable distance showing no signs of feeding on the trail, but occasionally they would leave the trail, usually near an open canopy patch of forest, meander through the off-trail section feeding as they went, before returning to the same or a different trail and continuing on. There are two probable reasons for this pattern of foraging. First, permanent elephant trails are found most often in closed canopy forests with high densities of fruit trees (Chapter 4), which contain low abundance of preferred understorey browse (Chapter 2), and also low abundance of lianas. Permanent trails also tend to deviate around thickets and light gaps, which are preferred feeding areas. Second, elephant activity is concentrated on trails relative to off-trails, which suggests that mortality rate through continuous browsing of edible plant species would be relatively higher on trails than off them, thus availability would be lower on trails. Elephant trails were however extremely important foraging areas for fruit (Chapter 4); thus when foraging for fruit elephants would be expected to use trails more than when they are browsing.

Fruit feeding

It is well established that compared to savannah elephants, forest elephants are highly frugivorous (Alexandre 1978; Short 1981, 1983; Gautier-Hion *et al.* 1985b; Dudley *et al.* 1992; Tchamba and Seme 1993; White *et al.* 1993; Feer 1995; Powell 1997). Wing and Buss (1970) and Chapman *et al.* (1992) showed that when savannah elephants have access to forest containing abundant fruits they appear to eat them with relish. White *et al.* (1993) found that elephants in the Lopé Reserve, Gabon, ate fruit from a minimum of 72 species, with fruit remains present in 82% of dung piles, a consumption far greater in range of species and frequency in dung than previous studies had indicated (citations above). In an extensive study of the role of forest elephants as seed dispersers in Cameroon, Powell (1997) identified 93 species of germinating seedlings in dung piles. In the Ndoki Forest, elephants consumed at least 96 species of fruit from 35 families, and fruit was present in 94.4% of dung piles.

Elephants in Ndoki ate fruit consistently throughout the year, though there were marked seasonal and inter-annual differences in the mean number of species consumed and species composition. Across all three years, mean monthly number of species per dung pile ranged from 2.3 in January, the lowest month, to 5.9 in June, with a mean of 4.3 species per dung pile. The data show that while some species of fruit provide elephants with staple items in the diet, such as *Omphalocarpum elatum* and *Duboscia* spp, *Strychnos aculeata*, and

Myrianthus arboreus, they are also highly opportunistic. The majority of fruit species were recorded in dung in just one or two months of the study. The wide range of species consumed allows elephants to exploit at least some fruit throughout the year. Rainfall was a good predictor of both the numbers of species consumed per month, and the number of species per dung pile. Thus in low rainfall periods elephants must increase their consumption of browse to compensate for the reduced availability of fruit. Given the spatial distribution of fruit-rich versus browse-rich areas across the Ndoki Forest, this dietary shift implies that to forage efficiently, elephants should shift their use of space from fruit-rich *terra firma* closed canopy forests during high rainfall periods, to open canopy *terra firma* and swamp forests during periods of low rainfall.

CONCLUSIONS

1. Ndoki elephants ate a variety of plant foods including leaves, bark, wood, stems, roots, and fruits. A minimum of 351 species, from 73 families, involving 725 plant parts were consumed. Trees and lianas accounted for the majority of food species (57% and 20% respectively). Monocotyledons made up 13% of species. Leaves were the most frequently consumed items and also the most diverse, with at least 288 species recorded as food. Barks from 121 tree and liana species were also consumed. The remains of at least 96 species of fruit from 35 families were identified from dung piles. Ndoki elephants had the most diverse diet of any elephant population yet studied.
2. Leaves were the most commonly consumed plant part for trees, lianas, and shrubs. Elephants consumed terminal twigs of lianas more readily than those of trees or shrubs, while bark made up nearly 25% of feeding events involving trees, compared to just 7.3% for lianas. Bark of shrubs was consumed only when wood was also selected. In the case of THV, leaf+stem and leaves were most frequently selected, but roots accounted for over 25% of feeding records.
3. Foraging frequency (number of feeding events km^{-1}) involving non-fruit foods was high in swamps compared to *terra firma* forest. Among *terra firma* forest types, browsing rate was highest in open canopy conditions, particularly light gaps, and lowest in closed canopy forest. Among swamps, elephant foraging frequency in the northern swamps of the Mokala/Lola Rivers was more than twice that of the Likouala swamps, thus browse food density was thought to be highest in the northern swamps, moderate in the Likouala swamps, and lowest in *terra firma* forest. However, foraging frequency was exceptional in *Raphia* spp. dominated swamps, which cover vast areas

of the Likouala swamps, but in which data were not collected, and it is likely that foraging frequency in the Likouala swamps was under-estimated.

4. Fruit remains were recorded in 94% of 860 dung piles analysed over nearly three years. Species of both the Sapotaceae and the Tiliaceae were recorded in over 50% of dung piles (59.5% and 86.4% respectively). Fruit consumption was low during dry periods but became a major part of the diet as fruit availability in the forest increased. Both the number of fruit species per dung pile, and the total number of fruit species consumed per month, were significantly positive correlated with rainfall.

CHAPTER 4. FOREST ELEPHANT TRAIL SYSTEMS

INTRODUCTION

How organisms disperse within heterogeneous or patchy habitats to make efficient use of resources and ultimately maximise fitness is a central theme in ecology (MacArthur and Pianka 1966; Fretwell and Lucas 1970; Weins 1976; Levin 1992). Food is arguably the most important of resources for many animals, at least in a proximate sense, and foraging behaviour and its evolution is one of the most widely studied areas of ecology. Foraging strategies are thought to have evolved through differential survival and reproduction (natural selection), in order to optimise foraging efficiency in the short term and maximise fitness in the long term (MacArthur and Pianka 1966; Charnov 1976; Stephens and Krebs 1986). Whether the currency of foraging success is ‘energy maximisation’ (Fryxell 1991) or ‘time minimisation’ (Bergman *et al.* 2001) the central point is that foraging efficiency should be maximised within the constraints of environment or physiology.

Animals searching for food in heterogeneous environments must decide on a course of action in response to three basic questions: 'when to forage, what to forage for, and where to forage' (Menzel 1981). If foraging optimally, the solution to these questions lies in minimising the effort required in finding and acquiring food, and maximising the energy gain from food. Animals should be expected to preferentially use areas where gain is maximised and travel costs between areas (patches) of high gain are minimised. A large number of models of foraging behaviour have been developed based on predictions of the rules by which animals search for food at different spatial scales of heterogeneity and also for different food characteristics (Bell 1991; Roese *et al.* 1991; Spalinger 1992; Ward and Saltz 1994; Gross *et al.* 1995; Moen 1997; Grünbaum 1998). Small-scale rules may apply to foraging within a single patch of high food availability, whereas the path between patches may be determined by a different set of search rules (Gross *et al.* 1995). If animals within a population are using the same rules to optimise movements between patches of high quality food, the tendency will be for concentrations of movement activity to form along high gain, low cost routes.

Repeated travel across a surface by animals that are capable of modifying their environment may lead to the formation of trails. Environmental modification may range from the deposition of 'chemical signposts' - pheromones along foraging trails in the case of many ant species (Holldobler and Wilson 1990; Watmough and Edelstein-Keshet 1995a, b; Schweitzer *et al.* 1997), to the mechanical cutting of trails through the erosion of soil and vegetation on rangelands by the hoofs of large bodied ungulates (Lange 1969; Arnold 1978; Walker 1986; Ganskopp *et al.* 2000). The assumption that, at least for livestock, these trails are pathways of least resistance (minimum cost) between target areas of high gain within the habitat (Weaver 1951; Arnold 1978) was recently supported with quantitative data from domestic sheep movements across a rugged terrain (Ganskopp *et al.* 2000).

Like ants and sheep, African elephants are capable of modifying their environment, and do so on a suitably elephantine scale (Laws 1970; Kortland 1984; Western 1989a). Moss (1988) described three large trails used seasonally by migrating elephants in Amboseli, Kenya, one of which was large enough to be mistaken for a road by cartographers. Ruggiero and Fay (1994) described trail networks connecting licks in saline complexes in the savannahs of Central African Republic. Williamson (1975) mentioned large, well used elephant trails following the troughs of Pleistocene dunes in Wankie National Park, and cites Smithers (1971) who suggested they were created as a result of elephant movement from Botswana. Short (1983) and White (1992) suggest elephant trails in the forests of west and central Africa may link important fruit trees. In the Odzala National Park, Congo Vanleeuwe and Gautier-Hion (1998) characterised several types of elephant trails, and showed that they provide easy access to forest clearings (*bais*), and possibly dense stands of Marantaceae, an important elephant food source (Chapter 3). However, there was little or no quantitative data presented in these studies with which to verify these observations.

Elephant trails are a conspicuous feature of the Ndoki Forest of northern Congo. Since trails are constructed as a result of repeated movement to important resources (above), it was predicted that trails would link those resources offering the highest net gain for the lowest costs. It was also hypothesised that the multiple scales of spatial and temporal heterogeneity on which resources were distributed would determine the most efficient foraging strategy for elephants, which in turn would drive the formation of trails. Identification of the factors most influencing trail formation and geography would help identify the resources of prime importance in driving elephant ranging behaviour and seasonal movement. The goals of this study were the following:

1. To describe qualitatively the structure of elephant trails in the Ndoki Forest.
2. To determine which resources were important for the formation of elephant trails. Specifically, it was predicted that trail density would be positively correlated with

proximity to watercourses and swamps, fruit tree abundance, THV food abundance, and with proximity to *bais*.

3. To test the hypothesis that 1) fruit tree density is positively correlated with proximity to elephant trails, but that non-elephant food trees show no relationship with distance to trails, 2) that trail intersections contain particularly high abundance of important food resources
4. To synthesise these data into a number of conclusions about how the patterns of resource distribution drive foraging patterns, which shape the formation of elephant trails, which in turn may be vectors for elephant seasonal movements and ranging which determine distribution.

STUDY SITE AND METHODS

Study site

The spatial distribution of elephant trails in relation to vegetation type, rivers, and swamps was investigated via two sets of east-west transects located south of the Nouabalé-Ndoki National Park (Figure 4.1), both sets non-randomly selected to meet a combination of scientific and conservation goals. The first location was the Goualougo Triangle (Figure 4.1), an area of ca. 29,000ha of *terra firma* forest bordered by extensive swamps, which at the time of the study was outside the National Park and in the Kabo Logging concession. Reconnaissance surveys (Fay *et al.* 1990; Blake *et al.* 1994) had previously identified the triangle as an area of outstanding ecological integrity due to the complete absence of humans over at least several decades. While the longevity of trails is not known, this area was thought to provide the best available example of an elephant trail system constructed largely in the absence of human influence. Data on the value of the area for elephant conservation were critical to provide evidence of its importance for the NNNP, and justify the argument of park managers that it should be taken out of commercial forestry land use legislation and incorporated into the National Park. The second location was immediately south and east of the National Park, and occupied the swathe of forest from the Ndoki/Goualougo Rivers to the Likouala swamps, also chosen for ecological and conservation reasons. Anecdotal evidence suggested that the Bodingo Peninsula, to the east of this area (Figure 4.1), was an elephant access corridor to the Likouala swamps and higher north-south trail abundance on the peninsula would be good evidence of this. The conservation application of site selection was that a major logging road was planned through the area to link the Kabo and

Loundougou concessions (Figure 4.1). In this chapter the ecology of trail systems is described, while the implications of the study for conservation are left until Chapter 7.

Data on the relationship between elephant trail characteristics and resources (*bais* and fruit trees) was collected from a total of nine elephant trails distributed widely through the NNNP (Figure 4.1). *Bais* were selected based on two criteria; their known importance for elephants, and their location in primary forest which showed no visible sign of human disturbance, including logging, which may radically alter the species composition and structure of tropical forests (Johns 1988; White 1994e; Plumptre 1996a) and so influence the distribution and foraging patterns of forest elephants (Barnes *et al.* 1991; Struhsaker *et al.* 1996). The nine *bais* selected were the most heavily used 'elephant *bais*' within the National Park (Blake, pers. obs.)

Methods

TRAIL GEOGRAPHY

Path of least resistance survey tracks (Hall *et al.* 1997; White and Edwards 2000b; Blake in press) are illustrated in figure 4.1. Direction was maintained using a combination of compass for east-west headings, with deviations from the heading due to obstructions kept below 40°. A Garmin 12LX™ Global positioning System (GPS) was used to keep a running tally of cross-track errors and to navigate back to the desired track. A continuous tracklog was recorded with fixes every 15 seconds. The GPS memory was capable of storing 1024 fixes (ca. 4 hours of continuous operations) and when memory was close to full the tracklog was downloaded to a Hewlett-Packard palmtop computer. Distance was also measured using standard forestry measuring equipment (Hip-chain and Topofil). All data were recorded into waterproof notebooks with a time reference from a digital watch synchronised to the nearest second with GPS time, and a distance reference indicated by the hip-chain.

A running rélévé of vegetation type and all fruitfall was recorded following the methods described in Chapter 2, with additional ecological data collected as follows. All signs of elephants were recorded including direct observations, vocalisations, feeding remains (following the protocol described in chapter 3), and dung. For each dung pile observed from the survey track, age class (fresh, recent, old, and very old) and perpendicular distance from the track were estimated and recorded. The locations of all elephant trails which crossed the survey track were recorded, the width was measured to the nearest 5cm at ground level, and each was given a subjective size (small, medium, large) and use (poor, moderate, and heavy) classification based on physical attributes. The orientation of each trail was measured in both directions using a sighting compass from the middle of the trail. Records of trails were systematically recorded in swamps, though since trails could not be reliably identified in swamps where ground was often inundated with up to 1m of standing water, these data have not been included in the analyses below.

TREE SPECIES COMPOSITION ABOUT ELEPHANT TRAILS

The structure and composition of vegetation in relation to elephant trails was quantified using two methods: first, from a comparative study of trail intersections and paired random locations in the forest, and second from a survey of large trees (>40cm dbh) along, and with perpendicular distance from, nine large elephant trails distributed across the NNNP.

Trail intersections were targeted since they are obvious focal points of the trail system. During seasonal surveys, a sample of random trail intersections was selected as foci for a pair of nested plots. Two hours were chosen at random from between 9AM and 3PM, and the first trail intersection encountered after each hour was surveyed to avoid biasing intersection selection. The centre of the trail intersection defined the centre of two nested circular plots of $200m^2$ and $400m^2$. All trees >10 cm DBH within the $200m^2$ plot were identified and measured (DBH), and in the $400m^2$ plot, all trees over 50 cm DBH were identified and measured. A random compass bearing and a random number between 50 and 100 were selected using the random number function of a pocket calculator. These values were used to locate the second of the pair of nested plots, in which the same procedures of tree enumeration were followed. A distance of between 50 and 100m was selected because it was thought to be far enough from the intersection to not be influenced by its vegetation, but near enough to be in comparable conditions.

For the trail vegetation survey, nine elephant *bais* were non-randomly selected in the NNNP as foci for the study. *Bai* selection criteria included that the *bai* was currently being heavily used by elephants, was in primary forest, and had elephant trails radiating from it into *terra firma* forest. A large elephant trail was randomly selected from each *bai*, following a brief survey of each major trail leaving the *bai* to ensure that the trail climbed into *terra firma* forest and did not follow a watercourse, where soil water regimes could have had confounding effects on vegetation characteristics, and that the trail did not end close to the *bai*. From the selection of trails that met these criteria, one was selected randomly. Each trail was followed for 4 km or until it ended (in one case only), using the convention of taking the largest trail at intersections. The inventory started at the point when the trail entered *terra firma* forest on exiting the *bai*. Trail width was measured every 50m at ground level along the trail, and assigned a subjective size class (small, medium, large). The location and characteristics (number and width of radiating trails) of all trail intersections were recorded. A complete count of all trees greater than 40cm dbh within 10m either side of the trail was completed, noting the distance of each tree along the trail and its perpendicular distance from the trail. A running rélévé of general vegetation type was recorded. Every 200m along the trail, a perpendicular transect was run from the trail to a distance of 100m, alternating between left and right, and all trees 10m or less from the transect were identified and measured (Figure 4.2). The trail was mapped using a sighting compass, clinometer, markers and topofil. A GPS track (non-selective availability) of each trail was taken with a fix every 5 seconds.

Figure 4.1. Survey routes for elephant trails study

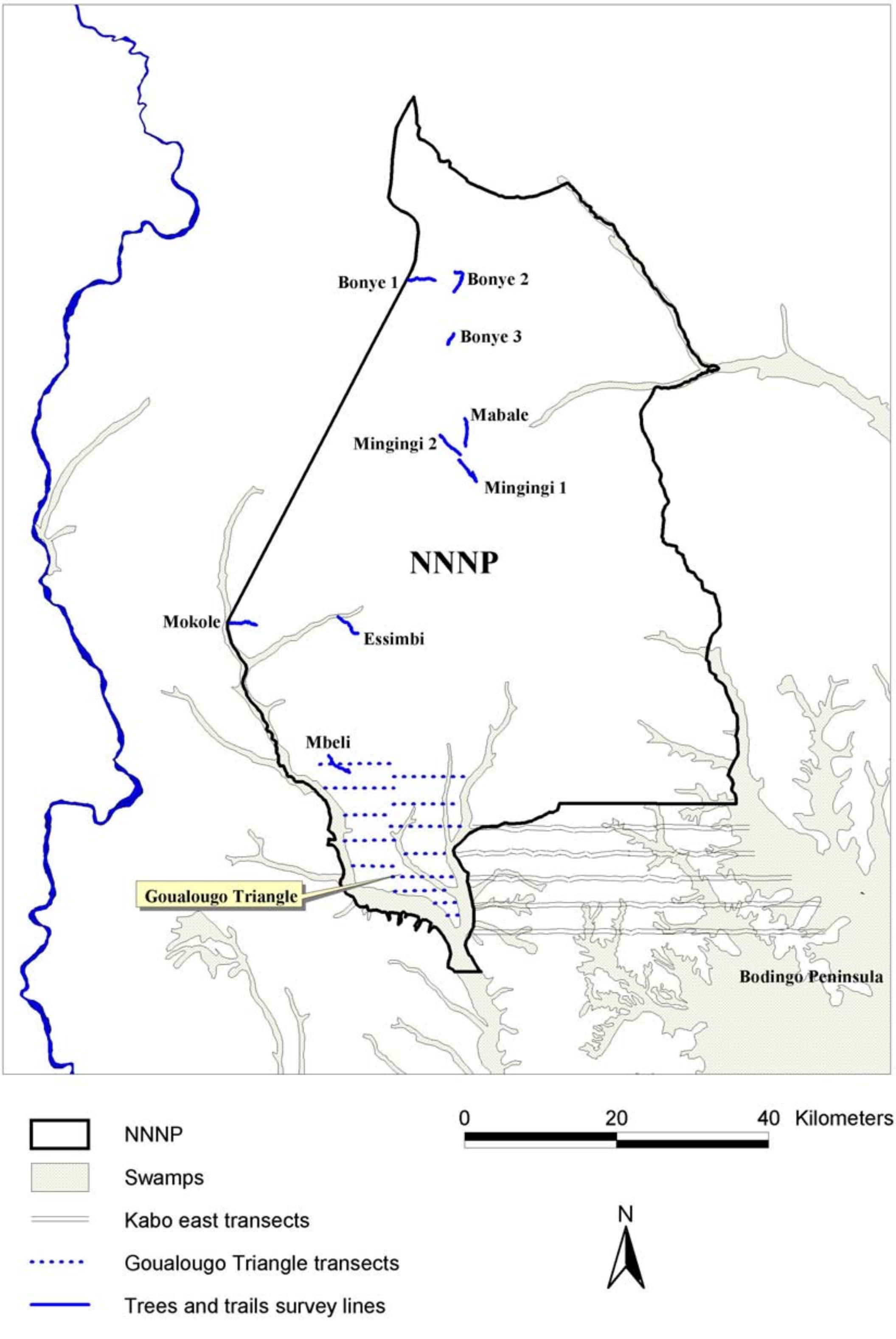
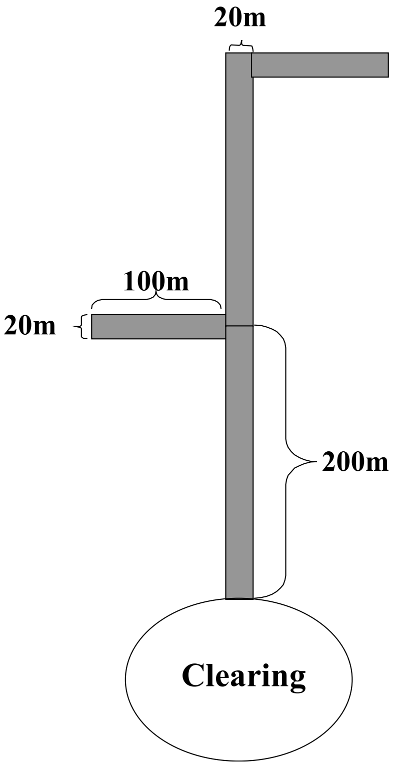


Figure 4.2. Transect and trail sample units



RESULTS

General trail characteristics

Permanent elephant trails were categorised into three types; *bai* trails, fruit foraging trails, and riverine trails. *Bai* trails, as the name suggests, led to and often connected *bais*, with almost straight routes even when separated by 10km or more. On entering *bais*, trampled vegetation, bare earth, or grass on trails was up to 15m wide with a main central passage of bare earth up to 3m wide. *Bai* trails were often almost straight-line links between *bais* when inter-*bai* distances were small (under ca. 5km). More usually however *bai* trails became smaller and more sinuous after 1-2 km and dissolved into riverine or fruit foraging trails. Fruit foraging trails were trails that appeared to trap-line between favoured fruit trees, and trail intersections appeared to be based around fruit trees, a hypothesis that was tested in this study. At large fruit trees, these intersections took the form of large circular patches of trampled vegetation under the canopy of the central fruit tree, with cleared understorey. Fruit foraging trails were rarely more than 1m wide, with clearly defined edges.

Riverine trails were a conspicuous part of the elephant trail system. While quantitative data were rarely collected on them, a large amount of time was spent walking them taking descriptive notes. The principle characteristic of riverine trails was their size and longevity, following the biggest rivers through the region. Figure 4.3 shows the locations of verified riverine trails, which indicates four main characteristics. First, they often extended as unbroken trails for several tens of kilometres, fording small streams and tunnelling through thick vegetation where necessary. Second, they were most often associated with the larger rivers in the region that had clearly defined swamp/*terra firma* vegetation interfaces. Third, they adhered to the interface often not more than ca. 10m from the swamp boundary and almost never more than 100m. Fourth, in all cases where trails follow larger rivers, the trails diffused into a capillary network of smaller trails on approaching the headwaters, when terrain became more undulating, and the river branched more frequently. Large riverine trails were commonly, though not exclusively, associated with *Gilbertiodendron dewevrei* forest (Figure 4.4), which occupied much of the riverine vegetation throughout the Nouabalé-Ndoki National Park (Chapter 2). The Mabale, Bonye, and Ndoki Rivers all had bands of *G. dewevrei* forest running almost unbroken from the lower headwaters to the park limits, and each had large elephant trails running their length. However, the lower Ndoki River and the northern branch of the Mokala, had mixed species forests and large trails were still present. *Gilbertiodendron dewevrei* forest with its open understorey and almost no lianas, resulted in easy establishment and maintenance of trails. It was frequently the case that when trails passed from *G. dewevrei* forest to mixed species or vine forests the condition of the trail immediately deteriorated, which since the animal traffic was the same, indicated that trail maintenance was more difficult in these forest types.

Figure 4.3. Verified large riverine trails in the Ndoki Forest

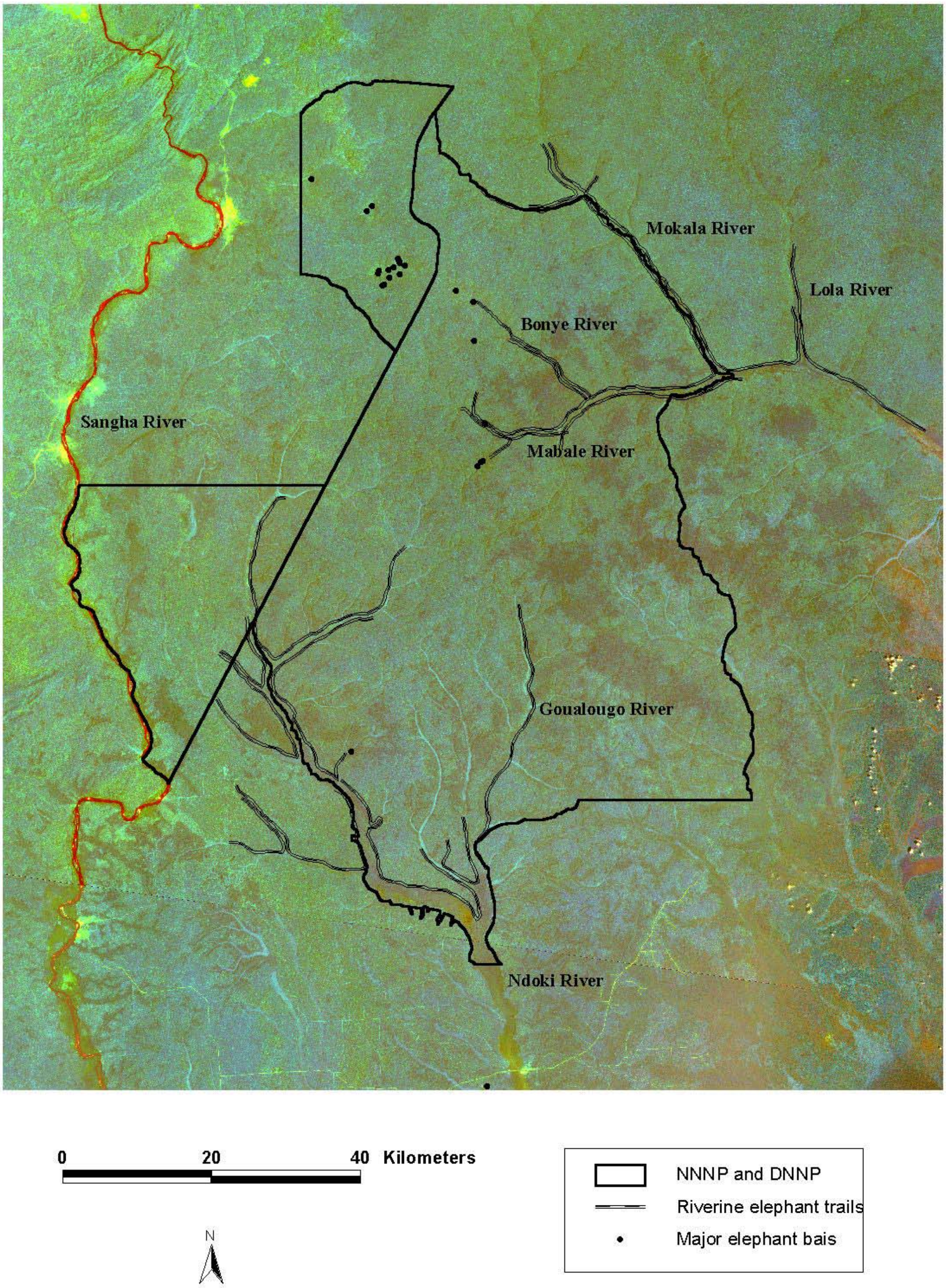


Figure 4.4. A large riverine elephant trail through *Gilbertiodendron dewevrei* forest on the Mabale River.

TRAIL DISTRIBUTION

A total of 2823 elephant trails were crossed throughout the 287 km of *terra firma* forest surveyed, or a mean of 9.82 (SD 4.62) trails km^{-1}, with a mode of 9 trails km^{-1}, and a range of 1 to 27 trails km^{-1} (Figure 4.5). Trail width varied from 35-100cm, with a mode of 50cm (32.3% of trails), and the width band between 40 and 50cm accounted for 78% of all trails (Figure 4.6). These small trails made up the majority of trails (49.3%), followed by medium (50-70cm) (37.1%) and finally large trails (70-100cm) (13.6%). The subjective classification of trail size was tested by measuring width on the ground, and there were highly significant differences in the mean width of the three trail size classes, which indicated that the subjective classification was reliable (Kruskal-Wallis Test: χ^2: 1504, df = 2, $P < 0.001$, Figure 4.7).

Figure 4.5. Frequency of trails km^{-1}

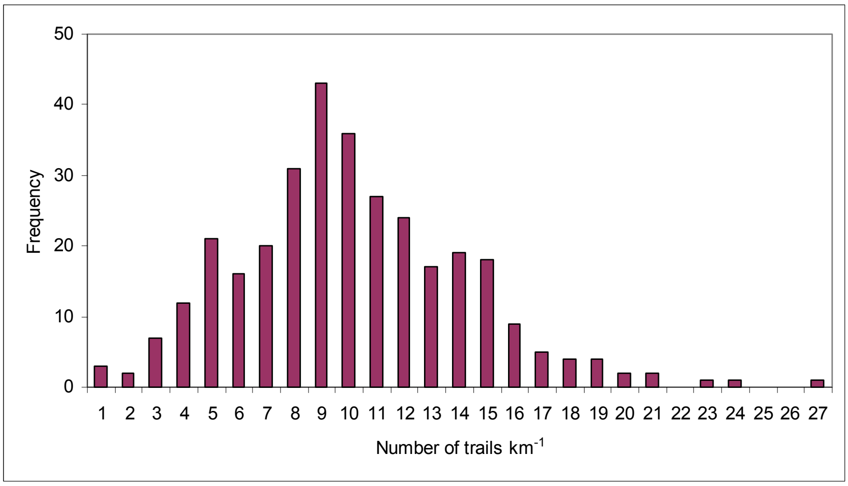


Figure 4.6. Trail width frequency

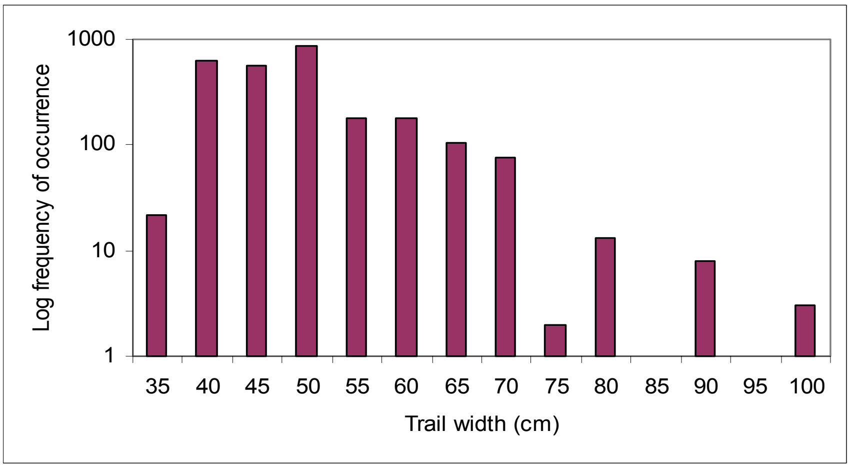
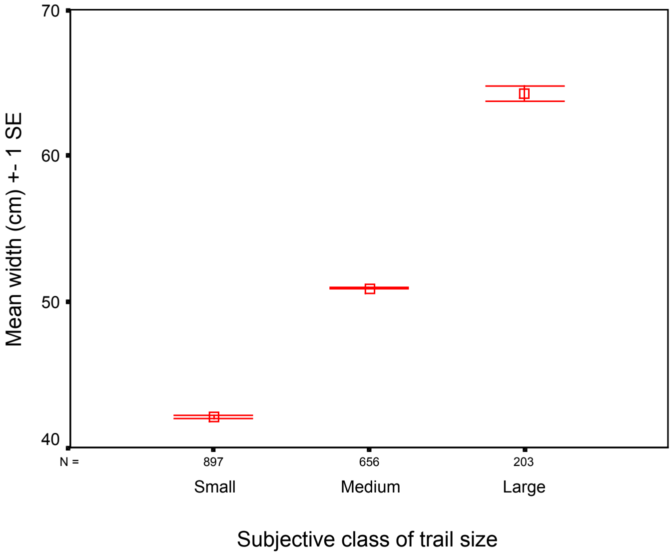


Figure 4.7. Mean width (cm) of subjective trail size classes



Trail frequency by vegetation

Since vegetation type was described in considerably greater detail for the Goualougo Triangle portion of the survey than the Kabo East portion, only those data were used to assess differences in trail density with vegetation type. The mean number of elephant trails across all vegetation types was 9.8km^{-1}, with a range from 0.8 km^{-1} in VLF to 16.7 km^{-1} in MCF (Figure 4.8). The difference in trail density by vegetation type was highly significant (Kruskal-Wallis Test: $\chi^2 = 138.2$, df = 8, $P < 0.0001$). Since data on tree nor THV abundance were not collected during this study, the hypothesis that trail density was positively correlated with elephant fruit tree density and overall tree density was tested using tree density data from different vegetation types calculated in Chapter 2. Trail density was significantly positively correlated (Spearman's Rank Correlation, all tests one-tailed) with both elephant fruit tree density (rho = 0.679, N = 7, $P < 0.05$) and the density of all trees (rho = 0.893, N = 7, $P < 0.005$) (Figure 4.9). There was no relationship between trail frequency and THV abundance by vegetation type, which suggested that THV had no influence on either elephant trail construction or location.

Figure 4.8. Mean number of elephant trails km^{-1} by forest type

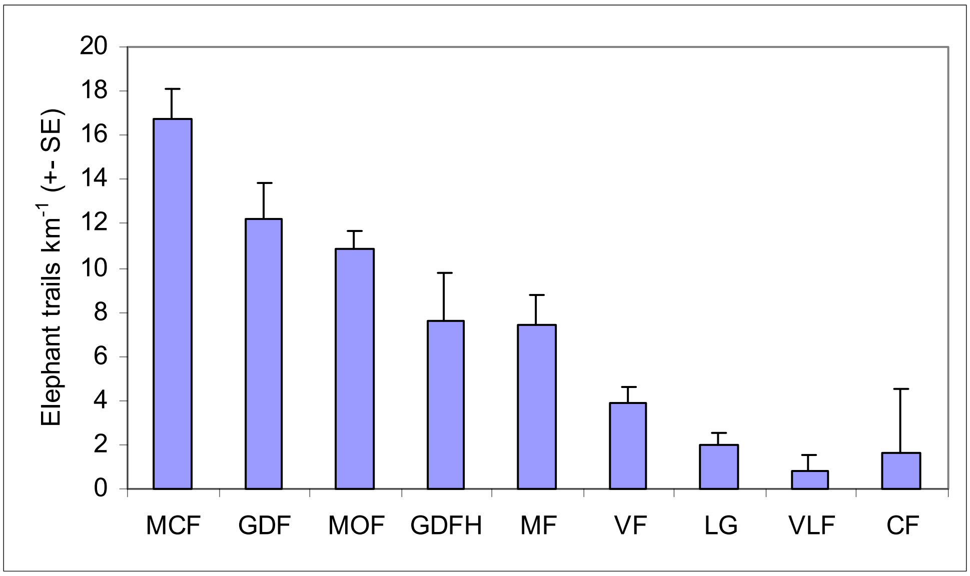
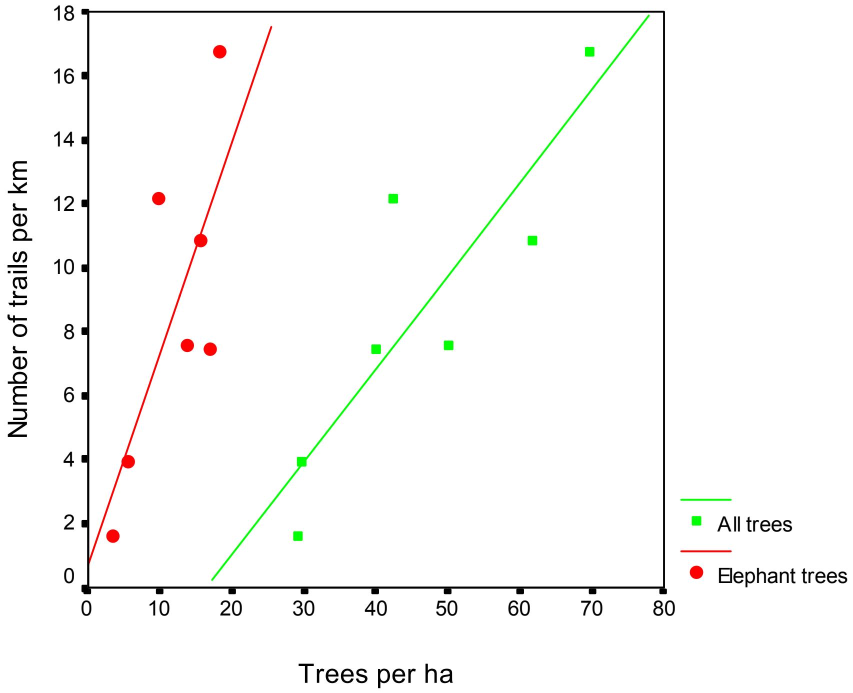


Figure 4.9. Change in trail frequency with the density of large trees



Elephant trails in the Goualougo Triangle and on the Bodingo Peninsula

On descending through the Goualougo Triangle from the then southern border of the NNNP, trail frequency of all, medium, and small trails increased significantly with decreasing latitude, (All, $F_{(1,85)} = 6.25$, $P < 0.05$; Medium, $F_{(1,85)} = 7.773$, $P < 0.01$; Small $F_{(2,84)} = 4.572$, $P < 0.05$). There was no change in the frequency of large trails with distance form the southern border. In the Kabo logging concession, there was no difference in trail frequency with either distance from water, latitude, or proximity to the Likouala swamps. There was a trend toward increasing trail frequency on the Bodingo Peninsula compared to the rest of the Kabo concession, though it failed to reach significance (Mann-Whitney U test (one-tailed): z = -1.590, p = 0.056). However, when trail data were divided by size class the frequency of medium trails was significantly higher on the peninsula (Mann-Whitney U test: z = -1.886, p = 0.028). This indicated that the Bodingo Peninsula was a region of high elephant movement, possibly due to fruit tree density on versus off the Peninsula (though fruit tree density across the Kabo concession are unavailable with which to test this hypothesis), or that the Peninsula may constitute an access corridor between the Likouala swamps and *terra firma* forests to the north.

Trails and bais

A total of nine trails originating from *bais* were surveyed over a distance of 33.7km (8x4km, 1x1.7km) following the methods described earlier. *Bais* always have watercourses running through them (Chapter 2), and are therefore situated in river valleys. The trail system originating in *bais* may be extremely well developed and trails are often arranged radially from the focal drinking points in the *bai* (Figure 4.10). Trails exiting *bais* may follow either the watercourse or make their way through *terra firma*, and the latter were selected for this study. The physical structure of the trail system and the tree species composition changed considerably with distance from the *bais*. Trails originating (or passing through) *bais* are well trampled, devoid of vegetation, and often several metres across as they exit the *bais*. In one case on leaving the Mingingi *Bai*, a single trail (not surveyed in this study) was measured at over 20m in width. All trails appeared to become smaller and more tortuous with distance from *bais*, which were tested using regression analysis of distance from *bai* in 100m segments on mean trail width. Trail width decreased significantly with distance from *bais* (Figure 4.11, $r = 0.254$, $F_{(1,588)} = 40.467$, $P < 0.001$) with a mean in the first 100m of 137 cm, declining quickly to 94cm between 100-200m, and only 55cm at 4000m. An index of tortuosity was calculated as the mean change in trail heading divided by the length in metres between heading measurements, and it did not change significantly with distance from *bais*.

Figure 4.10. Bonye 1 showing the characteristic trail system of a *bai* heavily frequented by elephants

Trail intersections formed conspicuous foci to the trail system, which ranged from a single trail branching off the main trail, to multi-trail intersections involving up to 7 trails radiating out from the centre point. The number of trail intersections decreased significantly with increasing distance from *bais* (Linear regression: $r = -0.679$, $F_{(1,38)} = 32.559$, $P < 0.001$) (Figure 4.12), and the mean number of trails crossed on perpendicular transects (Figure 4.13) also decreased significantly with increasing distance from *bais* (Linear regression: $r = -0.644$, $F_{(1,18)} = 12.751$, $P < 0.005$). Trails therefore became bigger, more intensively used, and the trail network became more intricate with proximity to *bais*.

Figure 4.11. Mean trail width with distance from *bai*.

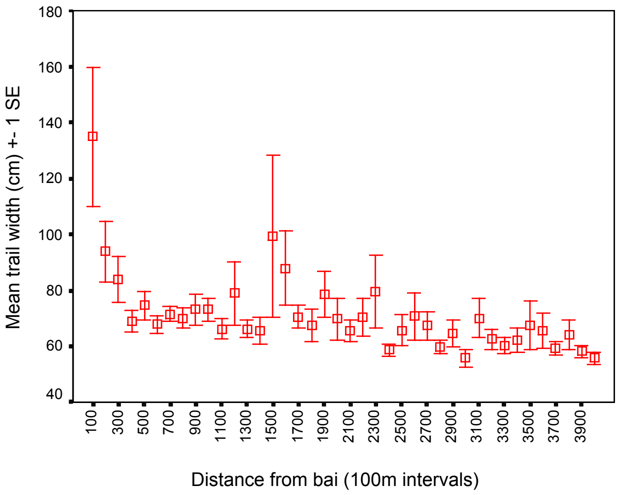


Figure 4.12. Mean number of trail intersections with distance from *bais*

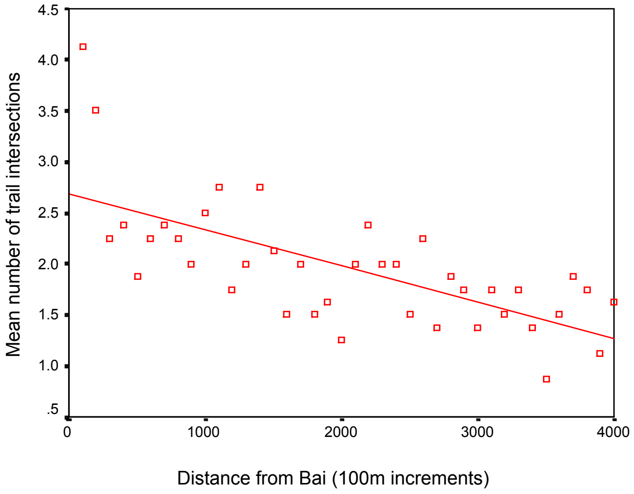
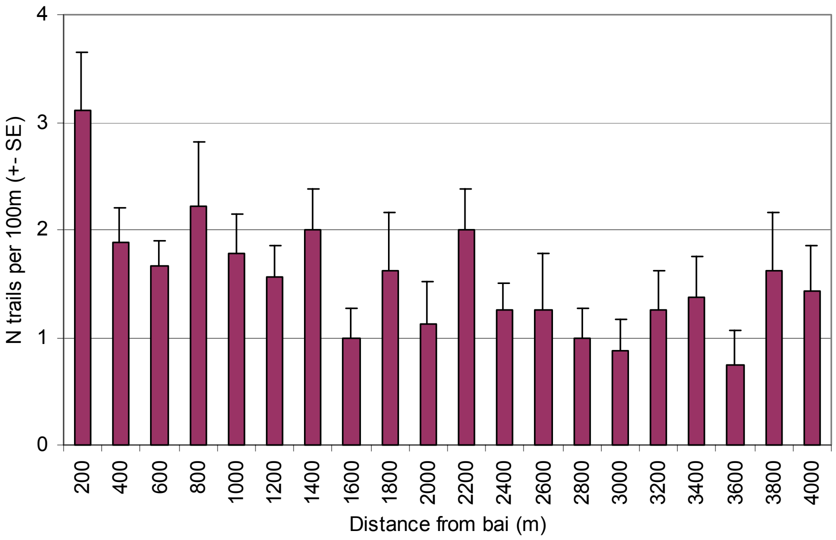


Figure 4.13. Mean number of trails crossed on 100m transects perpendicular to vegetation survey trails

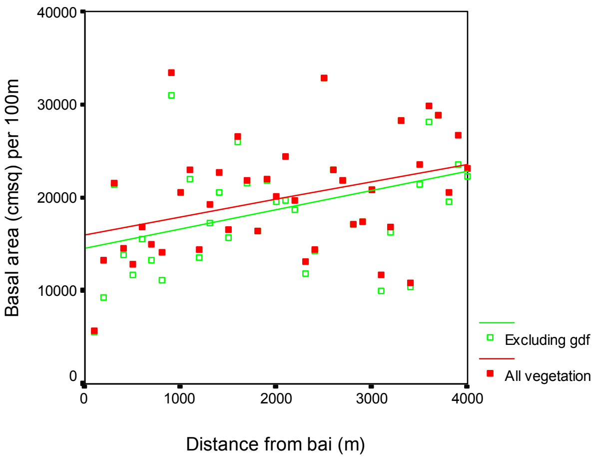


Trees and trails

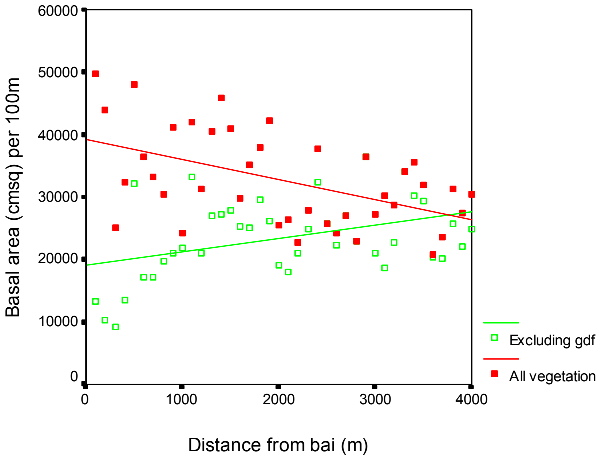
The abundance of elephant fruit trees and non-elephant trees with distance from *bais* was investigated. Because *Gilbertiodendron dewevrei* forest (GDF) was clumped around *bais* in some cases, two analyses were carried out, one including GDF and the second excluding GDF survey sections. In both cases, the basal area of elephant fruit trees increased significantly with increasing distance from *bais* (Linear regression analysis: $r_{(\text{all vegetation types})} = 0.362$, $F_{(1,39)} = 5.742$, $P < 0.05$; $r_{(\text{excluding GDF})} = 0.390$, $F_{(1,39)} = 6.821$, $P < 0.05$), and there was no significant difference between these relationships ($t = -0.289$, $df = 76$, ns) (Figure 4.14a). When all vegetation types were included in the analysis, there was a strong negative correlation between tree basal area and distance from *bais* ($r = -0.498$, $F_{(1,39)} = 12.525$, $P < 0.001$). When GDF was excluded the slope of the regression line became significantly positive ($rs = 0.398$, $F_{(1,39)} = 7.116$, $P < 0.01$) (Figure 4.15b).

