FRUGIVORY AND SEED DISPERSAL: ECOLOGICAL INTERACTIONS BETWEEN BABOONS, PLANTS, AND DUNG BEETLES IN THE SAVANNA-FOREST MOSAIC OF WEST AFRICA

DISSERTATION ZUR ERLANGUNG DES

NATURWISSENSCHAFTLICHEN DOKTORGRADES

DER BAYERISCHEN JULIUS-MAXIMILIANS-UNIVERSITÄT WÜRZBURG

VORGELEGT VON

BRITTA K. KUNZ

GEBOREN IN FRANKFURT AM MAIN

WÜRZBURG 2008

Eingereicht am: 17.12.2008

Mitglieder der Promotionskomission:

Vorsitzender: Prof. Dr. Martin J. Müller

Gutachter: Prof. Dr. K. Eduard Linsenmair

Gutachter: Prof. Dr. Eckhard Heymann (DPZ, Göttingen)

Tag des Promotionskolloquiums: 10. Juli 2007

Doktorurkunde ausgehändigt am: ___________________

One that would have the fruit must climb the tree.

Thomas Fuller
Gnomologia 1732

Olive baboons feeding on fruits of *Lannea acida* (Anacardiaceae)
at Comoé National Park, Ivory Coast

Table of Contents

Chapter 1

General Introduction, Focal Taxa, and Study Site 1

Chapter 2

Diet and Behavioural Ecology of Olive Baboons in the Comoé National Park 51

Chapter 3

Chapter 4

Chapter 5

Chapter 6

Chapter 7

Chapter 8

Chapter 1

General Introduction, Focal Taxa, and Study Site

This chapter outlines the theoretical background of frugivory and seed dispersal, their importance particularly in tropical ecosystems, and the two groups of seed dispersers my research focused on: primates (*i.e.* olive baboons *Papio anubis* Lesson 1827) and dung beetles (Coleoptera, Scarabaeidae).

I start with some brief definitions prior to reviewing the current hypotheses on the general advantages of seed dispersal for plants. Following is an overview of the different modes of seed dispersal, in which I focus on the mode relevant for my study: endozoochorous seed dispersal by vertebrates. Under this topic, I specify morphological fruits traits that may affect a frugivores' choice of fruit, and explain how different frugivores may differ in their contribution to plant fitness. One important aspect of this contribution is the spatial distribution of seeds, which sets the template for post-dispersal processes. I briefly discuss two post-dispersal processes, secondary seed dispersal and post-dispersal seed predation, which both may exert selection pressures conflicting those by primary dispersers. Subsequently, I summarize further evidence against the once favoured view of a close coevolution between species of plants and frugivores. I deal with one of these conflicting factors, pre-dispersal seed predation, in more detail, because primates may also act as important pre-dispersal seed predators for their food plants.

I then highlight the region of the world where plant-frugivore-interactions are most prevalent and where my research took place – the tropics – and describe the importance of primates and dung beetles for seed dispersal in these diverse ecosystems. Finally I provide a description of the study site and an outline of the following chapters' content.

1. 1 SEEDS, FRUITS AND DIASPORES

The '*seed*'[1] is the offspring of an adult plant of the division Spermatophyta derived from sexual reproduction. It is the fertilized ovule at the state of maturation and disjunction from the parent plant (Strasburger *et al.* 1991). In gymnosperms, the seed is the embryo embedded in the female gametophyte. In angiosperms, the seed is the embryo plus food storage organs (endosperm, cotyledons) surrounded by a seed coat, the testa (Howe & Smallwood 1982).

Seeds fulfil several distinct functions for the plant: provisioning and protection of the developing embryo, multiplication, release of genetic variability to the external environment, and often also perennation, and dormancy (Harper *et al.* 1970). Originally, the seed was the item of dispersal before morphological connections with other parts of the maternal plant evolved (Strasburger *et al.* 1991): the fruits.

A '*fruit*' is the mature gynoecium in the Spermatophyta, with or without (parts of) other floral organs. It encloses the ripening seed(s) and may aid seed dispersal. A fruit may either drop off the parent plant at fruit maturity (indehiscent fruit), open and release the ripe seeds (dehiscent fruit), or be harvested by a fruit or seed eating animal (Strasburger *et al.* 1991).

A '*diaspore*' is the propagative structure of a plant (or fungus) that is dispersed (Howe & Smallwood 1982). It may be identical to the fruit but can also be a single seed (or spore), an entire infructescence (or parts of it), or vegetative parts that aid dispersal of the plant (Strasburger *et al.* 1991). In a few plants, the whole aboveground part of the plant serves as a diaspore, being drifted away by wind (Strasburger *et al.* 1991).

The reproductive structures of many Spermatophyta, and in particular angiosperms, have developed an enormous diversity of morphological modifications from a variety of anatomical origins that enhance dispersal of seeds (van der Pijl 1982; Dirzo & Domínguez 1986; Herrera 2002). Structures that facilitate dispersal of the diaspore by wind can, for example, evolve from the seed coat, ancestral arilloids, the ovary, or calyx tube. The part edible by frugivorous animals can be homologous with the seed coat, an outgrowth of the seed coat or from ancillary floral structures like bracts (seed aril), an outgrowth from the endocarp, or a tissue derived from the ovary wall (van der Pijl 1982; Strasburger *et al.* 1991). I henceforth use the terms 'fruit' and 'seed' in their ecological sense (regarding seed

---

[1] The term 'propagule', in contrast, refers to *any* plant material used for the purpose of plant propagation. In asexual reproduction a propagule may be any vegetative plant part from which a new individual may develop. In sexual plant reproduction, the propagule is a seed and the two terms are often used as synonyms.

dispersal), not in their strict morphological sense.

The great functional convergence of fruits suggests consistent selective pressure favouring dispersal of seeds (Herrera 2002). In view of the cost to the plant of producing the morphological features associated with dispersal of seeds, one would expect some advantages to dispersal (Howe & Smallwood 1982).

1. 2 WHY DISPERSE SEEDS? POTENTIAL ADVANTAGES OF SEED DISPERSAL

Two processes in the reproductive cycle of the otherwise sessile higher plants - sexual reproduction and offspring dispersal - require movement of some reproductive plant structure. In Spermatophyta, sexual reproduction requires that pollen grains travel to meet female gametophytes, and offspring dispersal involves the movement of seeds some distance away from the parent plant (Herrera 2002; see also Levin *et al.* 2003).

Seed dispersal is the spatial distribution of viable seeds away from the parent plant (Nathan & Muller-Landau 2000). It is the link in the demographic transition between the ripe fruit crop on the plant and the whole recruitment cycle (Jordano & Godoy 2002). Dispersal of seeds takes place at the plant's final stage of each reproductive episode, and can thus potentially "screen off" previous selection effects in the reproductive cycle (e.g. effects of pollination and fruit growth).

Regarding scale, two major types of dispersal can be distinguished: (1) dispersal relevant to immigration at geographical scales, and (2) dispersal relevant to colonization of new sites in the same general area/community where the parent plant lives (Dirzo & Domínguez 1986).

Seed dispersal not only is important for range expansion of species and the fitness of individual plants, it is a key process for determining the spatial and genetic structure of plant populations (Jordano & Godoy 2002; Levin *et al.* 2003). The genetic consequence associated with seed dispersal is that it prevents or reduces the local genetic differentiation of plant populations (Herrera 2002).

Seed dispersal also sets the template for post-dispersal processes such as secondary seed dispersal and seed predation, and thus affects patterns and rates of early seed survival and seedling establishment (Jordano 2000, and references therein). Eventually, adult plant dispersion results form the interactions of seed distribution and seed and seedling survival.

Howe & Smallwood (1982) summarized three hypotheses that point out the different potential benefits of seed dispersal. These hypotheses are not mutually exclusive. Many plants may benefit from more than one advantage (Wenny 2001).

(A) The '*Escape-hypothesis*' was first formulated by Janzen (1970) and Connell (1971). It predicts that near the parent plant, where seed and seedling densities are generally highest, increased competition among seedlings and increased attacks by distance-responsive and/or density-responsive enemies (seed predators, herbivores, pathogens) result in a disproportionate high offspring mortality. Distance from the parent plant and seed/seedling density are generally correlated because the area into which seeds can be dispersed around the source increases with increasing distance. Seed dispersal benefits plant recruitment by moving seeds away from the source and decreasing seed density.
Many studies have found a higher probability of survival for distant seeds and/or seedlings than for those close to the parent plant or close to other conspecifics (e.g. Howe & Smallwood 1982; Augspurger 1984; Clark & Clark 1984; Harms *et al.* 2000; Balcomb & Chapman 2003; Jansen *et al.* 2008). However, the degree to which seed and seedling mortality occur beneath parent plants varies widely among species (reviewed in Howe 1989; see also Augspurger 1984; Howe *et al.* 1985; Willson & Whelan 1990b; Chapman & Chapman 1996). In a few studies, seeds far away from the source performed poorly (Augspurger & Kitajima 1992; Chapman & Chapman 1996). Exceptions can be found e.g. where parent plants are associated with mutualists such as mycorrhizae (Wilkinson 1997) or where nurse plants provide a favourable microenvironment for plant recruitment in arid ecosystems (Tewksbury & Lloyd 2001). In some cases, siblings may profit from the proximity of genetic relatives, but the mechanisms are not clearly understood (Willson *et al.* 1987, and references therein).
In contrast Hubbell (1980) suggested that, despite low survival, recruitment should always be higher close to the parent plant because of the disproportionately high seed density. The high seed density can lead to satiation of predators and to an increased number of seeds that establish (Augspurger & Kitajima 1992; Burkey 1994; Crawley 2000; Boudreau & Lawes 2008). This may still be the case if the number of seeds killed increases with seed density, yet the proportion of seeds killed does not increase disproportionately (reviewed in Howe & Smallwood 1982).

(B) The '*Colonization hypothesis*': For most plants successful colonization of new sites depends upon the passive arrival of seeds. In contrast to pollen dispersal, plants do not have a definite 'target' for their seeds and favourable germination sites are often spatially and temporally unpredictable and out of control of the parent plant (Herrera 2002). In the view of an environment that is in constant flux (disturbances, succession, flux of species) it is advantageous for plants to distribute their seeds widely so that some seeds eventually reach appropriate sites (e.g. tree fall gaps in forests). This may be particularly important in species in which the seeds and seedlings require different conditions for germination and establishment than the adult plant (Willson & Traveset 2000, and references therein).

(C) The '*Direct dispersal hypothesis*': According to the direct-dispersal hypothesis, seeds are dispersed into certain suitable microsites (often called 'safe sites') where they have a higher probability of germination and survival compared to random sites. Direct dispersal thus has two components: (1) non-random arrival and (2) survival in predicable sites. The overall result is a disproportionate effect on plant recruitment.

Classic examples of 'directed dispersal', as it was called by Howe and Smallwood (1982), include:

(a) Mistletoes dispersed by passerine birds to host plant branches of a certain range of size (Reid 1991). Seeds not eaten by birds and seeds falling to the ground do not establish.

(b) Dispersal of elaisome- or aril-bearing seeds by ants to their nest sites. After consumption of the seed appendage, the seeds are discarded to a refuse pile, the relatively high nutrient content of which may enhance seedling growth (reviewed in Howe & Smallwood 1982). Other authors, however, argue, that dispersal by ants into their nest may not be true direct dispersal, as seeds get aggregated, leading to a high seedling competition (e.g. Stiles 2000).

(c) Dispersal of pine seeds to caches by corvids (reviewed in Wenny 2001).

In a recent review Wenny (2001) suggested that direct dispersal might be more common than previously believed. According to Wenny (2001) plants need not special adaptations for direct seed dispersal. Particular foraging preferences, habitat preferences and defecation patterns of dispersers can result in non-random distribution of dispersed seeds to sites that are more suitable for plant establishment than random sites (Wenny 2001). In this view, seed dispersal by birds to forest gaps (Hoppes 1988; Levey 1988; also reviewed in Wenny 2001), to perches, lek sites, or nest sites (Kinnaird 1998; Wenny & Levey 1998), and seed dispersal by mammals to sleeping sites or latrines (Pigozzi 1992; Julliot 1996b; Fragoso 1997; Voysey *et al.* 1999b) have potential for directed dispersal (Wenny 2001).

Directed dispersal can, however, also be disadvantageous, for example, when bats disperse seeds to roosting sites in caves.

Herrera (2002) further classified the benefits of seed dispersal into two major categories: benefits related to departure form the site of the seed source, and benefits of arrival at a new site.

'*Departure-related benefits'* include the above-mentioned escape from seedling competition and high mortality under the maternal plant, but also escape from (auto)allelopathy (when plants produce chemicals that inhibit germination of seeds, including those of the own species).

'*Arrival-related benefits*' include advantages from the quick occupation of vacant (micro)habitats (e.g. forest gaps, new volcanic islands).

In contrast to the arrival-related benefits, the departure-related benefits of dispersal are relatively predictable and under the control of the maternal plant (Herrera 2002). One would thus expect that the evolution of traits enhancing departure (e.g. morphological modifications, fruit conspicuousness, nutritious reward) would be strongly favoured (Herrera 2002).

1. 3 FRUIT SYNDROMES, DISPERSAL VECTORS, AND MAIN FUNCTIONAL CATEGORIES

Morphological modifications of diaspores that enhance seed departure from the maternal plant are very widespread in many communities across the world (Dirzo & Domínguez 1986). A '*fruit or dispersal syndrome*' is a particular non-random combination of morphological fruit traits that is associated with seed dispersal (van der Pijl 1982; Howe 1989; Charles-Dominique 1993). The most commonly used classification system of dispersal syndromes is based on the vector of dispersal, "typically inferred from diaspore and seed morphology" (Levin *et al.* 2003). The main '*vectors of dispersal*' are either abiotic (wind: anemochory, water: hydrochory) or biotic (the plant itself: autochory (e.g. ballistically), animals: zoochory) (van der Pijl 1982; Levin *et al.* 2003).

Dispersal by animal vectors can be further classified into '*main functional categories*': external seed transport (synzoochory) or internal seed transport (endozoochory), and active or passive seed acquisition (Stiles 2000). Animals acquire seeds passively by picking them up incidentally with the skin, fur or feathers from the vegetation or ground (Herrera 2002). Active seed acquisition can be divided into whether the animal (a) harvests seeds during seed predation of which some escape later consumption (= imperfect harvesting, e.g. cache-hording birds and rodents), or (b) ingests the seed incidentally while feeding on other parts of the diaspore (Herrera 2002).

Regarding active seed acquisition by animals, dispersal syndromes can further be differentiated according to the taxonomic groups of disperser, e.g. chiropterochory, ornithochory, saurochory, mellichory (reviewed in Théry *et al.* 1998).