Figure 4.14. Elephant fruit tree and non-elephant tree basal area with distance from *bais*

a) Elephant fruit trees



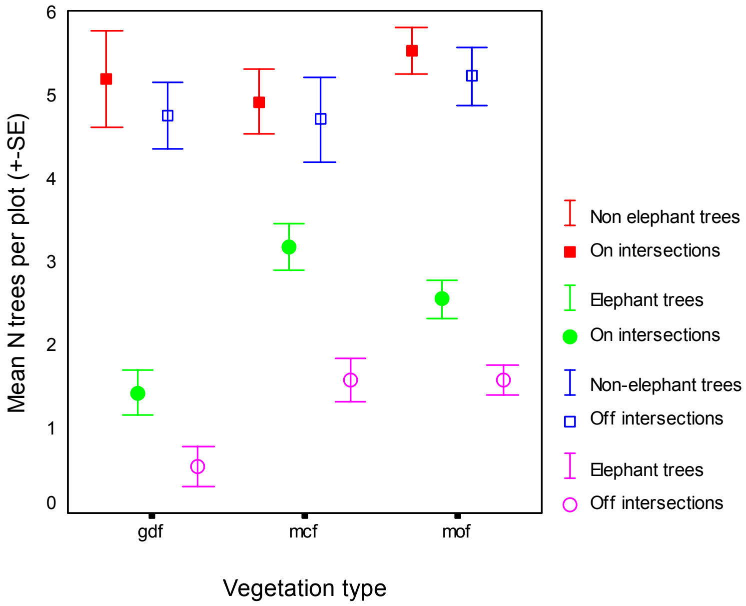
b) Non-elephant trees



TREES AND TRAIL INTERSECTIONS

A total of 115 pairs of nested plots was enumerated, giving a total surface area of 2.3ha enumerated for each in the pair of on:off trail intersections for trees over 10cm dbh, and 4.6ha for trees over 50cm dbh. Of 187 species identified, 48 were species whose fruits were known to be eaten by elephants (Chapter 3). Of all trees, non-elephant trees were more common both on and off trail intersections (Figure 4.15). There was no significant difference in the abundance of non-elephant trees by vegetation type, or by plot location (ANOVA: vegetation, F = 1.242 $_{(2,222)}$, P = 0.291; location (on or off intersection), F = 0.251 $_{(1,222)}$, P = 0.617). By contrast, elephant trees showed highly significant differences in stem abundance both by vegetation type and location, being twice as abundant on trail intersections compared to off them (Figure 4.15). The interaction between vegetation and location was non-significant, indicating that vegetation had little effect on the scale of the abundance difference with location (ANOVA: vegetation, $F_{(2,222)} = 8.764$, $p < 0.001$; location (on:off intersection), $F_{(1,222)} = 22.505$ $P < 0.0001$; interaction, $F_{(2,222)} = 1.010$ $P = 0.366$). Elephant trees were most abundant on intersections in mixed closed forest (MCF) (Tukey's HSD test revealed significant differences between GDF and other vegetation types, but no significant difference between mixed open forest and mixed closed forest). For trees of all species, stem abundance was variable, but not significantly different between vegetation types, but was significantly higher on intersections compared to off them (ANOVA: vegetation, F = 2.265 $_{(2.450)}$, P = 0.105; location on off intersection, F = 7.873 $_{(1,450)}$, P <0.01).

Figure 4.15. Mean number of 'elephant' and 'non-elephant' trees on and off trail intersections



Similar trends were observed when the basal area of trees was compared across vegetation types and intersection/non-intersection sites (Tables 4.1 and 4.2). For all vegetation types, elephant fruit tree basal area was significantly greater on than off intersections, with an 8.5 fold increase in mean basal area on compared with off intersections. In the case of GDF, there was a 30-fold increase in basal area on intersections compared to off them. There was no significant difference in basal area on versus off intersections for non-elephant trees.

Table 4.1. Basal area ha^{-1} of trees on and off trail intersections

		Elephant fruit trees		Non-elephant trees	
Vegetation	Plot type	On intersection	Off intersection	On intersection	Off intersection
GDF	200m^2	31.35	1.01	41.01	28.27
MCF	200m^2	55.48	4.84	18.63	19.57
MOF	200m^2	28.16	5.65	19.79	16.59
GDF	400m^2	14.99	0.85	26.26	16.47
MCF	400m^2	34.54	2.81	8.86	9.03
MOF	400m^2	18.98	6.45	7.29	6.94

Table 4.2. Significance tests of the difference in basal area by vegetation and on/off intersection for elephant fruit and non-elephant tree species

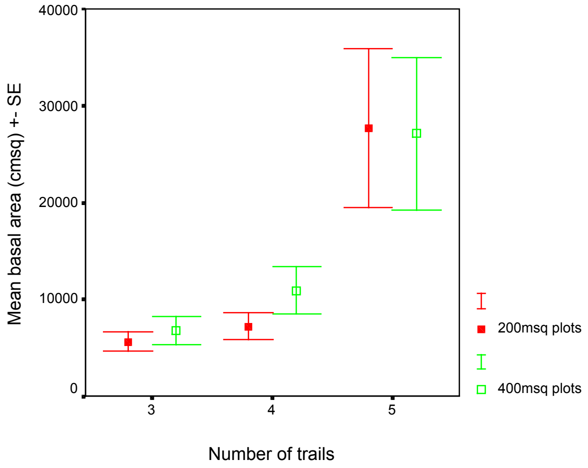
ANOVA (ln or square root tranformations in all cases resulted in homogeneity of error variance)				
	200m^2 plots		400m^2 plots	
	$F_{(df)}$	P	$F_{(df)}$	P
Elephant fruit trees				
Vegetation	11.529 $_{(2,222)}$	<0.001	3.731 $_{(2,222)}$	0.025
On/off intersection	46.404 $_{(1,222)}$	<0.001	42.85 $_{(1,222)}$	<0.001
Interaction (vegetation/intersection)	1.8 $_{(2,222)}$	ns	4.199 $_{(2,222)}$	<0.05
Non-elephant trees				
Vegetation	1.725 $_{(2,222)}$	ns	12.732 $_{(2,222)}$	<0.001
On/off intersection	1.633 $^{(1,222)}$	ns	1.015 $_{(1,222)}$	ns
Interaction (vegetation/intersection)	0.193 $_{(2,222)}$	ns	0.003 $_{(2,222)}$	ns

Intersection size and tree abundance

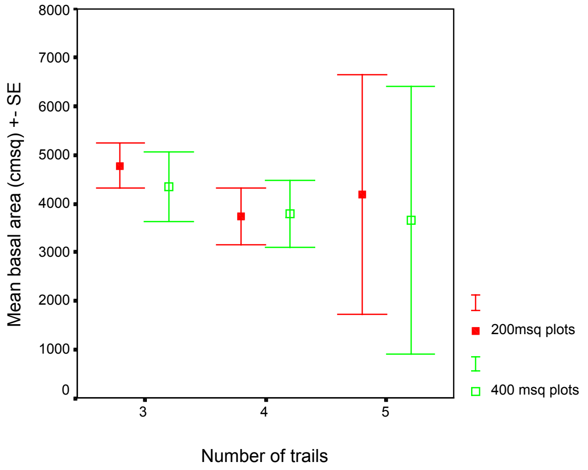
Intersections formed the foci of the trail system rather like the hubs and spokes of a wheel. It was hypothesised that as the number of spokes off the intersection increased, fruit tree abundance (as indicated by basal area) would also increase. The graphs below (Figure 4.16a,b) show mean elephant fruit tree and non-elephant fruit tree basal area with respect to number of trails at intersections. As predicted there was a significant increase in elephant tree basal area with increasing number of trails at intersections (ANOVA (using square root transformed basal area) for 200^2 plots, $F_{(2,110)} = 10.444$, $P < 0.001$; for $400m^2$ plots, $F_{(2,110)} = 9.6$, $P < 0.001$). Post hoc tests (Tukey's LSD) suggested that for $200m^2$ plots there was no significant difference between 3 and 4 trail intersections, however for $400m^2$ plots Tukey's LSD indicated that the basal area for all three intersection types was significantly different ($P > 0.05$ in all cases). There was no significant difference in basal area with number of trails at intersections for non-elephant trees (ANOVA, (square root transformation of basal area), for $200m^2$ plots, $F_{(2,110)} = 0.1$, ns; $400m^2$ plots, $F_{(2,110)} = 0.476$, ns).

Figure 4.16. Mean tree basal area per plot by number of trails on intersections

a) Elephant fruit trees



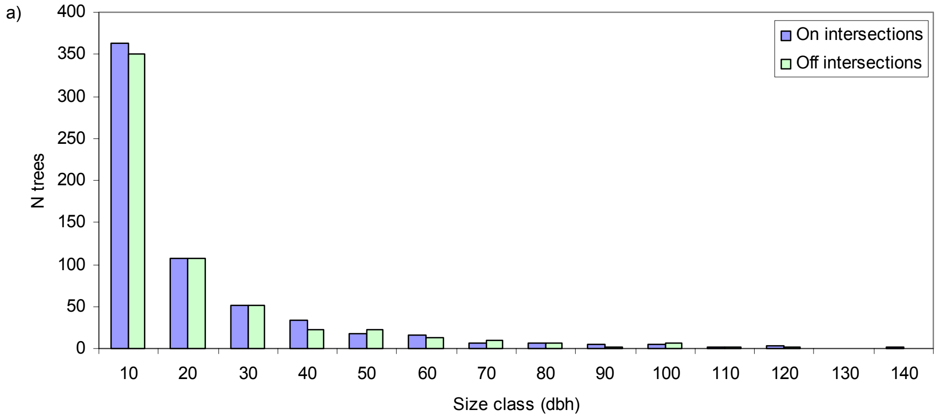
b) Non-elephant trees

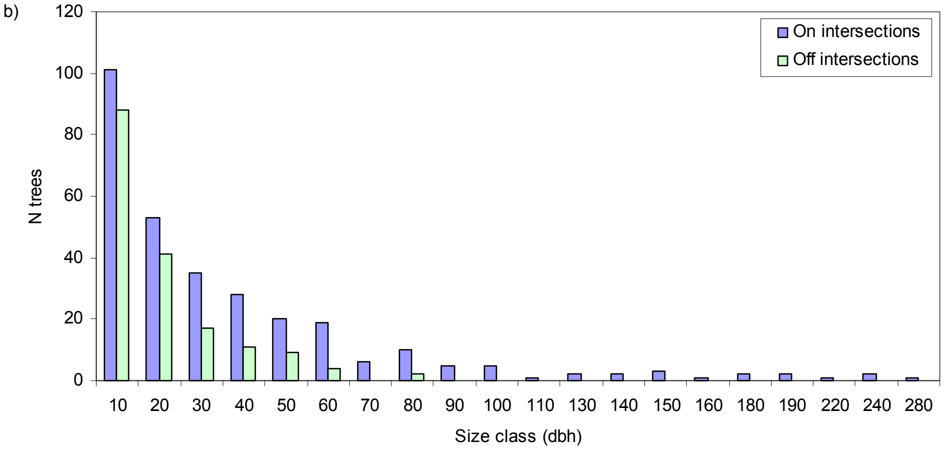


Size class distribution and trail intersections

Trees enumerated in 200m^2 plots were used to assess differences in the size class distribution of elephant and non-elephant trees. Since most elephant trees tend to be large growing species and there is an abundance of non-elephant trees in the understorey which never attain large size classes, only those tree species for which individuals could reach 50cm dbh or greater were included in the analysis. Figure 4.17a shows the size class distributions, measured in dbh increments of 10cm, for non-elephant tree species both on and off intersections, while Figure 4.17b shows data for elephant tree species. Elephant trees reached considerably larger dbh than non-elephant trees, with the largest non-elephant tree in the 140cm size class, while elephant trees as large as 280cm dbh were measured. Only 8 elephant trees over 140cm dbh were recorded all of which were on trail intersections. The largest elephant trees measured off intersections were 80cm dbh. For non-elephant trees, a sign test revealed there was no significant difference in size class representation on and off intersections. For elephant trees, the total number of trees was significantly higher for every size class on, compared to off, intersections (sign test: $P < 0.001$, $N = 21$).

Figure 4.17. Relationship between size class for a) non-elephant trees and b) elephant fruit trees on and off trail intersections

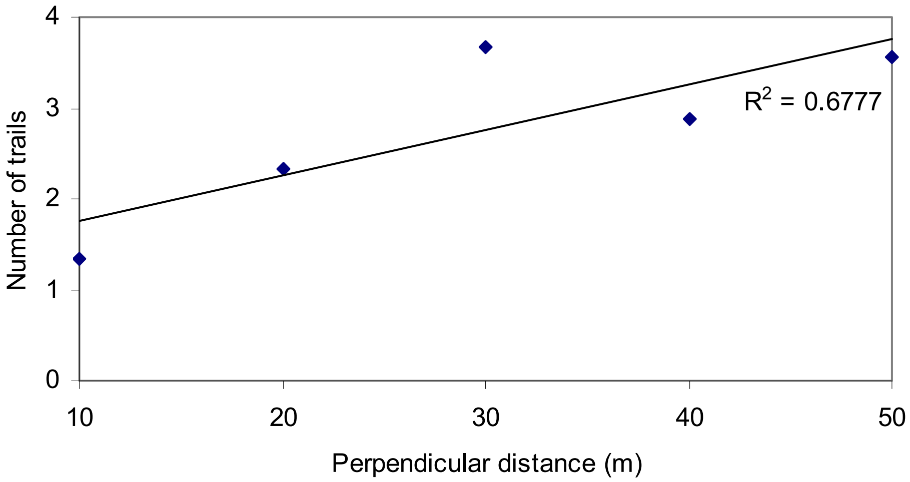




Tree composition with perpendicular distance from elephant trails

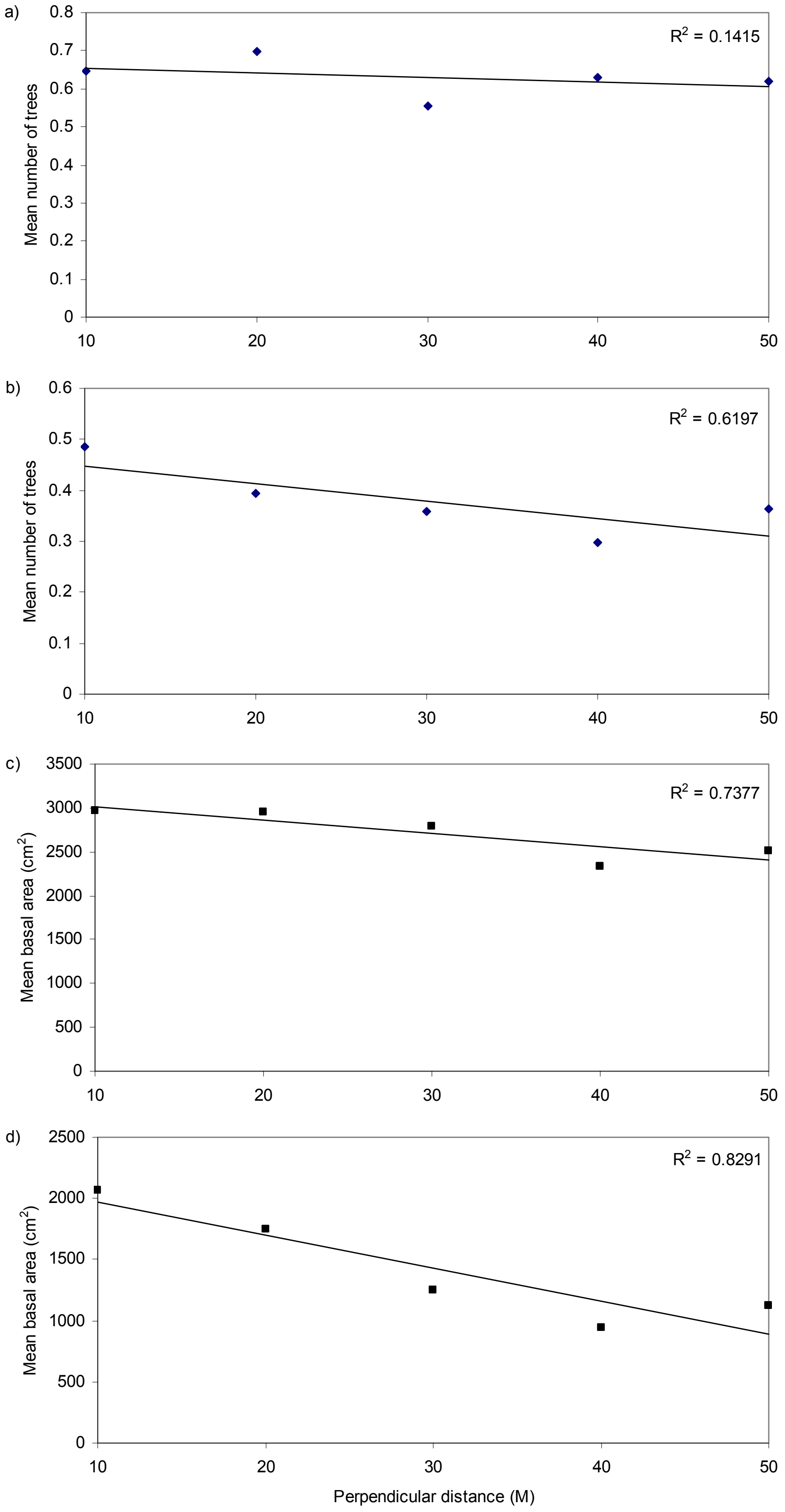
A total of 3523 trees over 40cm dbh from at least 151 species was identified and enumerated from the 9 elephant trails and corresponding perpendicular transects, of which 1673 trees were enumerated on transects. Two factors confounded data analysis of the distribution of trees with perpendicular distance from the trails. First, there were no data on trail distribution after the end of each transect, which could have influenced the abundance of trees on the second 50m of the transect. Second, as distance from the principal trail increased, the likelihood of a trail approaching, but not crossing, the transect increased. The first source of error was eliminated by removing data from the latter half of the transect from the analysis which was also thought to reduce the bias of the second source of error.

Figure 4.18. Trail distribution with distance from the principal trail



The apparent trend of increasing number of trails with distance from the principal trail did not reach statistical significance (Linear regression, $r = 0.823$, $F_{(1,3)} = 6.13$, ns) (Figure 4.18). There was no significant change in the number of non-elephant trees (Figure 4.19a) or elephant fruit trees (Figure 4.19b) with perpendicular distance from the principal trail (non-elephant trees: $r = -0.376$, $F_{(1,3)} = 0.533$, ns; elephant trees: $r = -0.787$, $F_{(1,3)} = 4.889$, ns). When basal area was calculated, there was again no significant change in non-elephant tree (Figure 4.19c) values with distance from the trail ($r = -0.376$, $F_{(1,3)} = 0.495$, ns), while there was a significant decrease in elephant tree basal area (Figure 4.19d) ($r = -0.911$, $F_{(1,3)} = 14.552$, $P < 0.05$). That basal area of elephant trees decreased with distance from the trail, yet the number of trees did not, indicated that trees in larger size classes were aggregated about the principal trail.

Figure 4.19. Mean number of trees and basal area (cm^2 per 10m transect segment) with perpendicular distance from survey trails



DISCUSSION

The results of this study have shown that there are at least three critical habitat components involved in the construction of trail systems by elephants; large rivers, *bais*, and fruit trees. Specifically it has been shown that 1) elephant trail density, individual trail development and size is highest in close proximity to *bais*, 2) the overall density of trails throughout the Ndoki Forest is close to one trail per 100m of linear distance ($9km^{-1}$), 3) trail density increases with elephant fruit tree density, 4) elephant fruit trees are heavily aggregated about elephant trails particularly at trail intersections, and 5) large rivers on flat terrain often with extensive swamps and open understorey vegetation are associated with the development of large trails. Each of these is an important resource, the exploitation of which should have evolved to maximise the efficiency of acquisition (Stephens and Krebs 1986).

Evolution of elephant trail systems

If food resources were super-abundant and uniformly distributed, animal foraging strategies would be based only on the effects of temporary local depletion. Rules governing decisions on ranging would be based on factors such as the cost of locomotion, risks of predation, and constraints of social interactions (Bell 1991). As the heterogeneity of resource distribution increases, adaptations for efficient exploitation must become more complex and may involve decision making over several spatial and temporal scales (Bell 1991). In patchy habitats, one set of searching rules may govern mechanisms for locating widely dispersed patches e.g. pseudo-random walks, straight walks, systematic searching, (Jander 1975; Hoffmann 1983) or 'kinesthetic input' mapping (the use of sensory information in searching) (Carde 1984; Wiltschako 1984). Different rules may determine how long to remain in a patch, or when to leave a patch which is no longer profitable. This implies some assessment of patch quality - the 'Marginal Value Theorem' (Charnov 1976). In addition to environmental and social issues, physiological cues and constraints, and cognitive ability, including spatial memory, may also play significant roles in foraging behaviour (Allman 1977; Clutton-Brock 1980; Menzel 1981; Milton 1981b, 1988; Cheney and Seyfarth 1990; Barton 1996).

In Chapter 2 it was demonstrated that different resources required by elephants are distributed over different spatial and temporal scales. Mineral deposits are located in *bais*, which are both rare across the landscape and locally clumped. While location remains constant, mineral availability may fluctuate, as may the physiological needs of elephants for mineral supplements. Free running water (rivers) is spatially clumped yet dependable (at least in tropical forests) and stationary. Swamp browse is clumped according to the distribution of swamps, and also on a within-swamp scale, as a result of the heterogeneity of swamp vegetation. *Terra firma* browse is ubiquitous throughout *terra firma* forests, yet the quality and quantity is spatially heterogeneous. Light gaps and open vegetation offer high abundance, high quality browse while closed canopy forests contain low quantity and quality forage. Environmental factors governing the temporal change in browse quality (e.g. rainfall, soil moisture gradient, and insolation) result in a variable spatial distribution. While the quality of browse is patchy on several spatial scales (e.g. individuals trees, to vegetation types, to environmental gradients), on the range of scales at which an elephant is capable of foraging, there are few areas where suitable browse is completely absent. Thus, patchiness is a continuum of quality rather than a discreet presence/absence distribution (except on the scale of the distribution of individual plants). Fruit is widespread throughout *terra firma* forests, is spatially and temporally clumped, and patch quality is unpredictable. The variation in availability is high, from extremely dense clumps under heavily fruiting trees, to large areas (up to several kilometres) which may contain little or no fruit. Given these differences in the distribution of resources, elephants would be expected to search for each in a different way, which in turn should be reflected in the structure of their trail system. Superimposed on resource distribution are the constraints of locomotion, predation, and sociality mentioned above.

The spatial scale of the proximate resource (e.g. leaf, fruit, mineral, water), and its persistence will also determine an animal's foraging strategy. *Bais* are big patches, may attract several hundred individuals in a single day (Turkalo and Fay, 2001), and the resource is found in quantities probably only limited by the animal's intake rate (at least on an ecologically meaningful time scale). The payback from *bais* is thus predictable and large, and depletion of that resource negligible (i.e. the presence of one elephant prior to the arrival of a new individual will not diminish mineral availability). There are only a limited number of elephant *bais* in the Ndoki Forest (several tens), thus the increasing concentration of elephant traffic at these fixed point locations with a dependable resource, would be expected to create an increasingly intense trail network with proximity to the *bai*.

The physiological need of elephants for browse is nearly continuous for adequate maintenance and growth. Forage quality is dispersed on the spatial scales of large regions within the forest (vegetation types), to high and low quality patches within vegetation types, to individual plants within these patches, and ultimately to individual branches or leaves on plants. There may be several thousand potential browse plants per hectare of forest. The amount of food at any one high quality small scale patch (a plant) is variable from a few leaves to several kilogrammes of succulent pith, but one feeding event on one plant, no matter how big, will not satiate the elephant on its own, and the elephant has to move to another plant, most likely on the second scale of 'patchiness', e.g. another plant within a light gap. The payback from any one patch is smaller as patch size decreases, and the elephant is obliged to move on to new patches on all spatial scales. Once a small-scale patch (a single tree or branch) has been visited, the resource has been depleted perhaps to zero, and it is costly to return to the same patch until it has been replenished. In the case of palatable leaves, replacement for an individual plant may take weeks, months, or the onset of the next wet season. Thus it is most efficient to devise a set of search rules for browsing which take into account the high probability of finding a browse patch (compared to finding a *bai* for instance), the dispersal of high quality patches on several spatial scales, the small payback per browse patch, and depletion of the resource after feeding. The combination of these factors would tend to discourage the development of permanent trails as individual patches are too small and too dispersed, the probability of finding another by chance is relatively high, the payback is low, and return to the same place in the short-term is costly.

In terms of its spatial and temporal distribution, patch size, payback, replenishment rate, and physiological requirement, fruit lies somewhere between the two extremes of *bais* (localised in space, single spatial scale, rare, high payback, undiminishable by repeated visits, occasional physiological requirement) and browse (widespread, multiple spatial scales, low payback, diminishable and slowly renewable, continuous physiological requirement). Fruit trees are found throughout all *terra firma* forest types, but like browse, patchiness is high in time and space. Patch size ranges from the fruitfall under an individual tree in a dense stand of fruit trees (2 scales), to widely dispersed individual trees in poor habitats. Individual spatial patches have finite temporal existence, which is the fruiting period of the tree, while the location of the tree remains constant over most foraging time scales, and usually the lifetime of an elephant. Considering first the patch size of the fruitfall under a single canopy, during fruiting periods the payback is relatively high. Unlike browse, even if a single elephant depletes the entire fruit stock under the tree, during the fruiting period of that tree there will be a rapid replacement of fruit under the tree as new ripe fruit continues to fall. Thus, there is good reason to return to the same site soon afterwards, since if fruit was found on one day there is a high probability that it will be found again a short time later. There is also a strong incentive for another animal to visit the tree soon after a previous animal since it is unlikely that the first elephant found or desired all of the fruits available at the time of the visit. The rewards of high payback and profitability of repeated visits would lead to permanent trail establishment built around fruiting trees, as apparently is the case in the Ndoki Forest and elsewhere (Short 1983; White 1992; Powell 1997).

FINDING AND EXPLOITING RESOURCE PATCHES

Animals may use a variety of sources of information when searching for resources (Bell 1991). Usually there will be some environmental cue to assist foraging. Cues may be patch-specific' (smell, sight, or sound), or environmental (light, heat, or topography). Environmental cues give way to patch-specific cues as scale decreases. The ability to use cues may vary from a simple taxis towards a stimulus (e.g. phototaxis to light), which requires no cognitive capacity, to a complex set of relationships such as the knowledge that rainfall leads to new leaf production at the end of some habitat gradient or specific part of the environment (e.g. elephants hear thunder which signals new grass production in the savannahs of Amboseli at the end of the dry season (Moss 1988)).

Browse and fruit have different environmental and patch-specific cues depending on spatial scale. Browse is more abundant in light gaps (Struhsaker *et al.* 1996; Chapter 2) thus light levels through the canopy could indicate a high quality browse patch. Once in the patch (light gap) a different search image may take over to locate leaf patches. The cues for fruit may also be on several levels. In Ndoki, elephant fruit abundance is positively correlated with rainfall, and since fruit is found in *terra firma* forests, this could indicate to a cognisant elephant that its search should be in *terra firma* when rainfall is high. Fruit trees are more abundant in closed canopy forest (Chapter 2); therefore searching in low light levels should increase the probability of finding fruit. Many elephant fruits smell strongly, some make a distinctive sound when they hit the ground, while others attract a variety of conspicuous animals such as chimpanzees and gorillas, all of which may indicate the presence of fruit. Rivers and swamps are found in valley bottoms, an excellent environmental cue to help an elephant locate a generally profitable area. Once there, the most efficient way to find good patches would presumably be to follow the *terra firma*-swamp interface and use other environmental cues such as light, sound, or sight to locate accessible water, rather than a more random search.

TRAILS AND TREES: CHICKENS AND EGGS

In this study it was argued that the spatial aggregation between fruit trees and trails is the result of the effect of heterogeneity of fruit and fruit tree distribution on elephant foraging mechanisms. The extent to which elephants may influence the distribution of these fruit trees has not been discussed. Elephants are excellent seed dispersers of numerous species (Powell 1997; Chapter 3) which presumably improve the germination and subsequent survival of seeds (Chapman *et al.* 1992). Thus, the distribution of elephant-dispersed plant species may be strongly determined by the distribution and ranging patterns of elephants themselves. Areas of the forest in which elephants are found in high densities will have a higher rate of seed deposition (through dung) than low elephant density areas. This presents a chicken and egg problem for the relationship between elephant trails and elephant fruit trees. Two competing hypotheses are immediately obvious: 1) Elephants forage and construct their trail system with respect to and in response to the underlying distribution of fruit trees caused by a variety of edaphic, environmental, and ecological processes, 2) Elephants, through the spatial variability in their ranging behaviour create an irregular density surface of seed rain through the forest, which determines the spatial distribution of trees, and feeds back positively to the spatial distribution of elephants themselves. A third hypothesis is that the distribution of both trees and elephants is a combination of 1) and 2). Data from this study cannot respond to these hypotheses, though future research in this area is important, particularly as range restriction, logging, and population decline will increasingly influence the ecological role of elephants in Africa's forests.

CONCLUSIONS

1. Observations revealed three important habitat components involved in the construction of trail systems; large rivers, *bais*, and fruit trees. Vegetation structure may also influence trail system development. Large trails often followed watercourses, particularly along the *terra-firma*/swamp interface of large rivers, where they sometimes continued, unbroken, for tens of kilometres. These trails were most frequently associated with riverine *Gilbertiodendron dewevrei* forest, which, due to its open understorey, was thought to facilitate trail formation and maintenance over forest types which had more abundant understorey vegetation, including lianas.
2. Surveys across a wide swathe of the Kabo logging concession showed that trail density was high in *terra-firma* forest, with a mean of 9trails km^{-1}. The density of trails increased with the density of large trees, particularly with the density of elephant fruit trees.

3. The trail system proliferated with increasing proximity to *bais*. Trial width, intersection frequency, and trail density all increased with proximity to *bais*. The largest trails observed in the entire forest were associated with large, active *bais*.
4. There was a high level of association between trails, trail intersections and elephant fruit trees, which was not observed for non-elephant trees. Fruit tree density was higher at trail intersections than at random locations in the forest, and the basal area of elephant fruit trees on intersections increased as the size of the intersection (based on the number of associated trails) increased. The basal area of elephant fruit trees decreased significantly with perpendicular distance from trails, while there was no change in basal area for non-elephant trees.
5. It was hypothesised that elephant trail systems develop as a result of optimal foraging patterns of elephants. Ubiquitous resources (such as browse) which offer a low payback and which are readily depleted do not encourage repeated visits by foraging elephants, and therefore are not associated with the formation of trails. Clumped resources (such as water, *bais*, and fruit) which provide a high payback, which are temporally reliable and not immediately depleted, do encourage repeated visits by elephants. It is these resources that do appear to promote trail formation, and may be important determinants of elephant ranging and distribution.

CHAPTER 5. THE ECOLOGY OF ELEPHANT DISTRIBUTION IN THE NDOKI FOREST

INTRODUCTION

Survival, fitness, and evolution of animals is dependent on their ability to efficiently exploit important resources (MacArthur and Pianka 1966). Since food is a critical resource, survival and reproductive success ultimately depend on the efficiency of foraging strategies (Schoener 1971; Stephens and Krebs 1986; Moen 1997). In heterogeneous environments, foraging efficiency is constrained by ranging ability (Mace and Harvey 1983), energy requirements and gut capacity (Demmet and Van Soest 1985; Owen-Smith 1988), and cognitive ability (Bell 1991; Grünbaum 1998) all of which are scaled in some proportion with body size (McNab 1963; Peters 1983; Edwards 1996). Large terrestrial animals have lower specific energy requirements than small ones (Peters 1983), can tolerate lower quality food (Bell 1970; Geist 1974; Jarman 1974), range further than small ones (McNab 1963; Lindstedt *et al.* 1986), and have larger total home ranges (Harestad and Bunnell 1979; Kelt and Van Vuren 1999). Thus large-bodied animals should to be better adapted to cope with spatial and temporal variation in the distribution of food resources than small ones.

Elephants (*Loxodonta africana)* are excellent examples of large-bodied, opportunistic, generalist herbivores. Since the early work of Merz (1981) and Short (1981, 1983) in West Africa, biologists have recognised that there are considerable ecological differences between forest and savannah elephants, particularly in the distribution and quality of important resources (e.g. food and water). These differences influence feeding ecology, which in turn affects ranging patterns, distribution, abundance, and social organisation (MacArthur and Pianka 1966; Fretwell and Lucas 1970; Stephens and Krebs 1986; Krebs and Davis 1993).

Savannah elephants are grazers/browsers which usually live in semi-arid, seasonal habitats where dry season drinking water may be restricted to a few, widely separated sources (Owen-Smith 1988). Access to drinking water is a critical issue for savannah elephants because of their large body size (Owen-Smith 1988), exposure to direct sun (Barnes 1983b), and high fibre diet (Laws *et al.* 1975; Barnes 1982) which create prodigious drinking water requirements. During the dry season savannah elephants rarely venture more than a day's walk from permanent water holes (Leuthold and Sale 1973; Western 1975; Eltringham 1977; Western and Lindsay 1984) with the exception of small isolated populations specially adapted for life in desert conditions (Viljoen 1989b; Lindeque and Lindeque 1991). With the coming of the rains, temporary water sources dot the landscape and savannah elephants disperse out of restricted dry season range close to water into larger wet season ranges (Leuthold and Sale 1973; Western 1975; Barnes 1983b; Verlinden and Gavor 1998). They may also migrate to spatially discrete wet season areas, often over 100km away to graze in areas of high grass productivity (Viljoen 1989b; Lindeque and Lindeque 1991; Tchamba *et al.* 1995; Thouless 1995; Verlinden and Gavor 1998). Primary productivity in savannahs increases with rainfall (Norton-Griffiths 1975) and movements into upland areas are partially governed by food quality. However upland areas often maintain high quality forage throughout the year, but these may remain inaccessible to obligate drinkers such as elephants during dry periods (Western 1975). Water and not forage distribution is thus the primary determinant of savannah elephant distribution.

Forest elephants are generalist browsers and facultative frugivores, with grass making up a minor part of the diet (Short 1981; Dudley *et al.* 1992; Tchamba and Seme 1993; White *et al.* 1993). Like savannahs, African forests also experience extended dry seasons, but total annual rainfall is higher than in the savannah and permanent surface water tends to both cover a higher percentage of the forest landscape and be more evenly distributed (Powell 1997). Forest elephants are rarely more than a few kilometres from permanent drinking water, thus drinking water availability would seem unlikely to constrain access to food resources or drive ranging, habitat selection, or long distance movements (Short 1983; Dudley *et al.* 1992; Powell 1997). Initial data from telemetry studies implied that forest elephants do not make large-scale migratory movements such as those exhibited in savannah elephants (Powell 1997; J-M Fromment pers. comm.). However, more recent telemetry studies using collars fitted with Global Positioning Systems (GPS) conclusively showed that forest elephants may make movements of over 100km when their range is not restricted by human activity (Chapter 6).

If drinking water availability does not drive distribution and large-scale movements by forest elephants, then what does? Short (1983) and Powell (1997) argued that ripe fruit availability was a determinant of forest elephant distribution, and White (1994d) suggested that elephants may move into super-abundant fruit patches from as far away as 50 km. While fruit may make up a considerable portion of the diet, forest elephants maintain a high fibre intake throughout the year consisting of leaf browse, wood, bark, roots, stems, and aquatic vegetation (Short 1981; White *et al.* 1993). Mineral deposits, which are known to strongly influence the distribution of savannah elephants (Weir 1972; Ruggiero and Fay 1994), are also centres of aggregation for elephants in forests (Turkalo and Fay 1995; Klaus *et al.* 1998; Querouil *et al.* 1999). In tropical forests, the distribution of these resources is patchy on a variety of spatial and temporal scales across landscapes (Leigh and Smythe 1978; Van Schaik *et al.* 1993; White 1994c; Leigh and Windsor 1996; Struhsaker 1997; Tutin *et al.* 1997a; Chapman *et al.* 1999) comprising both consistent (the spatial distribution of water) and irregular (spatio-temporal abundance of fruit) elements. Habitat heterogeneity across a continuum of scale may result in habitat selection involving diet choice, patch use, or migratory movements (Orians 1991; Travis and Dytham 1999) leading to aggregation and elevated densities of foragers in high quality habitat patches compared to patches of low quality (Senft *et al.* 1987; Kotlier and Weins 1990; Fryxell 1991; Turchin 1991; Bailey *et al.* 1996). Forest elephant trails have been shown to connect clumped resources, which offer high payback for foraging effort, including minerals in *bais*, water and swamps, and fruit, which may therefore direct elephant ranging and distribution (Chapter 4).

In this chapter, elephant distribution in the Ndoki Forest is described in response to a suite of ecological and human factors. A number of predictions of elephant responses to change in resource distribution were tested:

1. Since they require year round access to drinking water (Western 1975) which is highly clumped in space, elephants should show a permanently clumped distribution in proximity to watercourses in tropical forests.
2. Forest elephants should tolerate high bulk, low nutritional quality foods when more nutritious foods such as fruit are scarce or unavailable. During such times, elephants should forage in patches where browse availability is high (such as swamps and light gaps), leading to increased elephant abundance in these areas.
3. Not only should elephants forage in areas with abundant browse, they should also track the distribution of high quality browse, characterised by the availability of new leaves of browse species.
4. Due to its high nutritional value, fruit should be preferentially exploited over browse when available, and elephants should adjust their foraging pattern to track the spatial and temporal distribution of fruit patches. Elephant abundance should therefore track the distribution of fruit.
5. Permanent trails are conduits for elephant movement, therefore elephant abundance should be highest on, compared to off, trails. However, since fruit trees are highly

aggregated on elephant trails, and browse is associated with open canopy forest away from trails (Chapter 4) use of trails by elephants should increase during periods of high fruit availability.

6. Since rain forest vegetation is notoriously nutrient poor, elephants should be aggregated at sources of minerals, and the scale of aggregation should increase as mineral availability increases or during times of physiological stress (extended periods of low rainfall).
7. Due to high poaching levels in African forests, elephant distribution is negatively correlated with human abundance (Barnes *et al.* 1991). Elephants should respond negatively to increases in human activity level, which may over-ride the ecological basis of their foraging and distribution.

METHODS

Field methods

In March 1998, a 'path of least resistance' foot survey track (White and Edwards 2000a) of 253km total length was established which traversed the Northwest Southeast drainage gradient (Figure 5.1). The logistical problems imposed by the scale of the study precluded stratified random sampling procedures. The track was non-randomly located to maximise sampling effort across a diverse range of habitat types, ecological and human influence gradients previously identified. Surveys were repeated seasonally, four times per year over 2 years starting in the same month each year and each took approximately 1 month to complete. Data collected included track, attributes of vegetation, elephant dung counts, elephant feeding including fruit consumption, and climate, each of which is explained below. The track and all data collected were geo-referenced using a GPS. A single observer (SB) was responsible for quantitative observations and data collection for all surveys. A second person, a Bayaka guide, was responsible for initially marking the survey track (with occasional machete cuts), and for following the exact route on subsequent surveys.

TRACK

During the first survey, compass headings were used to maintain the desired direction of travel along a path of least resistance or 'recce' (Walsh *et al.* 2001) track. An attempt was made to remain on permanent elephant trails, though if these deviated widely from the desired direction, a compass bearing was resumed until the next trail was found. A continuous record of trail type was kept, characterised as no trail, human trail, or elephant trail, with elephant trails subdivided as small, medium, or large, based on qualitative assessment of width, depth, and presence of blockages and debris. Throughout the study the track was logged using a Garmin 12LX GPS with an external antenna worn under a cap. The GPS was set to record a fix every 10 seconds or approximately one fix every 10m. Whenever the GPS memory was full, data were downloaded into a Hewlett-Packard Palmtop computer (HP 12LX). All attribute survey data were recorded into field notebooks with time (a digital wrist-watch was set to GPS time to the nearest second and verified each day) which allowed every datum to be geo-referenced to a GPS fix. During one survey, distance along the track was measured using topofil to accurately measure vegetation types and elephant trail segments.