For example, fruits characteristic of the 'bird-dispersal syndrome' are small, brightly coloured drupes or berries (Knight & Siegfried 1983; Balasubramanian 1996; Herrera 2002). Fruits associated with seed dispersal by mammals tend to be larger and dull coloured (Knight & Siegfried 1983; Cooper *et al.* 1986; Balasubramanian 1996; Herrera 2002; Schmidt *et al.* 2004; but see Whitmore 1998).

Phylogenetic constraints on dispersal modes may vary across plant families (Willson & Traveset 2000). Some families (e.g. Liliaceae) and genera (e.g. *Acacia*, *Pinus*) have evolved a great variation in dispersal modes (Willson & Traveset 2000). In the relatively small tropical family of Lecythidaceae (about 450 species) diaspores are dispersed by birds, primates, fish, water, wind or gravity (reviewed in Howe & Smallwood 1982). In some species, different types of seeds or diaspores can be produced even within an individual (polymorphic seeds, e.g. with and without appendages for wind dispersal in *Leontodon* spp., Asteraceae) (Strasburger *et al.* 1991). Other (higher) taxa are less variable (Willson & Traveset 2000).

On the other hand, seed dispersal is seldom mediated by a single vector or dispersal agent (Higgins *et al.* 2003; Levin *et al.* 2003; Vander Wall & Longland 2004). I address this issue in more detail in the section 'Secondary Seed Dispersal'.

1. 4 SEED DISPERSAL BY ANIMALS

For many species of plants, animals provide the means for seed mobility (Jordano 2000). Animals as distinct as molluscs and annelids (Stiles 2000), ants (Andersen 1988), fish (Gottsberger 1978), frogs (Fialho 1990; Da Silva & Britto-Pereira 2006), reptiles (including lizards, tortoises and snakes, Fialho 1990, Traveset 1995), birds (e.g. Murray 1988; Wheelwright 1988; Izhaki *et al.* 1991), mammals (including bats, Medellin & Gaona 1999; Shilton 1999, and carnivores like bears and tigers, Kitamura *et al.* 2002) disperse seeds of plants. The vast majority of animals that act as seed dispersers, however, are vertebrates and ants. Among vertebrates, birds and mammals are probably the most important seed dispersers in terms of the number of dispersed seeds (Stiles 2000; Herrera 2002). Most vertebrate-dispersed seeds are passed through the digestive tract (Stiles 2000).

1.4.1 FRUGIVORY AND ENDOZOOCHOROUS SEED DISPERSAL BY VERTEBRATES

'*Frugivory*' is "the ingestion of fruits, whether or not seeds are digested" (Howe 1989). Many plant species produce fruits[2] that are adapted to consumption and potential seed dispersal by animals (Howe 1989). These fruits commonly have edible appendages (e.g. seed arils) or tissues surrounding the seeds (i.e. fruit pulp) that reward some nutrient benefit in exchange for the potential service of moving the seeds away from the source (Herrera 2002). In turn, fruits are a primary food sources for many animal species, at least temporarily (Willson & Traveset 2000).

---

[2] I term the package made up of the seed(s) plus the accessory nutritious tissues that are used by animals as food 'fruit' also it does not always originate from the ovary (see 'Seeds, fruits and diaspores').

As generally both partners gain some benefit from the interaction, the plant-seed disperser relationship often is called a mutualistic one (Herrera 2002). However, the outcome of ecological interactions is often complex and context-dependent. For example, animals select food items based on a complex set of criteria, including temporal and spatial food availability, perceptive abilities to locate food, morphological constraints, food quality, the animals' own nutritious requirements, and avoidance of toxins (Jordano 2000; Stiles 2000).

1.4.1.1 Diaspore Design and Effects on Fruit Choice and Seed Dispersal by Frugivores

Relevant morphological fruit traits that may influence an animal's choice of fruit include fruit type, fruit and seed size, and fruit colour (e.g. Howe & vande Kerckhove 1981; Knight & Siegfried 1983; Gautier-Hion *et al.* 1985; Janson *et al.* 1986; Stanley & Lill 2002; Jansen *et al.* 2004).

Fruit Type

Plants bearing soft, fleshy fruits like berries, drupes or functionally analogous structures represent the most widespread and diverse vertebrate-plant dispersal system (Herrera 2002). Other fruit types can set string constraints to fruit and seed handling, e.g. when pulp and seeds are protected in hard, indehiscent capsules or pods that can only be opened with strong teeth, bills, fingers, or elaborated fruit handling techniques (Janson 1983; Pratt & Stiles 1985; Stiles 2000).

Fruit and Seed Size

Fruit and seed size (respectively seed mass), which are typically correlated (Mack 1993; Leishman *et al.* 2000), are two key traits in plant-frugivore interactions (Herrera 2002). Relative to the body size of the frugivore, both set limitations to handling and ingestion of whole fruits/seeds by the animal (Wheelwright 1985; Jordano 2000).

The body size of frugivorous vertebrates spans about five orders of magnitude, ranging from tiny birds of 10-12 g (the flycatcher *Piprimorpha oliginea*) to the African elephant (*Loxodonta africana*) weighing 5,000-7,500 kg (Howe 1989).

Fruits and seeds dispersed by animals also vary considerably in size. Small seeds of *Miconia argentea* (Melasomaceae) weigh only 0.01 g whereas *Balanites wilsoniana* (Balanitaceae) seeds are as heavy as 40 g (reviewed in Howe 1989). Fruits may weigh up to several kilograms as in *Kigelia africana* (Bignoniaceae). Within families, Paleaotropical fruits tend to be larger than Neotropical ones (Mack 1993). Most fruit traits of vertebrate-dispersed plants show phylogenetic inertia, but size is an exception (Alcantara & Rey 2003, and references therein).

In general, both fruit and seed size of Angiosperms are correlated with the size of the frugivores that consume the fruits (Janson 1983; Alcantara & Rey 2003, and references

therein; see also Jordano 1995a). Small fruits with small seeds are typically dispersed by a greater number of animals than large fruits with large seeds (Wheelwright 1985; Howe 1989; Jordano 2000; Stiles 2000). Large soft fruits, that contain many small seeds, however, can also be dispersed by small frugivores, that are able to peck and swallow seeds with pieces of the pulp (Jordano 2000). Fruit and seed size seems less limiting in mammals than in birds; fruits eaten by mammals tend to be larger (Janson 1983; see also Wheelwright 1985). Seeds larger then 30 mm may be exclusively dispersed by large mammals (Tutin *et al.* 1991; Chapman *et al.* 1992). Some authors argue that some large frugivores like large monkeys are likely to ignore small fruits (≤ 0.5 g), probably because they are less profitable to exploit than large fruits (Howe 1989, and references therein).
On the other hand, size preference of small over large seeded fruits in birds (e.g. Jordano 1995b; Stanley & Lill 2002) may reduce costs of seed processing (Stanley & Lill 2002). In several bird species, seed size can influence the probability of seed regurgitation. Small birds tend to regurgitate more seeds per plant species than large birds (reviewed in Stiles 2000). In primates, seed size influences whether seeds are dropped during feeding or swallowed (Corlett & Lucas 1990; Kaplin & Moermond 1998). Data indicate that New World primates select smaller and larger seeds of some plant species, respectively, than available, when feeding on pulp or seed-arils (Howe & vande Kerckhove 1981; Garber & Kitron 1997; Stevenson *et al.* 2005). However, seeds of other plants are ingested irrespective of available size within the plant species (Russo 2003; Stevenson *et al.* 2005).

Seed size not only varies among species, but probably due to environmental effects during development often also among individuals of the same species, within plants, within infructescences (e.g. in panicles), and also within multi-seeded fruits (reviewed in Harper *et al.* 1970; see also Michaels *et al.* 1988; Leishman *et al.* 2000).
The seed size represents the amount of maternal investment to an individual offspring (Leishman *et al.* 2000). Given a defined amount of resources available to reproduction, an increase in seed size will reduce the number of seeds produced (seed number-seed size trade-off, Harper *et al.* 1970). Hence seed number and seed size represent alternative strategies in the deposition of reproductive resources (Harper *et al.* 1970). Seed size can also have consequences for early seed survival (see 'Post Dispersal Seed Fate') and seedling vigour. Seedlings emerging from larger seeds seem to generally have better competitive abilities and to survive better under environmental stress (reviewed in Leishman *et al.* 2000).

Fruit Colour

The importance of the many different colours of fruits is not completely clear, but the non-random use of certain fruit colours within animal guilds suggests the importance of at least certain colours as a signal to frugivores (Stiles 2000). Fruit colours can enhance conspicuousness of fruits and detection by frugivores and advertise far-ranging information on fruit maturity (Cooper *et al.* 1986; Giles & Lill 1999; Schaefer *et al.* 2004; Schmidt *et al.* 2004). Red and black fruits exhibit stronger contrasts against a background of foliage than other colours (Schmidt *et al.* 2004). 'Green' often signals unripeness and unpalability (but see Knight & Siegfried 1983; Herrera 2002).

The perception of the colour signal depends, however, on the contrasting sensory capacities of the receiver. In general, birds are tetrachromatic and UV-A sensitive (Varela *et al.* 1993; Bennett & Théry 2007), whereas most terrestrial mammals are dichromatic (Dominy *et al.* 2003). Among the primates, humans and all Catarrhines are trichromatic, which enables them to discriminate red-green (Dominy & Lucas 2001). In New world primates, males are dichromats in most species and about 60% of females are trichromats (Dominy & Lucas 2001, and references therein). Most nocturnal mammals seem to locate fruits by smell (e.g. civets) rather than vision, and colours of fruits dispersed by nocturnal frugivores are often dull (Whitmore 1998).

Fruit choice by frugivores on the basis of colour has been investigated most intensively in birds. Frugivorous birds often discriminate fruits on the basis of fruit colour and show preferences for brightly coloured (red, orange and black) as well as UV-reflecting fruits over white and dull (green and yellow) fruits (McPherson 1988; Sanders *et al.* 1997; Honkavaara *et al.* 2004). Red and black globally are the dominant fruit colours of bird-dispersed fruits (Willson & Whelan 1990a; Herrera 2002). Green and unripe fruits are avoided by many frugivorous bird species (Knight & Siegfried 1983; Sanders *et al.* 1997; Schaefer & Schaefer 2006). Ripe fruits that are green, yellow or brown tend to be dispersed by mammals (Herrera 2002; Urbani 2002), though diurnal Old World primates also heavily consumed brightly-coloured fruits (Gautier-Hion *et al.* 1985).

Fruit colour, however, may also be aimed at factors unrelated to consumption by dispersers. Phenolic pigments stored in the fruit husk can, for example, have antifungal effects. Red fruits are 'inconspicuous' for insect predators (Willson & Whelan 1990a). Fruits may be green because of photosynthetic compensation (Cipollini & Levey 1991).

1.4.1.2 Fruit and Seed Treatment, and the Effectiveness of Frugivores as Seed Dispersers

Regarding, for example, a small territorial, non-migratory bird and an elephant, it is evident that frugivores differ in the types and sizes of fruits they can select for consumption. According to their morphology, anatomy, physiology, and behaviour, animal species, even within the same frugivore guild (e.g. frugivorous birds), will also differ in their contribution as seed dispersers to the future reproduction of a given plant (reviewed in Schupp 1993; Stiles 2000). This contribution, called '*effectiveness of a seed disperser*' (*sensu* Schupp 1993) has a quantitative and qualitative component:

- The '*quantitative component*' includes the number of seeds dispersed per plant (a function of the number and duration of feeding visits to a plant and the number of seeds dispersed per visit).
- The '*quality of a seed disperser*' for a given plant depends on its external and internal seed processing behaviour as well as on the probability of dispersed seeds to become adult plants (Schupp 1993).

Differences among dispersers in the number of feeding visits to a certain plant can result from differences in the species' abundance, in the importance of (certain) fruits in their diet, and in their temporal and spatial reliability of visitations (throughout the fruiting season, the years; visiting some or all trees in a population) (Schupp 1993).

How a fruit/seed is handled by a frugivore while feeding affects the number of seeds handled per visit and the number of the handled seeds that are actually dispersed. Frugivorous birds, for example, may either swallow whole fruits and regurgitate or defecate seeds away from the parent plant, or ingest pulp and juice and drop the seed at the feeding place, or remove bits of pulp from the fruit while feeding (Moermond & Denslow 1985; Levey 1987; Jordano 2000).

Fruit and seed treatment by the frugivore as well as the physiology (gut retention times) and the ranging behaviour of the animal (habitat and microsite selection, rate and directionality of movement away from the parent tree, latrine use, use of roosting sites) will largely determine where dispersed seeds will land (Wenny 2001; Jordano & Godoy 2002), whether seeds will be deposited singly or in clumps (Schupp 1993) or otherwise aggregate (e.g. directed dispersal). Some microsites into which seeds are delivered are more suitable for germination and seedling establishment than others, the result of which can be extremely heterogeneous seedling recruitment patterns (Schupp 1993; Jordano & Godoy 2002) (see also section 'Why Disperse Seeds? Potential Advantages of Seed Dispersal'). Small vertebrates like bats or small birds usually drop, regurgitate or defecate single seeds or small numbers of seeds rapidly within a few meters from the source (scattered-dispersal) (Howe 1989). Larger frugivores (≥ 3 kg body weight) generally retain seeds for longer periods in the gut, may disperse seeds over larger distances, and tend to deposit several to large numbers of seeds per faecal clump. Most clumped dispersal is by mammals, but some large birds like the cassowary (*Casuarius casuarius*) also deposit seeds in clumps (reviewed in Howe 1989). The probability for a seed to establish from defecation can depend on the number of conspecifics and other seed species in the dropping (Loiselle

1990; Kaspari 1993), hence competition in faecal clumps can be an important component of the quality of dispersal (Schupp 1993). Seeds dispersed in a clumped manner may be more vulnerable to post-dispersal removal by seed-eating rodents and ants than scattered-dispersed seeds (e.g. Kaspari 1993; Zhang & Wang 1995).

A potential benefit of endozoochorous seed dispersal is enhanced germination after passage through the gut of the frugivore, e.g. through abrasive effects on the testa. Internal treatment of seeds is influenced by the morphological (long or short gut), physical and chemical conditions in the gut. Seed ingestion and gut passage can alter either or both the rate of and time to germination (Lieberman & Lieberman 1986; Barnea *et al.* 1990; Izhaki & Safriel 1990; Yagihashi *et al.* 1999; Nchanji & Plumptre 2003), but the effects are variable and seem to depend on the plant and/or animal species involved (Lieberman & Lieberman 1986; Barnea *et al.* 1990; Izhaki & Safriel 1990; Traveset & Verdú 2002). In a review of 351 germination experiments from different biomes and habitats, Traveset & Verdú (2002) found that gut passage mostly had a positive effect on germination percentage. Overall, birds and bats had stronger positive effects on germination than non-flying mammals and reptiles, probably due to the shorter gut passage time of birds and bats (Traveset & Verdú 2002). Germination of seeds from dry fruits, however, was generally negatively affected by ingestion. The positive effect on germination was higher on large than on small and medium sized seeds, and was more pronounced in the tropics than in temperate zones (Traveset & Verdú 2002). (The latter may, however, result from the fact that tropical plants often have larger seeds than plants in the temperate zone, see Harper *et al.* 1970).

In addition, deposition of seeds with dung may provide a nutrient source for early seedling growth (Stiles 2000). However, post-dispersal seed predators are often attracted by the smell of the dung (see also 'Post-Dispersal Seed Fate').

What disperser characteristics will be most important for the qualitative component of seed dispersal depends on the most critical advantage of dispersal for the plant. If escape from the vicinity of the parent plant is critical, disperser attributes that aid movement away from the parent plant and conspecifics will be most important. If distance from the parent tree is crucial for seed survival, an important component of disperser effectiveness will be how far away seeds are dispersed (Jordano 2000). If colonization to suitable but unpredictable sites are crucial, than widespread dispersal of seeds may be most important (Schupp 1993). In any case, the spatial distribution of the seeds determines the conditions under which the seeds live or die.

1. 5 THE SPATIAL DISTRIBUTION OF SEEDS: SEED RAIN, SEED SHADOW, AND DISPERSAL DISTANCES

The *seed rain* is the flux of seeds from reproductive plants without considering space explicitly (Nathan & Muller-Landau 2000).

The *seed shadow* is the spatial distribution of dispersed seeds in relation to their source and other conspecifics (Nathan & Muller-Landau 2000; Jordano & Godoy 2002). Seed shadows have two horizontal dimensions for most plants (epiphytes have a third, vertical dimension) and can be described by two factors: (1) the number (or density) of dispersed seeds in relation to the distance from the source, and (2) the directionality with regard to the seed source (Willson & Traveset 2000).

In most plant species, the vast majority of seeds fall beneath the parent plant or are dispersed within several meters. Generally, only a few seeds are dispersed over very long distances. In the majority of empirical seed dispersal data, the seed density-distance relationship thus follows a leptokurtic distribution, with a high peak relatively close to the seed source and a very long tail (Stiles 2000; Willson & Traveset 2000; Clark *et al.* 2005). Clark *et al.* (2005) found that the seed shadow of animal-dispersed tree species was best described by an inverse power function, whereas Gaussian- and Student *t* functions best fitted the seed shadow of wind-dispersed tree species.
Several factors outside of the plant's control can alter the seed shadow from random distribution. Abiotic means of dispersal may accumulate seeds, e.g. downwind, downstream, or downhill (Willson & Traveset 2000). Many frugivores create a highly heterogeneous and aggregated seed rain (see 'Fruit and Seed Treatment'). As a consequence of aggregated seed shadows most sites in the landscape receive no or few seeds despite high fruit production - seed delivery is insufficient to saturate suitable microhabitats for plant establishment. This so called 'dissemination limitation' or 'dispersal limitation' may be a rather general characteristic of frugivore-generated seed shadows (Jordano & Godoy 2002; Muller-Landau *et al.* 2002).
Geritz *et al.* (1984) calculated optimal dispersal curves as a function of seed production, safe site area, and boundary of the habitat. They showed that dispersal curves with short tails are most efficacious when safe sites are small or few propagules are produced. Longer dispersal curves are more advantageous when safe sites are larger or more propagules are produced. Plants that disperse over short distances might compensate for their poor spatial dispersal by means of extended dormancy, thus dispersing in time (Willson 1993).

Morphological adaptations to seed dispersal generally increase dispersal distances yet vary in their effect on distances achieved. Typically, long-distance dispersal capacity is higher in wind- or vertebrate-dispersed plant species than in species dispersed by ants or by ballistic mechanisms (Willson & Traveset 2000). Seeds that reach distant islands were often carried by water, wind or inside bird guts or feathers (reviewed in Willson & Traveset 2000).

In contrast to Willson (1993), Clark *et al.* (2005) found that animal dispersed species had longer mean dispersal distances than wind-dispersed species (but lower fecundity). Seed shadows, however, can vary widely even within species and dispersal vectors (Clark *et al.* 2005). Long-distance seed dispersal can also result from non-standard means of dispersal (that is when seeds are transported by means other than diaspore morphology indicates, e.g. wind transport of seeds that lack obvious appendages of increased air resistance) (Higgins *et al.* 2003).

The ability of a species to reach distant habitats may be a critical feature in maintaining biodiversity, particularly with regards to an increasing habitat fragmentation (Ouborg *et al.* 1999; Levin *et al.* 2003). The seeds in the 'tail of the distribution' (*sensu* Portnoy & Willson 1993), though less common, potentially spread the genes more widely and help maintaining the genetic diversity of the plant species' metapopulation (Portnoy & Willson 1993; Stiles 2000; Herrera 2002). In addition, where density-dependent mortality factors are active, even low levels of long-distance seed dispersal may become disproportionately important for plant recruitment (Portnoy & Willson 1993; Nathan & Muller-Landau 2000).

However, the probability for any seed to establish is very low (Wenny 2001, and references therein). Some authors argue, that the post-dispersal processes (as a whole) are likely to have at least an effect on the spatial distribution of plants within communities as great as primary dispersal itself (Chambers & MacMahon 1994). The effectiveness of a seed disperser (*sensu* Schupp 1993) cannot be accurately evaluated without considering the post-dispersal fate of seeds (Estrada & Coates-Estrada 1986; Garber & Lambert 1998; Andresen & Levey 2004; Vander Wall *et al.* 2005).

1. 6 POST-DISPERSAL SEED FATE: WHAT HAPPENS TO A SEED AFTER PRIMARY DISPERSAL?

Seeds may be destroyed after primary dispersal (also called 'initial dispersal') by abiotic and biotic factors. They may land in habitats or microsites unsuitable for germination, may be attacked by fungi and pathogens, may be eaten by granivores, or burrowed at depths too deep for seedling emergence (Fenner & Thompson 2005). Processes like post-dispersal seed predation and secondary seed dispersal can alter the template set by primary dispersal (Nathan & Muller-Landau 2000).

1.6.1 POST-DISPERSAL SEED PREDATION

Dispersed seeds represent a diverse and spatially heterogeneous resource, and most of the animal species involved in post-dispersal seed predation are mobile, generalist herbivores, such as insects (mainly ants and beetles), crabs, fish, birds, and mammals (especially rodents) (Crawley 2000; Hulme & Benkman 2002).

Post-dispersal seed predation reduces the number of dispersed seeds and affects the spatial distribution of seeds (Hulme & Benkman 2002). Post-dispersal seed predation rates can be very variable in space and time (Schupp 1988a; Crawley 2000), depending, for example on the kind of animal that defecates the seeds and how much dung is defecated, what seeds are dispersed, how many seeds are dispersed and where the defecation lands (Janzen 1986; Schupp 1988b; Brewer & Rejmanek 1999; Alcantara *et al.* 2000; Andresen 2002b; see also Fenner & Thompson 2005). Some authors argue that post-dispersal seed predation often is more severe than pre-dispersal seed predation (Crawley 2000; Hulme & Benkman 2002), with rates averaging about 60% (Hulme & Benkman 2002). Losses of up to 100% of the dispersed seeds may be achieved (Andresen 1999; Crawley 2000; Wenny 2000). Yet it may lead to marked effects on seedling recruitment only when recruitment is not microsite-limited (Crawley 2000).

In studies of post-dispersal seed fate, however, seed removal from primary deposition sites often is equated with seed predation without considering secondary dispersal, hence predation rates are potentially overestimated (reviewed in Vander Wall *et al.* 2005).

1.6.2 SECONDARY SEED DISPERSAL

Seed dispersal often is a multi-step process that includes more than one dispersal agent or means of seed movement. Ants, dung beetles, birds, rodents, and abiotic factors can disperse seeds secondarily from the place of primary deposition (Vander Wall *et al.* 2005). Gravity, for example, can move primary dispersed seeds downhill in steep terrains, eventually by the aid of wind and water (see also Kaspari 1993; Chambers & MacMahon 1994). Seeds that are dispersed ballisticly or by birds from the parent plant may be further dispersed by ants (Westoby & Rice 1981; Böhning-Gaese *et al.* 1999). Seeds that are wind dispersed may be further dispersed by cache hoarding rodents (reviewed in Vander Wall & Longland 2004). Seeds that are transported in animal guts may be removed from dung piles by dung beetles (Scarabaeidae), rodents, or ants (Kaspari 1993; Levey & Byrne 1993; Andresen 1999; and reviewed in Vander Wall & Longland 2004).

Combining two (or more) means of dispersal can increase the benefits of seed dispersal and reduce seed mortality (Vander Wall & Longland 2004) (see Table 1). Plants that are clump-dispersed usually do not produce more than one adult from a single faeces. Secondary seed dispersal can reduce the spatial patchiness of dispersed seeds by scattering seeds locally, thereby also reducing seedling competition (Howe 1989; Kaspari 1993; Böhning-Gaese *et al.* 1999; Feer & Forget 2002).

Secondary seed dispersal often moves the seeds to discrete microsites favourable for seedling establishment (e.g. below ground) (Vander Wall & Longland 2004). Seeds dispersed secondarily from faeces by rodents, dung beetles, or to ant nests often have a higher probability of seedling establishment than seeds remaining at the primary deposition (reviewed in Vander Wall & Longland 2004).

Burying may decrease the risk of being eaten by a seed predator (Andresen 1999; Fenner & Thompson 2005), prevent seeds from desiccation (Vander Wall & Longland 2004) and may facilitate seed germination (Estrada & Coates-Estrada 1991; Estrada *et al.* 1993; Feer 1999) but the effects are species specific and are related to depth of burial, soil conditions (Price & Correll 2001) and seed size (Fenner & Thompson 2005).

Primary and secondary dispersal agents do not necessarily favour selection of the same diaspore traits. For example, cache-hoarding rodents may select for large seeds of wind dispersed species (e.g. pine seeds), but aerodynamic constraints will result in shorter primary dispersal distances of these large seeds (Vander Wall & Longland 2004).

In the following section I will further define what militates against the once favoured view of close coevolution between plants and their animal dispersers.

Table 1 General comparison between primary and secondary seed dispersal following Vander Wall & Longland (2004)

	Primary seed dispersal (Phase I)	**Secondary seed dispersal (Phase II)**
Benefits	Reduction of high seed density and seedling competition near parent plant; colonization of new sites	Reduction of seed predation; (further reduction of seed density and seedling competition)
Dispersal distances	Often relatively large (except ballistic dispersal)	Short in comparison to Phase I
Sites	Often undirected and unpredictable, often unsuitable	More or less directed, often predictable, suitable sites
Deposition	Mostly on soil surface	Often burrowed or cached
Likelihood of establishment at deposition site	Often low	Often increased relative to Phase I

1. 7 COEVOLUTION BETWEEN PLANTS AND THEIR SEED DISPERSERS?

Snow (1971) suggested that the production of abundant, conspicuous, easily accessible and nutritious fruit crops is designed to attract the greatest number and variety of disperser possible. This led to the dichotomy view of specialist versus generalist fruit plant species and disperser quality with the implication of a close coevolution between certain pairs or small sets of species. Large, single seeded fruits with pulp of high nutritive value would be associated with high-quality seed dispersal by specialized frugivores, whereas watery, carbohydrate-rich fruits with numerous seeds would be dispersed primarily by opportunistic frugivores (reviewed in Howe & Smallwood 1982; Whitmore 1998; Jordano 2000; Wenny 2001).

As studies frequently failed to find clear adaptations, at least of plants to their animal dispersers (Herrera 1986), the paradigm of disperser-plant coevolution changed to a diffuse, weak mutual, non species-specific adaptation between large groups of plants and groups of dispersers (Janson 1983; Howe 1984a; Jordano 1995b; Lambert & Garber 1998; Herrera 2002).

Several facts conflict with a tight coevolution between species pairs of plants and animal dispersers:

- No obligate mutual dependences between species pairs of plants and animals are known (Herrera 2002). Plants are rarely dispersed by one animal species alone (Herrera 2002). Only a few exceptions have been found, e.g. African elephants (*Loxodonta africana*) are probably the only seed dispersers of *Balanites wilsoniana* (Chapman *et al.* 1992). The once favoured notion of the endemic tree *Calvaria major* and the dodo (*Raphus cucullatus*) has been dismissed by further investigations (Witmer 1991). Frugivores frequently face temporal shortages of fruits and shift their diets accordingly to other (taxonomically unrelated) fruit plant species, other plant parts or animal prey (Jordano 2000; Herrera 2002). The variable (and often unpredictable) fruit availability adds an important stochastic component to plant-frugivore interactions. Consequently, selection pressures associated with the interactions between plants and their seed dispersers will also vary in space and time and limit the possibilities of frugivore specialization on plants (Jordano 2000; Herrera 2002). Mutualism must thus often rather represent chance association, not coevolution, and examples in which one animal taxon is identifiable as the most important local mutualist for a plant may often reflect relative abundance of the species, not foraging specialization (Howe 1984a).
- Trade-offs against selective forces imposed by abiotic factors and non-mutualistic organisms. The same traits that are important in plant-frugivore interactions (e.g. crop size, fruit colour, pulp constituents) may also affect the interplay between plants and fruit /seed damaging agents (seed predators like frugivorous insects, pathogens) and are

likely to exhibit some evolutionary pressure (reviewed in Herrera 1986, 2002; see also Chambers & MacMahon 1994).