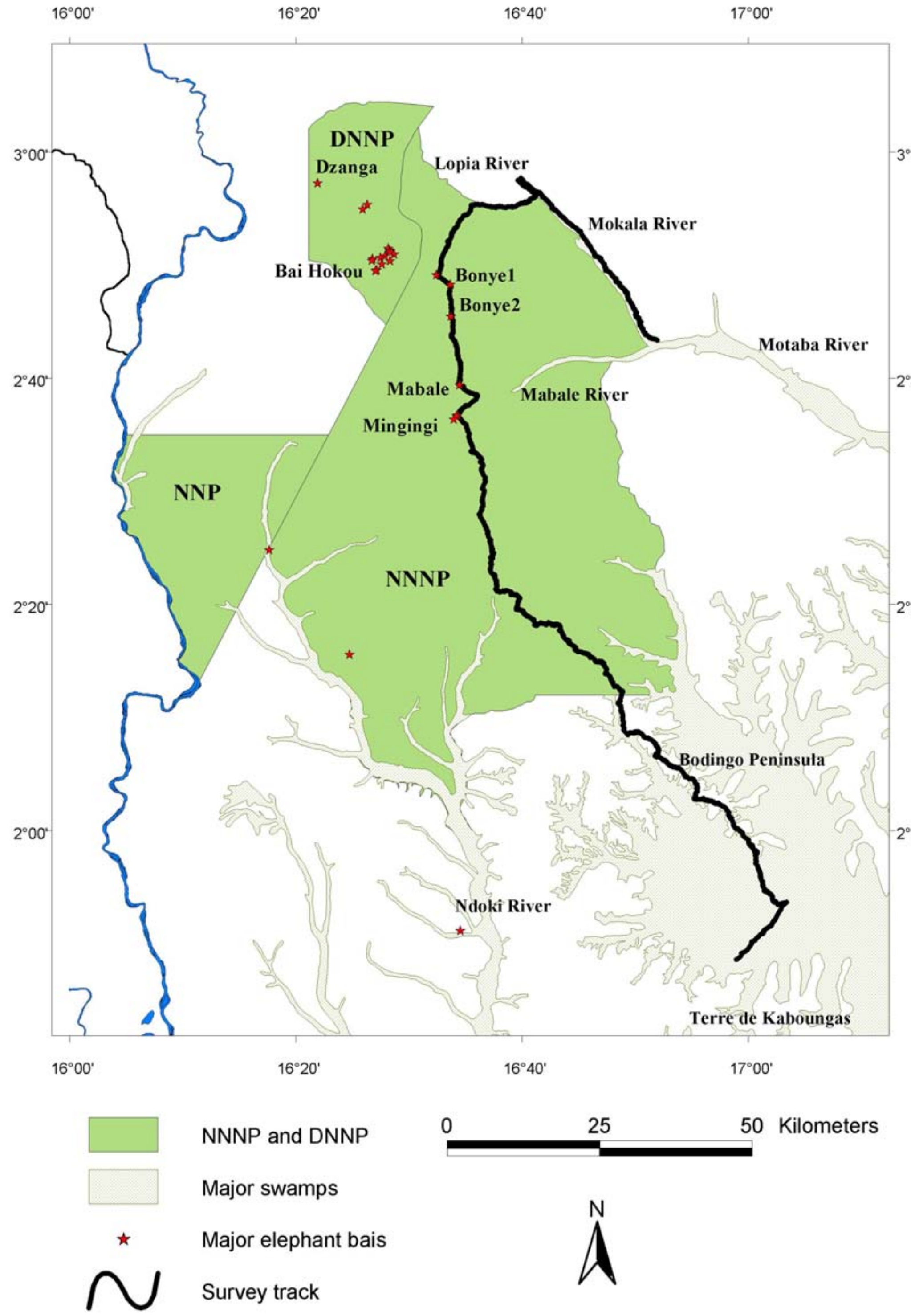
VEGETATION

Methods of vegetation classification and data collection were described in Chapter 2.

ELEPHANT ABUNDANCE

Dung counts were used to estimate elephant abundance in *terra firma* vegetation. All dung seen from the survey track, including piles in an advanced state of decay, was recorded, including estimates of age (fresh, recent, old, and very old) and perpendicular distance from the track. No attempts were made to quantify either defecation rate or dung decay. Constant dung pile decay and defecation rate were assumed for a single survey. Therefore dung was thought to provide a reliable estimate of the spatial distribution of elephants. However, in swamp and seasonally flooded forests, dung could not be reliably counted due to flooding.

Figure 5.1. Elephant seasonal distribution survey track



FRUIT CONTENT OF ELEPHANT DIET

The fruit content of elephant dung piles was discussed in Chapter 3, in which the collection of data used in the analysis below was described.

HUMAN ACTIVITY

All sign of human activity of any age was recorded. Sign included machete cuts, camps, shotgun shells, honey and fruit harvesting sites, fires, rubbish, footprints, forestry prospection transects, vocalisations and direct encounters. Only sign judged to be fresh or recent was used in data analysis.

RAINFALL AND TEMPERATURE

A research team at the Mbeli *Bai* research station in the Nouabalé-Ndoki National Park collected rainfall and temperature data. Data were collected from two locations at the site, one in a small clearing (30m radius) in the forest and one at Mbeli *Bai*, a large *bai* of ca. 8ha. The mean monthly rainfall across both sites was used as an estimate of mean regional rainfall.

Analytical Methods

Two classes of analyses were performed: 1) separate analyses of the distribution of dung and covariates, and 2) a spatial model relating covariate values to dung encounter rate. Pearson's product moment correlation was used (assuming statistical significance at $p \leq 0.05$) to investigate whether covariates such as fruiting score, monocot fresh leaf score and dicot fresh leaf score varied as a function of the amount of rainfall, the distance from rivers, or the distance from the southeast terminus of sampling. In many of the analyses both rainfall in the month of the survey and rainfall in the month preceding survey were used. Both months were tried because, although it was suspected that rainfall should influence characteristics such as fruiting and new leaf production, a clear mechanistic understanding of these processes was unavailable to predict how lagged the response to rainfall should be.

Pearson's product moment correlation was used to examine regularity in the pattern of fruiting between years. In this analysis the survey line was divided into 225 non-overlapping segments and the correlation coefficient was calculated between fruiting score in the first year and fruiting score in the second year. This analysis was performed separately for each of the four pair of surveys (1x5, 2x6, 3x7, 4x8). Neighbouring segments were then aggregated into larger lengths (i.e. 2km, 3km,….20km) and the correlation coefficient between years was calculated at each segment length scale. The correlation coefficients at different scales were not statistically independent; therefore a randomisation test was used to examine whether the degree of fruiting correlation between years changed significantly with increasing length scale. In each realisation of the test, the position of 1km segments was randomised, after which the correlation in fruiting between years at each spatial scale was recalculated. The correlation between the fruiting correlation coefficients and segment size was then calculated. This process was repeated 1000 times. Cases in which the observed correlation between fruiting correlation coefficients and segment size was greater than 95% of the randomised correlations were considered to be statistically significant.

A SPATIAL MODEL

The survey line on which data were collected in this study was not randomly or systematically placed. Thus, the data do not provide unbiased estimates of dung encounter rate and are not appropriate for analysis using standard random sampling methods. Instead a spatial model was used that cuts the survey line into a series of small segments and uses the values of environmental covariates to predict dung encounter rate in each segment. The analytical approach followed the general outline for spatial modelling of transect data set out by Hedley *et al.* (1999) although since perpendicular distances were estimated and not measured, estimates are of dung pile encounter rate, not dung pile density (Walsh *et al.* 2000; Walsh *et al.* 2001). A major advantage of the spatial modelling approach is that it does not assume random sampling, but merely requires reasonable spatial coverage. To the extent that sampling covers all of the major sources of variation in animal density, a spatial model can provide valid inferences about how environmental covariates influence animal distribution (Hedley *et al.* 1999).

The first step in the analysis was to divide the survey track into a series of non-overlapping segments, each one kilometre in length. One kilometre was chosen because it was felt that neither the accuracy of GPS positions taken under thick forest cover, nor the accuracy of the satellite images or conventional maps used to calculate the position of segments with respect to topographical features, were high enough to support a smaller segment size. All 1km segments consisting entirely of swamp or inundated forest were excluded from the analysis, leaving a total of 225 segments for analysis. For each segment, for each of the eight sampling periods the values of several environmental covariates were estimated. These included fruit abundance score (FRUIT), the amount of human sign (HUMAN), proportion of the segment that lay on an elephant trail (TRAIL), the amount of terrestrial herbaceous vegetation (THV), the new leaf scores for monocotyledons (MONOCOT) and dicotyledons (DICOT), and the distance of the segment from the terminus of *terra firma* sampling in the southeast corner of the study area (DISTSE). In addition, the distance of each survey segment from the closest river (DISTRIV), major swamp (DISTSWAMP), or forest clearing (DISTBAI) were estimated. A binary variable (FORESTRY) was used to describe forestry prospection activity on the Bodingo Peninsula. This variable assumed a value of unity for all segments that lay on the Bodingo Peninsula during the last three sampling periods (after the initiation of logging prospection). All five previous surveys of these segments and all surveys of all other segments received a value of zero. Rainfall during the month of each of the eight sampling periods was used in modelling seasonal movements. All segments within a given sampling period were assigned the same rainfall value.

Covariate estimation

Covariate data attached to each survey segment were generated in one of two ways. Geographical or ecological gradient covariates values (DISTSE, DISTRIV, DISTSWAMP, and DISTBAI) were calculated as the straight line distance in kilometres from the centroid of each survey segment to the edge of the nearest feature of that covariate type (i.e. the southeast terminus of the survey, rivers, swamps, and *bais*). Calculations were made in the Geographic Information System (GIS) ArcView 3.1 (ESRI, Redlands, California). All data collected during surveys were assigned the value of the 1km segment in which they were collected, and used to generate covariate values for each segment as follows.

FRUIT: The sum of abundance scores of all fruiting events recorded was calculated in each survey segment for species found in more then 1% of dung piles sampled (SCORE). Following the dung analysis study, all fruit species were assigned an importance rank (RANK) based 0n their frequency of occurrence in dung piles, which were grouped into five classes as follows (>50% = 5, 40-50% = 4, 25-40% = 3; 11-25% = 2, ≤ 10 = 1). The covariate FRUIT was the product of SCORE x RANK for each segment.

HUMAN: The sum of fresh and recent human signs recorded in each segment. Fresh and recent were defined as having occurred in the period between surveys (3 months), which was estimated for the first survey. Machete cuts and footprints that were clearly made by the same group of people and that continued along the survey track were counted as a single sign for each segment in which they fell. Human sign such as permanent human trails or forestry transects that traversed the survey route, multiple camps, and fire sites were summed for each segment.

TRAILPCT: The total length in meters of each survey segment that occurred on an elephant trail. No distinction was made in the value of the covariate between trails of different size.

THV: The mean of the sum of abundance ranks of each taxon of THV per plot for all plots within each segment, for known elephant food species only.

MONOCOT: The mean of new leaf scores for all taxa within each segment, for elephant food species only.

DICOT: The mean score of new leaf for all size classes per plot within each segment, for all known elephant food species.

Modelling procedures

A generalised linear model (Hedley *et al.* 1999) was used to describe how the environmental covariate values prevailing in each segment affected the number of dung piles (*N*) observed in that segment. Rather than the more familiar additive effects of linear regression, the model assumed multiplicative covariate effects,

$$N = \alpha \; f(x_1)\, f(x_2) ... f(x_m) \,,$$

where α is a constant, x is the value of a covariate, and the subscripts index each of m different covariates. For most of the covariates considered the simple linear form

$$f(x) = 1 + \beta x$$

was used to describe the functional relationship between x and N. Thus, for these covariates, the multivariate predictor of the number of dung piles in a segment took the form

$$N = \alpha(1 + \beta_1 x_1)(1 + \beta_2 x_2)...(1 + \beta_m x_m) \,,$$

with the constraint $f(x) >= 0.001$. In this formulation the constant α can be thought of as an "intercept": the number of dung piles expected when all covariate values for a segment are equal to zero (which may never occur in practice). For segments that were partially swamp forest and partially *terra firma* forest, the number of dung piles predicted by the spatial model was multiplied by the proportion of the segment in *terra firma* forest and compared only to the number of dung piles observed in the *terra firma* portion.

Although this model structure has many attractive attributes, it creates a problem in representing the effects of covariates that quantify the distance of a given segment from some topographical feature (i.e. distance from a river, swamp, or *bai*). These topographical features tend to exert their influence on elephant distribution most strongly over a relatively limited spatial scale. Beyond this characteristic scale, these features appear to have much less impact on dung distribution. In an additive model, this would be handled simply by letting the covariate effect go to zero beyond the characteristic range, but in a multiplicative model, setting $f(x) = 0$ for one covariate, also renders the product of all covariate terms equal to zero (i.e. no dung, rather than no effect). To address this problem, a "sill" term (γ) was added to all of the "distance to" covariates so that when the slope parameter β was negative

$$f(x) = 1 + \beta x, \qquad 1 + \beta x > \gamma,$$

$$f(x) = \gamma, \qquad 1 + \beta x < \gamma.$$

In the case of positive β, the parameter γ acted to depict the level at which short scale covariate effects asymptoted on some "ceiling",

$$f(x) = \gamma, \qquad 1 + \beta x > \gamma.$$

Exponential functions were also used to try to describe both slope and sill/ceiling terms in the hope that the asymptotic shape of these functions would better describe the covariate effects, but in preliminary runs of the model, these functions produced no clear improvement in model fit and were computationally more expensive than the linear functions. Since the large number of parameters and models examined put a premium on computational efficiency, only linear terms were used in the analyses.

Seasonal Effects on Elephant Distribution

Central African forests show considerable interannual variation in rainfall. Therefore, rather than dividing the surveys into artificial seasons, rainfall in the month of survey was used as a predictor of the strength of covariate effects on dung pile encounter rate. For each of five covariates, the same exponential form was used to represent the impact of rainfall (r) on effect strength (β)

$$\beta' = \beta e^{\phi r}.$$

In this formulation, a positive fitted value of the constant ϕ indicates that the effect intensifies with increasing rainfall, while a negative value indicates that the effect strength diminishes. A value of ϕ that is not significantly different from zero indicates the lack of seasonal variation in effect strength for the covariate of interest. This treatment was applied to the covariates DISTRIV, DISTSWAMP, DISTBAI, DISTSE, and TRAILPCT.

For the covariate TRAILPCT, fruit availability was tried as a predictor of effect strength, using the sum of fruiting scores taken across all survey segments during a given season. This sum of scores was chosen rather than the fruiting score particular to each segment, because the daily ranging scale of elephants at Ndoki is roughly an order of magnitude larger than the 1km segments considered here (Chapter 6 telemetry data). Thus, the characteristics of foraging paths within a given segment probably reflected decisions about fruit and browse availability on a much larger spatial scale.

Finally, the FRUIT, MONOCOT, and DICOT covariates showed substantial spatio-temporal variation and therefore, had the potential to account for seasonal variation in elephant dung distribution. Thus, it should be noted that any seasonal variation in dung distribution captured through the application of the exponential term to the DISTRIV, DISTSWAMP, DISTBAI, DISTSE, and TRAILPCT covariates is above and beyond that captured by the FRUIT, MONOCOT, or DICOT covariates. Because MONOCOT and DICOT data were only collected during the second year of the study, two analyses are presented below: 1) an analysis for the full two year study that lacks monocotyledon and dicotyledon availability as covariates, and 2) an analysis of the second year of the study that includes these covariates.

Estimation and Model Selection

Each possible combination of the covariate and rainfall effects represents a different model of elephant dung distribution. In estimating parameter values for each model, it was assumed that the sampling error followed a negative binomial distribution. In other words, the probability of observing a particular number of dung piles in a survey segment (given some choice of model parameter values) was distributed according to a negative binomial distribution, with a mean equal to the predicted number of dung piles for that segment. A single value of the negative binomial dispersion parameter (k) was assumed to be common to all segments. Parameter values were then estimated under the principal of maximum likelihood using a trial and error algorithm, *Amoeba* (Press *et al.* 1986). The likelihood was evaluated for all possible models (i.e. all possible combinations of covariate effects). Because of the large number of parameters, the multiplicative form of the model, and the nonlinearity of some of the terms, the likelihood space contained many local maxima. Therefore, the optimisation of each model was started at two different initial conditions, for each of which two different "tolerances" were used to determine when a likelihood maximum had been reached. An algorithm in the spirit of simulated annealing was also implemented. Each time *Amoeba* indicated that a maximum had been reached, the parameter values were perturbed and the search continued. This process appeared to produce robust estimates of maximum likelihood for each model, but was extremely computationally intensive, at times requiring as many as 50,000 evaluations of a model before arriving at likelihood maximum. This computational intensity limited the number of alternative functional forms and covariate effects that could be examined.

Models were compared using model selection described by Burnham and Anderson (1998) most notably Akaike's Information Criterion (AIC). AIC is based on the principal of parsimony, balancing the likelihood score for a model against the number of parameters required to achieve that likelihood. AIC has a number of desirable features including the fact that it allows comparison of alternative models that do not form a nested set (as is the case here). A sample size corrected version of AIC was used here, and the model with the lowest AIC was considered to be the best model. A model confidence set: (a group of models that could not be considered significantly worse than the best model) was constructed by calculating the Akaike weight

$$w_i = \frac{e^{-0.5\Delta_i}}{\Sigma e^{-0.5\Delta_r}}$$

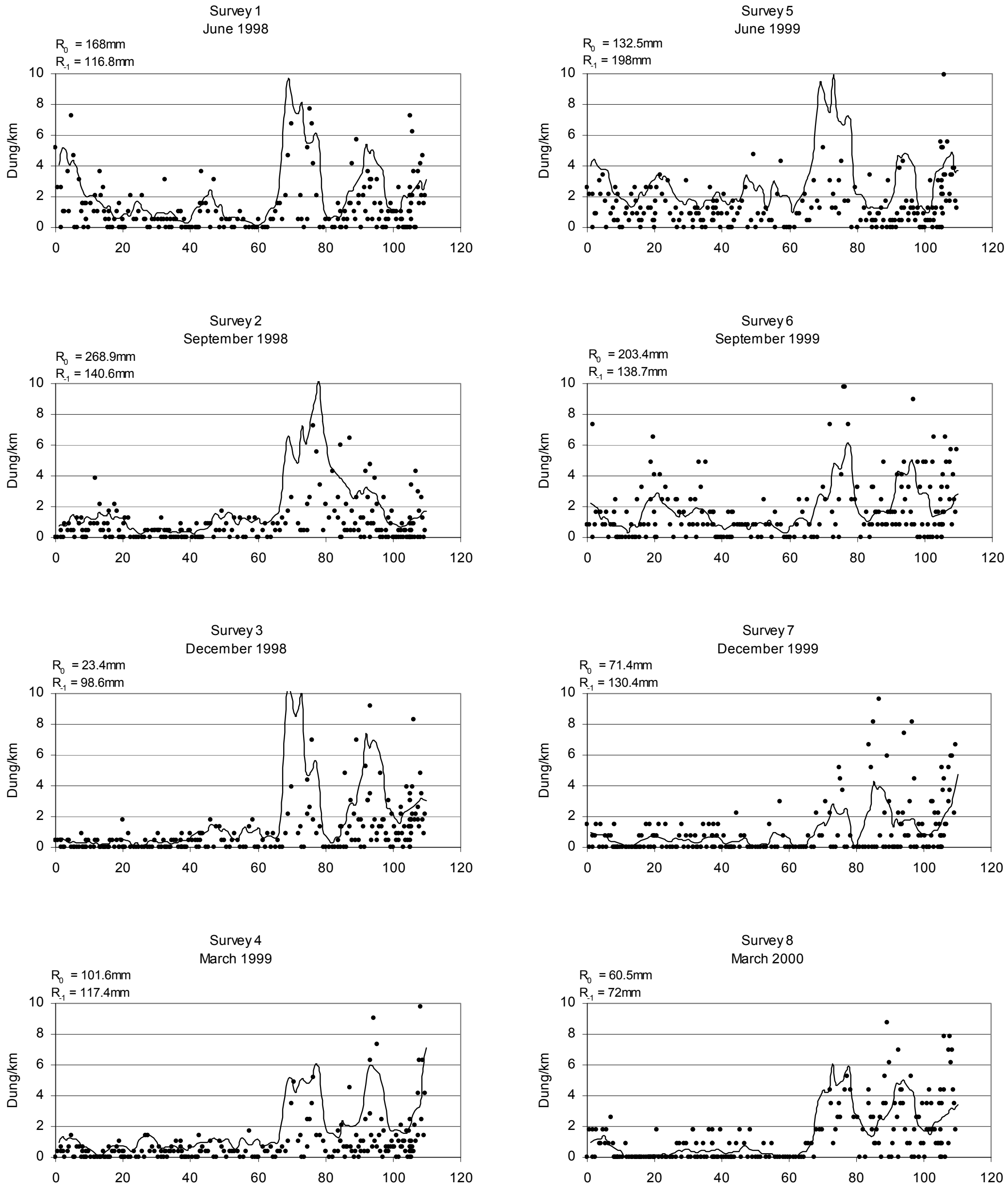
for each model, where Δ_i is the AIC difference between a given model and the best model and the summation is taken over all r models. Models were ordered in terms of increasing AIC and all models that fell below the point at which $\Sigma w_i > 0.95$ were considered to be part of the model confidence set. If a covariate appeared in at least one model in the confidence set, it was considered to have a significant effect on dung encounter rate. The relative strength of each covariate effect was evaluated in terms of the sum of Akaike weights for models in which that covariate appeared.

RESULTS

Dung Distribution

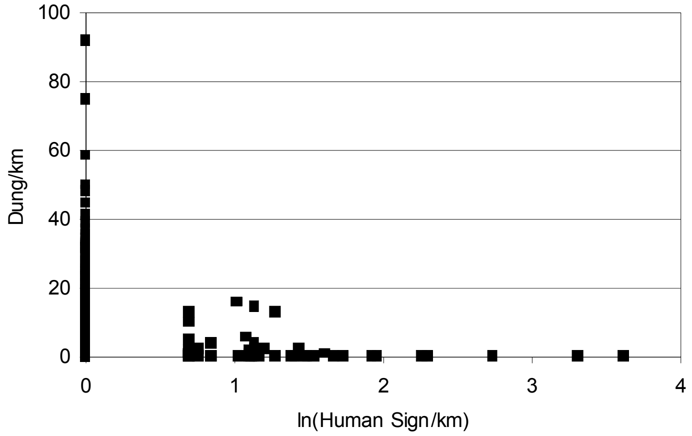
The most salient pattern in the dung data was a generally higher dung encounter rate in the northwest portion of the study than in the southeast (Figure 5.2). One factor contributing to the gradient in encounter rate was the spatial distribution of *bais*, which were clumped in the northern portion of the study area. Dung encounter rate in the survey segments adjacent to the Mokala river swamps were also usually high compared with the southeastern portion of the surveys. Qualitative observations of trail size, trampling, and damage to vegetation, were also particularly high in this section of the survey. Dung encounter rate in survey segments dropped sharply with increasing human sign (Figure 5.3), which reached its highest level near the southeast terminus of sampling during the last two surveys (Figure 5.4), after the initiation of forestry prospection in that area. The spatial gradient in dung encounter rate with distance from the southeast terminus also showed some evidence of the influence of rainfall (Figure 5.2), being most pronounced during the surveys 3,4,7, and 8, (drier pairs) and least pronounced during surveys 1,2,5, and 6 (wetter pairs).

Figure 5.2. Dung encounter rate plotted as a function of distance from the Southeast terminus of sampling.



Closed squares indicate dung/km for 1km survey segments. Lines show dung encounter rate smoothed over a 3km window. Dung encounter rates were normalised for the proportion of each segment lying in *terra firma* forest (see Methods). Rainfall in the month of the survey (R_0) and rainfall in the month preceding the survey (R_{-1}) are given above the upper left corner of each plot.

Figure 5.3. Dung encounter rate as a function of the natural logarithm of the rate of encounter for fresh human signs

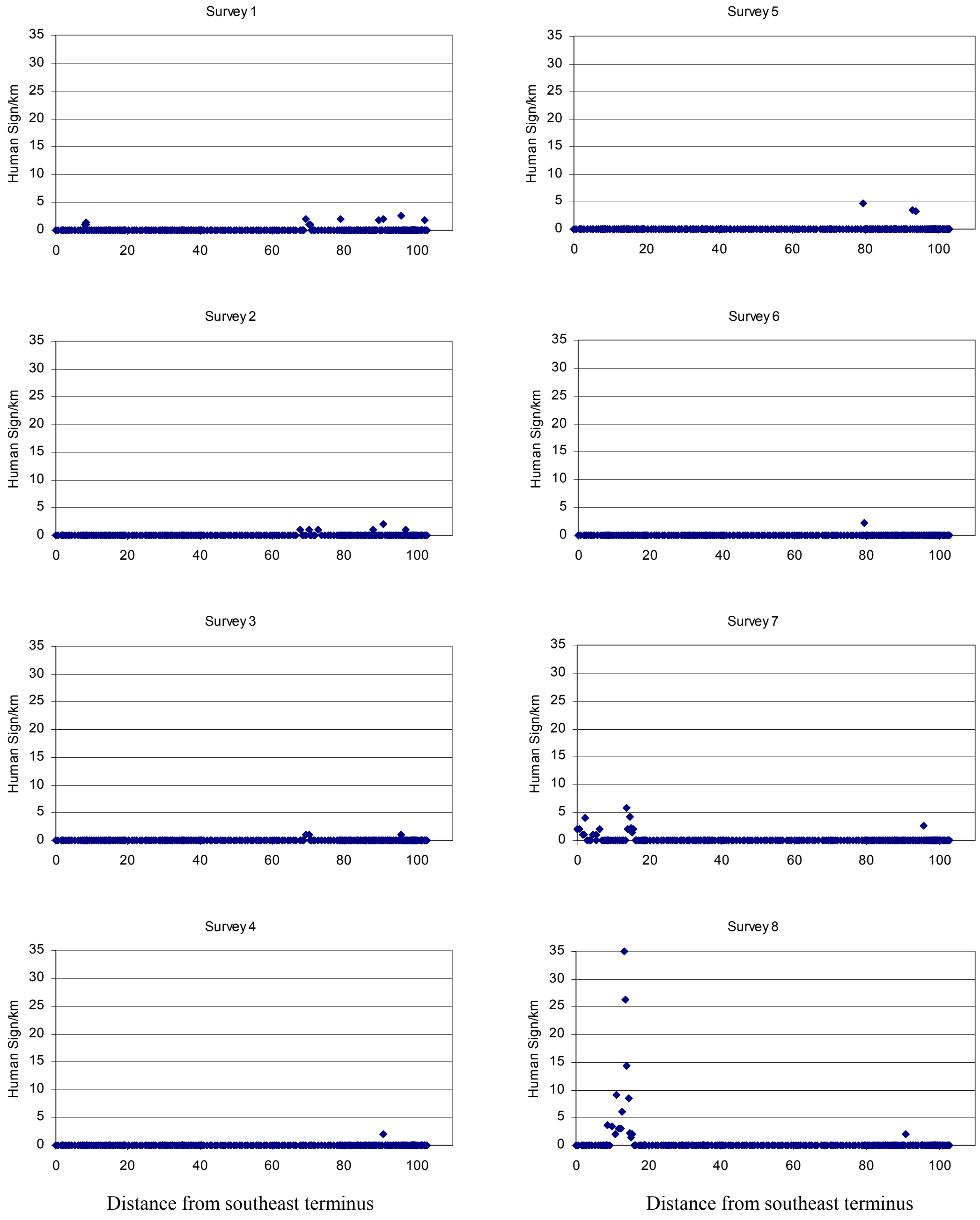


Each square represents data from a single 1km segment.
A total of 225 segments are included in the plot.

Fruit Distribution

Six patterns in the fruiting scores were noteworthy. First the initial and, particularly, second surveys showed highly elevated fruiting scores relative to the other six surveys (Figure 5.5). Second, when all survey segments were considered, there was no correlation between the fruiting score of a 1km segment in the first year and the score in the same segment in the next year (Figure 5.6). However, all four pairs of surveys showed significant effects of increasing segment size (increasing scale) on the fruiting correlation between years. Paradoxically, the correlation between years increased with scale for two of the surveys (Figure 5.6a,d) and decreased with scale for the other two surveys (Figure 5.6b,c). The explanation for this paradox is that a substantial proportion of segments had low fruiting scores in both years, which tended to force the inter-year fruiting correlation to be positive. When only segments with above average fruiting scores were included in the plot (Figure 5.6e-h), the two positive segment size effects disappear (Figure 5.6e,h) and the two negative effects (Figure 5.6 f, g) become even stronger. Thus, at larger spatial scales there is either no correlation or a negative correlation between years in the location of better than average fruit patches. And it is the location of superior fruit patches that seems most likely to determine elephant movement patterns.

Figure 5.4. Encounter rate of human sign as a function of distance from the southeast terminus of sampling.

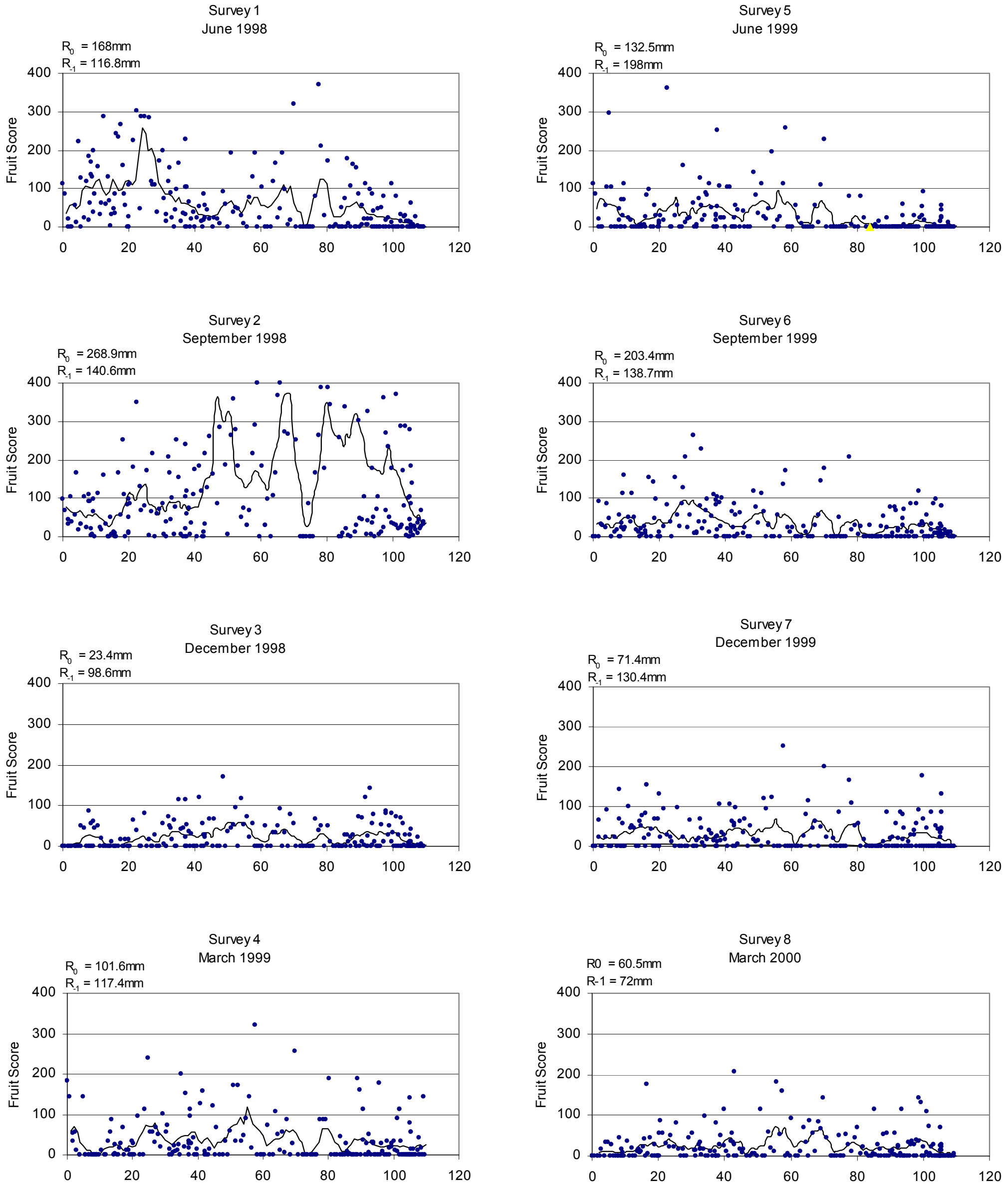


High encounter rates between kilometres 0 and 20 in surveys 7 and 8 were due to forestry prospection

The third pattern of interest was that fruiting scores were highly correlated with R_0, the amount of rainfall in the month of the survey (Figure 5.7). Fourth, the distribution of fruiting along the northwest-southeast axis of the study area appeared to change seasonally (Table 5.1). During the drier surveys, there was no correlation between the amount of fruiting and distance along the northwest-southeast axis. However, all four wet season surveys showed significant large-scale gradients in fruiting. In three surveys, fruiting decreased with increasing distance from the southeast terminus of sampling while in the wettest survey the rate of fruiting increased with increasing distance from the southeast terminus. Both the trend toward greater wet season fruiting in the southeast and the exception to that trend are of particular interest because they appear to closely mirror the distribution of elephant dung. The northwest-southeast gradient in elephant density (Figure 5.2) generally decreased as fruiting intensified in the southeast of the study area (Figure 5.5); and, of the four 'wet season' surveys (Surveys 1,2,5 and 6), the survey that showed the exceptional peak in fruiting in the northern half of the study area (Survey 2) also showed the lowest dung encounter rate in the southern half of the study area (Figure 5.2). All of the patterns observed in the data for the fruiting score also held for the raw number of fruiting events (i.e. uncorrected for fruit abundance or importance to elephants) (Figure 5.7).

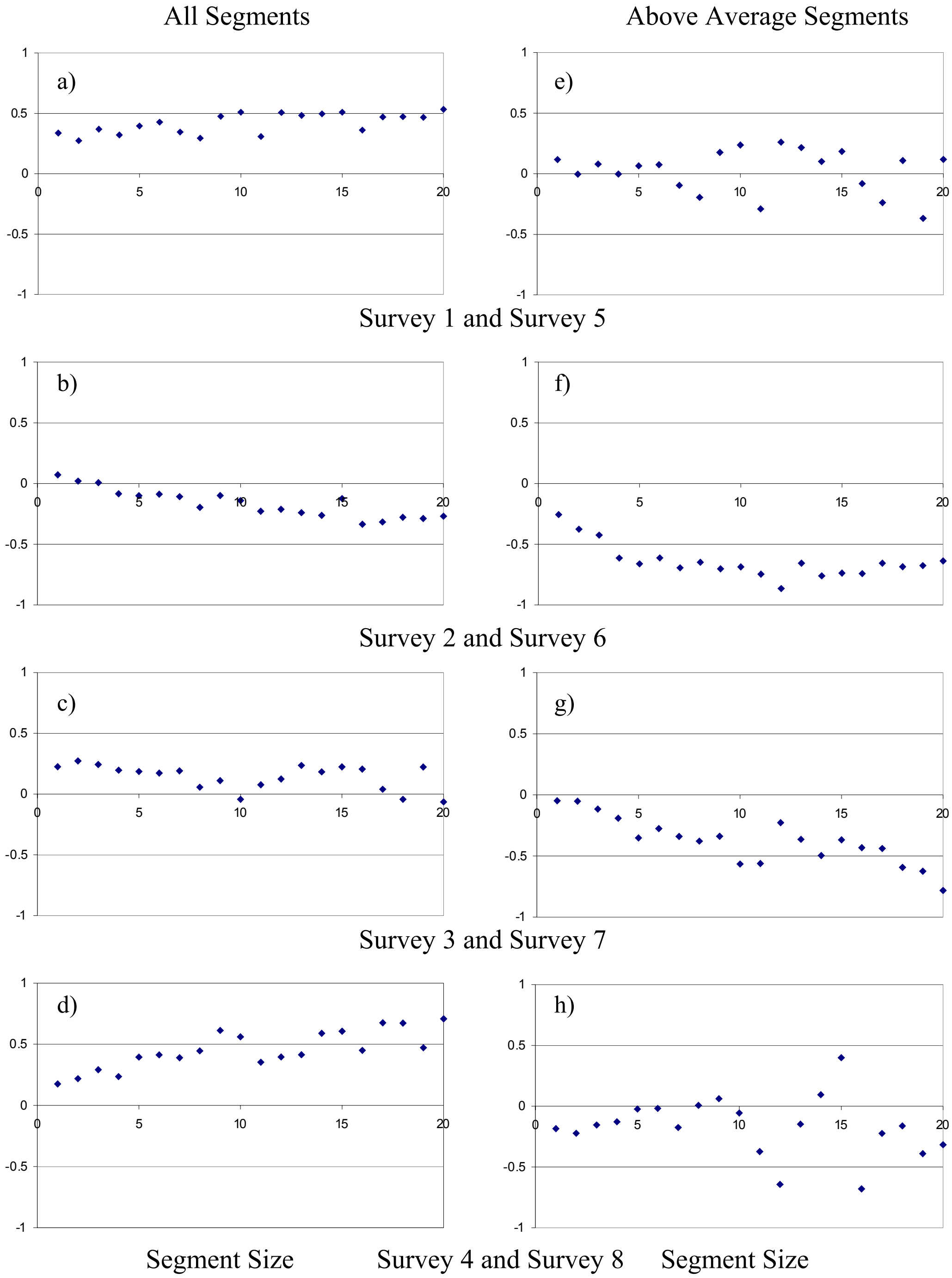
The fifth notable pattern in fruit distribution was the almost complete absence of fruit from survey segments in swamps. The mean of FRUIT values across all surveys was 3.4 in swamp segments compared to 88.0 in *terra firma* segments (Paired t test: $t = -3.264$, $df = 7$, p 0.014). Finally, the sixth important pattern was the positive gradient in fruit abundance with distance from the nearest river across all surveys, the slope of which increased dramatically with increasing total abundance of fruit for each survey (Figure 5.8). Thus fruit availability for elephants was consistently low in swamps and close to rivers, and increased in uplands with increasing overall fruit abundance.

Figure 5.5. Fruiting scores plotted as a function of distance from the southeast terminus of sampling.



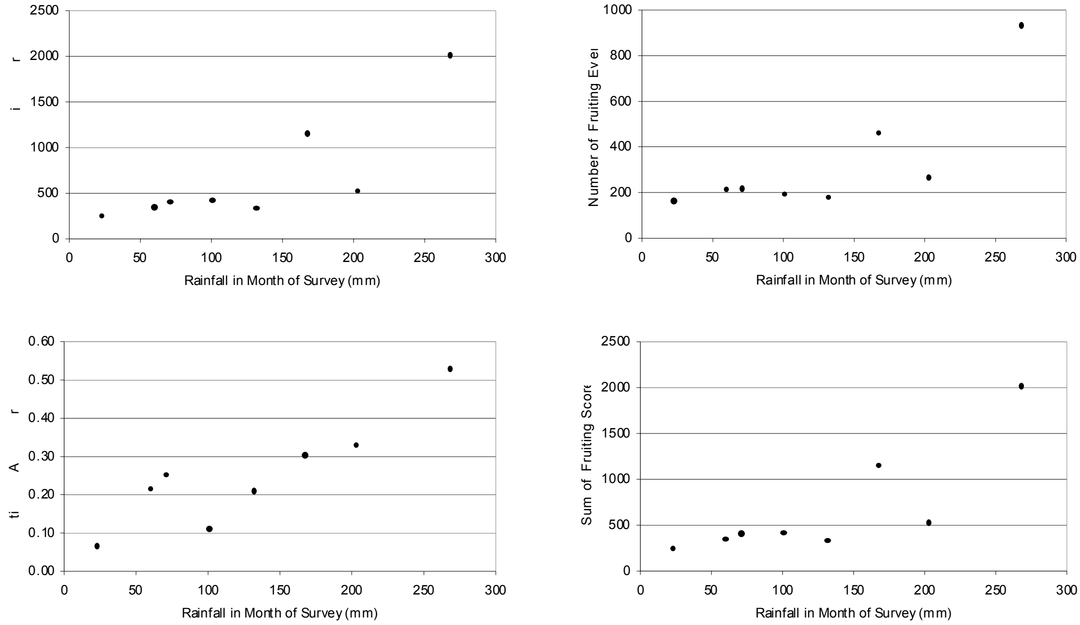
Fruiting scores were normalised for the proportion of each segment lying in *terra firma* forest. Points represent values for each 1km segment. Lines show fruiting score smoothed over a 3km window. Rainfall in the month of the survey (R_0) and rainfall in the month preceding the survey (R_{-1}) are given above the upper left corner of each plot

Figure 5.6. Between year correlation in fruiting score plotted as a function of segment size.



Each point represents a pair of surveys separated by one year. The left hand column uses all segments to calculate the correlation coefficient while the right hand column includes only segments which showed a better than average fruiting score in at least one of the two years. See text for results of randomisation tests for the significance of the relationship between correlation coefficient and segment size.

Figure 5.7. Correlation coefficient between fruiting score and the number of fruiting events (trees or lianas in fruit) plotted against rainfall in the month of the survey.

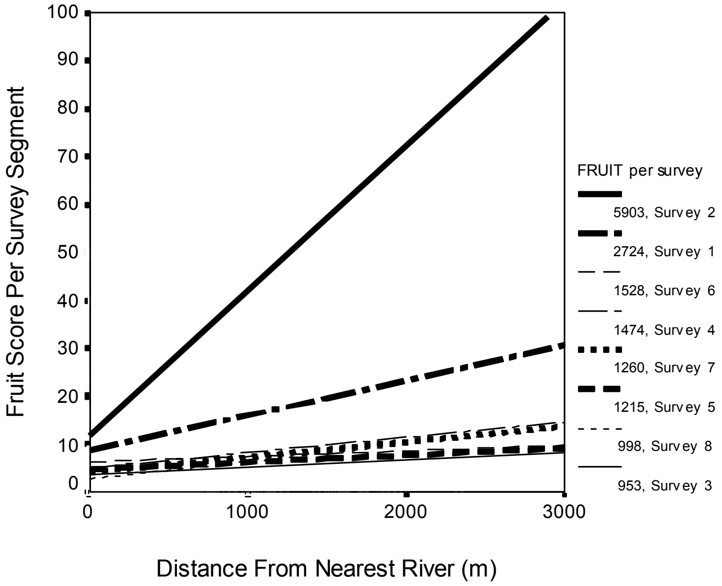


In the lower two plots fruiting scores were normalised by dividing by the highest score for that year. Correlation coefficients between fruiting and rainfall are respectively: a) r=0.82 , p=0.012 ; b) r=0.89 , p= 0.003; c) r=0.80, p=0.016; d) r=0.83 , p=0.13.

Table 5.1: Correlation coefficients between fruiting score and distance from the Southeast terminus of sampling for each of eight surveys. Rainfall values are for the month of the survey.

Survey	Pearson's r	Probability	Rainfall (mm)
1	-0.38	<0.0001	168
2	0.18	0.0055	268.9
3	0.01	ns	23.4
4	-0.07	ns	101.6
5	-0.28	<0.0001	132.5
6	-0.22	0.0011	203.4
7	-0.10	ns	71.4
8	-0.02	ns	60.5

Figure 5.8. Relationship between mean fruit score per survey segment and distance from nearest river in each survey period.



Sum of fruit scores in legend are the sum of fruit scores across the entire 225 survey segments

Browse Distribution

MONOCOT was positively correlated with DICOT in all four surveys for which data were collected (Table 5.2). This correlation held when data from all four surveys in the second year of the study were pooled and when the surveys were considered separately, although the correlation just missed significance in the third survey (the seventh survey overall). When scores for all segments within a given survey were summed, neither MONOCOT nor DICOT sums of scores were correlated with either R_0 or R_{-1}, rainfall in the month preceding the survey (Table 5.3).

Table 5.2: Correlation Coefficients between monocotyledon and dicotyledon new leaf scores.

Survey	Pearson's r	Probability	Rainfall (mm) in same month	Rainfall (mm) in previous month
5	0.15	0.0268	132.5	198
6	0.14	0.0362	203.4	138.7
7	0.12	0.0703	71.4	130.4
8	0.21	0.0018	60.5	72
Pooled	0.11	0.0007	--	--

Table 5.3: Correlation coefficients between new leaf scores and rainfall. Data from all surveys are pooled.

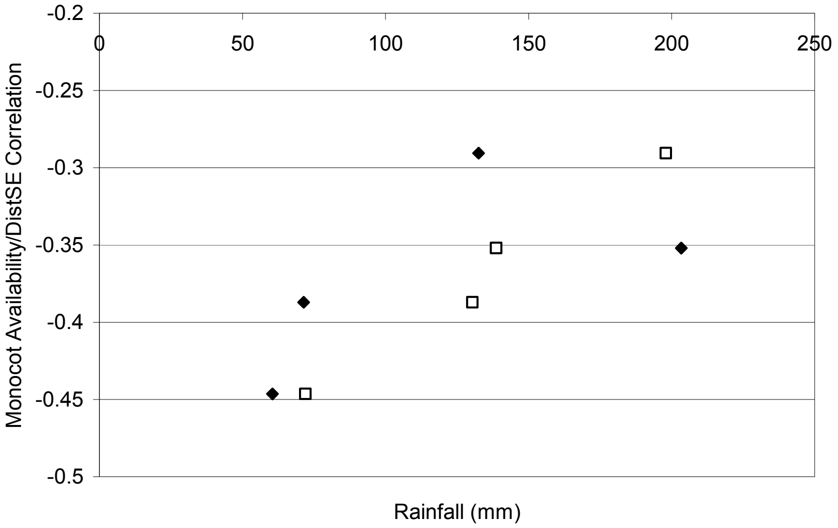
	Pearson's r	Probability
Monocot vs rainfall in same month	0.19	0.809
Monocot vs rainfall in previous month	0.08	0.918
Dicot vs rainfall same month	0.09	0.907
Dicot vs rainfall previous month	0.81	0.193

Monocotyledon new leaf scores tended to be negatively correlated with the distance from the southeast terminus of sampling (Table 5.4). This relationship was significant for the pooled data and for three of the four surveys when surveys were analysed separately. The strength of the negative correlation tended to weaken with increasing rainfall, and R_0 was a better predictor of the spatial gradient in monocotyledon score than R_{-1} (Figure 5.9). This relationship just missed significance (r= 0.94, p=0.06), which is highly suggestive given the low statistical power available with a sample of only four surveys. Abundance scores for THV decreased by more than 50% from the southeast to northwest extremes of the survey. Consequently, monocotyledon new leaf availability (the product of monocotyledon new leaf score and THV score) was always negatively correlated with distance from the southeast terminus (Table 5.5). For dicotyledons, the relationship between new leaf score and the distance from the southeast terminus of sampling was more variable (Table 5.6). In the eighth survey, DICOT showed a negative correlation with distance from the southeast while the relationship was positive in the fifth survey. The correlation was not close to significance for either the second or third survey. However, rainfall was an even better predictor of the spatial gradient in DICOT than it was for MONOCOT (Figure 5.10). The correlation between distance to the southeast terminus and DICOT increased strongly with R_{-1}. During the survey preceded by the heaviest rain, DICOT actually became greater in the northwestern part of the study area than in the southeast.