- Moreover, other stages of the life cycle, e.g. pollination, set constrains to fruit traits and time of fruiting (Jordano 2000, and references therein). Factors like climate (alteration of dry and rainy seasons), time needed for fruit growth, and the need of moisture for seed germination will also affect time of fruiting (Jordano 2000, and references therein). Adequate resource provision of seeds (reflected in seed mass) must be traded-off against dispersal probabilities and survival of seeds and seedlings (see also 'Post-Dispersal Seed Fate').
- The existence of sources of variance in dispersal that lie outside the control of the parent plant. These include growing-sites specific attributes, called the 'fruiting environment' by Howe (1984a) and Herrera (1986). For example, characteristics of the surrounding vegetation like height of plants or patchiness of the habitat and spatial and temporal interferences with other fruiting plants that attract the same seed dispersers can affect fruit removal rates and seed shadows of a given plant.
- Against previous assumptions of evolutionary plasticity in fruiting traits, several fruit characteristics seem to be subject to phylogenetic constraints, including fruit type and nutrient content of fruit pulp (reviewed in Herrera 1986). Many lineages of angiosperms with fleshy fruits have remarkably stable fruit traits since the Eocene and Oligocene, despite facing changing ecological conditions and a turnover in disperser faunas (reviewed in Herrera 1986; see also Jordano 1995a).
- Polygenetic inheritance promotes uneven rates of evolution among mutualists, leading, at best, to asymmetrical coevolution, in which one member of the pair has more potential to respond to selection from organisms outside the mutualism (Howe 1984a). Several studies confirmed enhanced genetic homogeneity of plant populations, with local generic structuring being less frequent among animal-dispersed plants. If animal seed dispersal consistently smoothes out spatial genetic variances of plant populations at large spatial scales, than animal-dispersed plants will have a low probability of regional differentiation, including adaptations to dispersal agents (reviewed in Herrera 2002).

The design of fruits is thus likely to be the resulting compromise from the many, potentially conflicting selection pressures. In the next section, I will address one of these conflicting selection pressures in more detail: pre-dispersal seed predators, which exploit the system without dispersing viable seeds.

1. 8 MOSTLY ANTAGONISM - VERTEBRATES AS PRE-DISPERSAL SEED PREDATORS

Neither disperse all vertebrates the seeds of the fruits they consume, nor are dispersed seeds always viable. Fruit thieves discard the seeds during pulp consumption (e.g. Levey 1987). Frugivores may temporarily feed on fruits prior to fruit and seed maturity (Foster 1977; Schaefer & Schaefer 2006). On the other hand, frugivores that swallow whole seeds while feeding on ripe pulp may defecate seeds that are not viable after gut passage (e.g. Idani 1986). Animals may also directly feed on seeds and destroy them during consumption (Hulme & Benkman 2002). In the latter three cases, the animals act as pre-dispersal seed predators.

In temperate woodlands, a few species of small mammals are the main pre-dispersal seed predators, whereas in the humid tropics, invertebrates as well as several species of mammals of different size play an important role (Hulme & Benkman 2002). In more arid ecosystems ants are pre-dispersal seed predators rather than dispersers of seeds (Hulme & Benkman 2002). Marked intercontinental differences in the relative importance of different guilds occur – rodents seem more important in terms of seed mass removed per time in the northern hemisphere and ants more in the southern hemisphere (Hulme & Benkman 2002).

Several bird species are granivorous, including some Passeriformes and pigeons, parrots (Psittaciformes), and gallinaceous birds (Galliformes), among others. Seed-eating mammals are found primarily within the rodents (Rodentia), including squirrels (Sciuridae), heteromyd rats (Heteromyidae), cricetid rats (Cricetidae), and murid rats (Muridae) (Stiles 2000). However, some seeds eaten by granivores may accidentally survive ingestion undamaged. Cache-hoarding seed eaters like some rodents and birds, that store seeds away from the parent plant for later consumption, can act as seed dispersers when seeds escape recovery (Vander Wall 1994; Herrera 2002; Jansen *et al.* 2004), i.e. during temporally superabundant seed crops (Forget *et al.* 2002; Herrera 2002; Jansen *et al.* 2004). Generally, however, survival and germination of cached seeds is low, often much less than 10% (reviewed in Hulme & Benkman 2002). It often remains unclear whether regeneration is higher in the presences or absence of cache-hoarding animals (Hulme & Benkman 2002).

Animals are expected to forage in a way that maximizes fitness. The nutritious content of the fruit pulp is the critical element in the plant-frugivore interaction (Herrera 2002). Though varying widely among fruit species, fruit pulp generally is best described by a high water content and an extreme deficiency in some compounds relative to others (Jordano 2000; Herrera 2002). Typically, the content of digestible energy is high relative to protein content (Jordano 2000; Herrera 2002). Lipid content can be relatively high, but shows large interspecific variation (Jordano 2000). The pulp also contains varying amounts and types of vitamins, carotenoids, amino acids and minerals (Herrera 2002). Frugivorous animals must cope with the nutritional constraints of fruits, particularly nitrogen deficiency. Many frugivorous animals regularly ingest some animal matter (Jordano 2000; Herrera 2002), are temporarily granivorous or feed on the seeds of certain plant species (Hulme & Benkman 2002). Compared to other plant tissues, seeds contain high contents of nutrients (Crawley 2000; Hulme & Benkman 2002). In particular, seeds of many legume species are rich in protein and are highly sought after (Whiten *et al.* 1991; Duranti & Gius 1997; Gathua 2000; Barnes 2001; Norconk & Conklin-Brittain 2004).

A frugivore thus may act as a pre-dispersal seed predator in some but not in other plant species (Jordano 2000; Herrera 2002), or in the same plant species in one fruiting season but not in another (Foster 1977; Schaefer & Schaefer 2006). Consequently, the traditional dichotomy into seed dispersers versus seed predators oversimplifies the interaction between animals and their food plant (Norconk *et al.* 1998).

1.8.1 Potential Effects of Pre-Dispersal Seed Predators on Seed Dispersal and Plant Recruitment

Pre-dispersal seed predators reduce the number of seeds available to dispersal. Up to 100% of the seed crop may be destroyed (Peres 1991; Tutin *et al.* 1996), but the proportion varies between habitats, locations, plant species and individual plants (Fenner & Thompson 2005). Moreover, a reduction in crop size may result in decreased visits by seed dispersers, both in numbers and in species, altering the seed shadow quantitatively and qualitatively (Dirzo & Domínguez 1986). Beyond a certain minimum crop size, plants may even become unattractive to dispersers (Dirzo & Domínguez 1986).

Seed predation can benefit biodiversity when the relative recruitment success of competitively superior plant species is reduced (Pacala & Crawley 1992; Howe & Brown 2001) e.g. if larger seeds, which often have better competitive abilities than small seeds, are the main targets of seed predators, or if seed predators select against the most abundant seeds at a site (Howe & Brown 2001; Hulme & Benkman 2002; Fenner & Thompson 2005). It may, however, affect plant recruitment and plant community structure only if regeneration is seed-limited (Fenner & Thompson 2005). 'Seed limitation' (also called 'source limitation') exists when fruit production is insufficient to produce enough seeds to reach all available safe sites, independent of frugivory activity (Muller-Landau *et al.* 2002). If plant propagation primarily is by vegetative means, if a large seed bank buffers seed losses, if large seed crops satiate seed predators (or alternatively seed predator densities are kept low by other factors such as predation), or if regeneration is microsite-limited, seed predation may be of minor importance for plant population dynamics (Hulme & Benkman 2002).

So far, I have given a general overview of seed dispersal with special emphases on the role of animals as seed dispersers and seed predators. The following sections highlight the region of the world where plant-frugivore-interactions are most prevalent – the tropics – and an important group of each primary and secondary disperser in these ecosystems – primates and dung beetles.

1. 9 FRUGIVORY AND SEED DISPERSAL IN TROPICAL ECOSYSTEMS

Many tropical ecosystems are characterized by a remarkably high biodiversity and plant-animal interactions play an important role in maintaining their structural and dynamic properties (Howe 1984b). Frugivory is seen as a central process for the natural regeneration of plant communities in tropical forests, where up to 94% of the woody plant species rely on endozoochorous seed dispersal by vertebrates (reviewed in Howe 1982, and Jordano 2000). There is evidence that tropical tree species deprived of their dispersal agents can exhibit severe recruitment decline (Chapman & Onderdonk 1998; Nuñez-Iturri & Howe 2007; Wang *et al.* 2007).

In general, the proportion of plant species with adaptations for endozoochorous dispersal is highest among trees and shrubs and lowest among herbs, hence decreases from forests to scrubland to herbaceous formations, and from tropical wet to dry habitats (Dirzo & Domínguez 1986; Howe 1989; Herrera 2002). Within each growth form, the proportion of vertebrate dispersed plant species decreases with increasing latitude, altitude and aridity (Willson *et al.* 1990; see also Dirzo & Domínguez 1986).

Frugivorous vertebrates also follow the overall latitudinal trend in terrestrial species diversity; most frugivorous species occur in the tropics (Herrera 2002). Important tropical frugivores include, among others, many species of birds (e.g. Heindl & Curio 1999; Loiselle & Blake 2002; Cordeiro & Howe 2003; Weir & Corlett 2006), bats (Medellin & Gaona 1999; Shilton *et al.* 1999; Hodgkison *et al.* 2003), civets (Engel 1999; Kitamura *et al.* 2002), duikers (Feer 1995; Hofmann & Roth 2003), elephants (Yumoto *et al.* 1995; Nchanji & Plumptre 2003), and many primate species (Lieberman *et al.* 1979; Tutin *et al.* 1991; Wrangham *et al.* 1994; Julliot 1996b; Chapman & Onderdonk 1998; Poulsen *et al.* 2001; Knogge & Heymann 2003; Bollen *et al.* 2004; Link & Di-Fiore 2006; McConkey & Chivers 2007).

The range of size of frugivores in the tropics is greater than in the temperate zone (Herrera

2002). Seed dispersal by vertebrates generally is associated with large seeds (Herrera 2002). As growth form and seed size are correlated, the frequency of plant species with large fruits is highest in wet tropical ecosystems; tropical forests include considerably larger fruits than temperate forests (Herrera 2002).

In contrast to their temperate counterparts, tropical frugivores generally exploit fruits whole year round, though seasonal dietary shifts occur (Jordano 2000).

Not surprisingly, studies to date on plant-frugivore interactions in the tropics focused mainly on forest ecosystems. Comparatively little is known about the role of vertebrate frugivores in seed dispersal and natural plant regeneration in drier and more open tropical and subtropical habitats, such as the savannas of Africa. Savanna ecosystems cover about 65% of the African continent (Tischler 1993). Africa's savannas are highly vulnerable to land degradation with considerable impacts on land cover and biodiversity (UNEP 2007). The populations of several major savanna tree species are declining (Gijsbers *et al.* 1994; Lykke 2000).

In West Africa, two floras intervene in the latitudinal belt of the Guineo-Congolia / Sudania transition zone and form the species rich forest-savanna-mosaic (White 1979; Poorter *et al.* 2004). Here, the number of woody fruit plant species providing fleshy fruits for dispersal by animals is particularly high (Hovestadt *et al.* 1999). However, factors influencing the interactions between the fruiting plants and their seed dispersers and seed predators in Afrotropical landscapes remain largely unknown (Githiru *et al.* 2002).

1.9.1 Primates as Seed Dispersers and Pre-Dispersal Seed Predators

Primates are among the major group of frugivores in the tropics (Lambert & Garber 1998; Stiles 2000); almost all diurnal primate species include fruits and seeds in their diet (Hladik 1981; Stiles 2000). Frugivorous primates are important seed dispersers and pre-dispersal seed predators for many of their food plant species (Lieberman *et al.* 1979; Gautier-Hion 1984; Zhang & Wang 1995; Julliot 1996b; Chapman & Onderdonk 1998; Norconk *et al.* 1998; Otani & Shibata 2000; Barnes 2001). With their often high biomass and relatively large home ranges, primates are able to harvest considerable amounts of fruit crops (Peres 1991; Chapman & Chapman 1996; Tutin *et al.* 1996; Voysey *et al.* 1999a). They are able to move high numbers of seeds over wide areas (Wrangham *et al.* 1994; Link & Di-Fiore 2006; McConkey & Chivers 2007). By choosing among and within fruiting individuals, they may thus be able to shift the overall fruit production towards a distinct subset of dispersed seeds (see also Jordano 1995b).

Like other frugivores, primates vary in their effectiveness (*sensu* Schupp 1993) as seed dispersers due to differences in morphology, physiology, feeding and ranging behaviour (Rowell & Mitchell 1991; Zhang & Wang 1995; Kaplin & Moermond 1998). Nonhuman primate species that include fruits in their diet range in size from the small dwarf lemurs (Cheirogaleidae), marmosets and tamarins (Callitrichidae), which weigh only a few hundred grams, to the large gorillas (*Gorilla gorilla*) (males weighing up to 175 kg) (Rowe 1996). Large primates with large home ranges and long gut retention times may disperse seeds over wider areas than small species with small home ranges which pass seeds rapidly through their digestive tract (see e.g. Garber 1986; McConkey 2000). Some primate species (i.e. species of the subfamilies Colobinae and Pitheciinae) are primarily granivorous and disperse seeds only occasionally (Harrison & Hladik 1986; Norconk *et al.* 1998). Several large primate species like baboons (*Papio* sp.) and chimpanzees (*Pan troglodytes*) disperse seeds in large faecal clumps, whereas smaller species like guenons (*Cercopithecus* spp.) and tamarins (*Saguinus* spp.) tend to disperse smaller seed numbers at a time (Lieberman *et al.* 1979; Wrangham *et al.* 1994; Poulsen *et al.* 2001; Knogge & Heymann 2003). Some species like spider monkeys (*Ateles* spp.) and howler monkeys (*Alouatta* spp.) may scatter seeds over small areas when defecating from trees (Andresen 2002b; Ponce-Santizo *et al.* 2006).

Unlike many other frugivores, primates are able to handle a wide variety of different fruit types and sizes. With their fingers and teeth they can handle and open even large, and indehiscent fruits with a hard pericarp (see e.g. Julliot 1996a).

Whether primates disperse the seeds of their food plants largely depends on the mode of oral seed processing during fruit consumption; primates may either swallow entire seeds, remove pulp and spit or drop the seeds, or masticate the seeds (reviewed in Lambert 2002). Some primate species are considered particularly important for the dispersal of large-seeded fruits, that many other frugivores cannot swallow, at least not without serious damage of the seeds (Chapman & Onderdonk 1998; Peres & van Roosmalen 2002; but see Dominy & Duncan 2005; Nuñez-Iturri & Howe 2007). On the other hand, many primates seem to drop large seeds rather than small seeds at the feeding site when feeding on fruit pulp or seed arils (Corlett & Lucas 1990; Kaplin & Moermond 1998; Dominy & Duncan 2005). Where separation of seeds from the pulp is difficult, primates may select small seeded fruits within a fruit plant species (Howe & vande Kerckhove 1981; Russo 2003; Stevenson *et al.* 2005). Primate body size is not always a reliable indicator for the size of dispersed seeds. Small tamarins disperse intact seeds as large as many other much larger primate species, including apes (reviewed in Garber & Kitron 1997). Evidence suggests that most seed species spat or defecated by primates are able to germinate (Chapman & Onderdonk 1998).