Table 5.4: Correlation coefficient between monocotyledon new leaf score and distance from the southeast terminus of sampling.

Survey	Pearson's r	Probability	Rainfall (mm) in same month	Rainfall (mm) in previous month
5	-0.19	0.0029	132.5	198
6	-0.09	0.1811	203.4	138.7
7	-0.25	0.0001	71.4	130.4
8	-0.37	<0.0001	60.5	72
Pooled	-0.22	<0.0001	--	--

Figure 5.9. Correlation coefficient between monocotyledon new leaf availability and distance from the southeast terminus of sampling plotted as a function of rainfall.



Closed diamonds use rainfall in the month of the survey (R_0), open squares used rainfall in the preceding month (R_{-1}). Relationship using rainfall in month before the survey is statistically significant (r=0.98, p=0.012).

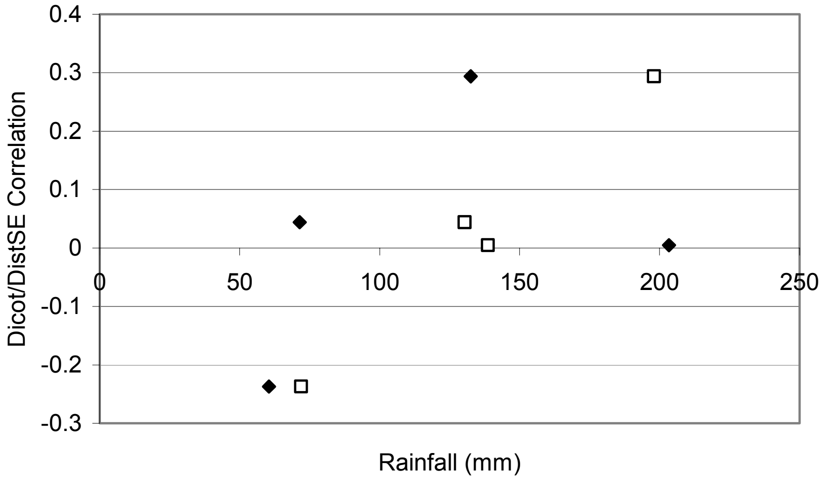
Table 5.5: Correlation coefficient between monocotyledon new leaf availability (the product of monocotyledon new leaf score and THV score) and distance from the southeast terminus of sampling.

Survey	Pearson's r	Probability	Rainfall (mm) in same month	Rainfall (mm) in previous month
5	-0.29	<0.0001	132.5	198
6	-0.35	<0.0001	203.4	138.7
7	-0.39	<0.0001	71.4	130.4
8	-0.45	<0.0001	60.5	72
Pooled	-0.36	<0.0001	--	--

Table 5.6: Correlation coefficient between dicotyledon new leaf score and distance from the southeast terminus of sampling.

Survey	Pearson's r	Probability	Rainfall (mm) in same month	Rainfall (mm) in previous month
5	0.29	<0.0001	132.5	198
6	0.00	ns	203.4	138.7
7	0.04	ns	71.4	130.4
8	-0.24	0.0003	60.5	72
Pooled	0.04	ns	--	--

Figure 5.10. Correlation coefficient between dicotyledon new leaf score and distance from the southeast terminus of sampling plotted as a function of rainfall.



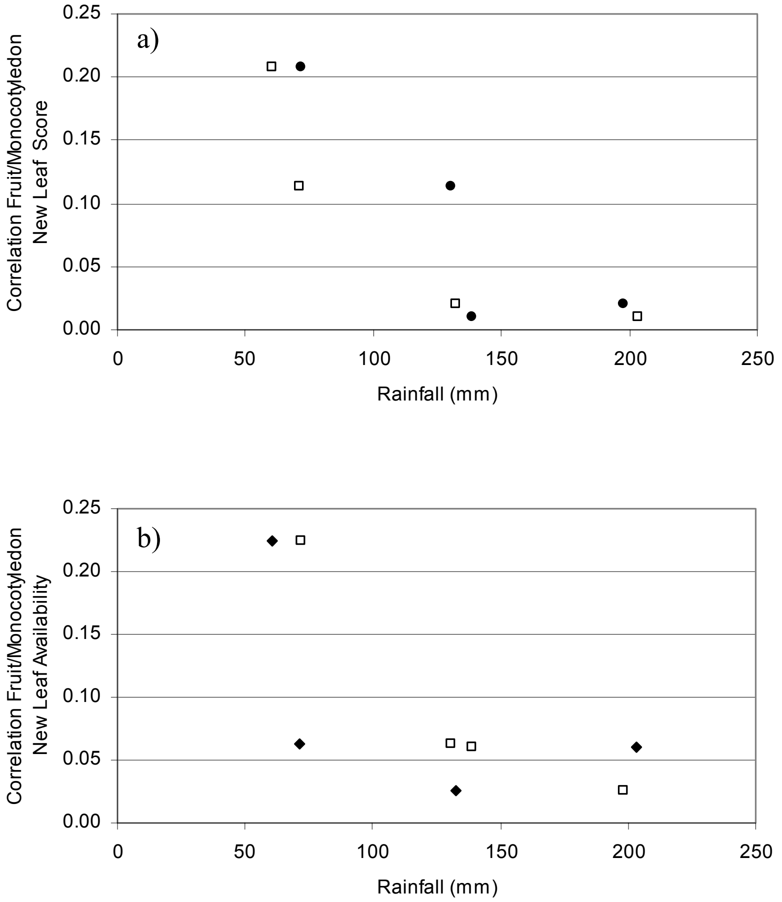
Closed diamonds use rainfall in the month of the survey, open squares use rainfall in the preceding month. Relationship using rainfall in the month before the survey is statistically significant (r=0.99, p=0.009).

Monocotyledon new leaf scores showed a very weak, but significant correlation with fruit scores when data from all four surveys were pooled (Table 5.7). Rainfall weakened the relationship between monocotyledon and fruit scores (Figure 5.11a). This trend was clearest for R_{-1}, in which case the correlation coefficient approached zero at monthly rainfalls of greater than 100mm. Although this relationship was not statistically significant (r=-0.854, p=0.145) when treated as linear, natural logarithm transformation of the correlation coefficients did yield a significant result (r=0.963, p=0.036). The relationship between monocotyledon new leaf availability and fruit score was also influenced by rainfall (Figure 5.11b), although the effect did not reach significance (r=-0.906, p=0.093), even with log transformation.

Table 5.7: Correlation coefficients between monocotyledon new leaf score and fruiting score.

Survey	Pearson's r	Probability	Rainfall (mm) in same month	Rainfall (mm) in previous month
5	0.02	ns	132.5	198.0
6	0.01	ns	203.4	138.7
7	0.11	0.0893	71.4	130.4
8	0.21	0.0017	60.5	72.0
Pooled	0.09	0.0099		

Figure 5.11. Correlation coefficient between a) fruiting score and monocotyledon new leaf score and b) fruiting score and monocotyledon new leaf availability plotted as a function of rainfall.



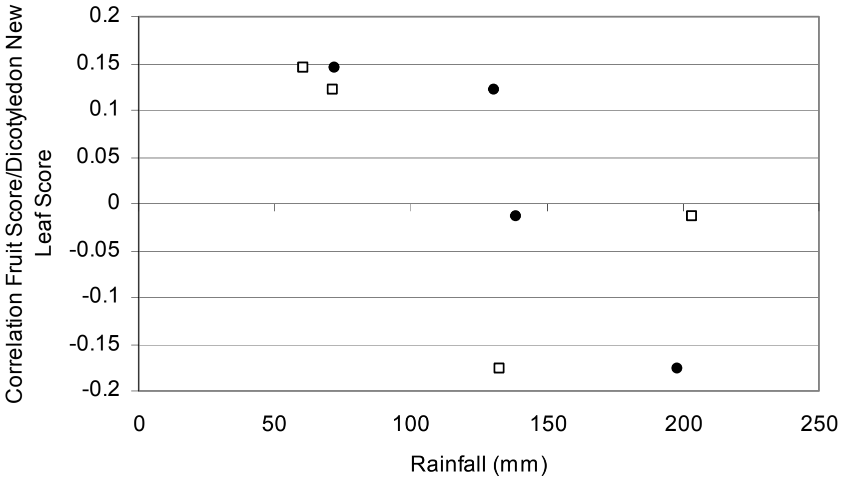
In a) closed circles use rainfall in the month of the survey, open squares use rainfall in the preceding month. In b) closed diamonds use rainfall in the month of the survey, open squares use rainfall in the preceding month. Relationship using rainfall in the month before the survey is statistically significant when correlation coefficients are natural log transformed (r=-0.96, p=0.036).

When all four surveys were pooled, DICOT did not show a significant correlation with FRUIT (Table 5.8). However, when the surveys were treated separately, the correlation between DICOT and FRUIT decreased with increasing rainfall (Figure 5.12). This trend was stronger for R_0 than for R_{-1}, but did not reach statistical significance. The DICOT/FRUIT correlation actually became significantly negative during the survey preceded by the highest rainfall (Survey 5). At this time, FRUIT increased strongly from northwest to southeast, while DICOT showed an increasing gradient in the opposite direction (Table 5.8). MONOCOT and DICOT revealed no significant trends with distance from rivers under any rainfall pattern, and therefore did not constitute a productivity gradient to influence elephant distribution.

Table 5.8: Correlation coefficients between dicotyledon new leaf score and fruitfall score with distance from southeast terminus of sampling

Survey	Pearson's r	Probability	Rainfall (mm) in same month	Rainfall (mm) in previous month
5	-0.18	0.0080	132.5	198
6	-0.01	ns	203.4	138.7
7	0.12	ns	71.4	130.4
8	0.15	0.0285	60.5	72
Pooled	0.01	ns	--	--

Figure 5.12. Correlation coefficient between fruiting score and dicotyledon new leaf score plotted as a function of rainfall.



Closed circles use rainfall in the month of the survey, open squares use rainfall in the preceding month

Spatial model

WITHOUT MONOCOT AND DICOT COVARIATES

For the full two-year analysis one model was superior to all others, with an AIC more than 6 units lower than the next best model. This model included eight of the nine tested covariates, lacking only an effect of timber prospection (FORESTRY) on the Bodingo Peninsula after the 5th survey (Table 5.9), though the negative effect of the more spatially precise HUMAN covariate was strong. Because there was only one model in the confidence set, it was impossible and unnecessary to compare and contrast covariates on the basis of their relative Akaike weights. However, it is worth mentioning that the DISTRIV covariate appeared to have a particularly strong effect on model fit, with the lowest AIC for a model not containing DISTRIV falling within 100 AIC units of the globally best model.

Table 5.9: Spatial model parameter estimates for combined data from both years.

Covariate	Parameter	Estimate
DISTRIVER	Slope	-23.61
	Limit	-1.24 (0.29)
	Seasonal	-7.86
DISTSWAMP	Slope	-44.13
	Limit	-1.3 (0.27)
	Seasonal	0.00015
DISTBAI	Slope	-23.26
	Limit	-1.67 (0.19)
	Seasonal	0.75
DISTSE	Slope	3.26
	Seasonal	-9.82
TRAILPCT	Slope	2.63
	Seasonal	-1.19
THV	Slope	-0.61
HUMAN	Slope	-2.23
FRUIT	Slope	2.12

Limit estimates are given both as raw parameter values and, in parentheses, as the exponential of the parameter value. Negative values of the “Seasonal” parameter indicate a weakening of the effect with increasing rainfall, while positive values indicate an intensification of the effect

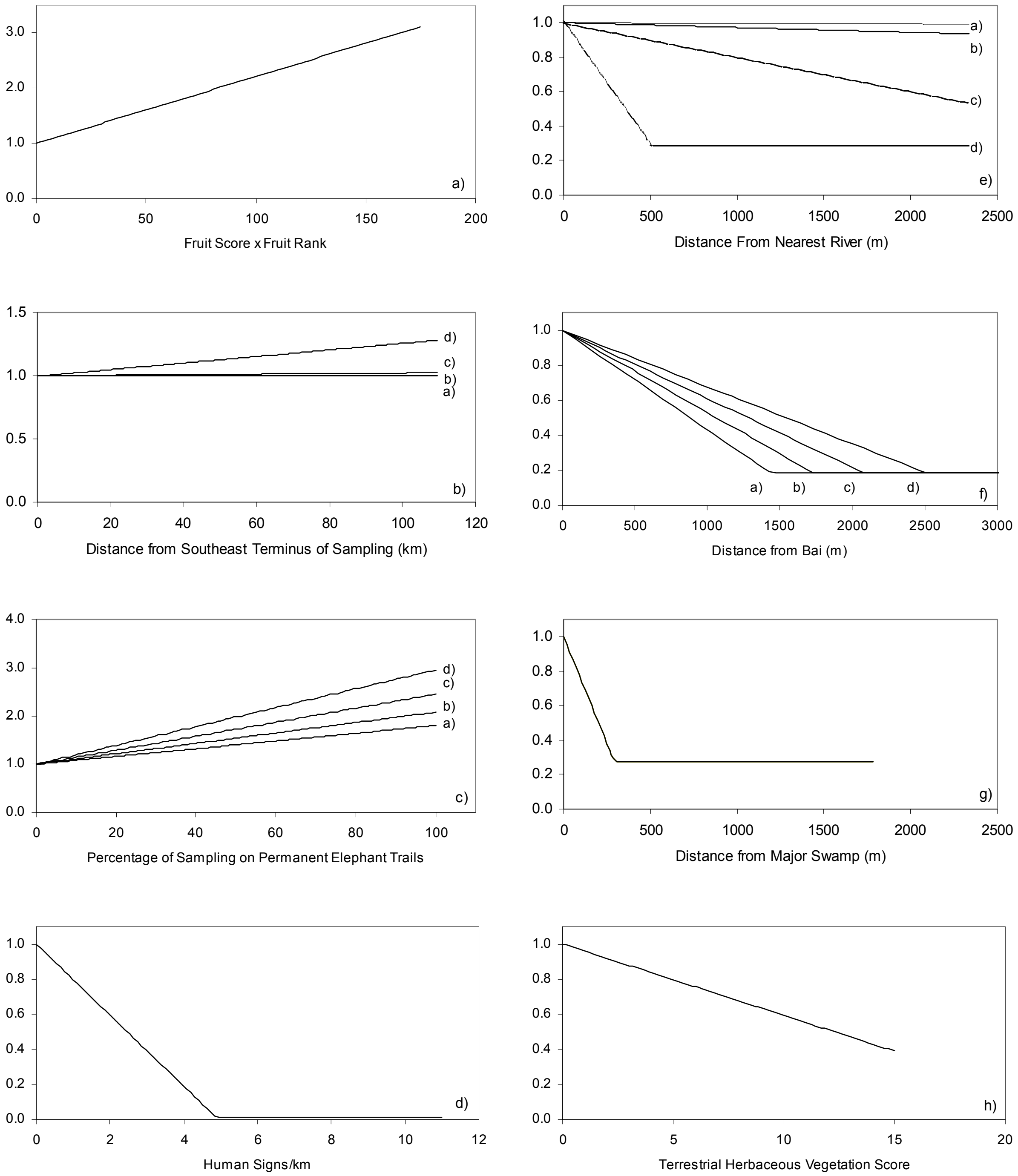
Perhaps the most notable result from the spatial model was the change in dung encounter rate which more than doubled over the range of observed fruit scores (Figure 5.13a). Dung also increased strongly with distance from the southeast terminus of sampling (Figure 5.13b) and with the percentage of sampling that lay on elephant trails (Figure 5.13c). The model also captured the strong negative effect of human sign implied in the raw data, predicting rapid decline to zero with increasing human sign (Figure 5.13d). As expected, dung encounter rate decreased strongly with distance from rivers (Figure 5.13e), *bais* (Figure 5.13f), and major swamps (Figure 5.13g). Contrary to expectation, dung encounter rate decreased strongly with increasing amounts of THV (Figure 5.13h).

The best model also showed seasonal effects for all five variables tested, with FRUIT performing better than did rainfall as a predictor of the degree of dung clumping on trails. The gradient in dung encounter rate around rivers weakened with increasing rainfall, showing a 70% drop in encounter rate over a range of only 300m during dry weather but a virtually flat distribution during high rainfall (Figure 5.13e). On a large scale, there was a similar effect of rainfall on the southeast-northwest gradient in dung encounter rate, with more dung in the northwest during the dry periods but little or no gradient during wet weather (excluding that captured by other covariates). The final three effects were contrary to *a priori* expectation, with dung becoming less clumped on trails and more clumped around *bais* as rainfall increased (the magnitude of the swamp effect was negligible with increasing rainfall).

WITH MONOCOT AND DICOT COVARIATES

In the analysis using data from year 2 only (no THV or Bodingo prospection effects), both MONOCOT and DICOT appeared in the 95% confidence set of models, which contained three models (Table 5.10). MONOCOT appeared in the best model and 3rd best model with a total Akaike weight of 0.82, while DICOT appeared only in the first model for an Akaike weight of 0.72. Unexpectedly, the signs of the effects for MONOCOT and DICOT were negative. That is, dung encounter rate decreased with increasing MONOCOT or DICOT. Otherwise, the results bore many similarities to the full two-year analysis. DISTRIV, DISTSWAMP, DISTBAI, DISTSE, and TRAILPCT appeared in all three models with the same effect directions and comparable magnitudes as in the two-year analysis. Fruit appeared in the first model (Akaike weight 0.72) while Human Sign appeared in the second and third models (Akaike weight 0.28).

Figure 5.13. Parameter estimates from the spatial model using both years of data.



The dependent variable in each plot (Y axis in all cases) represents the proportional change in dung encounter rate caused by the respective independent variable. Captions: a) maximum rainfall (100%), b) 75% rainfall, c) 50% rainfall, d) 25% rainfall.

The seasonal effect terms were more varied. The best model supported only three of the five possible rainfall effects (DISTRIV, DISTSWAMP, and DISTSE). The other two models each supported seasonal effects on all five covariates tested, with the second best model preferring a fruit effect on TRAILPCT and the third best model supporting a rainfall effect. The most intriguing seasonal result was a change in the direction of the effect of rainfall on the value of the DISTRIV covariate. Unlike in the two-year analysis, the clumping of dung piles around rivers actually increased with increasing rainfall. This effect was to a certain degree counterbalanced by the emergence of a much stronger seasonal effect on DISTSWAMP, with a strong decrease in dung encounter rate with increasing distance from major swamps during the dry weather but little or no effect during wetter weather.

Table 5.10: Spatial model parameter estimates for combined data from the second year only

			Model 1 AIC = 3310.16	Model 2 AIC = 3311.55	Model 3 AIC = 3312.11
Covariate	Parameter	Akaike Weight	Estimate	Estimate	Estimate
DISTRIV	Slope	1	-0.08	-0.35	-0.073
	Limit	1	-1.38 (0.25)	-1.50 (0.22)	-1.26 (0.28)
	Seasonal	1	4.47	1.52	4.41
DISTSWAMP	Slope	1	-11485.59	-9722.57	-8011.68
	Limit	1	-2.52 (0.08)	-2.14 (0.18)	-2.23 (0.11)
	Seasonal	1	-15.08	-14.89	0.43
DISTBAI	Slope	1	-42.78	-25.32	4.14
	Limit	1	-1.65 (0.19)	-1.73 (0.18)	-15.056 (0.001)
	Seasonal	0.47	-	1.52	2.29
DISTSE	Slope	1	67.71	2.6	4.42
	Seasonal	1	-11.94	-1.89	-4.1
TRAILPCT	Slope	1	1.79	21.66	1.42
Fruit on TRAILPCT	Seasonal	0.27	-	-2.88	-
Rain on TRAILPCT	Seasonal	1.0	-	-	0.43
MONOCOT	Slope	0.73	-0.051	-	-0.019
DICOT	Slope	0.53	-0.23	-	-
HUMAN	Slope	0.47	-	-2.19	-2.19
FRUIT	Slope	0.53	0.55	-	-

Limit estimates are given both as raw parameter values and, in parentheses, as the exponential of the parameter value. Negative values of the “Seasonal” parameter indicate a weakening of the effect with increasing rainfall, while positive values indicate an intensification of the effect

DISCUSSION

The results of this analysis support the idea that, like savannah elephants, forest elephants track a seasonal productivity gradient. Ndoki elephants concentrated activity in and near wetlands during the dry season then moved out into upland areas when high rainfall increased productivity there. However, the resource driving Ndoki elephant movement into upland areas was not new leaves, as it is for savannah elephants (Wing and Buss 1970; Leuthold and Sale 1973; Western and Lindsay 1984). DICOT showed no correlation with distance from rivers at any level of rainfall and both THV and MONOCOT actually showed a non-significant trend towards increased new leaf production around rivers during wet weather (i.e. in the direction opposite that of seasonal changes in elephant distribution). What did appear to draw elephants into upland areas was the high availability of fruit during the wet seasons. This effect was corroborated by the spatial model which detected a positive effect of fruit abundance on dung encounter rate, and fruit abundance increased with increasing distance from rivers, a relationship which became stronger with higher overall fruit availability.

Although there was strong evidence of a seasonal movement from wetlands to uplands, this seasonal cycle occurred on the inter-fluvial scale of only a few kilometres rather than over the landscape scale, as often seen in savannah elephants (Thouless 1995). In contrast to savannah elephants, the spatial model suggested a large-scale movement of elephants away from the major swamp, the Likouala swamps. During the dry season, dung encounter rate in the least productive part of the study area for browse (the northern half) actually increased while dung encounter rate in the more productive southern portion of the study fell to very low levels. However, the dry season aggregation of elephants in the northern part of the study area was not complemented by a consistent wet season movement to the south. Rather, large-scale changes in elephant distribution during the wet season appeared to track the large-scale distribution of fruit, which was more abundant in the southern part of the study area during three wet season surveys but not in the fourth. These results suggest that large-scale movement by Ndoki elephants is not a consistent annual migration between wetlands in the southeast and uplands in the northwest. Rather, ranging appeared to be partitioned into two distinct modes. During the dry season period of low fruit availability, elephants concentrated their activity around rivers and swamps in the northern part of the study area. During wet weather their distribution tracked the large-scale and irregular distribution of fruit.

Fruiting Regularity and Nomadism

The alternation between consistent dry season aggregation around rivers, swamps, and *bais*, and wet season nomadism following fruit patches may be typical of forest elephants in central Africa because of the complexities of fruit production in tropical trees (Van Schaik *et al.* 1993; Reich 1995; Chapman *et al.* 1999), which fall on a reproductive investment continuum analogous to the capital/income dichotomy in animals. At one end of the continuum lie tree species that carry over very few resources from previous years, basing current fruit reproduction mostly on current environmental conditions (primarily rainfall and insolation) (Chapin *et al.* 1990). For these species, peaks or troughs in environmental conditions lead to almost immediate peaks or troughs in fruit production. At the other end of the continuum are species that accumulate reserves over several years, producing few or no fruit until occasional heavy crops, or in extreme cases "mast" crops, are produced in response to some environmental trigger (Silvertown 1980; Tutin and Fernandez 1993; Van Schaik *et al.* 1993; Reich 1995). Thus, even if seasonal environmental cycles were highly regular between years, tree species would be expected to fall out of phase in fruit production as a function of their different sensitivities to the environmental cues that trigger fruiting and the extent to which they deplete nutrient reserves when they fruit. However, for masting and inconsistently fruiting species, the amount of fruit produced in a given crop depends not just on proximate environmental conditions, but also on conditions in previous years (Wright 1999). Thus, irregularities in rainfall and insolation, such as those caused by "El Niño" events probably jumble fruiting synchrony between species even further (Struhsaker 1997; Wright 1999). Good environmental conditions may increase and bad conditions decrease the fruit production of each species (Wright 1999). But because species differ in what triggers fruiting and how much they deplete reserves, each unique sequence of environmental conditions may not affect all species in the same way. Furthermore, inter-annual variation in within-year patterns of rainfall and insolation will inconsistently advance or retard fruit production of species between years.

The irregularity of fruiting cycles may lead to nomadism in forest elephants because tropical tree species tend to have spatial distributions that are clumped on scales relevant to animals with large home ranges (Jones 1955; Thorington *et al.* 1996; Chapman *et al.* 1997 Chapter 2). This large-grained clumping may be caused by variation in the abiotic habitat such as topography and soil nutrients (Gartlan *et al.* 1986), differences in disturbance history, particularly in human land use history (Aubreville 1962; Guillaumet 1967; White 2001), or stochastic colonisation processes (Hubbell 1979; Plotkin *et al.* 2001). The combination of large-scale spatial clumping of tree species and fruiting asynchrony between tree species is likely to produce an irregular pattern of fruiting. Between year variation in the amount of rainfall may also create variation in the large-scale distribution of groundwater, thereby creating large-grained spatial variation in fruiting phenology, even within species (Chapman *et al.* 1999). Whatever the cause, the large-scale distributions of high quality *terra firma* fruit patches in the Ndoki ecosystem were uncorrelated between years for two surveys and negatively correlated between years for two other surveys. This inconsistent pattern of fruiting is likely to lead to irregular wanderings in search of high productivity fruit patches rather than the kind of regular seasonal migrations seen in many savannah elephant populations. Like polar bears (Ferguson *et al.* 1998, 2001) and capuchin monkeys (Bitetti 2001), forest elephants appear to use a large home range to "smooth" irregular, large-grained variation in food availability. Elephants in savannah were unable to make exploratory journeys in search of high quality browse due to water constraints during dry periods (Western 1975; Western and Lindsay 1984). However forest elephants in Ndoki were never at physiologically dangerous distances from water, thus exploration in search of fruit was possible since the risks of drought, even in unfamiliar areas, was negligible.

Irregularity does not necessarily mean unpredictability. Elephants may use environmental rules of thumb to predict the location of high quality patches (Moss 1988; Foley 2001). For instance, elephants might know that increasing rainfall often signals upland fruit production, therefore a search rule might be to travel uphill and turn when going downhill. On a landscape scale they might also know that high fruit production in a patch in one year might indicate low fruiting in the same patch the following year. The large brain size of elephants should help them both store information on fruiting patterns and process this information in a sophisticated way (Dale *et al.* 1992). Frugivores in tropical forests appear to have better spatial memory capabilities than folivores which improves their ability to maximise foraging efficiency (Milton 1981a; Allman 1999), though Prins (1996) demonstrated that grazing African buffalo use a combination of rules of thumb and spatial memory to select high quality sward patches. It seems likely that frugivorous forest elephants develop a cognitive map (Gallistel and Cramer 1996) detailing the spatial location of zones of high fruit availability.

To the extent that the timing of high quality patches is unpredictable, large body size should be an advantage in exploiting ephemeral fruit (Lovegrove 2000), since efficiency of locomotion (Peters 1983; Owen-Smith 1988), fasting endurance (Millar and Hickling 1990), and tolerance of low quality forage (Geist 1974; Owen-Smith 1988) increase with body size. Furthermore, only young forest elephants are susceptible to predation by animals other than humans (Blake, unpub. data). Thus elephants should be able to make long, exploratory forays in search of high quality fruit patches with low risk of predation (except by humans) and, since at least low quality browse is ubiquitous, little risk of starvation if a high quality patch is not located. Savannah elephants are known to make rapid, large scale, roundtrips that appear to be exploratory forays during wet periods (Thouless 1995), while desert dwelling elephants do not make exploratory wanderings since they must track the distribution of scarce water holes (Viljoen 1989b). GPS telemetry work at Ndoki (Chapter 6) showed that forest elephants also make rapid, long-distance movements. The mean daily travel distance of collared elephants increased significantly with rainfall (which is highly correlated with fruit abundance) which suggested an increase in foraging for fruit over browse, as observed in folivorous/frugivorous gorillas (Goldsmith 1999). One interpretation of these observations is that elephants are making exploratory forays and staying only in areas that are particularly productive. The fact that these forays often tend to originate from and return to the neighbourhood of mineral clearings underscores the importance of mineral access to Ndoki elephants.

Dry season aggregation and migration

The dung data showed two foci of dry season elephant concentration, rivers and the northern part of the study area. The most likely explanation was not an increase in the requirement for water, but that riverine vegetation offered an abundance of aquatic herbs, semi-aquatic monocotyledons and preferred dicotyledons (Chapter 2), which provided a year round food source, particularly when fruit in *terra firma* forest was scarce. That elephant density in the northern part of the study area increased during the dry season is interesting since in *terra firma* habitats, the north was the area of lowest food availability in terms of new leaf production and THV abundance. This dry season aggregation in the north may be due to the local clumping of *bais* in the north. In the absence of strong energetic stress, mineral availability may drive the seasonal distributions of large mammals (McNaughton 1988, 1990; Murray 1995), including elephants (Weir 1972) in savannah environments. In the Serengeti the mineral gradient rather than the primary productivity (rainfall) gradient determined the seasonal migration patterns of many ungulate species (Fryxell and Sinclair 1988; McNaughton 1990; Murray 1995). However in the Serengeti, it was the elevated mineral composition of forage rather than the presence of saline licks which determined ungulate distributions, though underlying soil mineral concentrations were correlated with forage mineral levels for those ions important for migrating ungulates (McNaughton 1988, 1990). Dry season ungulate range was associated with infertile soils around permanent watercourses, whereas the wet season range was in fertile, volcanic, mineral rich soils with correspondingly high forage mineral concentrations, though these areas were not necessarily the most productive. By contrast, Weir (1972) showed that savannah elephants in Zimbabwe were attracted to mineral licks during the dry season, with vegetation characteristics apparently playing no role though analysis of forage nutrients was not carried out. Both mineral gradients of forage around pans and licks in otherwise nutrient poor landscapes and soil deposits within pans may also cause aggregations of herbivorous mammals, though when minerals are more homogeneously distributed across landscapes, they tend to have less influence on determining elephant distribution (Weir 1973).

In the Ndoki Forest, *bais* are analogous to the 'salt pans' of more arid regions of east and southern Africa (Weir 1969, 1972). Klaus *et al.* (1998) found that *bais* several kilometres west of the survey route in this study were located exclusively in doleritic intrusions, rich in minerals and clay. Sodium, potassium, calcium, magnesium, phosphorus, and manganese were found in significantly higher concentrations in Ndoki *bais* compared to non-*bai* soils (Klaus *et al.* 1998). All of these elements are important in explaining the seasonal movements of ungulates and elephants in east and southern Africa (Weir 1972; Kreulen 1975; McNaughton 1988, 1990; Murray 1995). Soils surrounding *bais* are mineral poor sandy alluvium (Klaus *et al.* 1998), which, coupled with the consistent drainage from northern uplands to the hydromorphous southeastern Likouala swamps, suggests that a soil mineral gradient and a complementary forage mineral gradients exists from northwest to southeast through the Ndoki. Thus as well as the *bais* themselves, browse in proximity to *bai* rich regions (the north) may have been selected by elephants during times of mineral deficiency.

It is well known that tropical forages are usually mineral-impoverished (McDowell 1985), and elephant diets may be permanently mineral-deficient. This would explain the year round clumping around *bais* in common with studies of a number of mineral-limited herbivores (Weir 1972; Kreulen and Jager 1984; Estkeen and Bornman 1990; Ruggiero and Fay 1994).

Why mineral requirements would increase during the dry season is less clear, though there are a number of possibilities. First, elephant diets fluctuate from highly frugivorous to highly folivorous during the dry season (Short 1981; White *et al.* 1993; Powell 1997). High folivory would increase consumption of toxic secondary chemicals contained in leaves resulting in reduced digestive capability (Oates *et al.* 1980; Waterman *et al.* 1980; Illius and Gordon 1996). The clay particles and minerals of *bai* soils may adsorb these chemicals and improve digestion of leafy browse (Oates 1978; Kreulen 1985; Knight *et al.* 1988). Second, the preference for swamp and lowland browse at the bottom of the forage mineral gradient suggests that mineral intake from forage increases during the dry season. Mineral supplementation either from *bais* or preferential foraging at the top of the forage mineral gradient would therefore tend to increase in dry periods. Third, since elephants are hind gut fermenters with some ability to digest cellulose using microbial fermentation (Hungate *et al.* 1959; Sikes 1971; Mikota *et al.* 1994) their requirement for sodium to assist microbial digestive processes would increase as the volume of gut contents increases. Presumably requirement for sodium increases during the dry season for elephants in the Ndoki Forest as the quality, digestibility, and absolute volume of gut contents increases when elephants shift from fruit to browse dominated forage. However, in temperate ecosystems aquatic vegetation may contain significantly greater sodium concentrations than terrestrial plants (Belovsky and Jordan 1981) and if this were the case in the Ndoki, elephant sodium intake may even increase with higher aquatic browse intake.

A fourth reason for mineral requirements leading to dry season aggregation around *bais* may be related to the social and physiological constraints on elephant reproduction. Observations at the Dzanga *Bai* suggest that the peak in mineral accessibility during the dry season is concurrent with significant peaks in the visitation rates of oestrous cows and musth bulls (Turkalo and Walsh unpublished ms). Bulls appear to use *bais* as leks and compete for control over seep holes. During the dry season (the period of peak mineral concentration), competition intensifies and holes become dominated by bulls in musth, who are apparently more attractive to females in oestrous presumably because they demonstrate dominance over competing males (Turkalo and Fay 2001). Physiologically, mineral deficiency is a major cause of infertility in many tropical mammals (Collier and Beede 1985), thus the timing of heightened reproductive activity when minerals in *bais* are most accessible may increase breeding success (Turkalo and Walsh, unpublished ms).

If a peak in mineral accessibility during the mid to late dry season drives concurrent peaks in oestrus and musth, then a peak in parturition at the beginning of the dry season is a necessary consequence of a 21 month gestation (Sikes 1971). The fact that parturition coincides with a time of low food availability suggests that either Ndoki cows find sufficient food reserves year round to maintain body condition, or that they rely on nutrient reserves accumulated during the previous wet season to support post-partum lactation. Qualitative observations of more than 2500 individually identified elephants made over more than 10 years show little evidence of condition loss, suggesting energy requirements are met even during the dry season (A. Turkalo, pers. comm.). This may be a consequence of large body size, since large animals invest less in reproduction and lactation relative to metabolic requirements than smaller ones (Millar 1977). While the energetic costs of reproduction may be met from food, the mineral requirements of lactation among herbivores are particularly high (Belovsky and Jordan 1981). Low sodium, calcium, and phosphorus intake from forage by lactating females may limit the reproductive success of feral donkeys in arid regions of Australia, whose high fibre diet further depletes minerals (Freeland and Choquenot 1990; Choquenot 1991). Forage calcium (Kreulen 1975) and phosphorus (Murray 1995) levels have been proposed as underlying reasons for the migration of female wildebeest in the Serengeti, who during lactation, move into pastures rich in these elements. Mineral licks may also provide important dietary mineral supplementation during lactation for both temperate and tropical female herbivores (Frazer and Reardon 1980; Tracy and McNaughton 1985; Moe 1993). Since the period shortly following birth usually requires the highest maternal investment among large-bodied herbivores (Owen-Smith 1988), it is not unreasonable to suggest that female forest elephants migrate into the mineral rich northern half of the Ndoki Forest following the dry season peak in parturition. While the basic social unit forest elephants is smaller than that of savannah elephants (White *et al.* 1993; Querouil *et al.* 1999; Turkalo and Fay 2001), there is evidence that they associate and travel in larger extended families which associate at *bais* (A. Turkalo, pers. comm.). Thus an influx into mineral-rich areas of either oestrous females, lactating females, or both, would with their associated family groups increase local population density.

It may appear paradoxical that the spatial model showed small-scale aggregation at *bais* increasing, not decreasing, with increasing rainfall. However an increase in the local density of elephants near *bais* would tend to flatten their distribution with distance to *bais* over a small spatial scale if dispersal was local. During wetter periods, dispersal is widespread since elephants track fruit over a large scale, and therefore the local increase of elephants near to *bais* probably dissipated. A high degree of residual clumping would remain in very close proximity to the *bais* if elephants were accessing them for short, rather than for extended periods, which would account for the steeper local gradient of dung distribution during the wet seasons.

The influence of humans

In common with numerous studies across central Africa (Barnes *et al.* 1991, 1995a,b, 1997b; Fay and Agnagna 1991a, c; Alers *et al.* 1992; Michelmore *et al.* 1994; Hall *et al.* 1997), the strong negative effect of human sign on elephant dung density indicated that the ecological determinants of elephant distribution were out-weighed by the influence of human activity. The spatial model implied that a frequency of just 5 human signs km^{-1} on surveys was sufficient to reduce dung density to zero. In an area as remote as the Ndoki Forest, where human sign frequency was usually nil (Figure 5.4), any influx of humans must represent a considerable impact on an otherwise undisturbed fauna. Of particular interest was not that the effect of humans was detected, but the speed with which elephants responded to the arrival of human activity. Data from surveys 7 and 8 (Figure 7.2) revealed that fresh dung deposition was reduced to nearly zero in the immediate prospection zone 10-18km from the southeast terminus of sampling. Forestry prospection is an intensive activity, in which large teams of 20 workers or more, often accompanied by their families, occupy a restricted area for periods of up to several months (Blake, pers. obs.). Straight-line transects are cut every 250m in a grid throughout the forest, and all exploitable trees are enumerated. Disturbance is intense. Usually, prospection teams rely on hunting wildlife as their only protein source. On the Bodingo Peninsula during surveys 7 and 8, several snare-lines and shotgun shells were seen away from the survey-line. The effect of humans, including forestry prospection, on elephant distribution was localised to the immediate areas of recent disturbance, which is probably why the covariate FORESTRY failed to reach significance in the spatial model, but HUMAN did. FORESTRY modelled the impact of logging prospection on elephant dung encounter rate over the length (33km) of the Bodingo Peninsula, while HUMAN modelled the same effect, but on the scale of 1km survey segments. The implications of human activity on elephant ecology and conservation are discussed at length in Chapter 7.

Caveats and Qualifications

Several factors suggest cautious interpretation of the results of the spatial model, including biases in the sampling plan, the failure of the chosen functional forms to adequately represent the biological reality, and flaws in the conceptual model of elephant ranging. For example, logistical and financial constraints meant that data collection was restricted to a single linear survey line traversing the major environmental gradient across the landscape rather than 2-dimensional spatial coverage. While the effects of the covariate suite on elephant distribution could be realistically modelled, it was not possible to confirm that an influx of elephants into one section of the survey was necessarily related to a decrease in another section (i.e. was the result of the same elephants moving between sections). For example, the sampling line ran parallel to major swamps at both the northeastern and southeastern ends of the study area, though sampling was relatively close to the swamp (<200m), in the northeast section but often much further (up to 1km) in the southeast. This was potentially a problem because the spatial model detected a strong peak in dung encounter rate within 200m of major swamps for all seasons. This peak probably represented the year round use of major trails that run along the edges of swamps (Chapter 4). Therefore, it is possible that a dry season drop in elephant density in the southeastern part of the survey line represented a local retreat into the swamp, rather than the large-scale distribution shift indicated by the spatial model. This possibility was examined by removing 50km of data from both the northeast and southeast extremes of the survey line and rerunning the spatial model. The results did not change qualitatively, with a large-scale movement towards the north still indicated during the dry season. Finally since this study was based on dung counts and not elephant counts, there was no way to determine relative elephant abundance in swamp habitats since dung decay processes are different in *terra firma* and swamps. Thus the quantitative estimate of swamp use was restricted to the gradient of dung density in *terra firma* with distance from the swamp edge.

Computational constraints meant that simplified functional forms were used to represent different covariate effects on elephant distribution. For example, the prediction that elephants tend to clump around rivers was modelled by representing dung encounter rate as a monotonically decreasing function of distance from rivers. Telemetry data (Chapter 6) suggest that this may adequately represent elephant distribution during the dry season, but that during the wet season elephant distribution probably becomes bimodal. A re-inspection of the dung data suggested a similar pattern, with lowland and upland areas showing peaks in dung concentration, and a lower density on intermediate slopes. Thus, although the spirit of the conceptual model of seasonal change in elephant ranging was correct, the functional form used to represent it was not accurate.

Another flaw of the conceptual model may have been responsible for the failure to corroborate the predictions made about the relationship between rainfall and the proportion of dung found on trails. The spatial model contradicted the prediction that a greater proportion of dung should be found off trails during dry weather, since it detected a significant trend in the opposite direction. The fact that the proportion of dung found on trails was not strongly correlated with any other covariate suggests that this was a “real” effect. Why the direction of the effect was opposite to the prediction is not clear, but the existence of any effect supports initial intuition that foraging mode varies with rainfall and the change in relative consumption of fruit and browse.

This study has been criticised for not attempting to estimate absolute elephant abundance in the Ndoki Forest, and that it merely provided a relative estimate of elephant distribution. An elephant population estimate of the Ndoki Forest was not a goal of this study for a number of reasons. First, the sampling intensity and therefore the effort required in providing an un-biased estimate of elephant dung density (Walsh and White, 1999) across an area as large as the Ndoki Forest was prohibitive given the primary goals of the study and the resources that were available. Second, in converting dung density into elephant density, at least two parameter estimates are required, namely elephant defecation rate and the decay rate of dung piles. Dung decay rate may depend on several environmental factors, the most important of which appears to be rainfall (Barnes, 2001 and references therein). Defecation rate is thought to be more consistent across seasons (Barnes, 2001), however in the Ndoki forest the large variation in diet composition, particularly in the ratio between browse and fruit, suggested that defecation rate was variable. Site specific studies were required to provide estimates of these parameters which, given their complexity (White, 1995, Barnes et al. 1994; Barnes 2001), was prohibitively expensive in time and resources. Third and most importantly, the goal of the study was to provide a coherent understanding of the factors governing elephant distribution and abundance, not a density estimate. This information was judged to have greater importance not just for scientific purposes, but also for management and conservation, and therefore was given priority in this study.

CONCLUSIONS

1. Elephant seasonal distribution in the Ndoki forest was governed by the spatial and temporal distribution of fruit, watercourses, swamps, and *bais*. Leaf abundance, or new leaf phenology of either dicotyledons or THV in terra firma forests was not found to influence elephant distribution. Indeed elephant distribution was negatively correlated with the gradient of THV abundance and new leaf production.
2. Elephants showed a strong permanent aggregation around large swamps, which was thought to be due to the high availability of browse foods of they provided.
3. During dry periods of low fruit availability, elephants were highly aggregated around watercourses. This was thought to be because fruit was not available in uplands, but abundant browse could be found in riverine habitats during dry periods. As rainfall and thus ripe fruit availability increased, the level of aggregation decreased, and in seasons of peak rainfall rivers had no effect on elephant distribution.
4. Elephants tracked the distribution of preferred ripe fruit. The spatial distribution of fruit was irregular, which appeared to encourage a quasi-nomadic searching behaviour. Forest elephants were probably able to be nomadic in their search for irregularly distributed fruit for several reasons. First, they were unconstrained by water availability, which was never at physiologically dangerous distances. Second, the probability of finding browse, even low-grade browse, was high since its distribution is ubiquitous. The large body size of elephants allows them to subsist on poor nutritional quality foods if throughput is high. Thus, elephants would be unlikely to suffer prolonged bouts of food scarcity if they failed to find fruit during an extended trip. Third, the large body size of elephants also allows them to range over large areas. Finally, fruit was superabundant in some patches in some seasons and thus the payback of locating a good patch was extremely high.
5. Elephants aggregated in the northern part of the study area during the dry season, contrary to the expectation that they would move preferentially into swamp-dominated areas. This was probably due to the highly localised distribution of *bais* in the north. . The influx of elephants into the northwest, which was against the gradient of leaf productivity, was probably driven by the elephants increased dry season physiological requirement for minerals, associated with reproduction and lactation. Dry season mineral supplementation may also have been a response to the digestive demands of an increase in browse consumption, when fruit became unavailable. There was a permanent gradient of increasing elephant density with proximity to *bais* at small scales, which became steeper, not shallower, with increasing rainfall. This was thought to be due to a

permanent local aggregation at the *bais*, accompanied by local dispersal in the dry season, and a more widespread dispersal during high rainfall periods.