Diminution or eradication of primate populations can negatively affect seed dispersal and local seedling recruitment of animal-dispersed plants (Chapman & Onderdonk 1998; Nuñez-Iturri & Howe 2007; Wang *et al.* 2007; see also Wright *et al.* 2000), many of which have some utility to humans (Lambert 1998).

Most of the approximate 240 extant nonhuman primate species (Rowe 1996) are tied to forests, and, not surprisingly, studies on the interplay between primates and their fruit plants mainly were conducted in forest ecosystems. Nonetheless, several primate species, including the olive baboon (*Papio anubis* Lesson 1827) range within the savannas of Africa.

1.9.1.1 The Olive Baboon (*Papio anubis* Lesson 1827)

Order Primates
  Suborder Anthropoidea
    Infraorder Catarrhini
      Family Cercopithecidae
        Subfamily Cercopithecinae
          Genus *Papio*

Within the higher primates (suborder Anthropoidea) baboons (*Papio*[3] spp.), like all Old World monkeys and apes, belong to the Infraorder Catarrhini. The distinctive feature, which separates the Catarrhines from the Neotropical Platyrrhini, is the shape of their nose: the nostrils in Catarrhines face downwards and are narrow. In the family Cercopithecidae, Old World monkeys (macaques, baboons, guenons, colobines) are separated from the apes. Anatomical features related to dietary adaptations further divide the Cercopithecidae into two subfamilies, Cercopithecinae and Colobinae. Baboons belong to the subfamily Cercopithecinae, characteristic of which are low cusp molars, consumption of fruits, and cheek pouches in which they can store food (Rowe 1996).

The phylogeny and taxonomy of the genus *Papio* still is disputed (Jolly 1998; Sarmiento 1998; Groves 2001, D. Zinner pers. comm.). Until further genetic analyses reveal more details, I follow Groves (2001) and distinguish five different species (chacma baboon *P. ursinus*, yellow baboon *P. cynocephalus*, olive baboon *P. anubis*, Guinea baboon *P. papio,* hamadryas baboon *P. hamadryas*). I henceforth refer to the first four species as 'savanna baboons', a term which separates the 'desert baboon' *P. hamadryas* by differences in habitat occupancy and socio-ecology (e.g. Melnick & Pearl 1987; Estes 1991).

---

[3] Some authors also include the three species drill (*Mandrillus leucophaeus*), mandrill (*M. sphinx*) and gelada (*Theropithecus gelada*) into the term 'baboon' but I will only refer to the genus *Papio*.

The status of the whole genus is at 'lower risk of extinction' (IUCN 2007).

The overall phylogeny combined with analyses of mDNA and fossil records suggest that the genus *Papio* originated and expanded from southern Africa at approximately 1.8 Ma (Newman *et al.* 2004). *Papio* thus emerged at a time when a global decrease in temperature and rainfall lead to a spread of grassland and scrub in Africa (Henzi & Barrett 2005). Baboons are still commonly associated with savanna habitats in West and East Africa, yet occupy a diverse array of climatic regimes and habitats from semi-dessert and thorn scrub to savanna, rain forest, coastal areas and sub-alpine grassland across their whole range in sub-Saharan Africa (Wolfheim 1983).

Due to their wide distribution and ecological flexibility, *Papio* spp. has long since been a focal target in studies on behavioural and ecological plasticity in primates (e.g. Hall & DeVore 1965; Rowell 1966; Altmann & Altmann 1970; Dunbar & Nathan 1972; Buirski *et al.* 1973; Harding 1976; Hamilton *et al.* 1978; Rhine & Westlund 1978; Anderson 1981; Post 1981; Strum 1981; Depew 1983; Whiten *et al.* 1987; Barton *et al.* 1992; Bercovitch & Strum 1993; Byrne *et al.* 1993; Dunbar 1994; Sapolsky 1996; Cowlishaw 1998; Castles *et al.* 1999; Zinner & Deschner 2000; Henzi & Barrett 2003; Warren 2003; Hill 2006).

Savanna baboons are known as eclectic omnivores (e.g. Altmann 1998). They include a variety of different plant items and animal matter into their diet (Hamilton *et al.* 1978; Harding 1981; Stacey 1986; Barton 1989). In a recent review Hill & Dunbar (2002) high-lighted fruits, leaves and subterranean items as the most important baboon food, but foraging profiles show a considerable variation across different sites (Whiten *et al.* 1991; Hill & Dunbar 2002). Field research up to date has focused on populations in East and southern Africa. Dunbar (1992) listed 31 *Papio* studies, of which only three were carried out on western populations. Several of these studies as well as more recent ones (e.g. Dunbar 1994; Bronikowski & Altmann 1996; Cowlishaw 1999; Hill *et al.* 2000; Hill & Dunbar 2002) deal with baboon (socio)ecology but there is very few data on how baboons, in turn, influence their environment, i.e. through seed dispersal and pre-dispersal seed predation (but see Lieberman *et al.* 1979; Refisch 1995; Hovestadt 1997; Gathua 2000; Barnes 2001).

Among the baboons, *P. anubis* is the biggest and most widely distributed species. With a body mass of 22-37 kg adult males double the weight of females (Rowe 1996). The range of the olive baboon extends from Mali and Guinea in the West throughout sub-Saharan West- and Central Africa to Ethiopia, Kenya, and northern Tanzania in the East (Sarmiento 1998; Groves 2001). Corresponding to the high ecological flexibility, olive baboons vary in their social organization. They form social groups ranging from small one-male-multi-female units to, more often, multi-male-multi-female groups comprising several dozens to a hundred individuals (Buirski *et al.* 1973; Nagel 1973; Rose 1977; Packer 1979; Barton &

Whiten 1993; Sambrook *et al.* 1995; Castles *et al.* 1999). Females are generally philopatric, whereas males emigrate with sexual maturity (Henzi & Barrett 2005).

Of the above-mentioned 31 baboon studies reviewed by Dunbar (1992) merely one investigated olive baboons in West Africa. Since Dunbar's review (1992), only one additional study on the behavioural ecology of western olive baboons has been reported (Nigeria, Warren 2003). Our knowledge on olive baboons in West Africa thus is very fragmentary. Data from Ghana (Depew 1983) and Nigeria (Warren 2003) suggest that western populations of the olive baboon form smaller groups, occupy smaller home ranges, and spend more time feeding on fruits and seeds than their conspecifics in East Africa. In West Africa the olive baboon is highly frugivorous, spending about 60% of feeding time eating fruits and seeds (Depew 1983; Warren 2003) and dispersing seeds of 31 to 51 dicotyledonous species per study site (Lieberman *et al.* 1979; Hovestadt 1997). Fruits of both forest and savanna species are consumed (Hovestadt 1997; Warren 2003).

Being a habitat generalist and able to move comparatively long distances, the olive baboon might act as a keystone species for the maintenance of the diversity of woody plants in the savanna-forest mosaic of West Africa.

1.9.2 DUNG BEETLES (COLEOPTERA, SCARABAEIDAE) AS SECONDARY SEED DISPERSERS

Recent studies in tropical ecosystems indicate that seed dispersal by vertebrates is often followed by secondary seed dispersal of rodents, ants or dung beetles from dung (Kaspari 1993; Levey & Byrne 1993; Adler & Kestell 1998; Blate *et al.* 1998; Shepherd & Chapman 1998; Andresen 1999; Alcantara *et al.* 2000; Forget *et al.* 2002; Jansen *et al.* 2002). Whereas rodents and ants are often simultaneously antagonistic and mutualistic towards seeds, dung beetles do not directly feed on seeds. They use the dung for feeding and to provision their larvae, and by removing small portions from the source they may accidentally disperse some seeds incorporated in the faecal material.

The true dung beetles[4] include the family Scarabaeidae (about 5,000 species), the subfamily Aphodiinae of Aphodiidae (about 1,850 species mostly in the genus *Aphodius*), and the subfamily Geotrupinae of Geotrupidae (about 150 species) (Hanski 1991).

Dung beetles range in body size from some small *Onthophagus* spp. weighing only about 3 mg to large dung beetles weighing 25 g (Cambefort 1984, 1991a). Generally, small species

---

[4] Some beetle species of other families (Hybosoridae, Chironidae, Trogidae) also use dung at the larvae or adult stage, and several species of Hydrophilidae and Staphilinidae use microorganisms or some components of the decomposing dung pat, the latter are usually not referred to as dung beetles.

are either diurnal or nocturnal, but most large species are nocturnal (Cambefort 1991a). Species do not fly all night or day but most have flight periods restricted to a few hours only (Cambefort 1991b).

Breeding pairs usually meet at the dung pat (Heinrich & Bartholomew 1979). The female or a pair of dung beetles burrow a nest in the dung pat or soil, into which a dung portion is moved and where oviposition takes place (Cambefort 1991c). Some species protect the brood during larval development (Cambefort & Hanski 1991).

Dung beetle fecundity generally is low (Cambefort 1991c). In some small species (e.g. *Sisyphus* spp.) the female may burrow a nest and lay an egg every three days, yet some large species (e.g. *Kepher* spp.) have only one offspring per year (reviewed in Cambefort & Hanski 1991).

Dung beetles can be divided into four behavioural and functional groups or guilds: dwellers (= endocoprids), tunnelers (= paracoprids), rollers (= telecoprids), and kleptoparasites (Cambefort & Hanski 1991):

- *Dwellers* (mostly Aphodiinae, typically small temperate species) directly feed at the faeces and deposit their eggs in the dung pat.
- *Tunnelers* (Geotrupinae and many tribes of Scarabaeidae) transport small dung portions into tunnels burrowed more or less vertically in the soil under or near the dung pat. The dung portion is then used for feeding by the adult or for breeding. Several brood masses may be deposited in one burrow.
- *Rollers* (many Scarabaeidae) form dung balls and roll them some distance away (up to 15 m Heinrich & Bartholomew 1979; up to 5 m Estrada & Coates-Estrada 1991) from the dung pat. Brood balls are often rolled by a pair of beetles. Subsequently, dung balls may be burrowed or attached against a tussock of grass. Balls that are not burrowed may be removed by other dung beetles.
- *Kleptoparasites* (Aphodiinae and Scarabaeidae) are very small dung beetles that do not make nests but use the dung portions relocated by tunnelers and rollers, clinging to the portions while these are being moved.

The dung beetles use a patchy, relatively small and highly ephemeral source at which severe competition can occur (Hanski 1991; Krell-Westerwalbesloh *et al.* 2004). Fights between individuals are common (Cambefort & Hanski 1991). Tunnelers and rollers monopolize at least small portions of dung by relocating it from the source (Heinrich & Bartholomew 1979; Cambefort & Hanski 1991). There is a clear hierarchy of guilds in their competitive ability (Doube 1990). Dung that is quickly removed by tunnelers and rollers cannot be used by dwellers (Doube 1990). On the other hand, rollers may not use dung that is colonized with a high number of dwellers (Heinrich & Bartholomew 1979).

Resource use may thus depend on quick arrival at the source (Krell-Westerwalbesloh *et al.* 2004) as well as on patch size. Dung patches vary in size from small pellets of about a gram to large elephant droppings weighing about 10 kg (Hanski 1991). During seasonal peaks of dung beetle abundances, colonization of a dung patch by dung beetles usually is within the first few minutes (Andresen 1999; Feer 1999).

Dung beetles seem to locate the resource by odour, though visual clues may also play a role (Cambefort & Hanski 1991, and references therein). Some species may sit in the fur of the 'host' and wait for defecation (Herrera *et al.* 2002, and references therein).
The main types of dung to be consumed by dung beetles are large herbivore and omnivore dung. Carnivore dung and small mammal dung is exploited by only a few dung beetles species (Hanski 1991; see also Krell *et al.* 2003). Many species use the more nitrogen-rich omnivore as immature adults, but the more carbohydrate-rich herbivore dung for breeding (Cambefort & Hanski 1991). In many species the larvae use the microorganisms in herbivore dung as food source (Cambefort & Hanski 1991).

Dung beetles are ubiquitous in warm temperate and tropical regions. They reach their peak diversity in the savannas of Africa, where they are associated with the rich mammal fauna of these ecosystems (Cambefort 1991b). African savannas harbour 75 genera and about 1,500 species of Scarabaeidae (~ 350 species of rollers and 1,150 species of tunnelers). Despite their lower diversity, rollers are about equally abundant in the West African savanna as tunnelers (Cambefort 1991b).
During the dry season, dung dries out quickly (Cambefort 1991b) and the soil is too hard for burrowing. Dung beetles in savanna ecosystems are thus generally most abundant at the onset and end of the rainy season. Some species reproduce only shortly after the first rains, whereas others reproduce and increase in number throughout the rainy season (Cambefort 1991b). During times of high dung beetle activity removal of dung takes place within a few hours. In West African savannas, the dung beetle community burrows an estimated $1m^3$ ton of dung $ha^{-1}yr^{-1}$ (Cambefort 1991b).

Dung beetle diversity, species abundance and guild distribution can have important implications for secondary seed dispersal. Rollers and tunnelers are the guilds that may scatter and/or burrow small numbers of seeds locally, thereby potentially reducing seedling competition and post-dispersal seed predation (Andresen & Levey 2004). Seeds buried by dung beetles are often more likely to escape detection by secondary predators than seeds on the soil surface (Estrada & Coates-Estrada 1991; Shepherd & Chapman 1998; Andresen 1999; Andresen & Levey 2004). Moreover, dung beetles burrow many seeds at a range of depths that is favourable for germination and seedling emergence (Estrada & Coates-Estrada 1991; Shepherd & Chapman 1998; Andresen 1999; Andresen & Levey 2004; but see Feer 1999). If germination takes place before larval development and feeding, the dung portions serve as organic fertilizer for seedling development (Vander Wall & Longland 2004).

The interaction between dung beetles and seeds, however, is complex and is influenced by many factors (Andresen 2002a). For example, the size of the dung pat can affect the mean number of dung beetle individuals and/or species at the resource (Peck & Howden 1984; Andresen 2002a) and the probability of seed removal by dung beetles (Andresen 2002b). Seed size can negatively affect both the rate of seed burial (Feer 1999; Andresen & Levey 2004) and burrowing depth (Shepherd & Chapman 1998; Andresen 2002a; but see Andresen & Levey 2004), as can dung beetle size (Feer 1999). Burrowing probability by dung beetles and burrowing depth, in turn is positively related with the amount of dung around the seeds (Andresen 2002a; Andresen & Levey 2004).

Where frugivores frequently disperse high numbers of seeds in single faeces and post-dispersal seed loss often is severe, secondary dispersal by rollers and tunnelers can be crucial for plant establishment (Andresen & Levey 2004). Yet, the role of primates and dung beetles for natural plant regeneration and biodiversity in West Africa remains largely unexplored.