6. Human activity strongly negatively influenced elephant abundance, and outweighed the ecological determinants of elephant distribution. On the Bodingo Peninsula, elephants quickly vacated areas of high human activity associated with forestry prospection. This was, however, a local effect, and did not cause elephants to leave the Peninsula completely. Forestry prospection probably prevented elephants from moving north-south along the Bodingo Peninsula, and cut-off access between the NNNP and the Likouala swamps.

ACKNOWLEDGEMENTS

The estimation of covariate values from the raw data was carried out using ArcView™ by myself. Peter Walsh carried out the spatial model analysis. He is thanked for his extensive help in both the analysis, and for the many stimulating ideas he generated on the implications of the data presented in this chapter on forest elephant ecology.

CHAPTER 6. THE MOVEMENTS OF INDIVIDUAL ELEPHANTS

INTRODUCTION

A wide array of factors influence patterns of ranging in animals most of which distil to a matter of ecological scale (Levin 1992). Body size and energy requirements, habitat heterogeneity, feeding ecology, social needs, and reproductive fitness are all tightly linked in a web of interactions that ultimately determines the evolution of ranging patterns and distribution. Home range is a fundamental measure of ranging behaviour, since within its boundary all of an individual's *'normal activities of food gathering, mating, and caring for young*' take place (Burt 1943). Foraging patterns, mate search strategies, avoidance of predators, and finding rest sites and shelter come together to produce an individual's home range.

Body size largely defines an individual's energetic requirements and predicts home range in some proportion to body mass (M). McNab (1963) demonstrated that home range size appeared to scale in proportion to $M^{0.75}$, while a number of more recent studies have shown that actually the power coefficient is significantly higher than 0.75 (Clutton-Brock and Harvey 1977; Harestad and Bunnell 1979; Mace and Harvey 1983; Lindstedt *et al.* 1986; Reiss 1988; Kelt and Van Vuren 1999). The mechanism which determines the relationship between mass and home range remains unclear but is, no doubt, largely a result of the influence of the interacting variables mentioned above (habitat heterogeneity, feeding ecology, predation, and social interactions) on the underlying energetic constraints of body size (Owen-Smith 1988). Since home range size is a compromise between metabolic requirements and social pressure (Damuth 1981), it is not surprising that there is no simple functional relationship with body size. Reiss (1988) cut to the ecological simplicity of the chase prior to a complex synthesis of available information stating - *'...it is hardly surprising that elephants range over larger areas than rabbits'*.

The concept of home range is important in defining the ultimate scale of ranging and all of its associated ecological interactions. Orians (1991) summarised perfectly the continuum of scale of habitat selection which ecologists attempt to define and compartmentalise. On the micro-scale, he conceptualised habitat selection as the fine-grained theory of optimal foraging or 'diet choice'. Somewhat larger scales imply differential use of space within a heterogeneous habitat matrix or 'patch use', while macro-scale habitat selection translated as 'emigration, immigration, and migration'. Populations of animals are made up of individuals, and it is the behaviours of individuals that characterise populations. Individual foraging strategies determine an individual's use of space and habitat preferences, which ultimately shape the pattern of aggregation seen in populations in heterogeneous environments (Fryxell 1991; Bailey *et al.* 1996). Therefore ranging patterns of individuals should reflect patterns observed at the level of populations.

In previous chapters of this thesis, the distribution of forest elephants and their resources were described. Chapter 2 described the spatial and temporal heterogeneity of food and minerals. Browse was ubiquitous, but quality and quantity were heterogeneous. Fruit was patchy across several spatial scales, was temporally predictable on short time scales (individual seasons), and irregular on longer time scales (seasons across years). Mineral deposits were spatially clumped in *bais* yet availability was temporally variable, and water was spatially consistent, clumped, and permanently available. Chapter 3 quantified the feeding ecology of elephants, describing the importance of different foods in the diet and some of the characteristics of foraging success associated with habitat conditions. Browse was permanently a large fraction of the diet, and fruit waxed and waned in some (unknown) proportion to availability. Chapter 4 described the trail system developed by elephants, which was thought to form as a result of resource heterogeneity and which underpins much of the pattern in ranging behaviour. Finally, Chapter 5 quantified the seasonal distribution of elephant dung piles on a number of spatial scales, from tens of metres to tens of kilometres and related spatial pattern to habitat quality and elephant nutritional and social needs.

Dung piles are not elephants, and extrapolations of 'dung' into 'elephants' are difficult (Barnes 2001). Even when the relationship is robust, the detail of the underlying elephant behaviour, which determines their distribution, is lost. Since almost all forest elephant ecological research is based on indirect evidence, there is little reliable information available on ranging characteristics of individuals (Merz 1986b), and the only convincing data comes from a satellite and radio-telemetry study in the forest of Cameroon (Powell 1997). Powell’s attempt to track forest elephants using telemetry provided important estimates of home range, however the paucity of data revealed limited details of ranging patterns. Furthermore the study region was heavily populated, and human activity had a marked impact on elephant movements. In the Ndoki Forest, human activities were extremely low over a region of more than a million hectares (Chapter 1), which provided an excellent opportunity to study the movements of individual across a gradient of human influence from high in the peripheries to negligible in the interior of the park. It was hoped that telemetry of elephants there would provide both site-specific information in the ecological context of the study area, and also data which could be applied in the wider context of forest elephant ecology throughout their range.

There were two broad goals of this study. First, the lack of information of any kind on forest elephant ranging, meant that telemetry data would provide the first detailed qualitative insight into the ranging of forest elephants. Descriptions of home range and basic summary statistics were worth reporting in the context of previous work on both forest and savannah elephants. The second goal was to test the conclusions of previous chapters of this study - to 'ground-truth' whether the patterns observed from secondary evidence (feeding behaviour in Chapter 3, and the distribution of elephant dung piles in Chapter 5) were reflected in the ranging behaviour of individuals.

Hypotheses

1. Fruit is seasonal, and its production is tightly correlated with rainfall. Patches of fruit are geographically clumped on the scale of metres, kilometres, and tens of kilometres and seasonally clumped. Dung surveys showed that elephants track fruit on several spatial scales. Forest elephants must therefore be sufficiently mobile to track fruit over large spatial scales, which should be reflected in the size of home ranges and travel distances.
2. Elephants need frequent access to drinking water, and chapter 5 showed generally high dung density in proximity to water, a trend that declined and even reversed in the wet season. Water is clumped, thus elephants should use areas close to water more frequently than their availability would suggest.
3. Swamp vegetation offers the highest payback (feeding stations per unit distance moved) foraging areas for browse (Chapter 3), thus elephants should show preferential use of swamps when food resources (i.e. fruit and high quality browse) are low in *terra firma* forests. This preferential habitat use should relax with increasing rainfall, which correlates with higher fruit and browse productivity (new leaves) in dry forest, and elephants should spend an increasing amount of time foraging in uplands.
4. Day range should increase with rainfall, a strong predictor of fruit abundance for at least two reasons depending on the mechanism of how elephants track fruit: 1) searching behaviour increases travel distance as elephants reconnoitre on an increased scale to find

fruit, 2) fruit patches are widely dispersed compared to browse patches, thus elephants need to move further to exploit those patches.

5. Speed of travel should increase with distance from water for three reasons. First it is mechanically more difficult to walk through swamps. Second, foraging in swamps should be more time-consuming, since browse feeding stations per unit distance were more frequent in swamp habitats compared to *terra firma,* and the ratio of feeding to walking should be higher in swamps. Thirdly, fruit density was correlated with distance from water (Chapters 2 and 5), thus elephants should forage for fruit mostly in uplands. The increased distance between fruit patches compared to browse, and the efficiency of walking on trails, would suggest greater overall speed during bouts of fruit foraging.
6. *Bais* are important permanent resources for elephants, though mineral availability increases in dry periods, which appears to attract elevated numbers of elephants. Collared elephants should increase their use of *bais* with increasing rainfall and reach maximum rates of use in the driest months.
7. In the absence of humans, elephant ranging is driven by their ecology. Human actions disrupt ranging patterns (Chapter 5). Collared elephants should avoid areas of high human abundance where protection is not vigorously enforced.

METHODS

This study was initiated in 1998 with a feasibility study of a GPS telemetry system previously only used in the savannahs of East Africa (Douglas-Hamilton 1998; Blake *et al.* 2001), and subsequent deployment on two forest elephants in the Dzanga-Ndoki National Park. Methodological details of the telemetry system and elephant immobilisation procedures were provided by Blake *et al.* (2001), which are summarised here.

The GPS telemetry system, manufactured by LOTEK Engineering (Toronto, Canada consisted of an 8-channel GPS receiver, with a built in RAM capable of storing over 3500 GIS fixes. Collars may be programmed to search for fixes at time intervals decided by the researcher, up to a maximum of one fix every five minutes. Battery pacification (capacity decay through lack of adequate draw of current) prevented low fix intervals (< 4 per day). Vertical and horizontal motion sensors record an index of animal activity before every fix attempt. Once deployed, a traditional VHF receiver allowed the collars to be located from an aeroplane, and an UHF modem link enabled communication between the collar and a remote laptop computer in the aeroplane. This link allowed data to be downloaded, RAM memory to be cleared, and the collar to be reprogrammed. With a regime of 8 fixes per day and minimal communications sessions, battery life, according to the manufacturers, was ca. 2 years.

A total of 6 elephants were immobilised over the course of the study and fitted with GPS collars. Field veterinarians of the Wildlife Conservation Society, who had extensive experience in wildlife immobilisation and handling techniques, supervised all procedures. All elephants were darted with Carfentanil hydrochloride (Carfentanil™) administered with either ‘Tel-inject™’ or ‘Dan-inject™’ delivery systems (rifle and darts). All animals were shot while they were drinking in *bais*, which allowed the field team to approach to 30-55 metres of the elephants and take a clear shot, almost impossible in the forest. An unobstructed view also allowed essential safety checks before final decisions on suitability for immobilisation were taken. Animals were only immobilised if they appeared to be in good health, were fully grown, were not members of an obviously larger group, and were not females with un-weaned offspring. Immobilisation of elephants usually occurred within 5-10 minutes following administration of carfentanil, during which time they were tracked from a distance judged not to be within earshot of the elephant, which could have induced panic. Skilled pygmy trackers were vital for the success of these operations. On finding a recumbent elephant, its neck was measured, and collars were fitted snugly and as quickly as possible taking care that all antennas (GPS and UHF) were situated in the centre of the top of the neck, and that the battery pack hung in a well-balanced position under the throat. Failure to position the antennas correctly would have resulted in the ears blocking signal transmission.

While elephants were immobilised a number of basic veterinary procedures were carried out, including collection of faeces, blood, hair, and ticks. Following collar attachment, elephants were administered with Naltrexone™, an antidote for Carfentanil and which reverses anaesthesia in 2-5 minutes. No mortalities occurred during or following immobilisations. There was good evidence to suggest that the immobilisation procedures did not have detrimental behavioural effects on the elephants. First, all stood easily, and walked away calmly into the forest on rousing, and on two occasions immobilised animals were observed later on the same day drinking calmly from exactly the same water holes in which they had been immobilised (Figure 6.1).

Figure 6.1. Sparkey approximately 8 hours post immobilisation

Following collar deployment, data were downloaded from the collars after the first month and approximately every three months thereafter. The GPS interval was set to record a fix every hour for the first month following immobilisation, and combinations of three hourly, hourly, down to every 10 minutes for one hour one day per week to track micro-scale movements. Fix intervals were maintained at 3 hourly intervals to provide data directly comparable with those collected for a sister project on savannah elephants (Douglas-Hamilton 1998).

The objective of the feasibility study was to test to collar performance on just two elephants in order to evaluate the chances of success of a larger scale project. Thus in October 1998, two elephants, a male and a female, were immobilised at the *Bai* Hokou complex in the Central African Republic. One collar, on the bull, failed immediately, while the female's collar gave one month of GPS positional data, before it too failed. However the VHF beacon continued to function, which allowed her to be relocated five times over a nine-month period using traditional aerial radio-tracking techniques (Blake *et al.* 1998). The failure of both collar GPS units within a month precluded deployment of further collars until reliability had been demonstrably improved. Following major changes to collar design and successful deployment on 6 elephants in east Africa, the forest elephant collaring programme was resumed in October 2000 with the collaring of a large bull at Mabale *Bai* in the NNNP. In

January 2001, a further 3 elephants, 1 bull and 2 females, were collared at *Bai* Hokou. The performance of these collars was excellent following deployment, providing both high fix acquisition success and communication system reliability. The difference in data quality and quantity between these collars, and those of the single collar deployed for the feasibility study, makes comparison of the two datasets difficult. The results presented in this chapter are therefore limited to data collected from the 4 individuals collared in 2000/2001, while the published paper describing the feasibility study is included as an appendix to this thesis. The data described below are preliminary and part of an ongoing study in which these collars will continue to collect data for at least 1 and it is hoped 2 years.

During initial planning for this study it had been proposed to deploy collars on known individuals from the Dzanga Bai study (Turkalo and Fay, 2001). Turkalo has 10 years of data on observations of hundreds of individuals and family groups made at Dzanga which show a variety of different visitation patterns, from almost daily visits, to some individuals which are seen only once or twice per year. It was hoped that telemetry data would shed light on the ranging patterns of these individuals. However, it was ultimately decided that immobilising elephants and deploying GPS collars at Dzanga Bai was would disturb the bai to an unacceptable level, with potentially negative consequences for the elephants. Thus Bai Hokou and Mabale Bai were chosen for their high visitation rates, and the first suitable animals that offered a shot were selected.

Analytical methods

Since most telemetry studies of elephants have used minimum convex polygons (MCP) (Southwood 1966) to estimate home range, MCP's were also calculated for the elephants in this study as an initial step in quantifying elephant ranging behaviour. All home range estimates were calculated using ‘The Animal Movement Program’ produced by the United States Geological Survey, a spatial analysis package which is seamless with ArcView™ GIS (Redlands, California).

TRAVEL DISTANCE AND SPEED ESTIMATES

Calculations of travel distance and speed using telemetry data vary according to the interval between locations, and short time intervals are better estimators of actual distance travelled than large intervals (Reynolds and Laundre 1990; de Solla *et al.* 1999). In this study, only those fix intervals of 1 hour were used to calculate hourly travel speed. Daily travel distance (path distance) was calculated by taking the average of mean hourly speed for those days in which at least 10 hours of hourly interval data were available and multiplying by 24. In large light gaps and *bais*, fix success rate for the telemetry system used was 100%, while across 'forest' vegetation types it dropped to a mean of 50% (Blake *et al*. 2001). Fixes while the elephants are in *bais* would therefore tend to bias the data toward ranging behaviour in *bais*, which was certainly different from that in the forest. A correction for *bai* activity relative to the forest was made by randomly dropping 50% of fixes within 250m of the geographic centre of *bais*.

DAILY AND SEASONAL EFFECTS ON LOCATION

Variability in fix intervals meant variability in the temporal auto-correlation between fixes. This was accounted for by selecting only those fixes at 0:00, 3:00, 6:00, 9:00, 12:00, 15:00, 18:00, and 21:00 hrsGMT for calculations of location means against geographic covariates. In the analysis of the distribution of elephants with respect to water, since *bais* are associated with watercourses, elephant visitation to them could potentially bias activity patterns associated with water. Therefore all GPS fixes within 500m of a *bai* were removed from the dataset before calculating mean distance from rivers.

To estimate use of habitat versus availability with distance from water, a minimum convex polygon of the range of the four elephants was constructed, and used to define the space potentially available to the elephants. A 100X100m grid (1ha cells) was established across the entire surface area of this polygon in GRID ArcView, with the centroid of each cell assigned a value of distance to the nearest river. Cells were then classified by 100m distance intervals, and the total area (number of cells) in each 100m stratum was calculated, which created zones of known area in increments of 100m from water. The percentage of total cells in each 100m distance class was then calculated. Using only ‘corrected’ telemetry data (above), and using only those fixes further than 500m from a *bai*, each fix was assigned the distance value of the grid cell in which it fell. Thus, a preference index for each 100m stratum could be calculated, by dividing the percentage of total fixes per distance class by the percentage of total grid cells in the same distance class. Values greater than 1 indicated a higher than expected use and less than 1 indicated lower use than expected.

RESULTS

Home range

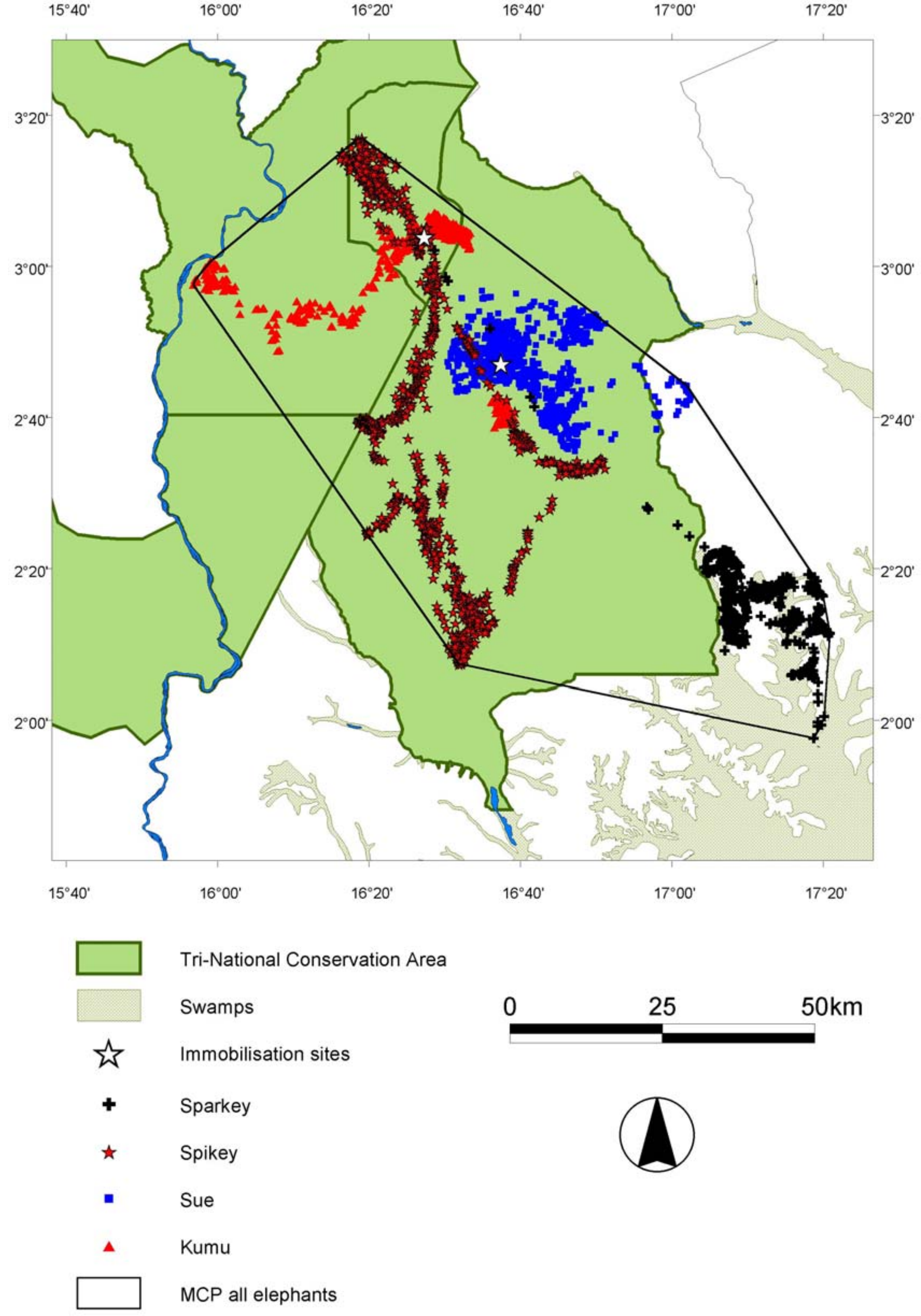
Minimum convex polygon home range estimates varied from 677 to 1977 km^2, with a mean of 1213km^2 (SD 548km) (Table 6.1, Figure 6.2). The maximum linear distance covered by each elephant ranged from 104km (Sparkey) to 40 km (Sue) (Table 6.1). The MCP for all elephants combined was 5246km^2. The total MCP for the four elephants combined (5246km^2) was larger than the surface area of both the Nouabalé-Ndoki and Dzanga-Ndoki National Parks (Figure 6.2).

Table 6.1. Minimum convex polygon home range statistics

Name	Sex	Date collar fitted	Last download	N days data	MCP (km^2)	Max. linear distance (km)
Sue	Male	29 Oct 00	15 July 01	260	677	40
Kumu	Female	29 Jan 01	5 Sept 01	148*	1058	58
Sparkey	Male	25 Jan 01	5 Sept 01	130	1140	104
Spikey	Female	26 Jan 01	5 Sept 01	223	1977	87
Mean					1213	72
Total MCP all elephants combined					5246	

* Data were lost between 6 April and 17 August 2001

Figure 6.2. Basic geography of collared elephant movements



Ranging

The mean travel distance for all elephants was 0.33kmhr^{-1} (SD 0.38), with a range from 3.3km to 0.0 kmhr^{-1} (Figure 6.3). Kumu had the highest average speed (0.51kmhr^{-1}) and Sparkey the lowest (0.2 kmhr^{-1}) (Table 6.1). The difference in average hourly speed between the four elephants was significant (ANOVA (log transformed dependent variable, speed): $F_{(3,548)} = 59.7$ $P < 0.001$). Mean travel distance was positively correlated with the proportion of days elephants spent in *bais* (Spearman's rank correlation, rho = 1.0, N = 4, P -; Table 6.2).

Figure 6.3. Range and frequency of travel distances per hour

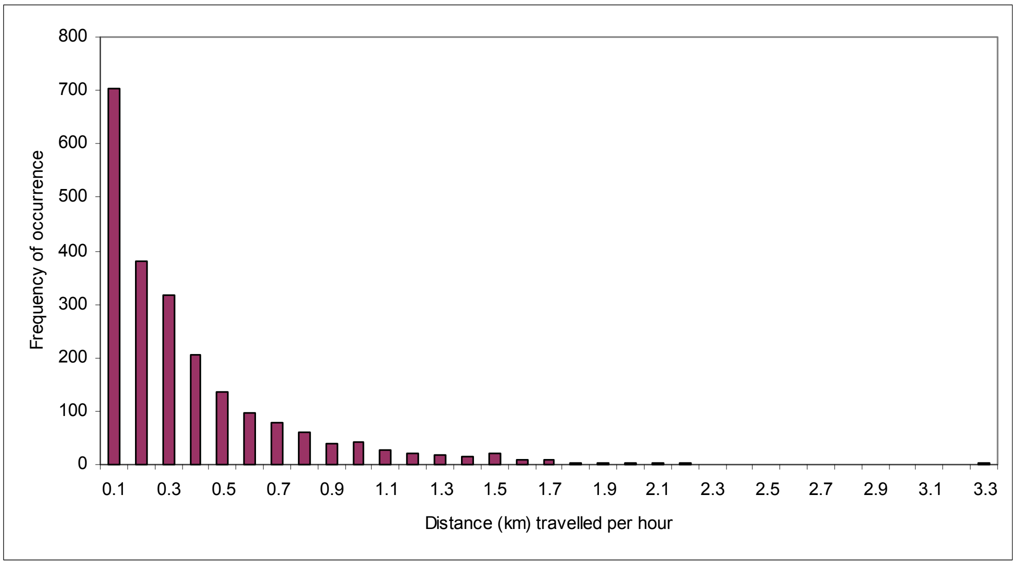


Table 6.2. Mean speed per hour for each elephant and proportion of days spent in *bais*

Elephant ID	Mean speed kmhr^{-1}	% of total days in *bais*
9a Kumu	0.51	57.8
99 Sue	0.37	49.4
bc Spikey	0.26	32.7
9d Sparkey	0.20	2.4

Daily path length varied between 2.13km and 22.45km, (mean = 7.84km, SD 4.23). The modal daily travel distance was 4km (Figure 6.4). Mean linear displacement at midday was 4.1km (SD 3.4) and at midnight was 3.4km (SD 3.2), which were significantly different (Mann-Whitney U Test: z = -2.582, P = 0.01) (Figure 6.5).

Figure 6.4. Frequency of occurrence of daily travel distance

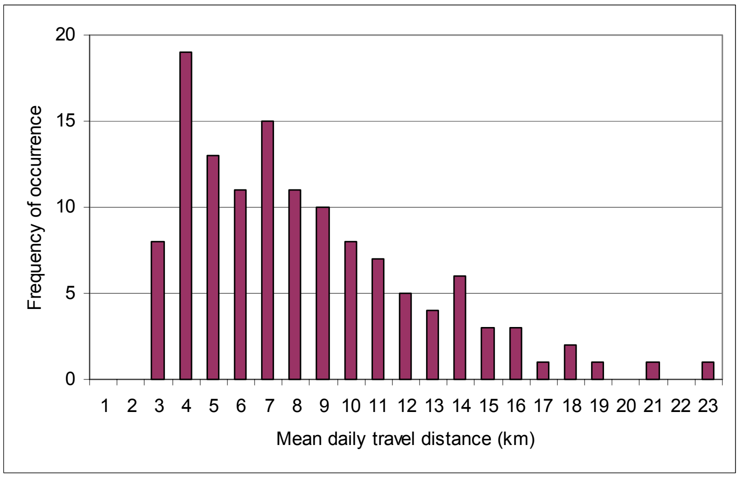
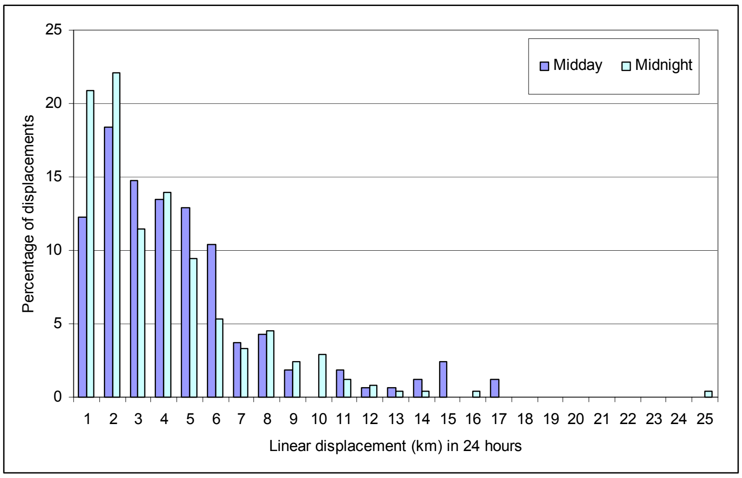


Figure 6.5. Linear displacement in 24 hours

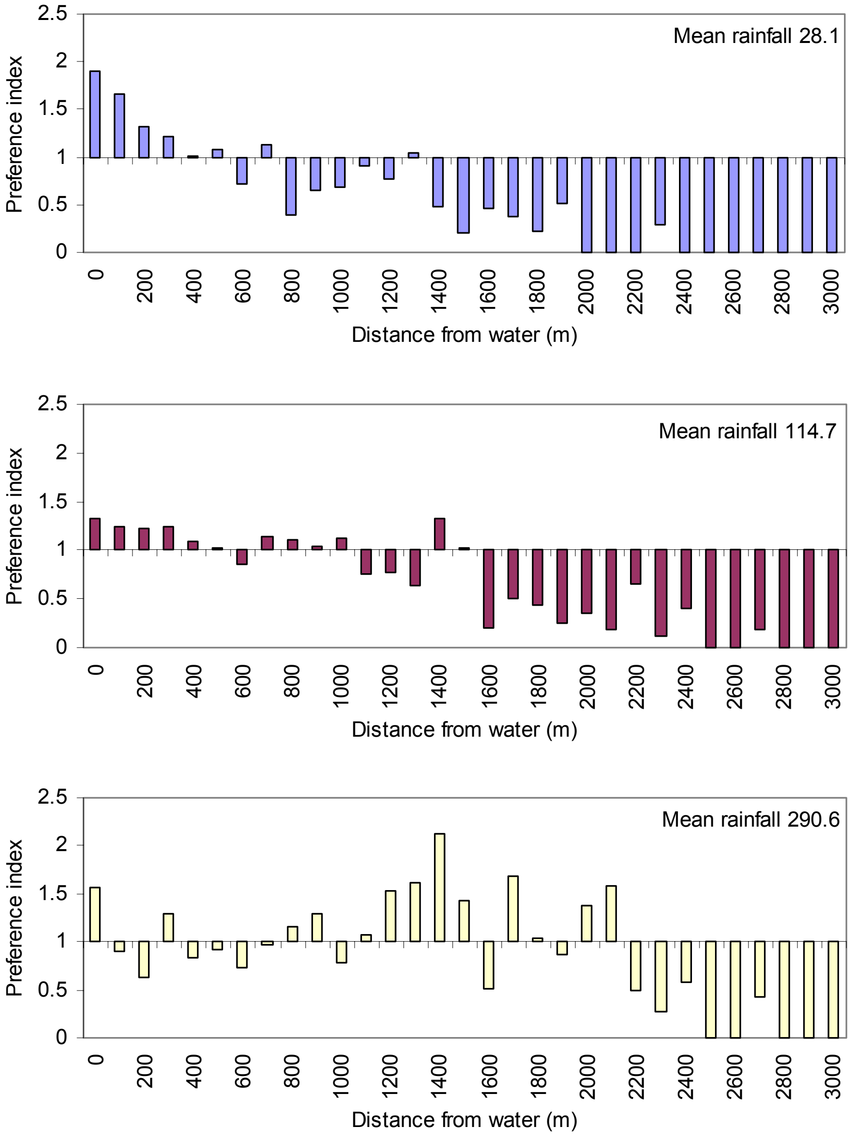


Seasonal effects on distribution and movement

RAINFALL AND DISTRIBUTION IN RELATION TO RIVERS

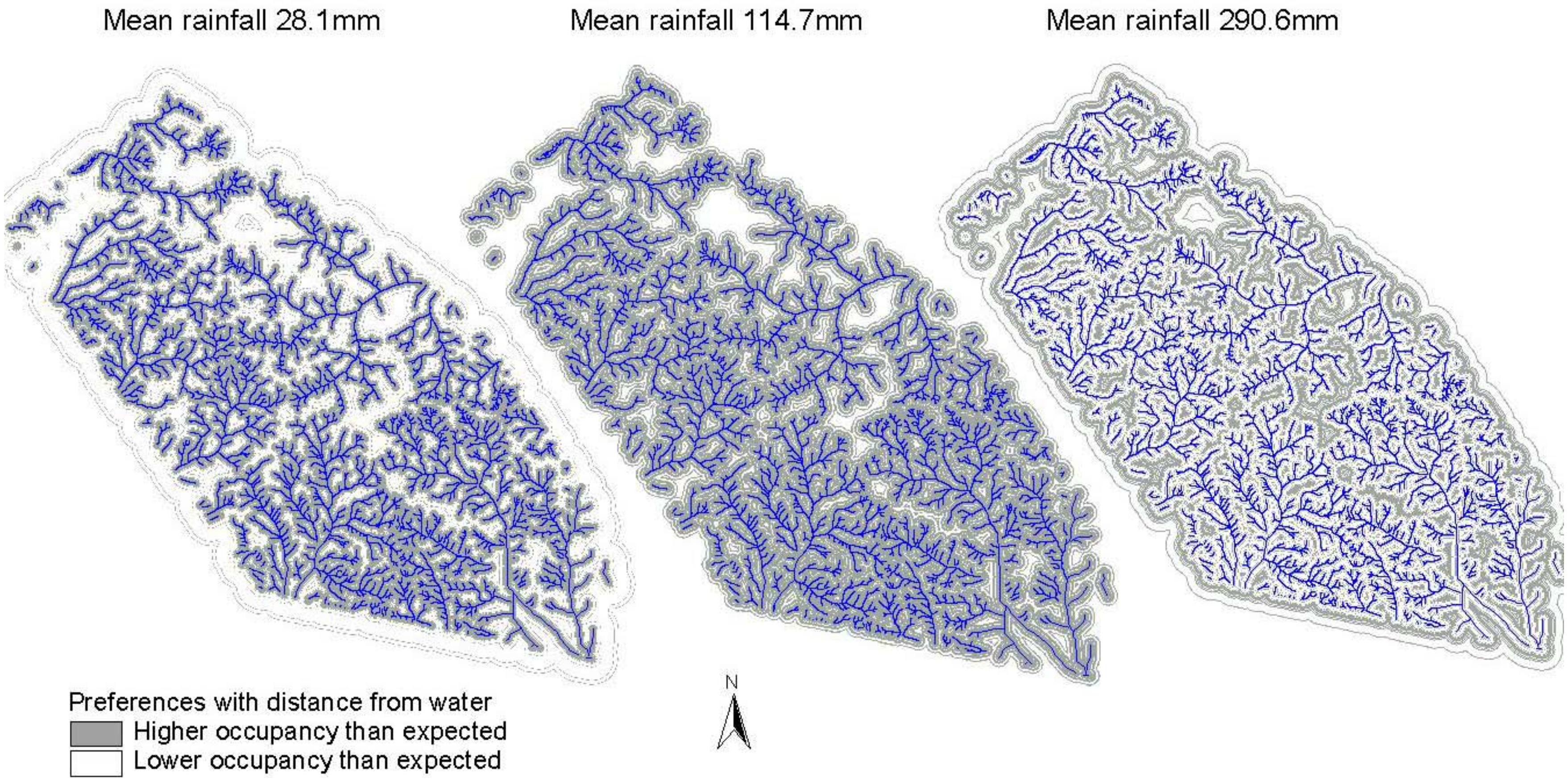
During low rainfall periods there was a sharp decrease in preference with distance from water (Figure 6.6), and forest beyond 600m from water was avoided (negative preference indices). All but 4 of the 43 zones further than 600m from water were used less than expected, and two of these (at 3600 and 4300m) were sampling artefacts, due to the small percentage of grid cells at these distances which allowed 1 fix to make the preference index greater then unity. At intermediate rainfall, the elephants also used zones close to water more than expected, though the preference index was lower for all distance classes in the region 0-600m than during the low rainfall period. Preference indices remained positive, with one exception, to a distance of 1100m from water. High rainfall months saw an extreme shift in elephant distribution with preference indices greater than 1 for only two of the 100m zones within 700m of water. At increasing distance intervals, preference indices were consistently greater than 1 until 2100m from water, after which elephants used remaining areas less than expected. These data clearly show the relaxation of the tight dry season clumping of elephants around watercourses as rainfall increases into the wet season, as elephants increasingly select upland areas. A geographical summary (Figure 6.7) models the change in elephant concentration within the MCP of all collared elephants in relation to rainfall.

Figure 6.6. Preference index of collared elephants with distance from water



Rainfall means were calculated by taking the average of the three driest months (Jan, Feb, and Mar 2001), the two wettest (Nov 2000 and Apr 2001), and the remaining five intermediate rainfall months (Dec 2000, and May, Jun, Jul, Aug 2001). October 2000 was excluded since there were only two full days of GPS fix data for a single elephant (99 Sue), and sample size was prohibitively low.

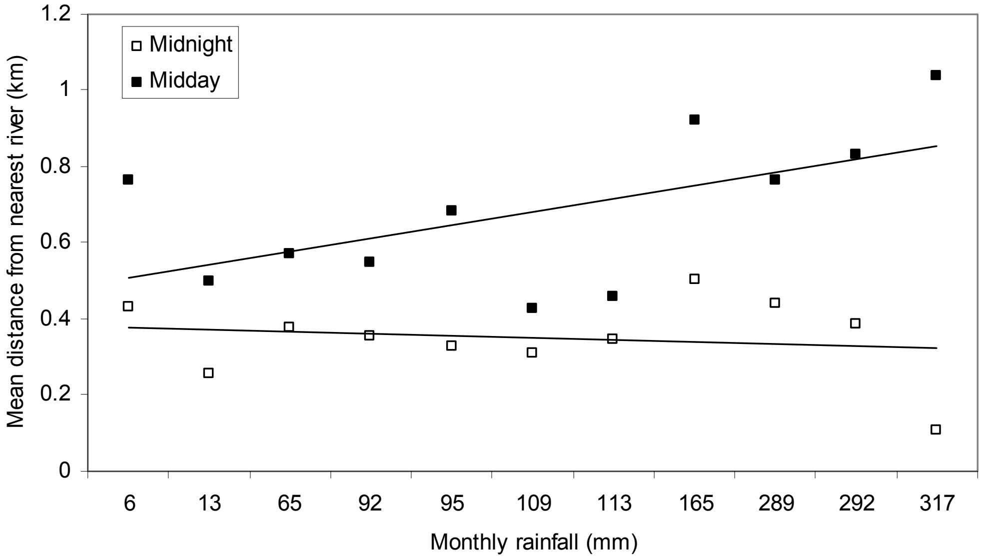
Figure 6.7. Change in elephant habitat preference in relation to distance from water by rainfall



As rainfall increased, the collared elephants habitat preferences shifted from close proximity to water courses to uplands

As rainfall increased, there was a significant increase in the mean distance of elephants from water (linear regression analysis of log distance from nearest water: r = 0.119, $F_{(1,2446)}$ = 35.265, $P < 0.001$). However, when the data were partitioned by time of day (midnight and noon) there was no significant increase in mean distance from water for midnight locations (r = 0.07, $F_{(1,300)}$ = 1.483, P = 0.224) , while the noon distribution remained significant though the relationship was weaker than for all data, probably due to smaller sample size (r = 0.106, $F_{(1,380)}$ = 4.314, $P < 0.05$) (Figure 6.8). The elephants were partitioning their seasonal use of space with respect to an underlying diurnal pattern, which remained consistent at varying rainfall levels (below). There was no effect of rainfall on mean distance from *bais*, which was highly variable among the different elephants and at different rainfall levels.

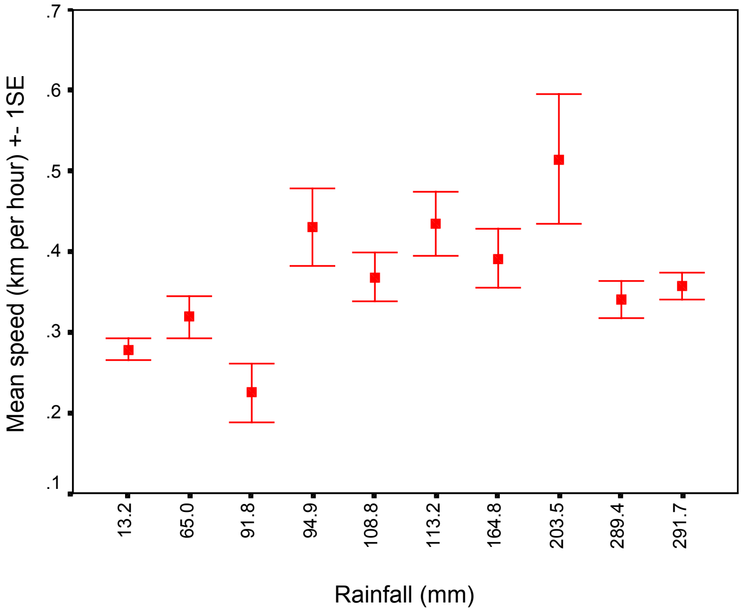
Figure 6.8. Distance from nearest water for all data, midnight, and midday fixes



TRAVEL DISTANCE AND RAINFALL

Using the dataset of 60 minute fix intervals corrected for *bai* use, regression analysis indicated that travel distance (speed) increased significantly with rainfall (log speed: r = 0.119, $F_{(1, 2194)}$ = 31.331, $P < 0.01$) (Figure 6.9). Despite this, there was no discernible difference in daily linear displacement with rainfall for either midday or midnight calculated displacement (Midday, $F_{(1,161)}$ = 0.754, $P > 0.05$; Midnight: $F_{(1,234)}$ = 1.030, $p > 0.05$).

Figure 6.9. Mean travel speed with rainfall

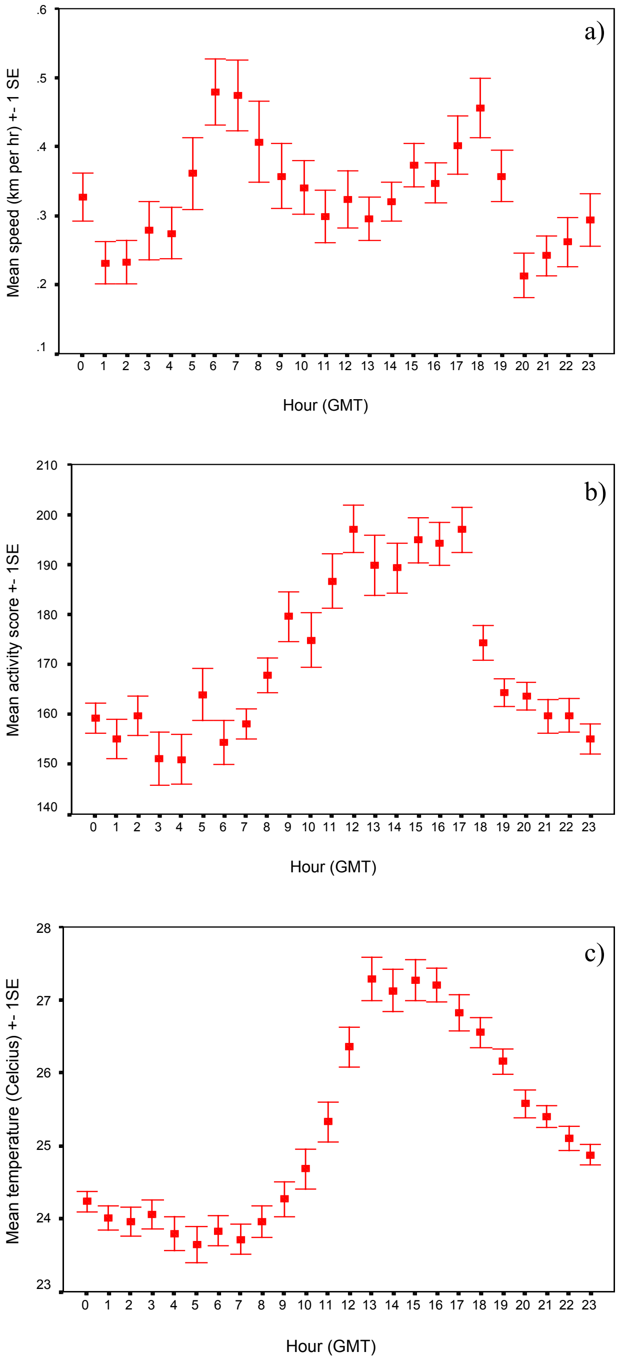


Patterns of diurnal movement

TRAVEL DISTANCE AND ACTIVITY

Mean travel distance per day was 7.8km, with a daytime (06:00 to 17:00) mean of 4.5km and night-time of 3.7km (Student's T test: $t = 2.36$, $df = 11$, $p < 0.05$). The diurnal pattern of travel distance was strongly bimodal (Figure 6.10a). Travel distance was lowest in the early hours of the morning between 1:00 and 2:00 GMT rapidly rising to a maximum of nearly 0.5km hr^{-1} at 6:00 and 7:00 GMT. Travel distance then waned to a midday low of ca. 0.3kmhr^{-1}, before rising to a second peak of ca. 0.5kmhr^{-1} at 18:00GMT, after which there was a steep decline to a night-time low. Data from the in-built activity sensor suggested a very different pattern of diurnal activity to travel distance, with a period of low activity throughout the night rising rapidly at daybreak to a single activity peak from 12:00 to 17:00 GMT (Figure 6.10b). There was no correlation between mean travel distance and temperature by hour (Pearson's correlation: $rs = 0.03$, $N = 24$, $P = 0.890$). The diurnal pattern of activity as recorded by the collars, tracked temperature change to a remarkable degree (Figure 6.10c) and the two were highly significantly positively correlated (Pearson's correlation: $rs = 0.795$, $N = 24$, $P < 0.01$).

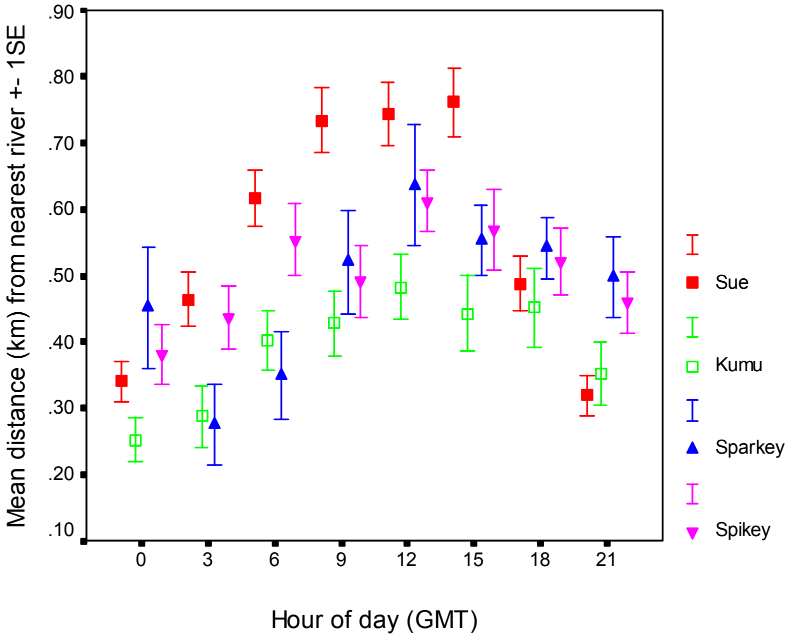
Figure 6.10. Daily pattern of mean distance travelled, activity index, and temperature for all fixes at one hourly intervals



DISTANCE FROM NEAREST WATER

There was a strong diurnal rhythm of elephant distribution in relation to water (Figure 6.11), with all individuals clumped around watercourses at night and in most cases most heavily at 00:00 GMT. As the morning progressed, there was a general movement away from water and swamps and into upland areas, where the elephants usually remained through the day until ca. 15:00GMT, after which they tended to move back toward watercourses. Mean speed also showed a diurnal rhythm, increasing weakly though significantly with distance from the nearest watercourse (Linear regression analysis, log speed: $r = 0.169$, $F_{(1, 2194)} = 64.175$, $p < 0.01$).

Figure 6.11. Diurnal elephant distribution in relation to rivers

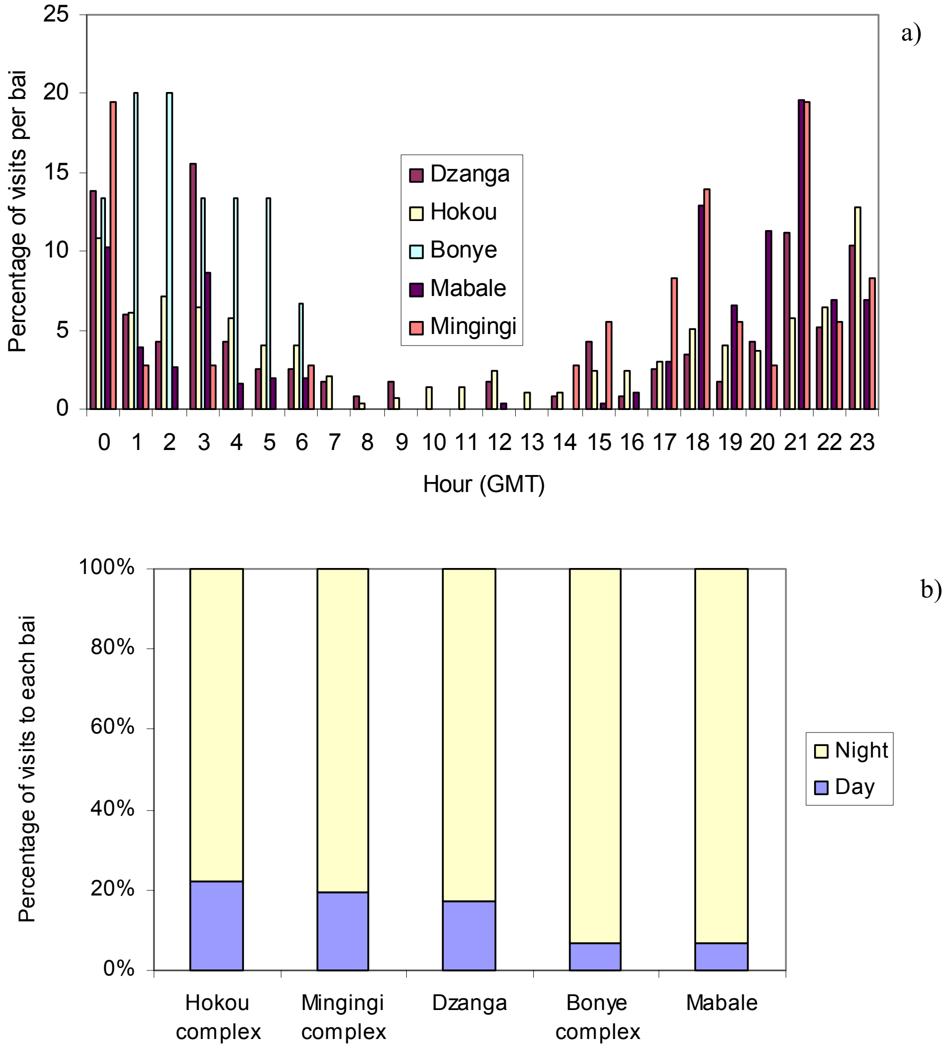


BAI VISITATION

To estimate *bai* visitation rates, it was assumed that all fixes within 500m of a *bai* constituted a visit to the *bai*. This radius took account of the size of *bais* (some of which are more than 200m long) and the interval between fixes for which there was no information on location, thus an elephant could visit the *bai* and leave between fixes. Combined data from the four elephants showed no overall diurnal pattern of *bai* visitation. However, when the data were partitioned to include only those elephants that used *bais* regularly, visitation followed a very clear pattern with activity in *bais* almost exclusively nocturnal or crepuscular (Figure 6.12a,b). Between 6:00 and 17:00 (50% of total time) only 15% of visits occurred and the difference between day and night visitation rates was significant (Wilcoxon signed ranks test: $z = -2.023$, $P_{(\text{two-tailed})} < 0.05$) (Figure 13b).

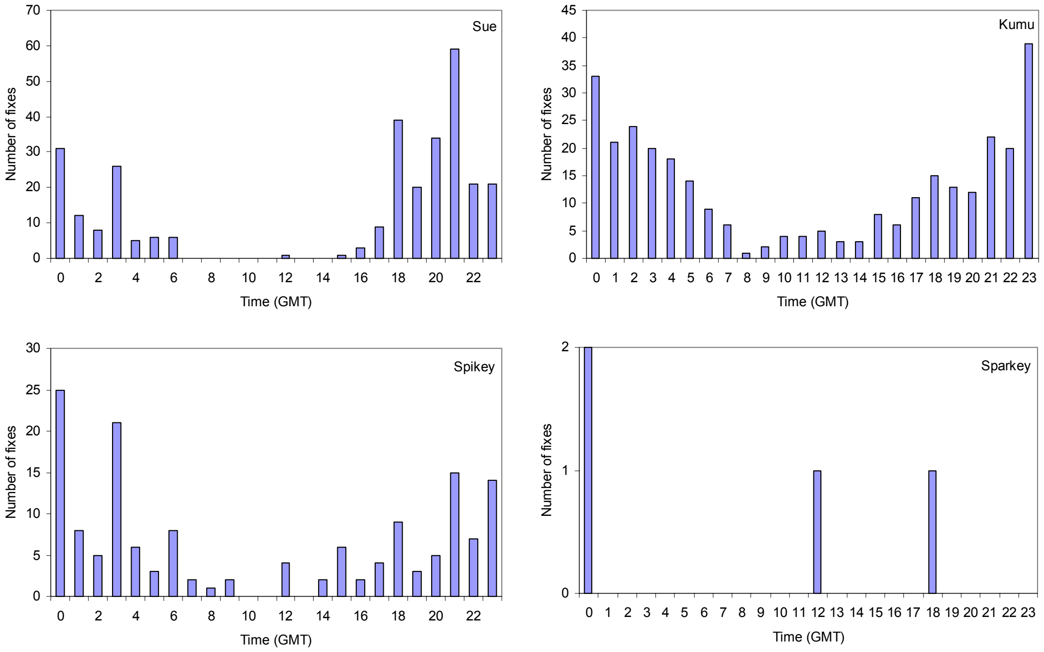
Sue showed a very strong diurnal pattern of activity based around a single *bai*, Mabale *Bai*, for the duration of the study (Figure 6.13). The duration of visits was very different for the three elephants that frequently used *bais*. Considering data collected during one-hour schedule periods only, the maximum number of hours spent in a *bai* (within 500m) was 9 in the case of Spikey, while Sue used the *bai* for 11 and 10 hours on one occasion each. Kumu used the *bai* for more than 10 hours on 39 days.

Figure 6.12. ***Bai*** **visitation by time, all elephants**



Night: 18:00 – 05:00
Day: 06:00 – 17:00

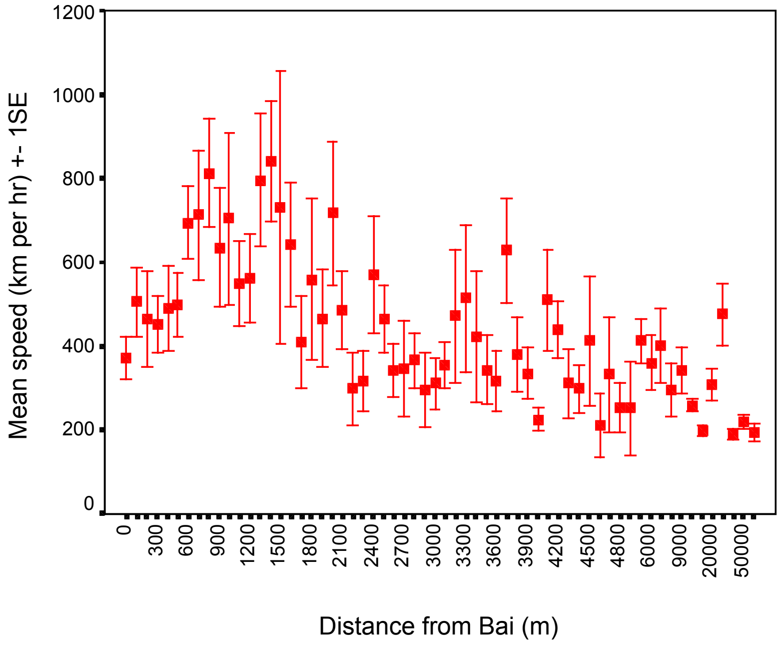
Figure 6.13. Diurnal pattern of *bai* use (note different scales on the y axis)



Speed in relation to bais

The speed of elephants varied considerably with distance from *bais* (Figure 6.14) with a significant decrease in speed with increasing distance (linear regression, Log speed: $r = 0.238$, $F = 132.318_{(1, 2194)}$, $P < 0.001$). The shape of the curve of speed against distance was not linear, with speed relatively constant within 500m of the *bai*. However, this was probably an artefact due to the collar's sampling schedules. The 1 hour fix interval was not sufficiently frequent to accurately detect animals entering or departing the *bai*, but would have included a certain time between fixes where the animal arrived at the *bai* sometime before the next fix was taken. The second bias may be because many of these fixes were during prolonged visits to the *bai* when the animal was moving within the *bai* between fixes. The predicted intercept (speed at *bai* - 0) from the regression equation was 0.24kmhr^{-1}, though due to the errors discussed earlier, the true mean speed at very close distances to *bais* was probably considerably greater than this.

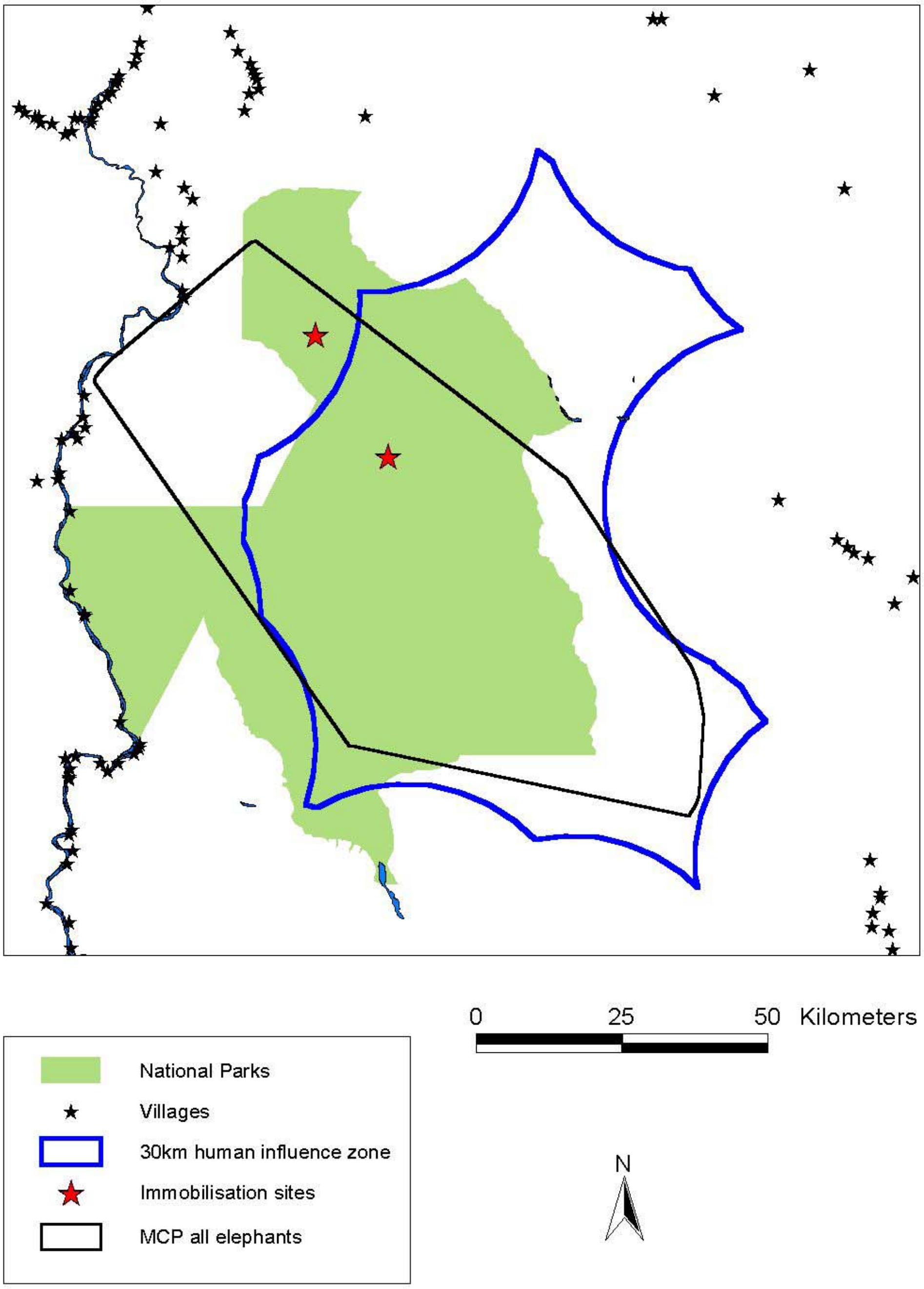
Figure 6.14. Mean speed with distance from *bais*



The effect of humans on elephant ranging

The first salient point to make is that of the four elephants, not a single individual ranged north of Dzanga *Bai*, yet all elephants moved long distances to the southeast (with the exception of Sue who remained rather sedentary), into the uninhabited and well protected NNNP. Figure 6.15 shows the individual paths and the minimum convex polygon (MCP) for all elephants in relation to National Parks, the Dzanga Special Reserve, and the 30km zone of influence around permanent human habitation (Chapter 1). The area of the MCP was 5246km^{-2} of which a total of 3597km^{-2} (68.2%) was inside the National Parks. Of the remaining 1649km^{-2} outside the Parks, 810km^{-2} (15% of the MCP) was outside the parks and special reserve, and also out of the 30km human influence zone, while the remaining 810km^{-2} (15%) was inside the 30km human influence zone. Of the entire 5246km^{-2} MCP, only 25km^{-2} (0.5%) was outside of any conservation management area and inside the human influence zone. While there were sampling biases in the choice of location for darting elephants (e.g. all elephants were collared inside national parks) which are discussed below, these statistics offer compelling evidence that the elephants avoided areas which were outside of protected areas and inside areas of human activity, while areas outside protected areas and where human activity was negligible were frequently used.

Figure 6.15. Combined MCP home range of collared elephants in relation to the NNNP and DNNP and a 30km human influence zone around permanent villages



DISCUSSION

This section discusses the results from this study in both a site-specific context and in comparison to data from other study sites, after which some generalisations are made which may be applicable to forest elephants throughout their range. Studies of African elephant ranging patterns have been biased toward savannah rather than forest elephants, and not until the mid-1990's did Powell (1997) succeed in satellite and radio-tracking forest elephants at a site in Cameroon. The study described in this chapter, which includes the preliminary work of Blake *et al*. (2001) (Appendix 1), was only the second telemetry study of forest elephants to be attempted, and the first using GPS to obtain high accuracy data in a relatively undisturbed forest.

Elephants collared in the extreme northwest of the Ndoki Forest ranged over much of the Ndoki landscape. The mean MCP of 1213km^{-2}, and mean linear coverage of 72km with a minimum of 40km were sufficiently large to track peaks of fruit production (Chapter 2 and 5), which were up to ca. 50km apart between seasons. Centres of fruit production are considerably closer than indicated from foot surveys along a single linear track, thus elephants seem well equipped to exploit food patches throughout the forest. Elephants were capable of linear displacements of up to 58km in 48 hours and frequently moved over 25km in 2 days. Thus their ability to track rapid changes in the geographic distribution of varied resources over a large spatial scale was evident.

Powell (1997) found that elephants in Cameroon had smaller home ranges than those reported here. In his study, two females and a male had MCP home ranges of 203.2, 328.7, and 598km^{-2} respectively, compared to a range of 677-1977km^{2} in the Ndoki Forest. A single immature bull recently collared in the Odzala NP (Congo) had an MCP home range of little over 100km^{-2}, nearly 20 times lower than Spikey, and 6 times smaller than Sue's (J-M Froment and W Karesh, pers comm.). There are methodological and environmental reasons that may account for these differences. The MCP is a crude estimator of the actual region over which animals range and may over-estimate the 'true' range (Harris *et al.* 1990). However, since it is the most frequently reported statistic in elephant studies, it is still the best means of comparison. Powell (1997) used harmonic mean and kernel range estimators, but since the Ndoki elephants have not yet provided a full year of data, more sophisticated analyses were avoided.

Issues of sample size also make comparison within and between sites difficult. Sample size (fix intensity and duration of study) was unfortunately low for Powell's study (1997), due to collar reliability problems, and his biggest sample size was 240 locations over 17 months for the bull, and only 23 locations for one of the cows. Asymptotes of home range were almost certainly not achieved for Powell’s females, and probably not for the bull. In Odzala, the fix rate was higher (ca. 2 fixes per day), however the duration was short (less than 1 year) and there were frequent long gaps between data points. Despite the high intensity of fixes in the present study, the home ranges calculated here were also over less than a year of data and it is unlikely that these elephants have yet used their full home ranges.

The second sampling problem is the number of individuals. Telemetry data have now been obtained from only 9 forest elephants, an exceedingly low number from which to make generalisations about a species and comparisons between sites, particularly when variation is high. At a single savannah study site (Laikipia district, Kenya) involving 20 individuals from the same population in the same habitat, elephant MCP home ranges varied from 102km^2 to 5527km^2, a 50 fold variation (Thouless 1996). In Tsavo NP, estimated home ranges varied between 400km^2 to 3700km^2 Leuthold (1977b) cited in Powell (1997), while Verlinden and Gavor (1998) (with a small sample of locations), reported a 123 fold difference between largest and smallest elephant home range in Botswana. Thus, variation among individuals within the same geographic region can be enormous. The variability in home range between Ndoki, Odzala, and Cameroon may indicate underlying ecological differences; however the small number of individuals and high variability prohibits anything more than speculation on home range differences and their causes.

The longest linear displacement recorded so far in this study was 103km (Sparkey). Verified reports of movements of over 100km in savannah habitats are rare. Early reports of enormous displacements quoted by Sikes (1971) appear to be gross exaggerations. The longest verified movement reported was 230km by a female elephant in Botswana (Calef cited as a personal communication by Dudley (1996). Dudley (1996) also cited Viljoen (1992), who claimed that desert elephants in Namibia could move 195km in a single day, with linear distances in excess of 70km per day, which seems hard to believe. For non-desert elephants, the longest linear distance covered appears to be 136km in northwestern Cameroon (Tchamba *et al.* 1995). Verlinden and Gavor (1998) state that elephants in northern Botswana moved up to 200km to reach dry season drinking water sources, but this was probably total distance travelled rather than linear displacement. Confirmation that elephants may move over 100km linear distance now comes from a number of study sites (Lindeque and Lindeque 1991; Tchamba *et al.* 1995; Thouless 1995, 1996; Verlinden and Gavor 1998). Sparkey's movements are comparable to these, but are more than double than the maximum of 42.5km recorded for forest elephants by Powell (1997). It is probable that 'normal' behaviour of elephants involves long distance movements of the order of 100km, but telemetry studies have been unable to confirm this as a widespread phenomenon since in most areas of Africa, elephant range has been disrupted by man (Douglas-Hamilton 1971; Cumming *et al.* 1987; Parker and Graham 1989a; Buss 1990; Caughley 1995).

Environmental conditions which might influence elephant ranging may be simply divided into two groups; ecological and human. The distribution of resources has a profound effect on elephant ranging patterns – abundant food usually means small home range (Leuthold and Sale 1973; Viljoen 1989b; Lindeque and Lindeque 1991; Thouless 1996). Thouless (1996) showed that home range was negatively correlated with rainfall, a strong predictor of primary productivity in tropical ecosystems (McNaughton 1985; Richards 1996). Forest elephants are outliers on the 'ln home range versus rainfall' curve (below the trend line) for savannah elephants, presumably because most of the primary production in forests occurs as leaves in the canopy, and is unavailable to terrestrial herbivores like elephants. Forest elephants are frugivorous, at least seasonally (Chapter 3), and frugivory is associated with increased home range size compared to folivory within taxa (Clutton-Brock and Harvey 1977), and within the same taxon when levels of frugivory change seasonally e.g. gorillas (Tutin 1996; Remis 1997; Goldsmith 1999). Thus, frugivorous forest elephants might be expected to have larger home ranges than their savannah grazer/browser counterparts.

Human disturbance influences both population distribution (Barnes *et al.* 1991; Fay and Agnagna 1991b; Alers *et al.* 1992; Tchamba *et al.* 1995; Tchamba 1996; Powell 1997) Chapter 5) and individual ranging patterns (Douglas-Hamilton 1971; Tchamba *et al.* 1995; Thouless 1996). Powell (1997) suggested that home ranges of individual elephants in Cameroon were shaped by the distribution of farms and logged forests, and that elephants avoided areas of current human activity. In the Ndoki Forest, three of the four elephants were collared to the north of the zone of minimum human disturbance. It is no coincidence that all elephants ranged south of the Dzanga *Bai*, which is close to villages and diamond camps at the northern limit of effective protection, yet all freely wandered into the vast uninhabited forest of the NNNP and beyond. The single contradictory evidence to the notion that elephants avoid high-risk areas was the westward range of Kumu (Figure 6.2) who crossed an active road and remained close to the heavily inhabited Sangha River for more than two weeks. Southeast Cameroon and villages along the Sangha River are notorious centres of poaching, which increases the local risk to elephants (Ekobo 1995; Eves 1998; Djoni 2000) (Blake, pers. obs). Powell (1997) found that collared elephants preferred secondary forest, which shaped their home ranges. It is probable that for Kumu, the attraction of the dense understorey of secondary forest close to the Sangha River, or perhaps ripe secondary forest fruit species such as *Myrianthus arboreus* common along the Sangha (Fay, 1997) overcame the associated risks.

The effects of rainfall on elephant distribution and ranging

Savannah elephants display two behavioural ranging mechanisms in response to rainfall and primary productivity. They may either migrate seasonally from one core area to another, depending on the availability of drinking water and forage quality (Tchamba *et al.* 1995; Thouless 1995, 1996; Verlinden and Gavor 1998), or as rainfall increases, elephants may expand out of restricted dry season ranges close to permanent water, and both water and high quality browse become available in uplands (Leuthold and Sale 1973; Western 1975; Williamson 1975; Eltringham 1977; Western and Lindsay 1984). 'Classic' elephant migrations (*'a seasonal two way movement involving a return to the area originally vacated and usually following traditional paths*' (Smith 1966) cited by Viljoen (1989b)) seem to occur where dry season rainfall is highly clumped and wet season rains reduce or eliminate the constraint of access to one or a few localised water sources.

Nowhere in the Ndoki Forest is more than ca. 5 km from permanent water, unlike savannah environments where areas may be several tens of kilometres from drinking water. Elephants can therefore never be at physiologically dangerous distances from water. The rapid drainage of tropical forest soils means that permanent drinking water never accumulates in uplands, and it is always clumped in rivers. Thus water probably imposes no restrictions on forest elephant ranging at large spatial scales, but does so on small scales. Therefore it is not surprising that movements of collared elephants were constrained on a physiological time scale (circadian) and a small geographical scale. On a large scale, long distance movements were possible at any rainfall level, which may allow elephants to be nomadic in their search of high quality forage, since there was no risk of being at physiologically dangerous distances from water.

The pattern of elephant distribution in relation to rainfall and water mirrored exactly the results of Chapter 5. In dry periods, elephants aggregate around permanent water, near which abundant browse may be found, but as rainfall increases they spend more time in uplands foraging for fruit. This range shift in response to increasing primary productivity (in this case fruit) in uplands with rainfall was similar to the macro-scale range expansion of many savannah elephant populations (above). The underlying reason was, however, different; forest elephants were unconstrained by water, continued to range widely under any rainfall regime, and were able to exploit high primary productivity at any spatial scale. Forest elephants chose not to use uplands because of poor foraging there in dry periods, unlike savannah elephants, which are obliged to remain sedentary around permanent water during low rainfall periods, even if upland productivity is high.

African great apes also change their ranging patterns in relation to fruit availability. Chimpanzees, which are obligate frugivores, increase their daily range and home range size to cope with decreasing fruit availability, rather than drastically modify their diet (Boesch and Boesch-Achermann 2000). In western lowland gorillas, which are facultative frugivores and adopt a different strategy, day ranges and home range size are positively correlated with fruit consumption (Goldsmith 1996; Tutin 1996; Remis 1997). Evidently the same is true for forest elephants in Ndoki, who increased their daily travel distances with increasing rainfall, a good indicator of fruit availability (Chapters 2 and 5). However, daily linear displacement did not increase significantly, which suggested that elephants restricted their foraging to localised patches despite their longer total day ranges.

Rainfall has a considerably different effect on the ranging patterns of desert elephants in Namibia, compared to forest elephants in the Ndoki (Viljoen and Bothma 1990). During the dry season desert elephants were often restricted to a single water hole from which they made daily foraging trips returning to the water hole at night. As the dry season progressed, food became depleted near to the waterhole and the elephants had to travel further to find good quality forage, while still obliged to return to the water hole at night, thus day range increased while 24 hour linear displacement was close to nil. With increasing rainfall, desert elephants could access a number of waterholes, thus could forage *en route* between holes, and day travel decreased but displacement increased.

The trend in shorter linear displacement distances of elephants at night compared with the day (4.1km (day) and 3.4km (night)) in the Ndoki forest was consistent with estimates made using VHF telemetry by Douglas-Hamilton (1971) who recorded displacements of between 0.2-8.2km and 0.4-3.5km for daytime and night-time travel respectively. In the Namib Desert, daily displacement of elephants ranged from 4 to 38km, with a mean of 12.9km, almost three times further than this study. No previous elephant studies using telemetry data have had sufficiently frequent fixes to provide estimates of daily path length, which are considerably different from the more frequently reported linear displacement. Merz (1986b) and Theuerkauf and Ellenberg (2000) measured the daily path lengths of forest elephants in Ivory Coast by tracking fresh prints. Merz found that elephants moved an average of 0.5km per hour, with a daily path length of ca. 12 km. Exceedingly small sample size (7 trail follows) and estimation of the age of elephant sign used to calculate travel time suggests that these estimates were unreliable. Theuerkauf and Ellenberg (2000), also with a very small sample size, calculated mean daily travel distance of 6.1km with no detectable seasonal difference. Wyatt (1974) followed savannah elephants and calculated a mean travel speed of 0.5kmhr^{-1} or 12km per day.

Diurnal patterns

Diurnal travel and activity patterns from this study are inconsistent with those of savannah elephants. In the Rwenzori National park, Uganda, elephants showed a marked decrease in activity between 03:00 and 07:00hrs (Wyatt 1974), which was exactly the timing of the daily peak in travel speed for Ndoki elephants. In Uganda, the decrease in feeding activity was accompanied by an increase in resting from 11:00 to 14:00 (Wyatt 1974), also recorded for elephants in Sengwa, Zimbabwe (Guy 1976), which is consistent with the drop in travel speed reported in this study. However in the Ngorongoro crater, Tanzania, there were two peaks in feeding at 13:00, and 16:00-18:00hrs and a corresponding decrease in walking (Kabigumila 1993). Unlike in Rwenzori, elephants in Manyara National Park displayed a bimodal pattern of movement, peaking in the early morning and late afternoon (Kalemera 1989), which closely resembled the bimodal peaks of movement in Ndoki. Kalemera (1989) stated that this diurnal rhythm was due to daily excursions too and from the large escarpment on which the elephants spend the night. The Ndoki elephants also showed a diurnal movement to and from uplands which was thought to explain the bimodal peaks in travel distance, though the directions of movement were the reverse of those in Manyara elephants.

Savannah elephants show little consistency in the timing of drinking and wallowing. In Uganda, elephants drink at any time (Wyatt and Eltringham, 1974), but in Manyara they visited the lake most often in the early evening (Kalemera, 1986). Why forest elephants should aggregate at rivers at night is unclear. Reasons might include avoidance of worrying insects, which can be very abundant near to watercourses during the day and can be bothersome to elephants (Blake, pers. obs.). Tsetse fly abundance diminishes rapidly with distance from water. Heat stress, which may cause savannah mammals including elephants to seek out water during the day seems unlikely, since aggregation at water would be expected when temperatures were highest, i.e. during the daytime. Safety may be a consideration, since elephants tend to make more noise in swamps and water compared to *terra firma* forest, which would alert diurnal predators (i.e. man). Elephants also find it difficult to flee when in swamps, and when disturbed by humans tend to panic, seemingly because of their relative inability to get away fast, unlike in *terra firma forest,* where they usually disappear quickly, quietly, and easily.

CONCLUSIONS

This study is based on less than a full year of data from four elephants. Conclusions are therefore preliminary and conservative, however these telemetry data of individual ranging patterns did confirm most of the conclusions on population scale distribution reached in Chapter 5. The following details are noteworthy:

1. Elephants in the Ndoki Forest had minimum convex polygon home ranges up to nearly 2000km^2. Elephants moved an average of ca. 7.8km per day, but were capable of ranging more than 25km in 24 hours, with linear displacements of up to 57km in 48 hours. The large home ranges and ability to travel quickly indicated that individual elephants were capable of tracking change in the geographic distribution of resources, particularly fruit, over all spatial and temporal scales within the Ndoki ecosystem.
2. Collared elephants showed a strong preference for close proximity to watercourses during dry periods, which shifted to a preference for uplands as rainfall increased. Coupled with an increase in day range with increasing rainfall, this suggested strongly that elephants relied on riverine and swamp browse during dry periods, and used uplands preferentially during wet periods to forage on fruit.
3. Forest elephant ranging patterns varied from central place foraging (Sue), to large-scale displacement followed by high fidelity to a restricted area (Sparkey), to quasi-nomadism (Spikey, Kumu). Forest elephants may have been capable of exhibiting these differences in ranging because they were unconstrained by the large-scale distribution of water and

browse foods, which were widely distributed and accessible. Therefore, the risk of quasi-nomadic wandering was low, while the payback of locating widely dispersed, high quality fruit patches was high.

4. *Bais* were clearly important throughout the study period for three of the four elephants, however, the dry season increase in the use of *bais* concluded in Chapter 5, was not confirmed from ranging data of collared individuals. One reason may have been that the study period has not yet included a full dry season for three individuals.
5. Elephants rarely visited *bais* during the day, which was thought to be a response to the risk of hunting by humans. The elephants appeared to use *bais* with the most recent history of poaching less in daylight hours than protected *bais*.
6. Collared elephants avoided areas of heavy human influence. Despite elephants all being collared in the north, ranging was rare outside of protected areas to the north, where human activity and elephant poaching were high. Sparkey concentrated his range almost exclusively outside the National Parks to the southeast, however the area he used was devoid of human activity during the study period. The remaining three elephants ranged largely within the confines of the National Parks.

CHAPTER 7. THE IMPLICATIONS OF FOREST ELEPHANT ECOLOGY FOR CONSERVATION

INTRODUCTION

Conservation of the world's remaining megaherbivores is one of the biggest challenges facing conservation in terrestrial ecosystems (Sukumar 1991; Owen-Smith 1998). They require enormous areas to accommodate large home ranges, seasonal migrations, and maintain viable populations (Beier 1993; Armbruster and Lande 1999). This brings them into direct competition with expanding human populations for land and other resources (Hoare 1999; Hoare and du Toit 1999), and to high hunting pressure (Sukumar 1991; Walpole *et al.* 2001). In many cases, they have high cultural and economic importance, which increases the tendency toward market driven over-exploitation (Barbier 1990; Emslie and Brooks 1999). The remaining extant species are often found in remote and impoverished regions of the globe which makes management logistically and technically difficult, and promotes exploitation by local people with few alternative sources of income (Milner-Guilland and Leader-Williams 1992; Berger and Cunningham 1994). The combination of these factors means that conservation is often critically needed, but is hampered by poor ecological understanding of the species, and even such basic information as numbers and distribution remain poorly quantified. In summarising the conservation implications of a central Africa-wide census of the status of forest elephants, Barnes *et al.* (1995a) listed four 'major constraints' on management ability; 1) ignorance of basic forest elephant biology, 2) ineffectiveness of wildlife departments, 3) corruption, and 4) the general difficulty of working in the forest zone, which combine to make forest elephants, unfortunately for them, an excellent example of this 'megaherbivore conservation syndrome'.

Successful conservation of forest elephants will ultimately involve actions on three inter-related levels: political, economic, and local. Politically, issues as wide ranging as the global demand for ivory and other products from central Africa's forests including timber, minerals, and meat must be addressed. The global inequality of wealth distribution and development, issues of over-consumption of natural resources in the developed world, and exponentially rising human populations and environmental degradation in the under-developed world are also critically important. Political solutions must be found for the growing immediate problems of civil unrest, expanding refugee populations and their resettlement, and the underlying reasons for instabiltiy in much of the developing world.

Economic solutions must be found to the inequality between the north and south in a framework promoting a true evaluation of natural resources, including forests and forest resources, in the global economy. Strategies must be developed for the long term financing of conservation and wise land use management of the central African forests. The third level, the local level, is concerned with the more immediate and practical problems of elephant and forest protection, and may range from education (development of conservation awareness, capacity building, resource management technical support), to identification of important populations of forest elephants, development and implementation of protected area management, law enforcement, scientific research, and coexistence of conservation actions with other local interest groups such as local people, loggers, hunters and miners. The local level cannot function without a supportive political framework, nor without the economic commitment to shape market forces at global, continental, and regional levels, and the financial resources to fund specific conservation actions on the ground.

This dissertation addressed the first of Barnes *et al.* (1995a) 'major constraints' and had two ultimate goals related to conservation. First was a site-specific motive to provide ecological information to help conservation efforts of the Ndoki elephant population. The second was to develop, from the results of this study and others, a series of generally applicable recommendations for improved management of forest elephants throughout their range. These goals were particularly concerned with the third level of actions outlined above, the local level and discussion of levels 1 and 2 is beyond the scope of this study. The aims of this chapter are to:

- summarise those aspects of forest elephant ecology identified by this study which have strong implications for management and discuss them in the context of conservation theory,
- summarise current land use practices and projected trends in the Ndoki Forest, discuss them and their implications for conservation in the light of forest elephant ecology,
- suggest practical ways in which land use management might be improved to promote successful conservation of forest elephants, based on the knowledge gained from this study and others.

This study was conducted in a relatively intact forest of high elephant density and low human population density. Much of Africa, even central Africa, does not enjoy this level of isolation and is populated, fragmented, and over-hunted. Obviously, elephant biology and conditions for conservation are different along the continuum from pristine to highly degraded landscapes. Emergency action may (or may not) be required in areas where poaching is rampant, and where populations are restricted to small numbers in isolated pockets surrounded by infrastructure and human development. In such situations, management options may be limited compared to those in large intact forest blocks in which continuous populations of elephants still occur. Large, isolated areas, like the Ndoki Forest, do still exist in some areas of central Africa, but they are dwindling fast. The recommendations from this study, which may be unrealistic or inappropriate in heavily impacted areas, are restricted to these remote landscapes.

Ecological conclusions from this study relevant to conservation

The single most important conclusion for management was the extent of the area over which forest elephants range (Chapter 6). Minimum convex polygon home ranges of four elephants were between nearly 700 and 2000km^2, and the maximum linear distance moved was over 100km. Four collared elephants ranged over a surface area larger than the combined areas of the Nouabalé-Ndoki and Dzanga-Ndoki National Parks. The elephants displayed a variety of ranging patterns from movement analogous to central place foraging, to semi-nomadic ranging, to abrupt, rapid long distance movement followed by extended sedentary periods. Forest elephants were found at varying densities throughout all vegetation types surveyed in the Ndoki Forest, from the deepest swamps, to upland plateaux of mono-dominant forest. During dry periods, they were aggregated near to rivers and avoided uplands. As rainfall increased, elephant habitat preferences switched to uplands. Aggregation near to large swamps was consistent throughout the year. Elephant distribution was determined by the distribution and abundance of fruit, and an underlying diurnal requirement for water and browse, which was most abundant in light gaps, open canopy forests, and particularly riverine and swamp vegetation. As fruit abundance increased, elephant distribution was determined by the macro-distribution of ripe fruit. The importance of fruit for elephants was highlighted by the geography and vegetation ecology of the elephant trail system, such that important elephant fruit trees were concentrated along elephant trails, particularly at trail intersections.

Elephant distribution was strongly influenced by the patchy distribution of minerals. *Bais* were centres of activity for three out of four GPS-collared individuals but there was no detectable pattern of use in relation to other environmental variables for these individuals.

Bais had a strong seasonal influence on elephant population distribution, with local aggregations occurring in the dry season, which brought a significant influx of elephants into the northern half of the study area. Minerals contained in *bais* may have been an important year round food supplement, becoming especially important during the dry season as a buffer against increasing nutritional and physiological stress. The distribution of resources varied on the landscape-scale with large distances separating seasonal peaks in fruit production, *bais*, rivers and swamps. Ranging and distribution patterns of forest elephants based on ecological constraints were severely disrupted by human distribution and activity. Collared elephants avoided areas of long term human presence, their range being largely restricted to the protected areas and their peripheries, where human impact was minimal. At the population level, elephants quickly vacated areas of rapidly increasing human activity, particularly those associated with forestry prospection; thus human activity rendered large areas of forest unavailable to elephants.

From the results of three years of intensive study, it is now known that elephants in the Ndoki Forest use swamps heavily; eat nearly 100 species of fruit; eat several hundred species of plant; use *bais*, especially in the dry season; may range over nearly 2000km^2, and avoid people when those people are perceived as hostile. What remains unknown is the size of the elephant population, its geographical limits, which resources are essential, and how serious their loss might be for the population. In undisturbed landscapes, all that management planning can do in lieu of a full understanding of ecological systems, is to attempt to maintain the status quo in those areas which are not heavily impacted by humans. Management decisions are always compromises between competing goals. In the Ndoki Forest, if elephant conservation were the only goal, managers may wish to increase favourable habitat by, for instance, creating large areas of open canopy forest and encouraging the spread of secondary growth while leaving fruit trees standing. However, Ndoki is as intact as any forest block in Africa, and manipulation of the system to favour a single species is incompatible with the greater site-based goal of ecosystem preservation. This is particularly true when the longer term ecological consequences of manipulative actions are unknown. Educated guesses based on the most robust information available is the best that can be done.

Fortunately, many ecological fundamentals are common across systems and species, and much empirical and theoretical work has provided an ecological framework useful for planning how to do conservation. In the following discussion, some of the most important aspects of this work are used to help fill the gaps in the understanding of forest elephant biology, and identify and frame appropriate conservation rules.

LAND USE, ELEPHANT ECOLOGY, AND CONSERVATION

Habitat loss and fragmentation

Elephants already live in a patchy world, and human land use only intensifies landscape patchiness through habitat loss and fragmentation (Meyer and Turner 1994). Since they are the most likely causes of the current increase in global extinctions across taxa (Wilcove *et al.* 1986; Wilcox and Murphy 1987; Primack 1998), habitat loss and fragmentation are central themes in conservation biology (Weins 1996). Fragmentation may occur across a continuum of spatial scales and intensities (Weins 1996). If separated by large distances and hostile space, patches may have properties similar to oceanic islands, while heterogeneous habitat mosaics of high and low quality patches within a variable matrix provide greater potential for connectivity, and ill defined patches of low heterogeneity may offer continuous habitat (Vandermeer and Carvajal 2001). The continuum of fragmentation is reflected in population structure, from quasi-total isolation, to isolated sub-populations with occasional dispersal, to continuous populations where conditions allow persistence everywhere albeit at different densities (Weins 1976; With 1997). Fragmentation reduces total habitat availability and redistributes the remaining habitat into a mosaic of patches, both of which may increase species extinction rates (Wilcove *et al.* 1986; Davies *et al.* 2001). Habitat loss is probably a more serious threat to population extinction when the two occur simultaneously (Fahrig 1997). Reduction in habitat availability decreases carrying capacity and population size, which increases the likelihood of extinction through deterministic threats or stochastic environmental events (Gilpin and Soulé 1986; Harrison and Taylor 1997; Davies *et al.* 2001). Fragment ‘edge effects’ (Lovejoy *et al.* 1986; Laurance 1991), which may include habitat modification (Saunders *et al.* 1991; Malcolm 1994; Laurance 1997) or increased conflict with humans (Mattson and Reid 1991; Woodroffe and Ginsberg 1998), also increase extinction probability within habitat blocks.

Matrix quality has a strong influence on between-fragment processes (Holt and Gaines 1993; Hanski 1999; Vandermeer and Carvajal 2001). Matrix quality may alter dispersal and colonisation rates (Stouffer and Bierregaard 1995), provide alternative habitat, particularly for generalist species (Whitmore 1997), and determine the severity of edge effects

(Mesquita *et al.* 1999), all of which influence population persistence (Etienne and Heesterbeek 2001). A high quality matrix surrounding a habitat patch may adequately buffer habitat loss within the patch and maintain low extinction probability, while in a poor quality matrix, loss of habitat has a dramatic effect on population persistence (Fahrig 2001). Not surprisingly, large habitat patches embedded in a high quality matrix afford the greatest chance of species conservation in the face of landscape fragmentation.