1. 10 STUDY SITE

I studied the interplay between plants, primates and dung beetles in the Comoé National Park (CNP) (08°30-09°36' N, 003°07'-004°25' W), Ivory Coast, West Africa. The CNP is located in the Northeast of the country, near the border to Burkina Faso and Ghana (see Figures 1 and 2). The national park covers approximately 11,500 km^2 at an altitude of about 250-300 m a.s.l. It is the largest savanna park in West Africa, and one of the biggest national parks worldwide (Poilecot 1991). Parts of the area have been under legal protection since 1926 as 'Refuge Nord de la Côte d'Ivoire', which was further extended to the 'Reserve de faune de Bouna' in 1953. The national park itself was created in 1968. Internationally recognized as a Biosphere Reserve under UNESCO's Man and Biosphere Programme, the CNP was inscribed on the World Heritage 'List' in 1983. Twenty years later, the UNESCO added the park to the 'List of World Heritage in Danger' due to the adverse effect of the present unrest in Côte d'Ivoire on the site (UNESCO, 1992-2008).

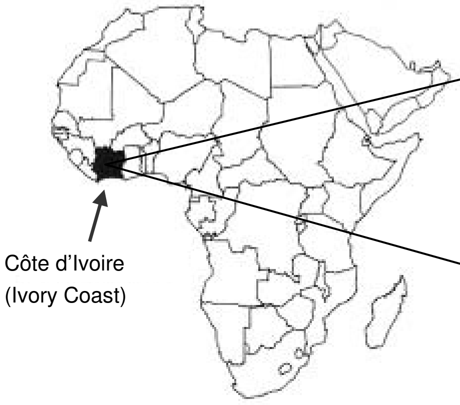


Figure 1 Location of the Ivory Coast within the African continent

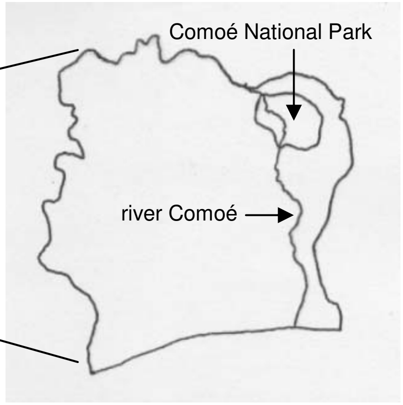


Figure 2 Map of the Ivory Coast
The Comoé National Park is situated in the North-East of the country, near the border to Burkina Faso in the North and Ghana in the East.

In West Africa, the zones of vegetation largely reflect the basic climatic zones (Lawson 1986). The southern park area is located in the species rich Guineo-Congolia / Sudania transition zone (following White 1983), where two distinct floras intervene and savanna dominates with humid forest elements scattered in the landscape (see White 1979; Poorter *et al.* 2004). The northern part belongs to the 'Sudanian regional centre of endemism' (following White 1983).

Due to the Comoé river, which crosses the national park from North to South for 230 km, the CNP comprises plants that are usually only found farther South.

My research focused on an area of about 145 km^2 in the southwest of the national park, East of the river Comoé (Figure 3). Different savanna formations[5] cover about 91 % of the study area and are interspersed by forest islands of different size and vegetation composition (7%). Gallery forest (2%) of up to 400 m width extends along the two main rivers (Figures 4a, b) (FGU-Kronberg 1979).

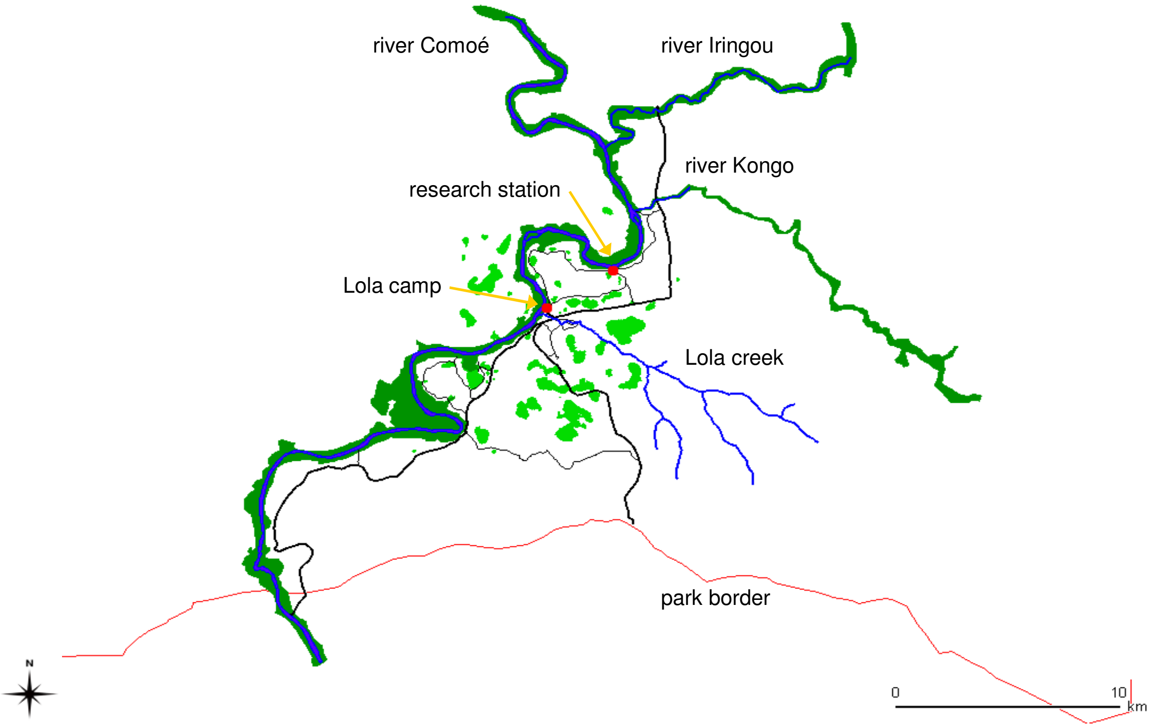


Figure 3 Map of the study area East of the river Comoé in the southern part of the Comoé National Park, north-eastern Ivory Coast (following Mühlenberg *et al.* 1990)
Rivers and creeks are drawn in blue with adjacent gallery forest in dark green. Forest islands are displayed in light green (only shown in and around the core research area). Main roads and side roads are shown as solid black lines. The red line indicates the southern border of the national park.

Hovestadt (1999) recorded 292 woody plant species in the study area of which 47% occurred in the gallery forest, 82% in the forest islands, 30% in the savanna, and 4% in all habitat types. About 70% produce fleshy fruits for consumption by animals (Hovestadt 1997). The proportion of evergreen plant species decreases from 50% in the gallery forest to 7% in the savanna (Hovestadt *et al.* 1999).

---

[5] I henceforth use the term 'savanna' to summarize different vegetation types in CNP with a percent cover of woody plants ranging from 20-70% (Hovestadt 1997). Following the vegetation classification of White (1983) in CNP these vegetation types include 'open bushland', 'wooded and bushed grassland', 'wooded bushland', and in the northern parts of the study area also '(*Isoberlinia*) woodland'.

The canopy of the gallery forest is dominated by evergreen trees such as *Cynometra megalophylla*, *Cola cordifolia,* and *Manilkara multinervis* (Porembski 2001). *Diospyros mespiliformis* can be locally abundant (Hovestadt *et al.* 1999). The canopy reaches a height of about 30 m, some emergent species (i.e. *Ceiba pentandra*) grow up to 40 m. Inside, the gallery forest shows no clear stratification. Lower trees and shrub species such as *Dialium guineense*, *Drypetes floribunda*, *Tapura fischeri* and lianas are abundant (Porembski 2001).

In most forest islands investigated by Hovestadt (1999) the canopy reaches greater height than the gallery forest (~ 40 m). Locally abundant tree species in the forest islands are *Diospyros mespiliformis*, *Diospyros abyssinica, Dialium guineense*, *Manilkara multinervis, Tamarindus indica and Anogeissus leiocarpa*. Many species in the forest islands are deciduous, but more humid forest islands are, like the gallery forest, dominated by the evergreen *Cynometra megalophylla* (Hovestadt *et al.* 1999).

The vegetation of the savanna in the study area is rather dense and scrubby and the grass grows up to several meters height which often makes it difficult to track and observe animals' behaviour in detail (Balzamo *et al.* 1980) (see also Figure 5). Locally most abundant woody plant species are *Terminalia avicennioides*, *Terminalia macroptera*, *Crossopterix febrifuga*, *Burkea africana*, *Detarium microcarpum*, and *Piliostigma thonningii* (Porembski 1991; Hovestadt *et al.* 1999). Towards the northern limit of the study area, *Isoberlina* woodland is locally present (Porembski 1991).

The habitat between savanna and forests changes abruptly. Savanna and gallery forests are often separated by a band of grass vegetation with few woody species (Porembski 1991), henceforth referred to as 'plains' (Figure 4b). Large areas of open grassland are lacking at the study site (FGU-Kronberg 1979; Pomeroy & Service 1986). The vegetation is described in more detail in Poilecot (1991), Porembski (1991, 2001) and Hovestadt (1997, 1999).

The savanna-forest mosaic in the Guineo-Congolia region is generally considered to be a secondary, but long established landscape, originating and maintained by extremely high fire intensities caused by humans (White 1983; Poilecot 1991; see also review in Sanford & Isichei 1986). Up to 95% of the savanna may be burned annually (Poilecot 1991). Forest islands remain where local edaphic conditions are favourable (Mühlenberg *et al.* 1990). On the other hand, some authors suggested that old termite mounts, with their particular edaphic conditions and partial protection against fire, serve as starting points for the formation of new forest islands (Mühlenberg *et al.* 1990; Porembski 1991). Using remote sensing data, Goetze *et al.* (2006), however, showed that the savanna-forest mosaic of the southern CNP was remarkably stable during the last 50 years. Forest island borderlines do not seem to extend into the savanna or only at very slow pace. Goetze (2006) thus argued that the savanna-forest mosaic in CNP should be considered semi-natural.

Figures 4a, b Arial views of the Comoé National Park, Ivory Coast

Fig. 4a *Foreground - the river Comoé and adjacent gallery forest of different extent. Background - savanna with forest islands*

Fig. 4b *The river Comoé with gallery forest, adjacent plain and savanna to the left*

Figure 5 Guinea savanna in the Comoé National Park during the rainy season

Figures 6a, b View from the vantage point ('Aussichtsberg') across the Guinea savanna during the rainy season (left) and the dry season (right)

Figures 7a, b View of the 'Gansé Plain' during the rainy season (left) and dry season (right)

The climate in the study area is characterized by a dry season from November to March/April (Figures 6a,b; 7a,b). Between January 1994 and December 1999 mean annual temperature was 26.3 °C, and mean annual rainfall was 1,053 mm (Figure 8). The annual average maximum temperature during the same period was 32°C, mean minimum temperature 20.6° C. During the dry season, dry winds from the Sahara (Harmattan) often bring daytime temperatures > 40° C and air humidity regularly drops down to 20% or even below. Nights are relatively cool (around 18° C, sometimes below 10°C). During the rainy season, daily variation in temperature is fluctuating around 31° C (max. mean) and 22 °C (min. mean).

Throughout the rainy season, a few rivers and several brooks drain the study area, and savanna ponds of variable size are abundant. Most of the brooks and waterholes as well as the smaller rivers desiccate during the dry season, and only the river Comoé and the lower part of its tributary Iringou reliably provide water whole year round.

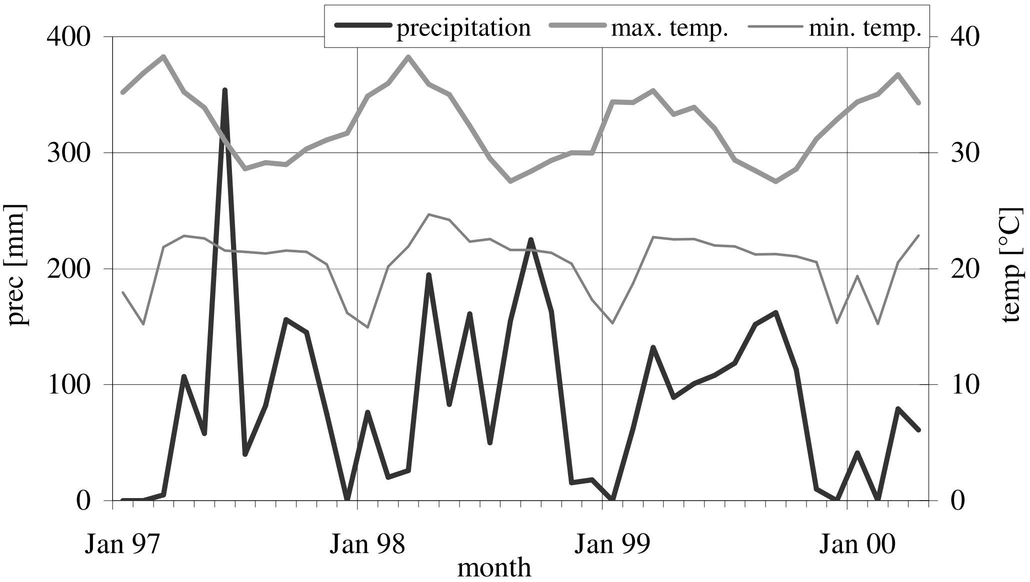


Figure 8 Precipitation and mean maximum and minimum temperature per month from January 1997 to April 2000 at the field station of the University of Würzburg (Lola Camp, 08° 45' 095" N, 003° 48' 990" W), Comoé National Park, Ivory Coast

The CNP also harbours a rich fauna. So far, 498 bird species (Salewski 2000; Salewski & Göken 2001; Rheindt *et al.* 2002), and 152 mammal species have been recorded (Poilecot 1991; Mess & Krell 1999; Fischer *et al.* 2002), among them 57 species of Chiroptera (J. Fahr , pers. comm.). Larger mammals include, for example, the African elephant (*Loxodonta africana;* though probably nearly extinct in CNP), hippopotamus (*Hippopotamus amphibius*), common warthog (*Phacochoerus africanus),* African buffalo

(*Syncerus caffer*), kob antilope (*Kobus kob kob*), Defessa waterbuck (*Kobus ellipsyprimnus defessa*), bushbuck (*Tragelaphus scriptus*), oribi (*Ourebia ourebi*), several duiker species (*Cephalophus* spp.), aardvark (*Orycteropus afer*).

The primate fauna is especially rich. Recent observations yielded nine diurnal species (Fischer *et al.* 2000), of which the olive baboon has the highest individual density and biomass (Fischer *et al.* 2000). Primate species other than baboons, with the exception of patas monkey (*Erythrocebus pata*), vervet monkey (*Chlorocebus aethiops*), and to a certain extent also white-crowned mangabey (*Cercocebus torquatus lunulatus*), are more restricted to forest habitats.