FRAGMENTATION AND ELEPHANTS

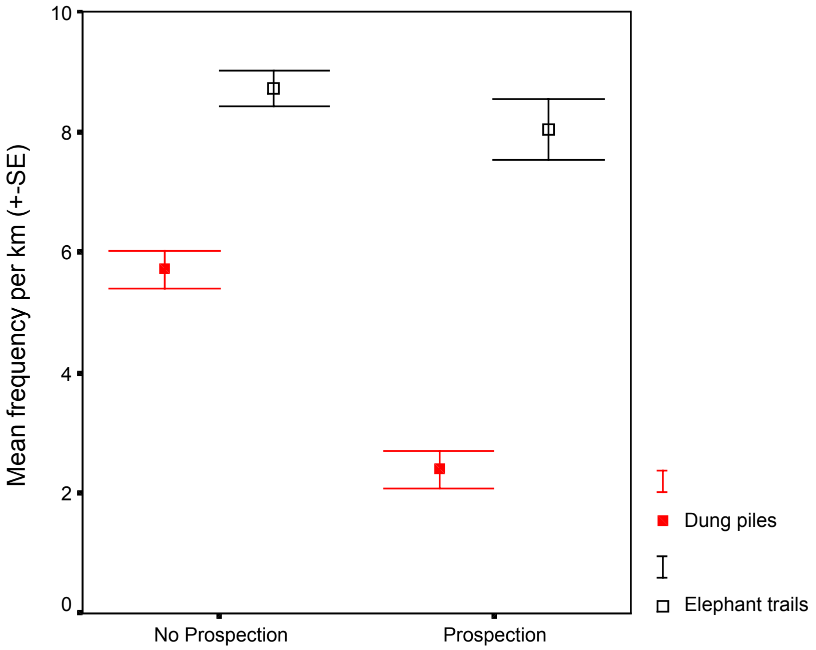
Fragmentation of habitat as a result of rapidly increasing human populations has been a hallmark of African elephant decline (Cumming *et al.* 1987; Parker and Graham 1989a; Buss 1990; Caughley 1995). In pre-Roman times, elephants were distributed almost continuously from the Mediterranean coast to the Cape, but now isolated populations are fragmented and scattered across sub-Sarahan Africa (Shoshani and Tassey 1996; Barnes 1998) often in sub-optimal habitats, having been displaced from more suitable conditions by humans (Parker and Graham 1989b). Humans ultimately determine the distribution of elephants. In Kenya in 1950, areas where human density exceeded 25km^{-2} did not support elephants (Parker and Graham 1989a), while in west Africa, elephants are restricted to the areas of lowest human population density (Barnes 1999). Rural human population density at 8.7km^{-2} in central Africa is lower than elsewhere on the continent (Bos *et al.* 1994; WRI 1994), and projections for the future indicate central Africa's rural human population density is likely to remain the lowest on the continent by 2020 (14.6km^{-2} compared to 37.3km^{-2} and 40.8km^{-2} for west and southern Africa respectively (Barnes 1999). While the increasing human popuation will increase the land area under slash and burn agriculture, projected relative deforestation rates for central Africa are lower than elsewhere (Barnes 1990), particularly for the last strongholds of forest elephants, Gabon and Congo (Fay and Agnagna 1991b; Barnes *et al.* 1995b). Of remaining elephant range, habitat fragmentation is most apparent in west Africa (Barnes 1999), where in 1984, elephants occupied ca. 232,000km^2, or just 6-7% of their estimated range in 1900 (Roth and Douglas-Hamilton 1991), and only 4.7% of the surface area of the region, compared to an estimated 17.3% and 28.9% in East and southern Africa. In central Africa, total range was estimated at 2,760,277km^2 or 51.6% of the land area (Said *et al.* 1995), which suggests that central Africa's forest elephants may be less likely to suffer severe consequences of fragmentation, at least in the short to medium term, than elephants elsewhere on the continent.

Evidence for fragmentation of forest elephant range in Central Africa

Despite these trends, there is strong evidence that human activities are fragmenting forest elephant range. A number of studies (Barnes *et al.* 1991; Fay and Agnagna 1991c; Hall *et al.* 1997) have shown that elephant density was determined by the distribution of human infrastructure (rivers, roads, and navigable rivers), even in remote forest areas. Powell (1997) found that elephant ranging was constrained by human distribution in Cameroon, while Alers *et al.* (1992) showed that large tracts of forest in DRC were devoid of elephants due to intense poaching pressure, which effectively isolated forest blocks that still contained elephants.

In the Ndoki Forest, elephants avoided areas of high human impact and vacated areas where human activity began in a matter of weeks (Chapter 5). Particularly striking was the negative effect of localised disturbance on elephant abundance resulting from forestry prospection. A parallel study (Blake and Nkamba-Nkulu, unpub. ms, Chapter 4) reinforced this conclusion with data on elephant and elephant trail abundance in prospection and non-prospection areas of the Kabo logging concession. They found a highly significant difference in elephant dung density between prospection and non-prospection areas (Figure 7.1). While there were no 'before prospection data' to demonstrate causation, the prospection and non-prospection areas were adjacent, in similar forest types, and were surveyed simultaneously (the dry season of 2000), so these data were highly suggestive that elephants left the area with the onset of prospection. The density of elephant trails was not significantly different between prospection and non-prospection areas (Figure 7.1), which suggests that the 'before prospection' elephant densities were similar. A qualitative difference in trail use was detected: in the non-prospection areas 37.3% of trails were classified as poorly used, whereas in prospection areas 64.3% were poorly used (Blake and Nkamba-Nkulu, unpub. ms), which suggests elephants had recently left the human activity areas, long enough for dung to decay and for trails to begin falling into a state of 'disrepair', but not long enough for them to disappear. These data were collected over a single month in both the prospection and non-prospection areas, which strongly indicates that any other interpretation of the data, such as a seasonal shift in elephant distribution in the prospection area but not in the non-prospection area, can be discounted.

Figure 7.1. Dung pile and permanent elephant trail frequency in logging prospection and non-prospection areas (from Blake and Nkamba-Nkulu, unpub ms).



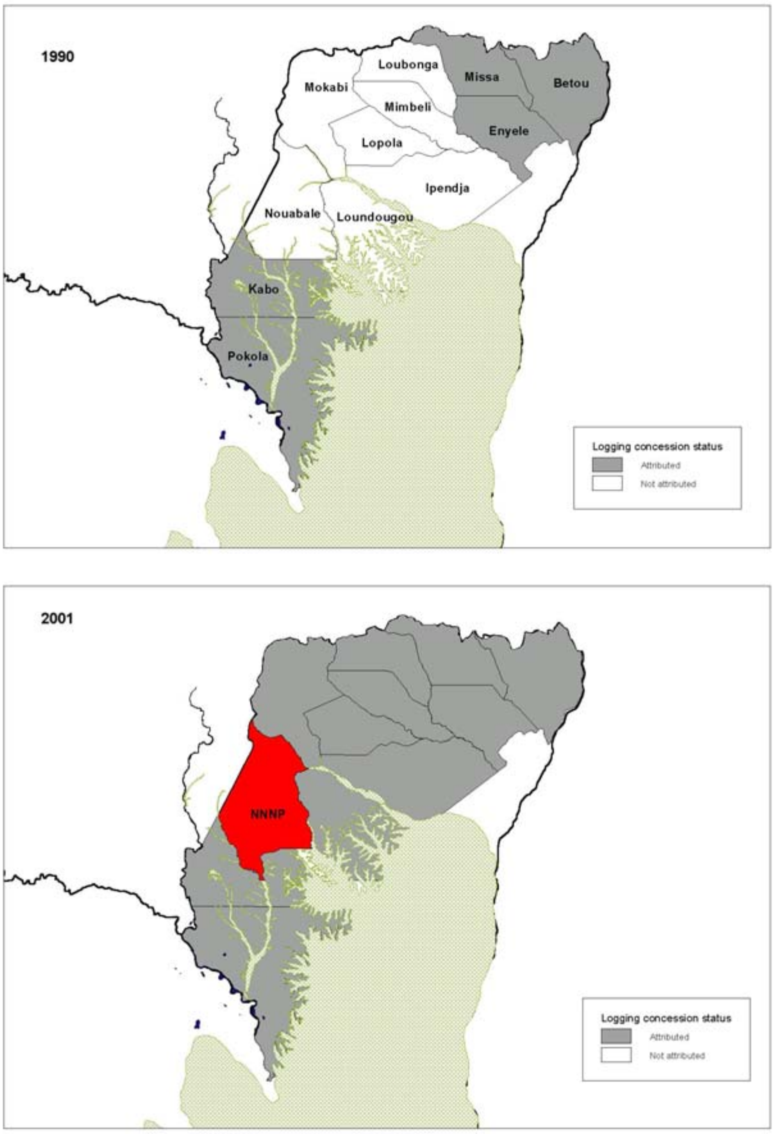
These examples show that, in central Africa, it is not habitat loss that is resulting in fragmentation. Rather it is the impact of human activities on elephant ranging behaviour and mortality which has fragmented the landscape. Since fragmentation is a 'disruption of continuity' (Lord and Norton 1990), this is as real an effect as loss of forest cover itself. Indeed, since Tutin *et al.* (1997b) showed that forest elephants in the Lopé Reserve Gabon, use forest fragments isolated by open savannah, albeit at lower densities than in continuous forest cover, intense human disturbance is perhaps a more severe form of discontinuity than loss of forest itself. Thus the fragmentation effect is one of a 'probability of mortality' surface by hunting across the landscape or region, with fragments defined by contours of low mortality, The surrounding matrix is a probability of mortality gradient, and hard edges are those areas in which elephants have been extirpated. Edges need not be physical barriers at all. A second probability surface leading to fragmentation is that of 'perceived risk' as defined by elephants themselves, much like humans avoiding dangerous neighbourhoods. There is no doubt that elephants can detect danger and modify their behaviour as a result of perceived threat (Lewis 1986). Telemetry data from this study suggested that is why elephants avoid *bais* during the day, and certainly elephants leave logging prospection areas because they are frightened (Chapter 5; This Chapter, Figure 7.1) rather than local extermination. The freehand illustrations of Fay and Agnagna (1991a), and the GIS generated maps of Michelmore *et al.* (1994) show the probable effects of these gradients on macro-scale fragmentation of elephant range across Congo and Central Africa.

A similar pattern of fragmented mammalian faunas probably exists across many human-influenced landscapes, and even continents where habitats themselves remain contiguous. A patchy distribution of either recruitment or mortality has led to the 'source-sink' theory (Pulliam 1988), in which high quality habitat patches where reproduction exceeds mortality serve as 'sources'. These sources providing surplus individuals that emigrate into lower quality habitat, or 'sinks', where mortality exceeds recruitment. In America during the early 1800's, often (wrongly) thought of as pristine habitat (Denevan 1992), the distribution of large mammalian herbivores (the preferred prey of indigenous humans) followed a density gradient which peaked in the 'war zones' between tribal homelands. Humans rarely ventured into these areas unless at war for fear of attack, thus hunting pressure was low and wildlife flourished in these 'game sources' (Martin and Szuter 1997). In African forests, not only elephants, but duikers (Muchaal and Ngandjui 1999), gorillas (Blake *et al.* 1995), and monkeys (Blake 1993) all increase in abundance with distance from hunted areas. However, animals with small home ranges do not have the geographical flexibility, nor perhaps the cognitive capability, to avoid hunted areas, and for these species it is hunting to local extinction which causes the spatial density gradient. Whether the cause is true habitat fragmentation or high mortality through hunting, the result is an increasing hostility of the matrix between high quality patches, which increases the risk from any of the plethora of extinction threats affecting small isolated populations (Gilpin and Soulé 1986). Ironically, this mechanism of spatially explicit mortality risk has been proposed as a framework for sustainable offtake for both meat production (McCullough 1996; Novaro *et al.* 2000) and for management of overabundant populations, including elephants, in wildlife reserves (Owen-Smith 1988; Whyte *et al.* 1998).

NNNP elephants and fragmentation

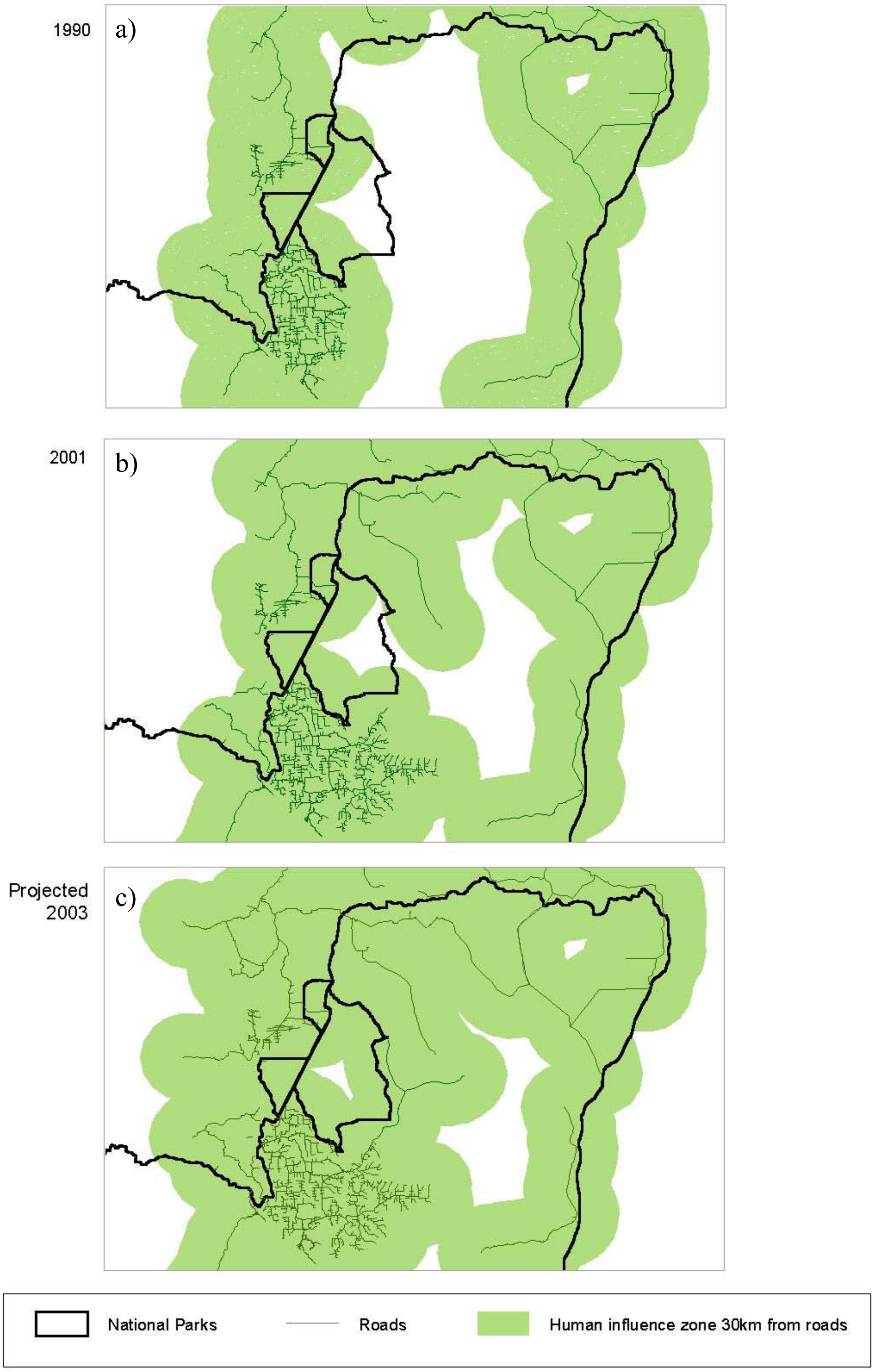
In 1990, the hallmark of northern Congo, including the Ndoki Forest, was large intact forest blocks free from human infrastructure development including roads and villages. Until a wave of poaching began in the 1980's elephants were relatively free-ranging across much of this unbroken habitat. The 1990's saw dramatic changes in land use in northern Congo (Chapter 1). In 1990, the total exploitable land surface area east of the Sangha River was ca. 4,060,530ha of which 1,7917,85ha (44.1%) was either attributed to a logging company or had been under production forestry (Figure 7.2). At the same time, no protected areas existed. In 1993, the creation of the NNNP took 386,000ha out of designated production forest, which by 2001, had grown to 422,000ha with the addition of the Goualougo Triangle to the park (Chapter 4). During the same period, the entirety of the remaining forest, some 3,638,212ha, or 89.6% of the *terra firma* forest had been attributed to logging companies (Figure 7.2). This will all be logging in the next ca. 25 years. Of the original forest cover, all of which was inhabited by elephants, only 10.4% (the NNNP) will remain intact (Figure 7.2).

Figure 7.2. The development of the forestry sector in northern Congo east of the Sangha River



The rapidly expanding logging industry of northern Congo since then has provoked the construction of a widespread logging road infrastructure to service active concessions. With roads comes settlement, market accessability, economic growth, over-exploitation of natural resources, loss of wildlife and further fragmentation of populations (Wilkie *et al.* 2000). Indeed, the location of roads, with their associated concentrations of human activity, was the single most important variable in determining elephant distribution in Gabon (Barnes *et al.* 1997b). Barnes et al. (1997b) stated that: '*The dung-pile gradient shows how elephants avoid roads and villages, resulting in a partitioning of the forest, with man living in a narrow ribbon along the roads and elephants in the depths of the forest*'. In 1990, the logging road infrastructure of the Ndoki Forest was concentrated to the south and west to facilitate logging in Kabo, Pokola, and the CAR. Humans rarely travel further than 30km on foot to hunt (Blake *et al.* 1997), and beyond this distance from roads, navigable rivers, and villages human impact was low (Fay and Agnagna 1991c), and these areas may be analagous to game sources ('wildlands' hereafter). The existing road system of 1990, with an associated 30km human influence zone contained the Dzanga-Ndoki National Park in its entirety and over half (2648km^2 or 62.7%) of the future NNNP, but left a huge forest swathe in the extreme north and centre of northern Congo completely road-free (Figure 7.3a). At the end of 2001, the road infrastructure of the Ndoki Forest and its associated 30km human influence zone had changed dramatically from its status in 1990 (Figure 7.3b). In the next 2 years, if road construction continues as planned, the scenario will be one of complete encirclement and fragmentation of the Ndoki Forest (Figure 7.3c). The remaining wildland in the 'Ndoki fragment' will be just 264km^2, in the core of the NNNP.

Figure 7.3. The growth of roads in northern Congo between 1990 and 2001, projected to 2003



Roads and human influence zones are inaccurate outside of Congo

CONSEQUENCES OF FRAGMENTATION FOR FOREST ELEPHANTS

If it is accepted that fragmentation of forest elephant habitat occurs as a result of human activity, then the consequences for both elephants and their habitat must be understood and brought into land management planning for successful conservation. While data to provide some insight into the mechanisms and impacts of fragmentation in forest elephants are scarce, several within- and between-fragment impacts are probable.

Loss of habitat

Chapter 5 showed that elephant distribution tracked the large-scale irregular distribution of fruit. Compression of elephants into small fragments must necessarily limit their ability to range in search of fruit, thereby increasing their rate of foraging on lower quality food resources such as tree bark and browse, which may inhibit forest succession (Struhsaker *et al.* 1996). Thus, range restriction may not only limit elephant food availability, and the carrying capacity of the remaining habitat in the short term, but lead to a spiral of habitat degradation and declining carrying capacity in the longer term, a well known phenomenon in savannah regions (Laws 1970; Leuthold 1977a; Eltringham 1980; Cumming 1982; Barnes 1983c, a; Lewis 1986; Dublin *et al.* 1990; Ben-Shahar 1993). In Kibale National Park, high rates of elephant damage to saplings (Wing and Buss 1970; Chapman and Chapman 1997; Struhsaker 1997) may reflect the fact that the National Park is too small to "smooth" large-scale variation in fruit availability, and thus elephants there may have little choice but to over-exploit browse food sources. The Nouabalé-Ndoki National Park did not adequately encompass the wet and dry season elephant aggregations nor the annual geographic distribution of fruit (Chapter 5), or the range of 2 of 4 collared individual elephants (Chapter 6).

With declining habitat availability, population size decreases, which increases the likelihood of extinction. In an attempt to determine a minimum reserve size for the African savannah elephant, Ambruster and Lande (1997) modelled the likelihood of extinction via stochastic mechanisms within reserves (fragments) of different sizes, with an initial density of 3.1 elephants mile^{-2} (1.2km^{-2}), over a range of culling intensities and with no colonisation. Their model suggested an area of 2590km^{2} was required to ensure a 99% probability of population persistence for 1000 years. By the same token, the probability of extinction in 100 years was low (<0.5%) in reserves of 100 miles^2, and negligible (<0.1%) for 200miles^2. Thus even in smaller national parks, stochastic population fluctuations are unlikely to lead to extinction in the short to medium term.

Despite the relative abundance of information on savannah elephant ecology and life histories, Ambruster and Lande (1997) suggested cautious interpretation of their data which promoted little confidence in their theoretical conclusions. However, it did promote the notion that in the absence of reliable information 'bigger is better', since the probabilitiy of population persistence for small reserves was significantly worse than for large ones. Compelling long-term data from two sites in Africa reinforce the importance of patch size and fragmentation on species survival. In Tanzania, Newmark (1996) found that extinction rates were inversely correlated with park size, strongly suggesting that fragmentation and insularisation were important contributors to extinction rates. In 6 Ghanain parks, reserve size and the size of surrounding human populations accounted for 98% of the variance in extinction rates (Brashares *et al.* 2001). The combination of logging roads leading to fragmentation and reduced patch size, and a concomitant increase in human population density in and around the periphery of the last large forest blocks, suggests catastrophe unless present trends can be reversed. The large body size of elephants makes then particularly vulnerable.

The tendency for elephants to retreat in the face of human activity means that the area that elephants are 'willing' to use may be considerably smaller than the actual size of a habitat patch or protected area. If elephants retreat some characteristic distance α in response to human activity on the borders of a (circular) protected area of radius r, with human activity up to the borders, the proportion (p) of the reserve that remains available and is "safe"

$$p = \frac{\pi(r-\alpha)^2}{\pi r^2} = \frac{(r-\alpha)^2}{r^2},$$

increases as reserve radius increases. Thus, the carrying capacity of reserves should increase faster than reserve area. In addition, both the enhanced ability to track fruit and the greater effective area of large reserves should decrease the incidence of human/elephant conflict on the periphery of reserves. For example, during the first survey of this study, the peak in fruit production near to the southeast of the NNNP was almost exclusively outside the Nouabalé-Ndoki National Park and would have been unavailable to elephants had the forestry prospection taken place prior to that survey. By the end of 2001, this area was lost to NNNP forest elephants as a result of logging developments and road building.

Edge effects

When animals become restricted into habitat patches, it is clear that those with large ranges will come into contact with, or traverse, the patch edge more frequently than those with small ranges. Woodroffe and Ginsberg (1998, 2000) showed that for carnivores in protected areas not only could edge effect mortality cause extinction, but that the likelihood of extinction was proportional to reserve size and home range size. Interestingly, the edge effect threat was a better predictor of extinction probability than population density, which suggested it outweighed stochastic extinction threats associated with small population size. Clearly the smaller the fragment, and the bigger the edge to area ratio, the greater the potential for animals to encounter hard edges, or cross soft edges. Although data showing a similar vulnerability across taxa were weak (Woodroffe and Ginsberg 2000), forest elephants share a number of traits in common with large carnivores, particularly large home range and high mortality caused through hunting, which might make them susceptible to similar threats.

Like some wild dog populations (Woodroffe and Ginsberg 2000), the edge for Ndoki elephants is the ‘elephant-human interface’, rather than a physical habitat boundary. Elsewhere in Africa this edge has resulted in the classic ‘human-elephant conflict’ problem, in which agriculture and human welfare suffer as a result of elephant damage to crops (Bell 1984; Parker and Graham 1989b; Thouless 1994; Hoare 1999), and in elephant poaching – the other elephant-human conflict story (Douglas-Hamilton and Douglas-Hamilton 1982). In a thorough treatment of elephants and human conflict in central Africa, Barnes (1996a) described how central Africa has witnessed a shift in the battle for dominance of the ‘edge’. Until well into the 20th century, elephants may have caused severe food shortages for humans through destruction of small-scale agriculture. With the directed resettlement of people by colonial powers larger villages were created, and the arrival of firearms allowed humans to reduce elephant numbers close to these larger human settlements. Agriculture developed and the balance of power at the edge shifted toward humans. Despite this, even today elephants may remain a problem to rural farmers in some areas (Lahm 1994), particularly where conservation efforts have been successful (Blake, pers. obs.).

Thus, encroachment by humans into elephant range can only have two outcomes; increased mortality of elephants through hunting and thus greater likelihood of extinction, or increased disturbance of humans by elephants. To alleviate these outcomes, drastic and costly intervention measures (e.g. electric fences and anti-poaching initiatives) are required but which are often ineffective in practice.

Dispersal between patches

Successful dispersal out of patches depends on, in part, the mortality risks associated with leaving the patch. Movements between habitat patches are important as recolonisation events for patches where local extinction has occurred (Levins 1969), and to mitigate genetic problems associated with small existing populations (Gilpin and Soulé 1986). In central Africa, it is impossible to assess the current state of fragmentation of the forest elephant population - whether they are still a single contiguous population, or a metapopulation fragmented on a macroscale, as suggested by the model of Michelmore *et al.* (1994) or divided into a number of completely isolated populations, each one currently undergoing further fragmentation. Elephants still cross the trans-Gabon railway (L. White, pers. com.), and they have recently begun to cross the Sangha River between Congo and Cameroon due to protection (Blake, pers. obs.), but it is very likely that an elephant has not crossed the Oubangui River, separating Congo and DRC, for at least 25 years. What may be more informative for conservation planning is to look at the distribution of the current system of national parks in the range of central Africa's forest elephants, which are increasingly likely to become the last elephant strongholds (Figure 7.4), and assess the likelihood of elephant transfer between them.

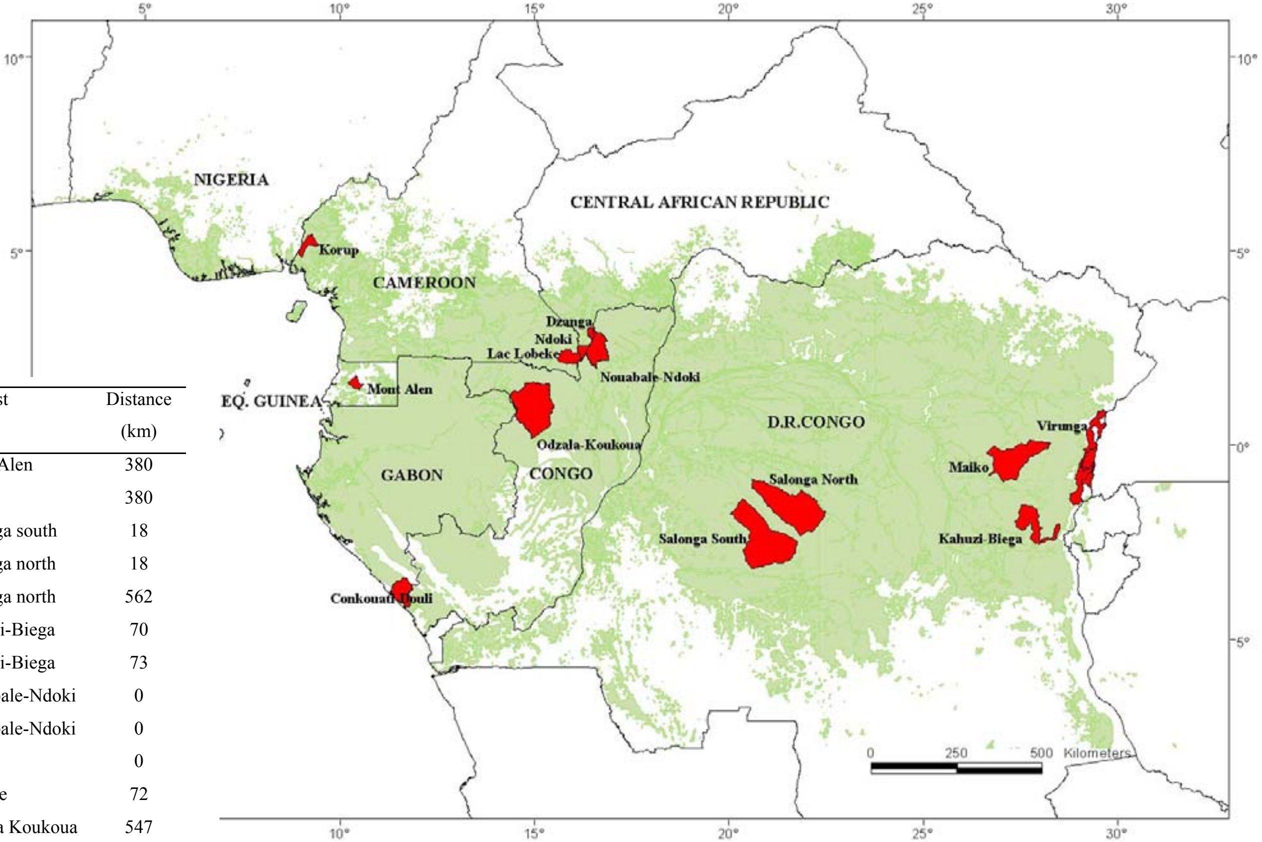
The closest distance between combinations of parks shows that 9 national park 'fragments' are found within the maximum known ranging distance for forest elephant of 103km (Chapter 6) (Figure 7.4). However 4 of these parks actually form a contiguous forest block (Ndoki, Dzanga, Nouabale-Ndoki and Lobeke) separated by rivers or international borders, and Salonga north and south are part of the same national park separated into two fragments by a narrow strip of hostile land (Figure 7.4). If only those fragments not physically connected are included, it would appear that elephants are physically capable of dispersing between just three sets of parks; 1) Salonga north and south, 2) the tri-national area and Odzala, and 3) Kahuzi-Biega, Maiko, and Virunga. Elephants have largely been eradicated from Kahizi-Biega and Virungas. Conkouati-Douli, Korup, and Mont Alen are all separated by at least 380km, and Salonga National Park in its entirety is separated by a minimum of 495km from the next nearest national park, Maiko. The physical distances separating these parks, and the multiple barriers to dispersal means they must actually be considered as oceanic islands in conservtion terms.

Habitat conversion and elephant ecology

Along with fragmentation, commercial logging also results in habitat modification, through reductions in tree abundance, creation of gaps and edges, increased understory growth, soil impaction, and arrested regeneration (Johns 1986; Skorupa 1988b; Whitmore 1990; Plumptre and Reynolds 1994; White 1994b; Struhsaker 1997; Kasenene 2001). Commercial mechanised logging usually results in a ca. 50% loss of all trees that were present before logging, though damage may vary from 5% to 80% of trees (Johns 1992). The 10% tree damage levels estimated by Wilks (1990) seem to be reasonable for high grade selective logging (White 1992), which is the usual forestry practice currently operating in much of central Africa (Whitmore and Sayer 1992). Thus, not only does forest exploitation cause elephants to vacate large tracts of land and increase mortality around roads and logging camps, but habitat modification alters the dynamics of edge effects and the quality of the matrix between intact fragments that remain occupied. Old logging areas, where roads have become abandoned and human activity has returned to very low levels, may once again be recolonised by elephants, while in areas where poaching has traditionally been very low or absent, elephants may continue to use logged forest even during logging operations (White 1992)

Studies focussing on primates have shown that light logging has little effect on biomass, but that heavily logging reduces the abundance of frugivorous primates (Skorupa 1988a). In the Lopé Reserve, logging appeared to be catastrophic to frugivorous chimpanzees whereas the more generalist frugivorous/folivorous western lowland gorilla quickly recovered (White and Tutin 2001). Folivorous primates may do better in logged forest, and densities may even increase in the absence of hunting, though studies are inconsistent (Johns and Skorupa 1987).

Figure 7.4. National Parks in the equatorial forest of Africa



National Park	Area (km^2)	Nearest	Distance (km)
Korup	1404	Mont Alen	380
Mont Alen	833	Korup	380
Salonga north	16235	Salonga south	18
Salonga south	18646	Salonga north	18
Kahuzi-Biega	5900	Salonga north	562
Virunga	7800	Kahuzi-Biega	70
Maiko	10830	Kahuzi-Biega	73
Dzanga	499	Nouabale-Ndoki	0
Ndoki	746	Nouabale-Ndoki	0
Lobeke	2082	Ndoki	0
Odzala Koukoua	13546	Lobeke	72
Conkouati Douli	3452	Odzala Koukoua	547
Nouabale-Ndoki	4220	Ndoki	0

Generalist feeders like elephants might be expected to do better than specialists in logged forests. In Kibale National Park savannah elephants prefer clearings and secondary vegetation over closed canopy forest (Wing and Buss 1970; Struhsaker *et al.* 1996). Indeed, Nummelin (1990) found ca. 6-fold increase in elephant abundance in heavily logged compared to unlogged forest, which he attributed to the high abundance of preferred browse in understorey tangles in light gaps compared with closed canopy forest. These results were corroborated from west Africa, where Merz (1981, 1986c) and Short (1983) both found that forest elephants foraged more heavily and spent more time in open canopy and secondary forests compared to undisturbed areas. White (1992) found that logging had no significant effect on forest elephant density in the Lopé reserve, but that they reached exceptional densities in Marantaceae Forest, a young forest type which may result from anthropogenic disturbance (Fay 1997; White 2001). Barnes *et al.* (1995a,b) showed convincingly that forest elephants were found in higher densities in secondary forest (though not necessarily logged forest) throughout central Africa, presumably, as in Kibale, for the more abundant browse they offered. However, in very heavily logged forest in Ivory Coast, forest elephants selected closed canopy patches, most likely because of increased risk of exposure in very large gaps and the high prevalence of unpalatable weeds (Theurekauf *et al.* 2001). Dudley *et al.* (1992) reported that the heavy fruiting of *Tieghemella africana* modified the seasonal distribution of elephants in Ghana, and suggested that the loss of these trees (a preferred timber species) through selective logging could seriously deplete elephant fruit food availability, and modify ranging patterns.

Industrial selective logging may have a different impact on elephant ecology depending on the structure and composition of the forest prior to felling. In open Marantaceae-dominated forests with abundant THV and irregular canopies which cover much of the forest mosaic of the Lopé Reserve, Gabon, densities of both the preferred timber species Okoumé (*Aukoumea klaineana*) and elephants are high (White 1994a). The impacts of logging in this vegetation type may be low. High natural tree mortality of Okoumé (and *Lophira alata*) as the forest matures, causes a proliferation of gaps, and logging may do little more than speed up this process. Logging in a mature, closed canopy forest with an abundance of elephant fruit trees, and a sparse understorey, might change forest structure more radically. Gap creation through logging and road building would stimulate the growth of understorey vegetation forming vine/woody tangles and/or Marantaceae thickets and increase preferred browse biomass for large terrestrial herbivores (Kasenene 1987; Brokaw and Scheiner 1989; Plumptre 1996a; Struhsaker *et al.* 1996). Collateral damage to elephant fruit trees through timber felling would be higher in mature mixed species forests due to the higher density of these species compared to, for instance, Marantaceae forest. Thus, the likely short term impacts of logging closed canopy forest on elephant ecology would be an increase in canopy gaps and understorey vegetation particularly THV and shade-intolerant woody species, and a reduction in abundance of preferred elephant fruit trees.

Old logging roads in the Ndoki Forest typically have very high densities of THV, particularly *Megaphrynium machrostachyum*, and a number of gap specialist dicotyledons, all of which are heavily browsed by elephants and which are rare in undisturbed forest (Chapter 3). These species may persist in dense stands on old roads, and even large skidder trails, for at least 20 years (Blake, pers obs), where they provide linear highly profitable foraging grounds for elephants, and where elephant browsing rates are high compared to closed canopy forests (Boudjan and Blake unpub data).

TREES, TRAILS, LOGGING ROADS, AND ELEPHANT ECOLOGY

In Chapter 4 it was demonstrated that there is a strong negative correlation between distance from elephant trails and important elephant fruit tree species, with a mean fruit tree density in a 20m strip either side of trails being 1.7 times greater than the 'background' density at greater distances. In many parts of Africa, logging roads, which often cut a wide swathe of 50m or more through the forest (Blake, pers obs), are often built along large elephant trails, particularly in areas of undulating terrain (L. White, pers. comm; C. Wilks, pers comm; M. Miller, pers comm). If the relationship identified in this study between fruit trees and elephant trails holds across central Africa, and there is evidence that it does (Short 1981, 1983; White 1992; Vanleeuwe and Gautier-Hion 1998), the propensity to build roads on trails would result in significantly greater loss of fruit trees than if roads were built randomly, or avoided if they trails.

Unlike permanent roads logging roads, secondary roads are important in terms of their direct effects on habitat quality since their density is high (typically in the Ndoki region 1 road km^{-1}) and their coverge is widespread. Secondary logging roads (which are kept open for the duration of felling) in the northern Congo usually involve a clearcut swathe of 30m which at the above density means a direct forest loss of 1.5%. The proportion of of large trees destroyed is more than this since felled trees from the road-bed topple, fracture, and damage trees along the route, and the climatological change through edge effects is responsible for further mortality (Kapos 1989; Ferriera and Laurance 1997). Wherever secondary forestry roads are constructed, one result of logging is a near complete destruction of the existing elephant trail system caused by fallen timber and tree crowns (Blake, pers. obs.). In its place is put a new path of least resistance trail network, the logging road and skidder trail system. On sections of elephant trails which foresters use as roadbeds, fruit trees - the underpinnings of trail system architecture - are lost. In other areas, a proportion of fruit trees may remain, but the connectivity between trees is lost. The efficiency with which elephants can exploit fruit must be reduced as a consequence, particularly if they use rules of thumb such as 'remain on upland trails' when nomadically foraging for fruit (Chapter 6). Presumably to continue exploiting fruit, elephants must cue in on new ways of navigating and travelling through the forest. It is probable that smell and sound (White 1992), or possibly even seismic ripples (Marchant 2001) of ripe fruit hitting the ground, may help elephants locate fruitfall. The effort involved in forcing a new trail through logged forest must be high even for an elephant; and the loss of trees and disruption of the trail system may considerably reduce elephant fruit foraging efficiency.

In logged forest, the new 'paths of least resistence' (roads and not elephant trails) have low or zero availability of fruit, high abundance of secondary monocotyledon and dicotyledon vegetation including favoured browse and easy travel compared to the logged forest. Elephants returning to logging areas preferentially use abandoned logging roads, skidder trails, and gaps where their rates of browsing are extremely high and fruit makes up little or no part of the food intake (Struhsaker *et al.* 1996). Elephant behaviour on the 'new trails' is radically different to their behaviour on natural trails where there is little or no browsing, seasonal fruit feeding, and fast movements (Chapter 3). If elephants can maintain a positive energy and mineral balance under logged forest conditions, the tendency toward nomadism and long distance movements in search of fruit would probably be reduced.

LOGGED FOREST AS AN 'ATTRACTIVE SINK'

In the Ndoki Forest, elephants range over a large spatial scale both inside and outside of protected areas (Chapter 6). If the road building and logging scenario described above continues, severe range restriction is the likely outcome. Elephants within the 'park fragment' may be compressed into a small core area with the the consequences of over-exploitation of resources, lowered carrying capacity, and re-establishment of ecological and demographic equilibrium at lower population size, with its associated negative deterministic and stochastic implications for viability. Initial compression may also be followed by re-expansion with the recession of logging to a new safe limit set by the level of human activity and permanent roads. Elephants could also continue to range widely, and be forced to use areas including logged forests to maintain positive nutritional balance, even where human activity and the risks of poaching remain high. Finally, elephants may positively select secondary forest in the aftermath of logging for its high food availability, despite the risk of poaching.

The first two scenarios are ecologically unrealistic since they imply an absence of dispersal across the edge of the safe range. This is unlikely since the edge is not a physically impermeable barrier, and as habitat availability becomes increasingly restricted, dispersal becomes more likely (Heino and Hanski 2001) as carrying capacity is reached or exceeded (Lidicker 1975). In the second two scenarios, sinks have the potential to reduce the source population, depending on mortality levels and immigration into the sink (Pulliam 1988). In a recent exercise Delibes *et al.* (2001), the implications of three source-sink scenarios - avoided sinks, neutral sinks, and attractive sinks - on population persistence were modelled. Results showed that populations persisted in the avoided sink scenario, but in the neutral and attractive sink scenarios, a threshold proportion of sink habitat existed above which the population declined rapidly to extinction, and the threshold sink size varied with habitat preferences. There is evidence from Congo that elephants, despite the rapid behavioural avoidance of humans in some circumstances (Chapter 5), may either fall into the attractive sink trap or be forced into it because of physiological necessity, if a resource is so important that it over-rides the associated risk of acquisition. Mouadje *Bai* in northwestern Congo, north of Odzala National Park is a good example, where despite being killed in the tens, and possible hundreds, every year (Fay 1996), large numbers of elephants continued to visit the *bai* to exploit mineral deposits. Similar observations have been made in DRC where tens or even hundreds of elephants are killed over long periods of time in poisoned waterholes (Alers *et al.* 1992). If elephants are fragmented into low quality ‘safe’ patches where mortality from poaching is low within a matrix of high food quality ‘unsafe’ habitat, they would have little choice but to forage in the high quality habitat. If poaching pressure were irregularly distributed in time and space within a large sink region such as a logging concession adjacent to a protected area, elephants may be unable to perceive the spatial distribution of high risk areas. Depending on the size of the source relative to the sink and the mortality rate, these sinks may have severe consequences for the population (Woodroffe and Ginsberg 1998, 2000), particularly if they are attractive (Delibes *et al.* 2001).

Elephant conservation and ecosystem function

African elephants have been labelled as keystone species (Western 1989a; Shoshani and Tassey 1996) because they influence ecosystem function in a number of ways. These include seed dispersal (Wing and Buss 1970; Alexandre 1978; Lieberman *et al.* 1987; Chapman *et al.* 1992; Powell 1997), seed and plant predation (Spinage and Guiness 1971; Barnes 1980; Eltringham 1980; Barnes 1985; Dublin *et al.* 1990; Ben-Shahar 1993; Plumptre 1996b), gap creation and trampling (Kortland 1984; Campbell 1991; Plumptre 1993), nutrient transport (Ruggiero and Fay 1994), mineral lick excavation and clearing formation (Turkalo and Fay 1995; Klaus *et al.* 1998), and creation and maintenance of trails (Short 1981; Vanleeuwe and Gautier-Hion 1998). Of particular interest in forests is the role of elephants in seed dispersal, since this is recognised as an important determinant of structure and species diversity in tropical forests (Jansen 1970; Hubbell 1979; Howe and Smallwood 1982; Tilman 1994; Fragoso 1997; Hubbell *et al.* 1999; Harms *et al.* 2000). Seed dispersal may be essential for the survival of some tropical tree species (Howe 1984; Pannell 1989). Since forest elephants disperse several hundred different species (Alexandre 1978; Merz 1981; Short 1981; Lieberman *et al.* 1987; White *et al.* 1993; Powell 1997), some of which have no other known disperser (Chapman *et al.* 1992), their fragmentation and decline has serious implications for the maintenance of forest diversity.

Dispersal away from the parent trees may be advantageous to seedling establishment (Jansen 1970; Connell 1971; Schupp 1992). Long distance dispersal, even when rare, may account for the successful and rapid spread of plant species across landscapes and even continents (Portnoy and Willson 1993; Clark 1998), and allow poor competitors to escape in space from good competitors (Dytham 1994; Holmes and Wilson 1998). Seeds can be dispersed by gravity, dehiscence, wind, water, and animal vectors. In forests, the first three mechanisms usually result in short dispersal kernels (Ridley 1930; Fox 1973; Augspurger 1986), with wind dispersal distances typically 10-40m, though rare events may dispers winged seeds up to 1km (Fox 1973). Given that ranging abilities in mammals and birds scale with body size (Peters 1983) large animals should transport seeds, on average, further than small animals, which should be reflected in the distribution of adult trees (Howe and Smallwood 1982). If long distance dispersal is evolutionarily advantageous (Smith 2001), the logical end point of the body size-seed dispersal continuum is the 'megafaunal dispersal syndrome' (Jansen and Martin 1982) which argues that certain plant species are adapted to long range dispersal by megafauna. In Brazil, the 'last of the neotropical megafauna' the tapir (*Tapirus terrestris*), was responsible for bulk long-distance dispersal (up to 2km) of a large seeded palm species (*Maximiliana mamripa*), which was reflected in the distribution of adult trees (Fragoso 1997; Fragoso and Huffman 2000) . Since they successfully disperse a large number of seed species, tapirs may influence population and community dynamics at the ecosystem level in tropical forests, which suggests their decline or loss would not only change the future distribution of the species whose seeds they disperse, but have far reaching consequences for ecosystem function (Fragoso and Huffman 2000).

Unlike tapirs, elephants are capable of dispersing seeds at least ca. 60km (Chapter 6). Blake and Walsh (unpub. ms) found that in the Ndoki Forest the spatial distribution of large (>40DBH) trees was closely correlated to seed dispersal mechanism. Patterns varied from most-aggregated for gravity and dehiscent species, less-aggregated for wind-dispersed, less still for species dispersed by animals not including elephants, less still for animal dispersed including elephants, finally to least-aggregated for obligate elephant dispersed species. Within elephant-dispersed species, high fruit preference also significantly decreased aggregtion (Blake and Walsh, unpub. ms). This strongly suggests that animal-dispersal, and elephant-dispersal in particular, plays an important role in the colonisation/competition tradeoffs between species, especially at large spatial scales. Like tapirs, decline in numbers and range restriction of elephants through habitat fragmentation, may have important negative consequences on the long term survival of their preferred fruit species and on the maintenance of species diversity of tropical forests. Declining numbers of elephants without fragmentation may reduce the total numbers of seeds dispersed, increase Jansen-Connell density-dependent mortality, reduce seed rain into suitable areas for establishment, and decrease the colonisation ability of poor competitors. Range restriction through fragmentation may compound all of the above, and may also reduce the distance over which seeds are moved, prevent important long-distance dispersal events, and reduce or eliminate colonisation across fragment boundaries, as has been observed for a number of primate-dispersed species (Chapman and Onderdonk 1998). The combined effects may tip the balance away from colonising and range expansion of fruit tree species, decrease their abundance and reduce total species diversity (Malanson and Armstrong 1996), which would propagate out across other taxa, particularly those with obligate relationships (Jansen and Martin 1982; Chapman and Onderdonk 1998; Anderson 1999; Wright *et al.* 2000).

RECOMMENDATIONS FOR ELEPHANT CONSERVATION

Elephant populations are being hunted, fragmented, and restricted throughout their range. An increasing human population and commercial interests in ever more remote forest areas, suggests this will continue. This is bad news not just for elephants, but for the ecosystem in which they are embedded – lose elephants and lose biodiversity. It is proposed that to conserve elephants successfully the effects of habitat fragmentation and loss must be minimised through a network of landscape scale, fully protected areas in the highest quality patches available, embedded within a matrix of variable land use in which direct competition between elephants and humans is minimised. In essence, this is little more than a reaffirmation of the proposal made by Barnes (1995) nearly a decade ago. Considerably more is now known on elephant ecology, and the impacts of human development on elephants, which point to specific actions that will help achieve this overall goal. These include:

1. core habitat protection
2. avoidance of further fragmentation of core areas by ecologically and socially optimal road planning
3. maintenance of high quality matrices outside of core areas
4. reduction of the opportunity for human-elephant conflicts
5. practical and applicable scientific research to help achieve 1-4

'Core' habitat protection

Site-based conservation to protect habitat in self-contained functional landscapes which are large enough to capture spatial heterogeneity of resources to maintain ecosystem processes will be essential. It is generally agreed that protected areas are vital to species conservation (McNeely *et al.* 1990). In east Africa, the utility of partially protected and multiple-use areas as primary conservation units has proved less than effective for elephants and other large mammals, and complete protection has been essential for successful conservation (Caro *et al.* 1998).

Unfortunately, even for species whose ecology and population dynamics are well understood, it is rarely possible to say 'how much habitat is enough' (Fahrig 2001). Evaluating habitat quality, its spatial variability, and the true numbers of elephants in anything but the most general terms (poor, moderate, good, low, medium, high) are still beyond current technical and personnel means which indicates that reserve size limitations will be best guesses using rules of thumb. Fortunately, field biologists (Brashares *et al.* 2001) and theoretical mathematical ecologists (Etienne and Heesterbeek 2001) agree on the rule of thumb that big and secure is better than small and unprotected. Decreasing the lowest local extinction probability is a better strategy for avoiding extinction that maintaining connectivity between population fragments (Etienne and Heesterbeek 2001); thus core protected areas are paramount. Home range analysis in Chapter 6 showed that range restriction is inevitable for most elephants even in the largest parks, and since few areas of sufficient size to provide unrestricted range still exist, national parks will remain too small to provide adequately for unrestricted movement. However, core areas of complete protection of at least several thousands of square kilometres within high quality matrices, would seem to be critical.

New protected areas – site choice

Principle considerations when choosing the sites of protected area sites for elephant conservation include ecological site characteristics (habitat quality, size, and carrying capacity), the ability to stop poaching, and the pressure of competing land use. Of the three, habitat quality is probably the least important, because it is human-induced mortality rather than habitat quality that causes extinction in wide ranging species, even when population density is low (Woodroffe and Ginsberg 1998, 2000). Uncontrolled hunting has a more rapid and severe impact on savannah elephants than habitat loss (Milner-Guilland and Beddington 1993). If the abilitiy to protect elephants is minimal, there is little point in pursuing core area development even if habitat quality is high. Kahuzi-Biega, a national park of 5899km^2 supported over 3000 elephants in 1995 (Hall *et al.* 1997), which suggests habitat quality was high. By 1999, the population had been reduced to just two families of elephants through poaching associated with mining the mineral Coltan (Columbo-tantelite) for the cell phone industry (United-Nations 2001), though this may be an over-exaggeration (J. Hart, pers. comm). The less catastrophic, but similar devastation of elephants in the parks of east Africa in the 1970’s and 1980’s also bears witness to the effect of poor protection in the face of poaching in high quality habitats (Malpas 1981; Douglas-Hamilton and Douglas-Hamilton 1982; Prins *et al.* 1994).

This does not mean that habitat quality is irrelevent. Certainly, it is desirable to maximise elephant abundance within the ecological limits of core areas. High carrying capacity is desirable, but secondary to management ability. Where possible then, features of primary importance should be included in integrally protected areas, and such as *bais*, open canopy swamps, closed canopy forest with high fruit tree density, and secondarised forest. Vegetation mosaics which include these features will promote high elephant carrying capacity.

Ecologically and socially optimal road planning

In a thorough treatment of the economic and ecological implications of road construction in central Africa, (Wilkie *et al.* 2000) concluded that road development will generate economic opportunities, attract people, and promote wealth creation. At the same time, roads increase ecological degradation of remote areas (Malcolm and Ray 2000; Wilkie *et al.* 2000). This presents a planning conundrum for governments, who are compelled to improve the well-being of their populace and increase the prosperity of their countries, but who also wish to avoid widespread ecological degradation (Djombo 1999). However, limited road development and the collapse of the existing road infrastructure in much of the Congo Basin, suggests that the opportunity still exists to strategically plan road development for maximal socio-economic benefit, and direct development and resource use away from large blocks of uninhabited and ecologically valuable forest (Wilkie *et al.* 2000).

Fortunately and almost by definition, the largest, most ecologically valuable forest blocks for forest elephants have no roads through them, and permanent human habitations are located around their peripheries. Therefore, maximising socio-economic gain and minimising ecological loss go hand in hand with linking the peripheral population centres, apparently an ideal solution for all. Unfortunately, the engine of road construction in central Africa is frequently the logging industry (Assene Nkou 1999), which is obliged to access remote forests for high quality timber. In isolated regions of central Africa, transport, including road construction, contributes the single greatest cost of timber production (Carret and Clement 1993). Since timber companies are usually from the private sector, economics encourages them to build straight roads through virgin forest, the absolute antithesis of what governments want, local people need, and ecologically sensible planning demands. Central African governments do not have sufficient resources to offer incentives, such as tax relief, to subsidise logging companies to build long costly roads, nor to maintain them following construction.

The action needed is clear if wildlands necessary for elephant conservation are to be preserved. The international donor community, including the World Bank and International Monetary Fund, which funds road development programmes around the world (Ostrom *et al.* 1993), must be encouraged to take on the responsibility of supplying the top-up funds required to finance these economically costly yet ecologically and socially beneficial road developments. The role of conservation science is to demonstrate the paramount importance of wise road planning for conservation and development and effectively communicate research results to governments and donors.

NNNP CASE STUDY: RE-LOCATION OF THE LOUNDOUGOU ROAD

The role of forestry in shaping socio-economic development in African forests was succinctly stated by Assene Nkou (1999): '*where the forestry sector passes, the road follows, and development with it*'. The road scenarios illustrated in figure 7.3 earlier show that the cordon of road infrastructure around the NNNP is close to completion. The permanent logging roads will become the future permanent transport and development roads for the north of the country, and are included in national planning as such. Permanent roads are being built to the north, south, and east of the National Park, which will result in two new roads spanning northern Congo which may provide direct road access from Bangui to Yaoundé, Douala, and the Atlantic coast.

There may still be time to relocate the road linking the Kabo and Loundougou concessions for the benefit of both human welfare and environmental well-being. A number of road-building scenarios for this strategically important section of the road network were proposed by the Nouabalé-Ndoki Project in 1997, which were considered by the CIB. The scenario with the lowest ecological impact in the NNNP and its elephants also had the highest socio-economic benefit, but was also the longest, most technically difficult to construct, and the most expensive. Under this scenario, the road would pass through the Terre de Kaboungas, cross a 14km section of the upper Likouala swamps, and link to *terra firma* near the village of Mbanza, before heading north through the Loundougou concession to the Motaba (Figure 7.5).

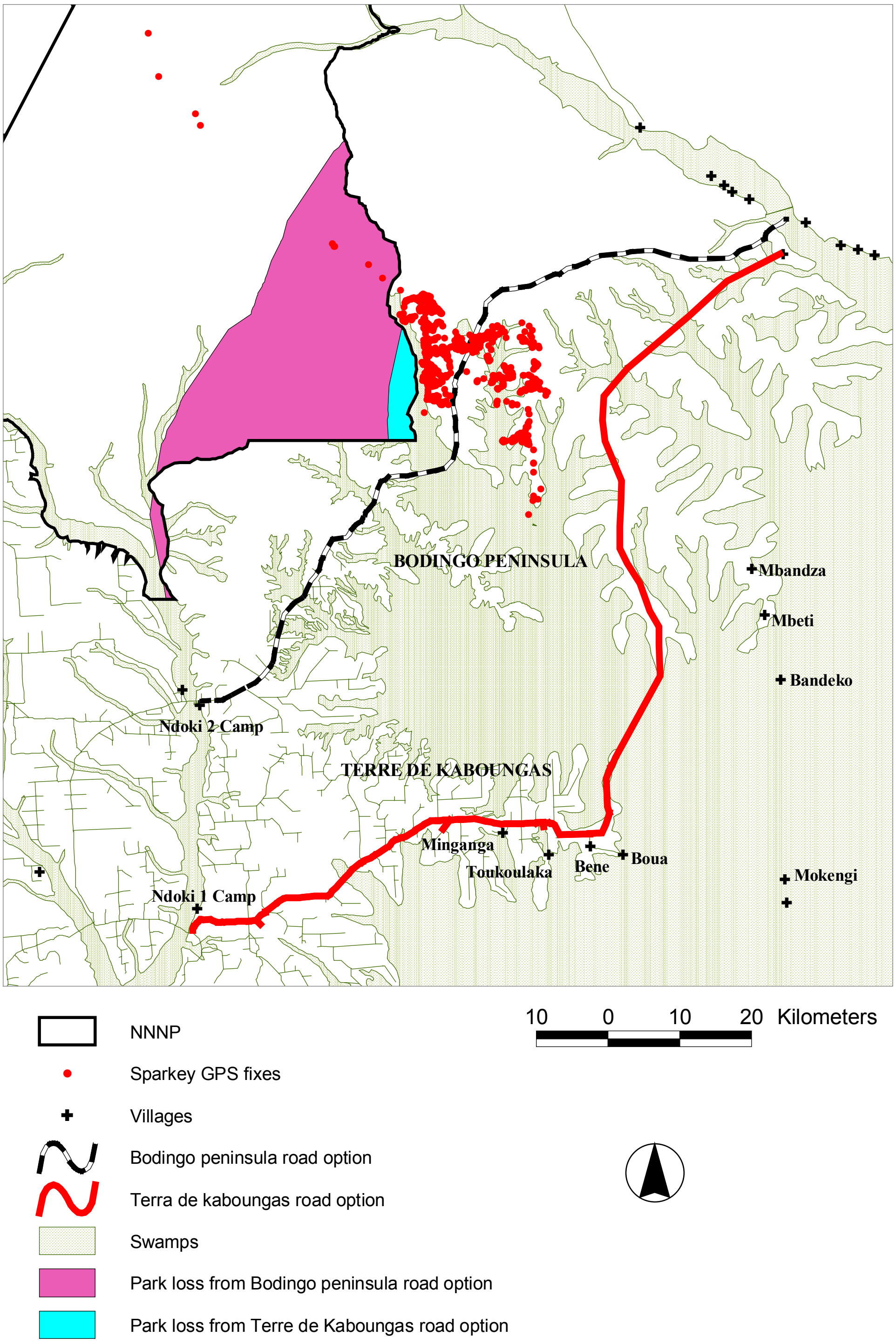
The most ecologically damaging scenario was also the least socio-economically attractive option, but was the shortest, easiest, and cheapest. This road would pass ca. 7km southeast of the NNNP, and traverse the western portion of the Loundougou concession. With no external funding, and a government needing rapid expansion of road infrastructure, there was little option but to choose the cheap option. This road is currently under construction across the Bodingo Peninsula (Figure 7.5).

A road across the Bodingo Peninsula would have just two villages along its length, one at either end. The Terre de Kaboungas option would link all of the villages of the Terre de Kaboungas with Poloka, and pass just 14km from Mbanza, and on to the villages along the Motaba River. Several thousand people would have access to this permanent, trunk road infrastructure, and the multitude of socio-economic advantages it would bring. The Bodingo Peninsula road would pass some 44km from the village of Mbanza and 40km from Minganga on the Terre de Kaboungas.

In terms of habitat loss and fragmentation, the advantages of the Terre de Kanboungas road are clear. Figure 7.5 shows that the Bodingo Peninsula road would cut off a significant portion of the southeastern home range of Sparkey, an elephant collared to the extreme northwest of the Ndoki Forest (Chapter 6). This road option would certainly restrict the ranging of a large number of Ndoki elephants, and completely block access to the high quality feeding grounds of the Likouala swamps. The 30km human influence zone would also penetrate the NNNP and affect some 830km^2 (20%). By contrast the Terre de Kaboungas road would enable elephants to access at least the northern reaches of the Likouala swamps, and the human influence zone would affect only 45km^2 (1%) of the NNNP.

The disadvantage to the Terre de Kaboungas road option is of course money. The remaining construction required to build the roads as depicted in Figure 7.5 are similar; 85km (Bodingo) and 86km (Terre de Kaboungas). The construction problems come in traversing swamp, and with the Terre de Kaboungas option, there is some 11.5km of swamp to traverse, compared to 5.5 for the Bodingo option. Dike construction costs per km are not available, but are considerably higher than building on *terra firma*. Ground-truthing by Blake (pers. obs.) and Malonga (2000) has shown that base maps often over-estimate the distribution of swamps, and it is likely that a considerable amount of *terra firma* along both routes would facilitate road building. The most significant cost, however, is not construction but the recurrent costs of timber transport. Based on 2000 transport and road maintenance costs (the responsibility of the logging company), and assuming an annual harvest of 100,000m^3, Blake (2000) calculated that the additional timber transport cost associated with the Terre de Kaboungas road option compared to the Bodingo option was US$495,805 per annum (an increase of 43%). This would amount to US$12,395,125 over the 25 years of the first logging rotation. The CIB is obviously unwilling, and the Government of Congo is currently unable, to finance the ecologically desirable road. In terms of international development spending, however, this is a paltry sum, and represents just 0.25% of Congo's current international debt.

Figure 7.5. Logging road options for the southeast of the NNNP.



Maintaining high matrix quality

The most important principle was discussed above – keeping human population centres and permanent roads as far from core protected areas as possible. These major roads will develop and in time become the limits of the matrix for fragmented elephant populations. On a site-based, landscape scale there are at least four other fundamental issues to be addressed in matrix management:

1. Poaching
2. Habitat change caused directly by humans
3. Habitat change caused by elephants
4. Human-elephant conflicts (aside from poaching)

POACHING

In the 1980s, poaching wiped out approximately half of Africa's elephants. Many essays have discussed poaching and anti-poaching policies and practices and their effectiveness in elephant conservation (Fay and Ruggiero 1986; Leader-Williams *et al.* 1990; Leader-Williams and Milner-Guilland 1993). Indeed poaching has even been discussed (though not recommended) in a suite of management 'tools' to combat the over-abundance of elephants in Ruaha National Park (Barnes 1983c). Having described the potential for poaching to eliminate elephants across large tracts of land above, clearly reducing elephant killing is the single most important issue for forest elephant conservation, but the application of anti-poaching initiatives is beyond the scope of this study.

HABITAT CHANGE CAUSED DIRECTLY BY HUMANS

Reduced impact logging

Some effects of logging discussed above are neutral or even potentially beneficial for elephants. However, long-term data on the ecological impact of logging are lacking, and a short-term increase in abundance may not reflect long-term habitat quality. An obvious negative consequence of logging on matrix quality is the destruction of elephant fruit trees. Recommendations to reduce the loss of fruit trees are to improve the location of secondary logging roads, and the protection of particularly important elephant fruit tree species through directional felling, and removal of these species from the list of exploitable trees:

Improved location of secondary logging roads

In the Ndoki Forest, because elephant fruit tree distribution is variable by vegetation type, and clumped heavily on elephant trails, secondary road location may have an enormous impact on the level of destruction of fruit trees. To minimise the loss of elephant fruit trees, secondary roads should be located in either mono-dominant *G. dewevrei* forest or in vine forest, where the density of elephant fruit trees is lowest (Table 7.1). They should not be built in *Terminalia* forest or mixed closed forest, which would eliminate a disproportionate number of important fruit trees. Unfortunately, these forest types contain low numbers of principle exploitable species, however, the spatial scale of the vegetation mosaic, with the exception of large upland patches of *G. dewevrei* forest is on a scale of tens and hundreds of metres rather than kilometres (Chapter 2); therefore a near straight path of least resistance route could avoid patches of particularly high fruit tree density. A practical benefit for road builders is that the lowest tree densities of all species are found in open canopy and mono-dominant forest types, which would make road construction considerable easier, faster, and therefore cheaper.

Elephant fruit tree basal area is ca. 1.7 times higher within 20m of a trail than the forest-wide value (calculated from data presented in Chapter 4). A secondary road every 2km at 30m width, built on permanent elephant trails will eliminate 2.55% of the elephant trees, compared to 1.5% with a random road placement. While this is only on average reducing mortality by 1% of total basal area, selection for suitable vegetation types and low trail densities (e.g. in *Gilbertiodendron dewevrei* forest and not on a trail) will further improve this ratio.

Table 7.1. Density of trees over 50cm dbh and frequency of elephant trails by forest type

Vegetation type	Trees ha^{-1}	Elephant fruit trees ha^{-1}	Entandrophragma spp. ha^{-1}	Elephant trails km^{-1}
Terminalia sp. forest	76.4	33.1	0.0	6.2
Mixed closed forest	69.6	18.2	2.7	16.8
Marantaceae forest	66.8	17.0	2.8	7.4
Mixed open forest	61.8	15.6	2.8	10.9
G. dewevrei forest with *H. dankelmaniana*	50.1	13.9	0.0	7.6
G. deweveri forest	42.4	9.7	0.4	12.2
Vine forest	29.8	5.5	0.5	3.9

Protection of important elephant fruit tree species

A number of families and species of particular importance in forest elephant diets should be targeted for special care during logging operations by removing them from the list of exploitable species, and reducing the mortality of these species through directional felling. A list of the most important species based on feeding rates (Chapter 3) is given below (Table 7.2). Of these species, only 4 are considered exploitable (*G. lacourtiana, A. congolensis, I. grandifolia, K. gabonensis*), and are rarely logged in northern Congo, though *A. congolensis* is frequently used in bridge construction. As tropical timber dwindles and second rotations begin, there will be more pressure to exploit these species which should be resisted.

In northern Congo, logging prospection teams identify, enumerate, and map all of the exploitable trees in a logging block ca. 1 year ahead of road building and felling. *Congolaise Industrielle du Bois* now digitise data which includes the density of exploitable trees in 2.5ha blocks. Important elephant fruit tree species (Table 7.2) should be similarly enumerated and maps used to plan directional felling procedures prior to logging. Directional felling involves careful planning, which would be time consuming and costly. However the benefits to vegetation, soil compaction, skidding operations, reduced accidents, and fewer damaged harvest trees, are clear and may be cost effective (Bertault and Sist 1997; Mason and Putz 2001). While the sheer size of central Africa's exploitable trees renders directional felling with precision difficult, it is probable that even a small increase in accuracy would systematically reduce the impact on important fruit trees. If current rates of loss of fruit trees are, for instance, one fruit tree needlessly damaged for every 10 trees felled, even a 10% reduction in damage over a 10,000ha logging coupe would save ca. 1000 important elephant trees.

Table 7.2. Species that should receive particular care during logging operations

Scientific name	Local Name	Currently exploited in northern Congo
Omphalocarpum spp.	Mobate	No
Manilkara mabokeensis	Moungenja	No
Gambeya lacourtiana	Bambu	Rarely
Autranella congolensis	Banga	Rarely, but used for bridge construction
Irvingia grandifolia	Mossombo	Rarely
Annonidium mannii	Mobei	No
Duboscia macrocarpa	Ngorouma	No
Treculia africana	Fussa	No
Klainedoxa gabonensis	Bokoko	Rarely
Tetrapleura tetraptera	Ekombolo	No
Panda oleosa	Kanna	No

HABITAT CHANGE CAUSED BY ELEPHANTS

Data from savannahs unequivocally show the profound effects of elephants on vegetation when numbers are artificially elevated. In the forest, poor estimation of elephant numbers, and the lack of data on vegetation biomass, vegetation mortality, and regeneration rates at different elephant densities, means that assessing the impacts of elephants on vegetation is speculative. Range restriction, population increase and decrease will modify feeding rates, seed dispersal rates, and may result in profound changes to vegetation in tropical forests, which will feedback to ecosystem processes including future carrying capacity. Too little is currently known to make serious recommendations, except to advocate applied research on elephant ecosystem dynamics which are discussed below.

HUMAN-ELEPHANT CONFLICT

If conservation of elephants is successful, and elephant populations expand within protected landscapes, conflict is an inevitable outcome. Co-existence of elephants and humans is unlikely, and the tendency to force co-existence increases as the range of one intrudes into the range of the other. As fragmentation reduces habitat and restricts ranging, more elephants are forced to encounter edges, and in a restriced area where food becomes limited, edges which include the secondary forest mosaic from slash and burn agriculture, will become attractive. If large areas are successfully protected and ‘good quality’ matrix is maintained, elephants will expand to fill the available matrix to carrying capacity, until they inevitably come into contact with humans, when they will become incompatible. Several strategies to reduce conflict are given below.

1. All human-elephant risk scenarios suggest one over-riding pre-emptive action – in undeveloped areas where there is still time, land use planning to keep elephant core areas as far from growing human population centres as possible. In this way elephants maintain access to their widely distributed resources, and humans are not expanding into high elephant density areas provoking immediate conflict.
2. Hoare (1999) showed that the spatial grain separating human settlement from elephant habitat was an important determinant of rate of conflict. At large grain (big blocks of each land use) crop raiding was lower than for fine grain (small land use blocks). Thus, single large areas for each of elephants and humans would seem the most sensible strategy in reducing conflict over the long term.
3. When elephants are at the edge, there are just three choices; the people move out, barriers to elephants (physical or fear) are erected and maintained, or the elephants are killed. Clearly the first is impractical, morally questionable, politically unfeasible, and following it to its ultimate conclusion would mean eradicating humans from the forest. The second is possible for small areas, but requires huge effort and often fails. The third, which has been presented as an option by Barnes (1996a), is both practical and possible, but is politically charged and biologically risky. Biological risk is reduced however if protected areas are large, and the numbers of elephants in them is high.

Applied research for conservation objectives

IDENTIFICATION OF POTENTIAL SITES

Clearly, the national park system, even with several new initiatives to create more parks in Gabon (L. White, pers comm), Congo (B. Curran, pers comm.), and elsewhere, is insufficient to ensure the continued survival of elephants at the site (population) or regional (species) level. Civil war, refugee crises, and expanding poor rural and urban populations all mean that existing protected areas, even if biologically pristine, are at risk of catastrophe. More legally mandated and adequately financed protected area landscapes are required. How should sites be identified? A possible methodology of applied research for site selection is given below, split into two stages: produce a basmap of 'elephant management suitability', and then inventory and ground-truthing within the most suitable sites.

Species survival planning in the wild often involves priority setting based on ecological databases (Wikramanayake 1998), with practical management considerations added later in the process, if at all (Sanderson *et al.* In press). While this is a useful first step in any data driven conservation planning process, it may be best suited for species with high genetic and ecological diversity, which already suffer high levels of fragmentation. It is perhaps less useful for generalist, recently fragmented species such as forest elephants. In Africa's forests, before humans had access to modern weapons, elephants existed everywhere (Barnes 1996a), though habitat determined abundance. Now elephants exist where people do not, and everywhere surveys have been conducted, it is people who determine elephant distribution. Therefore in priority setting, it is a more useful strategy to build the process from the perspective of human ecology and projected human development, and include elephant ecology later, rather than the other way around.

Basemap production

To select potential sites for new protected areas, a basemap of human influences is a critical first step. A GIS generated map should include human infrastructure including cities, towns, villages, roads, rivers, trade vectors, transport infrastructure, and the humam density gradient. Land use and projected land use must also be included. Existing regression models to predict the magnitude of human effects on elephants and habitat stability should be used when available (Barnes *et al.* 1991) Chapter 5; Fay, in prep.). The forest blocks with the highest potential to contain high numbers of elephants in areas of low current and projected human impact should be ranked by area, biggest first. Risk analysis should be carried out for each block, using predictions based on available human demographic data and government's land-use policy, about how human demographics and land-use will change in these areas. These should include likelihood of civil war and its associated impacts, immigration and human population expansion, the potential for industrial or artisinal mining, oil exploration, and logging. Habitat types should then be ranked for each block using available satellite imagery or existing survey data. Existing information on elephants should be quantified for each fragment, particularly poaching history. A final working document which ranks sites by current elephant management suitability and long-term risk should direct ecological and socio-economic ground-truthing surveys. Institutional programmes such as the Central African Regional Program for the Environment (CARPE) (Wilkie *et al.* 2000) and the Wildlife Conservation Society's Wildlands Project (E.

Sanderson, pers. comm.) have much of this information already contained in GIS form, and collaboration should make basemap production on this scale feasible

Groung-truthing surveys

A sample of sites should be selected for ground-truthing to test reliability of basemaps. Aerial reconnaissance using videography should be the first stage of ground-truthing, its purpose to identify human and habitat features not detected during basemap production, such as artisanal mining activity, illegal forestry, and fine-grained habitats of specific importance for elephants such as *bais*, Marantaceae forests, and open canopy swamp meadows. These features should be used in ground-survey planning. Reconnaissance biological and anthropological surveys should be conducted, the goal of which should be an objective test of conclusions drawn from the basemap. Data should be collected on human activity, elephant abundance, and habitat quality, following established methods (Barnes *et al.* 1997b; Walsh and White 1999; Walsh *et al.* 2000, 2001; White and Edwards 2000b; Barnes 2001) Chapter 5). If concordance is good (by some set of pre-determined objective criteria) between basemap predictions and ground-truthing of selected sites, a final list in rank order of suitability for elephant conservation should target the establishment of new protected areas. If concordance proved poor, the basemap would need revision, meanwhile sites of clearly high quality should be incorporated into conservation planning, in lieu of a final report. These methods have resulted in identification of a number of large intact forest blocks in Gabon where elephant densities are high, and conservation has high potential for success (http://www.savethecongo.org/maps.shtml.).

IMPROVING SURVEY METHODS FOR INVENTORY AND MONITORING

Measuring forest elephant conservation success requires accurate, precise, and timely results from monitoring. Low sensitivity of current monitoring methods usually means that substantial change in elephant abundance is required before it can be detected. Recent research on the relationship between dung density and elephant density (Barnes 2001), survey design efficiency and modelling of the spatial distribution of elephants, (Barnes *et al.* 1997b; Walsh and White 1999; Walsh *et al.* 2000, 2001) have increase the precision of elephant density estimation. Further research is needed to identify and quantify the effect of environmental covariates which influence the spatial distribution and local density of elephants to interpret density estimates and identify their likely causes. This study identified a number of covariates which significantly influence elephant distribution, some of which had a temporal component. For example, in the Ndoki Forest, fruit abundance varied over an order of magnitude in the same sample units in different sampling periods, and the range of fruit abundance resulted in a ca. 3 fold increase in elephant dung density (Chapter 5). Without collecting data on fruit abundance and including it in the analysis, there would be no way to interpret such fluctuations in elephant density, which would render monitoring data confusing for management.

In any future elephant surveys then, it would be useful to quantify the covatiates identified in this study that significantly influenced elephant distribution, and incorporate them into survey design and data analysis. Secondly, attempts should be made to identify additional covariates which influence elephant distribution to improve abundance estimates (Walsh *et al.* 2000).

Finally there is no adequate way to account for the proportion of time that elephants spend in swamps and rivers, which has important concequences for density estimates based on data only from *terra firma*. Consider two prospective reserves, one which is 100% *terra firma* and one which is 50% swamp. All of the dung from elephants in the *terra firma* site is potentially available for counting in a population survey. In the half swamp/half *terra-firma* site, if the elephants spend exactly half their time in swamps (assuming equal defecation rates in swamps and on dry land), then half the dung will be 'lost', and unavailable for counting. A dung count survey will thus underestimate the true number of elephants by half. As the swamp area or swamp attractiveness for elephants changes across or within sites, the error in density estimates of elephants from dung counts will also change by an unknown amount. Chapter 5 showed elephant aggregation around swamps was quite consistent but that it fluctuated seasonally around rivers. Different combinations of fruit availability, vegetation composition, and other factors will all change the time that elephants spend in swamps. Some way of calibrating *terra firma* elephant density estimates based on dung is needed to allow inter-site and within-site elephant density comparison, which could involve camera trap surveys or more widespread GPS telemetry to assess relative habitat use.

RESEARCH ON LOGGING AND ELEPHANT ECOLOGY

Quantifying ecological change caused by logging under different management scenarios will be important for landscape management planning as logging proceeds. Research should aim to answer at least the following broad lines of questioning.

- How do different logging practices in different habitats affect forest structure and composition in terms of elephant food availability?
- How do these differences influence elephant feeding ecology, and what does this mean for habitat preferences, ranging patterns, distribution, density and carrying capacity of logged forests compared to intact forests?
- What in turn do these changes mean for energy balance, reproductive rates, population dynamics and demography of elephant populations?
- How do changes in elephant ecology feed back into processes of forest dynamics? In particularly do high elephant numbers (the immediate objective of most site-based conservation) lead to habitat degradation, arrested succession, and threat to biodiversity as in savannahs? If so, what is an ‘acceptable’ elephant density, compatible with protected area ecology, elephant conservation, and silviculture?

ECOSYSTEM FUNCTION

A compelling argument linking elephants to biodiversity lies in the keystone species concept, the logic being that if the elephants are removed, biodiversity is necessarily reduced. While the concept is attractive, there are few supporting quantitative data. As the debate continues over the intrinsic worth of elephants in the face of growing human population growth, poverty, and land requirements, proponents of elephant conservation will need an increasingly persuasive argument as to why elephants matter. While in the short-term, understanding the dynamics of elephants as ‘ecosystem engineers’ will perhaps have little bearing on site-based management decisions, there is an immediate need to provide concrete examples of how elephants, by virtue of their body size, play a critical role in the maintenance of ecosystem level processes and biodiversity conservation, which are untimately relevant to human well-being. Fruitful lines of research in this area will include:

- How long distance seed dispersal by elephants affects competitive processes between plant species, and maintains tree species diversity and habitat heterogeneity

- How do the actions of elephants create and maintain forest clearings, both swampy *bais* and mineral *bais*, which are critical for a range of other large, charismatic mammals, as well as providing islands of radically different habitat from the surrounding forest which promote species richness?
- Do elephants, through the formation of trails and concentrated seed dispersal, create corridors of high fruit resource abundance which increases the local carrying capacity of other large frugivores and elephants themselves?
- How are these processes interrupted by range restriction, population reduction, and logging?

CONCLUSIONS

1. The discussion in this chapter has illustrated that habitat fragmentation, leading to habitat loss, and the re-distribution and isolation of remaining habitat, is occurring throughout the range of forest elephants in Africa's equatorial forests. Fragmentation is mostly due to the increasing risk of mortality with proximity to humans, who are concentrated along navigable rivers and roads, rather than the physical disappearance of elephant habitat. The development of extensive road infrastructure, primarily to service the rapid increase in large-scale mechanised logging, is dividing the last blocks of intact forest - the last elephant strongholds – in which the influence of human activity has traditionally been low.
2. Dramatic fragmentation of habitat is occurring even in the Ndoki Forest, a particularly isolated forest block, where conservation management has been active for more than a decade. A wildland area of at least 25,000km^2 outside of a 30km human influence zone around existing roads in 1990, will, if current plans for road-building continues, be reduced to an area of just 264km^2 in 2003, centred in the heart of the Nouabalé-Ndoki National Park. In northern Congo, the entirety of the *terra firma* forest outside of protected areas will be logged in the coming 25 years.
3. The large body size of forest elephants and the landscape-scale distribution of their resources, means that individual elephants have large home ranges, and therefore large areas are required to maintain viable populations. Elephants are particularly vulnerable to large-scale habitat fragmentation compared to smaller animal species with limited home ranges, since it cuts them off from important resources, and brings them increasingly into contact with a hostile 'edge', and high risk of mortality from poaching.

4. Small patch size reduces carrying capacity, which leads to population decline. The tendency for elephants to avoid humans may further reduce the 'effective patch size' of available habitat. Restricted ranging may cause elephants to over-exploit the remaining habitat within a patch, leading to a spiral of habitat distruction commonly seem in savannah elephant populations with restricted range. Small patch size will also increase the tendency for dispersal into areas of high mortality risk. Or, if logging around habitat patches improves habitat quality outside the patch, elephants may positively select logged forest. Uncontrolled hunting in these 'attractive sink' habitats may lead to rapid depletion of elephant numbers.
5. Evidence is building that it is not simply elephant loss that is of concern to conservation and environmental planning. Elephants are keystone species, which play an important role in ecosystem function including gap creation, excavation, trail formation, plant predation, and seed dispersal. Elephants disperse seeds from more than 100 plant species, over very large distances. Habitat fragmentation leading to range restriction and lower population size, may reduce the role of elephants in the creation and maintenance of diversity of habitats and species.
6. Based on the data collected in this thesis, a number of recommendations were proposed to improve the conservation of forest elephants. These included:
    - Protection of large core areas of suitable habitat, and preferably high-quality habitat, of at least several thousand square kilometres.
    - Avoidance of further fragmentation of core areas through ecologically and socially optimum permanent road planning.
    - Maintenance of high quality matrix outside of core areas by reducing
        - Poaching,
        - the impact of logging on important elephant fruit tree species through wise road placement and directional felling,
        - the likelihood of human-elephant conflict through coarse-grained land-use planning of core elephant habitat and areas for human development.
    - Scientific research to address specific management needs, including:
        - Identification of remaining suitable sites for elephant conservation that still exist.
        - Improvement of survey methods and data analysis for elephant monitoring purposes.
        - Quantifying the impact of different logging practices on forest elephant ecology, particularly how logging affects ranging, feeding ecology,

energetics, reproduction and demographics, and habitat carrying capacity.

- How do elephants influence the functioning of forest ecosystems, particularly as agents of habitat modification and seed dispersal?

CHAPTER 8. CONCLUDING REMARKS.

This study was initiated for two reasons. First, even in the 1990s, the collective knowledge of forest elephant ecology in the scientific literature was limited. Studies came mostly from the heavily disturbed forests of west Africa, where low numbers of elephants remained. With few exceptions, research on forest elephants in their last stronghold of central Africa, was based on dung counts to assess their status and distribution across the equatorial forest block, and the lack of basic biological information available on forest elephants was identified as a major constraint on effective conservation. The second reason for this study was the strong impression that the equatorial forest was not a safe green blanket, under which forest elephants had escaped from the massacres stimulated by the ivory trade in the 1980s, as was widely believed. Instead, it was clear from experience on the ground, that forest elephants had also been heavily hunted and were declining in numbers, their populations were being fragmented, and even in the most remote forest blocks remaining, humans were determining elephant distribution. This summary provides a final overview of the ecological context of the study, its main results, and its contribution to the understanding of elephant ecology and conservation.

1. Studies of the savannah elephant *(Loxodonta africana africana*) have shown that they are grazers/browsers, living in semi-arid habitats, occasionally in desert conditions, where dry season drinking water is restricted to a few, widely separated sources. Prodigious drinking requirements restrict the dry season ranging of savannah elephants to these permanent water sources. As rainfall increases, temporary water sources in uplands may become available, and savannah elephants either disperse into larger wet season ranges, or may migrate to spatially discrete wet season areas where grass productivity is high. Movements into upland areas are in response to high quality food availability, which increases with rainfall. However, upland areas may maintain patches of high quality forage all year, but obligate drinkers like elephants cannot access them. It is the distribution of water, not forage, which is the primary determinant of savannah elephant distribution.

2. By contrast, forest elephants (*L. a. cyclotis*) were known to be generalist browsers, with limited consumption of grass. Instead, fruit, a minor part of savannah elephant diet due to

limited availability, was clearly an important food source for forest elephants, but varied seasonally with availability in the habitat.

3. Like savannahs, African forests also experience extended dry seasons, but permanent rivers are abundant, widespread and reliable, and few locations in forests are more than a few kilometres from permanent water. Thus, it was always more likely that resources other than water determined forest elephant distribution, particularly given the high diversity and heterogeneity of rain forest habitats. For example, it was known that forest elephants were found at high densities in secondary forest, where browse abundance was high; and seasonally abundant fruit patches led to increased elephant abundance. Preliminary telemetry data had suggested that forest elephants ranged over relatively small areas, though extrapolations from dung counts suggested that they ranged further in response to fruit, and anecdotes suggested that elephant trails linked important fruit trees and mineral deposits. The spatial distribution of these resources, their importance as determinants of elephant distribution, and the scale over which elephants ranged, had obvious implications for protected areas management and conservation.

4. The Nouabalé-Ndoki National Park, established in 1993 in a remote area of northern Congo, was recognised as an important conservation area for forest elephants. The park's vegetation was intact, human density was low, and the area provided an excellent site (and one of the last) in which to study elephant ecology where human impact was minimal, and where elephant movements were largely unrestricted. While negligible in the interior, human impacts were increasingly severe toward the peripheries of the Ndoki Forest, regional land use was rapidly changing, and a gradient of human influence existed outward from the park's interior. Thus, the effects of high human activity, incipient encroachment, and the absence of humans on elephant distribution and ranging could all be investigated.

5. In contrast to previous research on forest elephant ecology, this study took a landscape-scale approach to data collection over a coarse-grained drainage gradient across the Ndoki forest, from northwestern uplands to extensive southeastern swamps, a gradient often recapitulated at smaller scales from inter-fluvial uplands to river valleys. Across these gradients, a 253km foot survey track was draped and repeatedly surveyed over two years. The aim of the survey was to quantify gross spatial and temporal patterns in forest structure, species composition, and resource availability for elephants. Temporal gaps in the survey data were

filled in at an intensive survey site. Against this backdrop, elephant distribution was quantified using dung counts. Diet was studied to determine the importance of different resources, and an estimate of foraging success in different habitats was calculated. Trail system geography and its association with forest structure and composition was quantified, to understand how resource distribution and preferences may influence foraging patterns, which result in permanent trails. Lastly, GPS telemetry enabled the ranging patterns of individual elephants to be determined, which 'ground-truthed' and tested the conclusions reached from the other datasets.

6. Spatial and temporal partitioning in the availability of several resources for elephants was revealed on several scales. Dicotyledon browse was most abundant in open canopy *terra firma* forest, light gaps and swamps, while monocotyledon foods were concentrated in *terra firma* forest to the southeast, and were superabundant in localised swamp patches. Production of new leaves was not correlated with rainfall, but a spatial gradient in new leaf production was. During periods of low rainfall, leaves were most abundant in the southeast, but became widespread as rainfall increased. Forest clearings, clumped in the northwest, contained high levels of minerals in seep-hole water, which were most concentrated during dry periods. Fruit availability was negligible in swamps, high in closed-canopy *terra firma* forest, and was highly irregular, though correlated with rainfall. Drinking water, confined to rivers, was widespread and abundant.

7. Elephants ate leaves, bark, wood, stems, roots and fruit from over 350 plant species, the most diverse diet ever recorded for any elephant population. Leaves dominated food selection, and browsing rates were highest in open-canopy forests, particularly swamps. Fruit consumption increased dramatically as its availability increased. Elephants constructed trail systems that allowed efficient exploitation of high payback resources, notably water, minerals and fruit.

8. Elephant abundance was consistently high in the northwest, probably because of the influence of forest clearings and high quality swamp habitat, around which elephants were permanently aggregated. During dry periods, elephant abundance increased in the northwest and in proximity to rivers. The influx of elephants into the northwest, which was against the gradient of leaf productivity, was probably driven by elephants increased dry season physiological requirement for minerals, associated with reproduction and lactation. Dry season

mineral supplementation may also have been a response to the digestive demands of an increase in browse consumption, when fruit became unavailable. As rainfall increased, elephants dispersed out of the northwest, selected upland forest, and tracked the patchy distribution of fruit across the landscape. Telemetry data revealed that individual elephants ranged over large areas (up to nearly 2000km^2), and travelled up to 57km in 48 hours, which allowed them to exploit resources over large spatial scales throughout the year. It also gave them unprecedented seed dispersal ability, which is important in the propagation of fruit trees and the maintenance of species diversity.

9. The above results show that, as suspected, it was the distribution of high quality resources that determined forest elephant distribution in the absence of human impact. Unlike savannah elephants, forest elephants were unconstrained by the distribution of water. The widespread distribution of browse, and the tolerance of elephants for low quality foods over extended periods conferred by large body size, meant that quasi-nomadic ranging in search of fruit patches was a low-risk strategy with a potentially high nutritional payback. Their long life and cognitive abilities, and their conspicuous trail system linking favoured resources, may allow elephants to develop rules of thumb, which help in their search for food and minerals which are distributed patchily in space and time.

10. The ecological determinants of elephant distribution were overruled by human activity, including forestry prospection, and elephants avoided areas of high human impact. Large-scale ranging patterns and the widespread distribution of their resources, mean that elephants are particularly vulnerable to habitat fragmentation caused by expanding human activities. Road building to facilitate logging in remote forest blocks was identified as a major threat to conservation. Immediate conservation actions were proposed, and the need for applied research was identified to ensure that they are carried out in the most appropriate way for both elephants and people.

11. This study showed clearly that the underlying habitat preferences of forest elephants were for those vegetation types that offered high browse and mineral availability, notably swamps, riverine forest, open-canopy forests and bais. It confirmed the overpowering role of fruit as a determinant of forest elephant distribution. High fruit availability released elephants

from their reliance on browse, which, since the two resources were spatially segregated, shifted elephant distribution towards closed-canopy forests and uplands. It confirmed that trail systems are constructed to maximise access to fruit trees, though bais, rivers and swamps were also important determinants of trail geography. Much of this was known or suspected before this study began, but no previous study has been conducted over such a large scale. It has therefore been crucial in clarifying and extending the findings of earlier, smaller-scale work.

12. Perhaps the most important contribution of this thesis is the confirmation that forest elephants range over a spatial scale far larger than previously suggested, which allows them to exploit resources on scales of over 100km. In Ndoki, an elephant may require browse from the Likouala swamps in the southeast, fruit from the middle of the park, and minerals from Dzanga Bai, in the extreme northwest of their remaining range. The same elephant may disperse a fruit tree seed from the heart of the park into the middle of a logging concession 60 or more kilometres away. If examples of functional forest ecosystems and the maintenance of species diversity in central Africa are global priorities, conservation planning on a spatial scale comparable to the wanderings of forest elephants is paramount. Meeting the immediate needs of humans living in remote forests through sensible road and infrastructure development is also in the best interests of forest elephant conservation. Commitment to sufficient funding for landscape planning outside of protected areas to maximise matrix quality is necessary if viable populations of elephants are to be maintained.

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