Unlike at many East African baboons study sites (e.g. Masai Mara, Ogutu & Dublin 1998; Laikipia, Mizutani 1999), the abundance of baboons' chief predators, leopards (*Panthera pardus*), lions (*Panthera leo*) and hyenas (in CNP: *Crocuta crocuta*) (Cowlishaw 1994; Barton *et al.* 1996), is low in CNP (Fischer *et al.* 2002).

Due to the poor ferralitic soils (Guillaumet & Adjanohoun 1971) and an extremely high abundance of tsetse flies (transmitting Nagana epidemic plaque to cattle) (Lawson 1986) the area was always sparsely populated by humans even prior to the creation of the CNP (FGU-Kronberg 1979; Lauginie 1995).

During the last thirty years, however, the human populace in the region grew rapidly (Lauginie 1995), imposing an increasing pressure on the natural vegetation (Goetze *et al.* 2006, and references therein). In the case of the CNP, local people frequently enter park areas adjacent to villages for wood and honey collection. Wood cutting is concentrated within 4 km inside from the park border, affecting about 40% of the forest islands in this strip of area (Goetze *et al.* 2006). Fruits are not intensively collected inside CNP. Poaching has become increasingly damaging during the last years (Hovestadt *et al.* 1999), diminishing the population of the African elephant and other big mammals (Poilecot 1991; Fischer & Linsenmair 2001).

1. 11 OUTLINE OF THE THESIS

Biological diversity and the mechanisms of its maintenance in the West-African Guinea savanna are still poorly understood, but interactions between fruiting plants and their fruit consumers are likely to be important. The role of primates and dung beetles for natural plant regeneration in this ecosystem remains largely unexplored. Combining direct observations, indirect methods and experiments, I investigated primary seed dispersal and pre-dispersal seed predation by olive baboons as well as secondary seed dispersal from baboon faeces by dung beetles in the savanna-forest mosaic of the Comoé National Park (CNP), north-eastern Ivory Coast.

The following chapter "***Diet and Behavioural Ecology of Olive Baboons in the Comoé National Park***" provides the basics to subsequently evaluate the baboons' role in seed dispersal and seed predation in the CNP and to calculate seed rain caused by baboons in the study area. Herein, I investigate baboon individual density and group sizes in CNP, and present data from a comparative study on home range, time budget and diet of two habituated baboon groups of different size. The results are published in *Folia Primatologica* (2007) 79: 31-51, http://www.karger.com/fpr, DOI 10.1159/000108384.

In "***Fruit Traits in Baboon Diet: a Comparison with Plant Species' Characteristics in a West African Savanna-Forest Mosaic***" I test whether the olive baboon in CNP predominantly includes plant species into its diet that have particular growth forms and morphological fruit traits. As trait use by primates might simply reflect availability among the species in the regional plant pool, I compare the frequency of occurrence of the traits in baboon diet to the entirety of the plant species in CNP. In addition, I analyse which suites of morphological traits best predict fruit choice and seed dispersal by baboons, respectively. (Data are submitted for publication.)

The chapter "***The Role of Olive Baboons as Seed Dispersers in a Savanna-Forest Mosaic of West Africa***", in which I provide quantitative and qualitative data on baboon seed handling and dispersal, aims at identifying the baboon's disperser effectiveness for selected plant species. Specifically, I focus on the species and number of seeds dispersed by the olive baboon in CNP, the sizes and damage of dispersed seeds, viability of ingested seeds, and estimate the number of seeds dispersed daily by the baboon population in the study area. The study is published in *Journal of Tropical Ecology* (2008) 24: 235-246, http://journals.cambridge.org/action/displayIssue?jid=TRO&volumeId=24&issueId=03&iid=1871996, © Cambridge University Press.

In the fifth chapter "***Changes in Baboon Feeding Behaviour: Maturity-Dependent Fruit and Seed Size Selection within a Food Plant Species***" I study the role of the olive baboon as seed disperser and pre-dispersal seed predator in a typical 'mammal-dispersed fruit' (*Parkia biglobosa*, Mimosaceae). The tree is one of the most important wild food plants for humans in West and Central Africa but little is known of the quantitative and qualitative dimensions of fruit choice and seed dispersal by its nonhuman consumers, and on the consequences of seed predation for regeneration of the tree. In CNP, baboons feed on unripe seeds as well as on ripe fruit pulp of *Parkia biglobosa*. I consider removal of unripe fruits and dispersal of ripe seeds by baboons from individual trees, and investigate whether baboons differentially select for seed number and seed size in unripe and ripe fruits. I discuss potential reasons for the different feeding strategies, and the implications of size selection during pre-dispersal seed predation and seed dispersal for tree regeneration. The data are published in *International Journal of Primatology* (2007) 28: 819-835. The original publication is available at http://www.springerlink.com, DOI 10.1007/s10764-007-9160-6.

In the sixth chapter "***Seed Size Selection by Olive Baboons***" I analyse whether olive baboons also select particular seed sizes in other fruit species and fruit types. I therefore compare sizes of seeds extracted from fresh baboon dung and from fresh ripe fruits in ten additional plant species commonly eaten by olive baboons at CNP. I discuss effects of other fruit traits and fruit availability upon seed handling and intraspecific seed size selection by baboons. The results are published in *Primates* (2008) 49: 239-245. The original publication is available at http://www.springerlink.com, DOI 10.1007/s10329-008-0101-6.

The following chapter "***Olive Baboons as Seed Dispersers of Typical 'Bird-Dispersed' Trees***" investigates the role of the olive baboon and other primate species as seed dispersers in comparison with birds in *Lannea* spp. (Anacardiaceae). First, I deal with the qualitative component of seed dispersal: the timing of frugivore feeding visits in relation to crop maturity and their treatment of fruits and seeds in *L. acida*. Second, I provide data on the quantitative contribution of the consumers to fruit removal and seed dispersal from *L. acida* and *L. welwitschii*. (Data illustrating the qualitative aspect of seed dispersal in *L. acida* are in press (*Ecotropica*); data on the quantitative aspects of seed dispersal are submitted.)

Seed fate after primary dispersal by baboons is addressed in the last chapter "***Habitat Differences in Dung Beetles Guilds (Coleoptera, Scarabaeidae) in a Savanna-Forest Mosaic of West Africa and Implications for Secondary Seed Dispersal from Baboon Faeces***". Herein I investigate dung beetle activity at baboon dung in the two main habitats in CNP, savanna and forest, both of which are intensively used by olive baboons. I focus on factors in the dung beetle community affecting secondary dispersal probabilities of seeds: species' and individual abundances of rollers and tunnelers, habitat preference of dung beetle species, and dung beetle size. For the first time comparative data on secondary dispersal of seeds by dung beetles in West Africa (seed species, seed sizes, dispersal distances) from both forest and adjacent savanna are provided. In the light of clear differences in dung beetle community structures between the two habitats I discuss secondary dispersal probabilities of seed species of different sizes naturally present in baboon dung in CNP. (Data are in preparation for publication.)

1. 12 REFERENCES

Adler, G. H. & Kestell, D. W. 1998. Fates of Neotropical tree seeds influenced by spiny rats (*Proechimys semispinosus*). *Biotropica* 30: 677-681.

Alcantara, J. M. & Rey, P. J. 2003. Conflicting selection pressures on seed size: evolutionary ecology of fruit size in a bird-dispersed tree, *Olea europaea*. *Journal of Evolutionary Biology* 16: 1168-1176.

Alcantara, J. M., Rey, P. J., Sanchez-Lafuente, A. M. & Valera, F. 2000. Early effects of rodent post-dispersal seed predation on the outcome of the plant-seed disperser interaction. *Oikos* 88: 362-370.

Altmann, S. A. 1998. *Foraging for survival: yearling baboons in Africa*. University of Chicago Press, Chicago.

Altmann, S. A. & Altmann, J. 1970. *Baboon ecology*. S. Karger, Basel.

Andersen, A. N. 1988. Dispersal distance as a benefit of myrmecochory. *Oecologia* 75: 507-511.

Anderson, C. M. 1981. Subtrooping in a chacma baboon (*Papio ursinus*) population. *Primates* 22: 445-458.

Andresen, E. 1999. Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rain forest. *Biotropica* 31: 145-158.

Andresen, E. 2002a. Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. *Ecological Entomology* 27: 257-270.

Andresen, E. 2002b. Primary seed dispersal by red howler monkeys and the effect of defecation patterns on the fate of dispersed seeds. *Biotropica* 34: 261-272.

Andresen, E. & Levey, D. 2004. Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. *Oecologia* 139: 45-54.

Augspurger, C. K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps and pathogens. *Ecology* 65: 1705-1705.

Augspurger, C. K. & Kitajima, K. 1992. Experimental studies of seedling recruitment from contrasting seed distributions. *Ecology* 73: 1270-1284.

Balasubramanian, P. 1996. Interactions between fruit-eating birds and bird-dispersed plants in the tropical dry evergreen forest of point Calimere, South India. *Journal of the Bombay Natural History Society* 93: 428-441.

Balcomb, S. R. & Chapman, C. A. 2003. Bridging the gap: influence of seed deposition on seedling recruitment in a primate-tree interaction. *Ecological Monographs* 73: 625-642.

Balzamo, E., Seri, B. & Kouako, K. 1980. Répartition géographique de *Papio anubis* dans le nord-est et le centre-sud de Côte d'Ivoire. *Primates* 21: 524-537.

Barnea, A., Yom, T. Y. & Friedman, J. 1990. Differential germination of two closely related species of *Solanum* in response to bird ingestion. *Oikos* 57: 222-228.

Barnes, M. E. 2001. Seed predation, germination and seedling establishment of *Acacia erioloba* in northern Botswana. *Journal of Arid Environments* 49: 541-554.

Barton, R. 1989. Foraging strategies, diet and competition in olive baboons. PhD thesis. University of St. Andrew, UK.

Barton, R. A., Byrne, R. W. & Whiten, A. 1996. Ecology, feeding competition and social structure in baboons. *Behavioural Ecology and Sociobiology* 38: 321-329.

Barton, R. A. & Whiten, A. 1993. Feeding competition among female olive baboons, *Papio anubis*. *Animal Behaviour* 46: 777-789.

Barton, R. A., Whiten, A., Strum, S. C., Byrne, R. W. & Simpson, A. J. 1992. Habitat use and resource availability in baboons. *Animal Behaviour* 43: 831-844.

Bennett, A. T. D. & Théry, M. 2007. Avian color vision and coloration: multidisciplinary evolutionary biology. *The American Naturalist* 169: 1–6.

Bercovitch, F. B. & Strum, S. C. 1993. Dominance rank, resource availability, and reproductive maturation in female savanna baboons. *Behavioural Ecology and Sociobiology* 33: 313-318.

Blate, G. M., Peart, D. R. & Leighton, M. 1998. Post-dispersal predation on isolated seeds: a comparative study of 40 tree species in a Southeast Asian rainforest. *Oikos* 82: 522-538.

Böhning-Gaese, K., Gaese, B. & Rabemanantsoa, S. B. 1999. Importance of primary and secondary seed dispersal in the malagasy tree *Commiphora guillaumini*. *Ecology* 80: 821-832.

Bollen, A., Van-Elsacker, L. & Ganzhorn, J. U. 2004. Tree dispersal strategies in the littoral forest of Sainte Luce (SE-Madagascar). *Oecologia* 139: 604-616.

Boudreau, S. & Lawes, M. J. 2008. Density- and distance-dependent seedling survival in a ballistically dispersed subtropical tree species *Philenoptera sutherlandii*. *Journal of Tropical Ecology* 24: 1-8.

Brewer, S. W. & Rejmanek, M. 1999. Small rodents as significant dispersers of tree seeds in a Neotropical forest. *Journal of Vegetation Science* 10: 165-174.

Bronikowski, A. M. & Altmann, J. 1996. Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. *Behavioural Ecology and Sociobiology* 39: 11-25.

Buirski, P., Kellermann, H., Plutchik, R., Weininger, R. & Buirski, N. 1973. A field study of emotions, dominance, and social behaviour in a group of baboons (*Papio anubis*). *Primates* 14: 67-78.

Burkey, T. V. 1994. Tropical tree species diversity: a test of the Janzen-Connell model. *Oecologia* 97: 533-540.

Byrne, R. W., Whiten, A., Henzi, S. P. & McCulloch, F. M. 1993. Nutritional constraints on mountain baboons (*Papio ursinus*): implications for baboon socioecology. *Behavioral Ecology and Sociobiology* 33: 233-246.

Cambefort, Y. 1984. Etude écologique des coléoptères Scarabaeidae de Côte d'Ivoire. PhD thesis. Muséum National d'Histoire Naturelle, Paris & University of Abidjan, Ivory Coast.

Cambefort, Y. 1991a. Biogeography and evolution. Pp. 51-67 In Hanski, I. & Cambefort, Y. (eds.). *Dung beetle ecology*. Princeton University Press, Princeton.

Cambefort, Y. 1991b. Dung beetles in tropical savannas. Pp. 156-178 In Hanski, I. & Cambefort, Y. (eds.). *Dung beetle ecology*. Princeton University Press, Princeton.

Cambefort, Y. 1991c. From saprophagy to coprophagy. Pp. 22-35 In Hanski, I. & Cambefort, Y. (eds.). *Dung beetle ecology*. Princeton University Press, Princeton.

Cambefort, Y. & Hanski, I. 1991. Dung beetle population biology. Pp. 36-50 In Hanski, I. & Cambefort, Y. (eds.). *Dung beetle ecology*. Princeton University Press, Princeton.

Castles, D. L., Whiten, A. & Aureli, F. 1999. Social anxiety, relationships and self-directed behaviour among wild female olive baboons. *Animal Behaviour* 58: 1207-1215.

Chambers, J. C. & MacMahon, J. A. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural managed systems. *Annual Review of Ecology, Evolution, & Systematics* 25: 263-292.

Chapman, C. A. & Chapman, L. J. 1996. Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. *Journal of Tropical Ecology* 12: 491-504.

Chapman, C. A., Chapman, L. J. & Wrangham, R. 1992. *Balanites wilsoniana*: elephant dependent dispersal? *Journal of Tropical Ecology* 8: 275-283.

Chapman, C. A. & Onderdonk, D. A. 1998. Forests without primates: primate/plant codependency. *American Journal of Primatology* 45: 127-141.

Charles-Dominique, P. 1993. Speciation and coevolution: an interpretation of frugivory phenomena. *Vegetatio* 107: 75-84.

Cipollini, M. L. & Levey, D. J. 1991. Why some fruits are green when they are ripe: carbon balance in fleshy fruits. *Oecologia* 88: 371-377.

Clark, C. J., Poulsen, J. R., Bolker, B. M., Connor, E. F. & Parker, V. T. 2005. Comparative seed shadow of bird-, monkey-, and wind dispersed trees. *Ecology* 86: 2684–2694.

Clark, D. A. & Clark, D. B. 1984. Spacing dynamics of a tropical rain forest tree: elevation of the Janzen-Connell model. *The American Naturalist* 124: 769-789.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and tropical forest trees. Pp. 298-312 In den Boer, P. J. & Gradwell, G. (eds.). *Dynamics of populations*. PUDOC, Wageningen.

Cooper, H. M., Charles-Dominique, P. & Vienot, F. 1986. The significance of the color of fruits as a function of the vision of the vertebrates that consume them. *Memoires du Museum National d'Histoire Naturelle Serie A Zoologie* 132: 131-144.

Cordeiro, N. J. & Howe, H. F. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences of the United States of America* 100: 14052-14056.

Corlett, R. T. & Lucas, P. W. 1990. Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaque *Macaca fascicularis*. *Oecologia* 82: 166-171.

Cowlishaw, G. 1994. Vulnerability to predation in baboon populations. *Behaviour* 131: 3-4.

Cowlishaw, G. 1998. The role of vigilance in the survival and reproductive strategies of desert baboons. *Behaviour* 135: 431-452.

Cowlishaw, G. 1999. Ecological and social determinants of spacing behaviour in desert baboon groups. *Behavioral Ecology and Sociobiology* 45: 67-77.

Crawley, M. J. 2000. Seed predators and plant population dynamics. Pp. 166-181 In Fenner, M. (ed.). *Seeds. The ecology of regeneration in plant communities*. CABI, Wallingford.

Da Silva, H. R. & Britto-Pereira, M. C. 2006. How much fruit do fruit eating frogs eat? An investigation on the diet of *Xenohyla truncata* (Lissamphibia: Anura: Hylidae). *Journal of Zoology* 270: 692-698.

Depew, L. A. 1983, Ecology and behaviour of baboons (*Papio anubis*) in the Shai Hills Game Production Reserve, Ghana. MSc thesis. Cape Coast University, Ghana.

Dirzo, R. & Domínguez, C. A. 1986. Seed shadows, seed predation and the advantages of dispersal. Pp. 237-249 In Estrada, A. & Fleming, T. H. (eds.). *Frugivores and seed dispersal*. Dr. W. Junk Publishers, Dordrecht.

Dominy, N. J. & Duncan, B. W. 2005. Seed-spitting primates and the conservation and dispersion of large-seeded trees. *International Journal of Primatology* 26: 631-649.

Dominy, N. J. & Lucas, P. W. 2001. Ecological importance of trichromatic vision to primates. *Nature* 410: 363-366.

Dominy, N. J., Svenning, J. C. & Hsiung, L. W. 2003. Historical contingency in the evolution of primate color vision. *Journal of Human Evolution* 441.

Doube, B. M. 1990. A functional classification for analysis of the structure of dung beetle assemblages. *Ecological Entomology* 15: 371-383.

Dunbar, R. I. M. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behavioural Ecology and Sociobiology* 31: 35-49.

Dunbar, R. I. M. 1994. Ecological constraints on group size in baboons. *Physiology and Ecology Japan* 29: 221-236.

Dunbar, R. I. M. & Nathan, M. F. 1972. Social organization of the Guinea Baboon, *Papio papio*. *Folia Primatologica* 17: 321-334.

Duranti, M. & Gius, C. 1997. Legume seeds: protein content and nutritional value. *Field Crops Research* 53: 31-45.

Engel, T. R. 1999. African civets, their ecology and role in forest regeneration. 12. Jahrestagung der Deutschen Gesellschaft für Tropenökologie, Ulm. p 24.

Estes, R. D. 1991. *The behavior guide to African mammals*. University of California Press, Berkley.

Estrada, A. & Coates-Estrada, R. 1986. Frugivory in howling monkeys (*Alouatta palliata*) at Las Tuxtlas, Mexico: dispersal and fate of seeds. Pp. 93-104 In Estrada, A. & Fleming, T. H. (eds.). *Frugivores and seed dispersal*. Dr. W. Junk Publishers, Dordrecht.

Estrada, A. & Coates-Estrada, R. 1991. Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions of Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 7: 459-474.

Estrada, A., Halffter, G., Coates-Estrada, R. & Meritt jr., D. A. 1993. Dung beetles attracted to mammalian herbivore (*Alouatta palliata*) and omnivore (*Nasua narica*) dung in the tropical forest of Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 9: 45-54.

Feer, F. 1995. Seed dispersal in African forest ruminants. *Journal of Tropical Ecology* 11: 683-689.

Feer, F. 1999. Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (*Alouatta seniculus*) in the French Guianan rain forest. *Journal of Tropical Ecology* 15: 129-142.

Feer, F. & Forget, P. M. 2002. Spatio-temporal variations in post-dispersal seed fate. *Biotropica* 34: 555-566.

Fenner, M. & Thompson, K. 2005. *The ecology of seeds*. Cambridge University Press, Cambridge.

FGU-Kronberg. 1979. Gegenwärtiger Status der Comoé- und Tai-Nationalparks sowie des Azagny-Reservats und Vorschläge zu deren Erhaltung und Entwicklung zur Förderung des Tourismus. Technical Report. Deutsche Gesellschaft für Technische Zusammenarbeit GmbH, Eschborn.

Fialho, R. F. 1990. Seed dispersal by a lizard and a treefrog. Effect of dispersal site on seed survivorship. *Biotropica* 22: 423-424.

Fischer, F., Groß, M. & Kunz, B. 2000. Primates of the Comoé National Park, Ivory Coast. *African Primates* 4: 10-15.

Fischer, F., Groß, M. & Linsenmair, K. E. 2002. Updated list of the larger mammals of the Comoé National Park, Ivory Coast. *Mammalia* 66: 83-92.

Fischer, F. & Linsenmair, K. E. 2001. Decreases in ungulate population densities. Examples from the Comoé National Park, Ivory Coast. *Biological Conservation* 101: 131-135.

Forget, P. M., Hammond, D. S., Milleron, T. & Thomas, R. 2002. Seasonality of fruiting and food hoarding by rodents in Neotropical forests: consequences for seed dispersal and seedling recruitment. Pp. 241-256 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation*. CABI, Wallingford.

Foster, M. S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* 58: 73-85.

Fragoso, J. M. V. 1997. Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *Journal of Ecology* 85: 519-529.

Garber, P. A. 1986. The ecology of seed dispersal in two species of callitrichid primates (*Saguinus mystax* and *Saguinus fuscicollis*). *American Journal of Primatology* 10: 155-170.

Garber, P. A. & Kitron, U. 1997. Seed swallowing in tamarins: evidence of a curative function or enhanced foraging efficiency? *International Journal of Primatology* 18: 523-538.

Garber, P. A. & Lambert, J. E. 1998. Primates as seed dispersers: ecological processes and directions for future research. *American Journal of Primatology* 45: 3-8.

Gathua, M. 2000. The effects of primates and squirrels on seed survival of a canopy tree, *Afzelia quanzensis*, in Arabuko-Sokoke Forest, Kenya. *Biotropica* 32: 127-132.

Gautier-Hion, A. 1984. La dissemination des graines par les cercopithecides forestiers africains. *La Terre et la Vie* 39: 159-165.

Gautier-Hion, A., Duplantier, J. M., Quris, R., Feer, F., Sourd, C., Decoux, J. P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C. & Thiollay, J. M. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65: 324-337.

Geritz, S. A. H., de Jong, T. J. & Klinkhammer, P. G. L. 1984. The efficacy of dispersal in relation to safe site area and seed production. *Oecologia* 62: 219-221.

Gijsbers, H. J. M., Kessler, J. J. & Knevel, M. K. 1994. Dynamics and natural regeneration of woody species in farmed parklands in the Sahel region (Province of Passore, Burkina Faso). *Forest Ecology and Management* 64: 1-12.

Giles, S. & Lill, A. 1999. The effect of fruit abundance, conspicuousness and sugar concentration on fruit colour choice by captive silvereyes. *Ethology Ecology & Evolution* 11: 229-242.

Githiru, M., Lens, L., Bennur, L. A. & Ogol, C. P. K. O. 2002. Effects of site and fruit size on the composition of avian frugivore assemblages in a fragmented Afrotropical forest. *Oikos* 96: 320-330.

Goetze, D., Hoersch, B. & Porembski, S. 2006. Dynamics of forest-savanna mosaics in north-eastern Ivory Coast from 1954 to 2002. *Journal of Biogeography* 33: 653-664.

Gottsberger, G. 1978. Seed dispersal by fish in the inundated regions of Humaita, Amazonia. *Biotropica* 10: 170-183.

Groves, C. P. 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington.

Guillaumet, J. L. & Adjanohoun, E. 1971. La végétation. Pp. 161-263 In ORSTOM (ed.). *Le milieu naturel de la Côte d'Ivoire*. ORSTOM, Paris.

Hall, K. R. L. & DeVore, I. 1965. Baboon social behavior. Pp. 53-110 In DeVore, I. (ed.). *Primate behavior. Field studies of monkeys and apes.* Holt, Rinehart & Wilson, New York.

Hamilton, W. J. I., Buskirk, R. E. & Buskirk, W. H. 1978. Omnivory and utilization of food resources by chacma baboons, *Papio ursinus*. *The American Naturalist* 112: 911-924.

Hanski, I. 1991. The dung insect community. Pp. 5-21 In Hanski, I. & Cambefort, Y. (eds.). *Dung beetle ecology*. Princeton University Press, Princeton.

Harding, R. S. O. 1976. Ranging patterns of a troop of baboons (*Papio anubis*) in Kenya. *Folia Primatologica* 25: 143-185.

Harding, R. S. O. 1981. An order of omnivores: nonhuman primate diets in the wild. Pp. 191-214 In Harding, R. S. O. & Teleki, G. (eds.). *Omnivorous primates. Gathering and hunting in human evolution*. Columbia Press, New York.

Harms, K. E., Wright, S. J., Calderon, O., Hernandez, A. & Herre, E. A. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404: 493-495.

Harper, J. L., Lovell, P. H. & Moore, K. G. 1970. The shape and size of seeds. *Annual Review of Ecology, Evolution, & Systematics* 70: 327-356.

Harrison, M. J. S. & Hladik, C. M. 1986. Un primate granivore: le colobe noir de la foret du Gabon; potentialité d'évolution du comportement alimentaire. *Revue d'Ecologie: La Terre et la Vie* 41: 281-298.

Hausfater, G. 1975. Dominance and reproduction in baboons (*Papio cynocephalus*). *Contributions to Primatology* Vol. 7. Karger, Basel.

Heindl, M. & Curio, E. 1999. Observations of frugivorous birds at fruit-bearing plants in the North Negros Forest Reserve, Philippines. *Ecotropica* 5: 167-181.

Heinrich, B. & Bartholomew, G. A. 1979. The ecology of the African dung beetle. *Scientific American* 241: 118-126.

Henzi, S. P. & Barrett, L. 2003. Evolutionary ecology, sexual conflict, and behavioral differentiation among baboon populations. *Evolutionary Anthropology* 12: 217-230.

Henzi, S. P. & Barrett, L. 2005. The historical socioecology of savanna baboons (*Papio hamadryas*). *Journal of Zoology* 265: 215-226.

Herrera, C. M. 1986. Vertebrate-dispersed plants: why they don't behave the way they should. Pp. 5-18 In Estrada, A. & Flemming, T. H. (eds.). *Frugivores and seed dispersal*. Dr. W. Junk Publishers, Dordrecht.

Herrera, C. M. 2002. Seed dispersal by vertebrates. Pp. 185-208 In Herrera, C. M. & Pellmyr, O. (eds.). *Plant-animal interactions. An evolutionary approach*. Blackwell, Oxford.

Herrera, E. R. T., Vulinec, K., Knogge, C. & Heymann, E. W. 2002. Sit and wait at the source of the dung - an unusual strategy of dung beetles. *Ecotropica* 8: 87-88.

Higgins, S. I., Nathan, R. & Cain, M. L. 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? *Ecology* 84: 1945-1956.

Hill, R. A. 2006. Thermal constraints on activity scheduling and habitat choice in baboons. *American Journal of Physical Anthropology* 129: 242-249.

Hill, R. A. & Dunbar, R. I. M. 2002. Climatic determinants of diet and foraging behaviour in baboons. *Evolutionary Ecology* 16: 579-593.

Hill, R. A., Lycett, J. E. & Dunbar, R. I. M. 2000. Ecological and social determinants of birth intervals in baboons. *Behavioral Ecology* 11: 560-564.

Hladik, M. C. 1981. Diet and the evolution of feeding strategies among forest primates. Pp. 215-254 In Harding, R. S. O. & Teleki, G. (eds.). *Omnivorous primates. Gathering and hunting in human evolution*. Columbia Press, New York.

Hodgkison, R., Balding, S. T., Zubaid, A. & Kunz, T. H. 2003. Fruit bats (Chiroptera: Pteropodidae) as seed dispersers and pollinators in a lowland Malaysian rain forest. *Biotropica* 35: 491-502.

Hofmann, T. & Roth, H. 2003. Feeding preferences of duiker (*Cephalophus maxwelli*, *C. rufilatus*, and *C. niger*) in Ivory Coast and Ghana. *Mammalian Biology* 68: 65-77.

Honkavaara, J., Siitari, H. & Viitala, J. 2004. Fruit colour preferences of redwings (*Turdus iliacus*): experiments with hand-raised juveniles and wild-caught adults. *Ethology* 110: 445-457.

Hoppes, W. G. 1988. Seedfall pattern of several species of bird-dispersed plants in Illinois USA woodland. *Ecology* 69: 320-329.

Hovestadt, T. 1997. Fruchtmerkmale, endozoochore Samenausbreitung und ihre Bedeutung für die Zusammensetzung der Pflanzengemeinschaft. Untersuchungen im Wald-Savannenmosaik des Comoé Nationalparks, Elfenbeinküste. PhD thesis. University of Würzburg, Germany.

Hovestadt, T., Yao, P. & Linsenmair, K. E. 1999. Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoé National Park, Ivory Coast). *Plant Ecology* 144: 1-25.

Howe, H. F. 1984a. Constraints on the evolution of mutualism. *The American Naturalist* 123: 764-777.

Howe, H. F. 1984b. Implications of seed dispersal by animals for tropical reserve management. *Biological Conservation* 30: 261-281.

Howe, H. F. 1989. Scatter and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* 79: 417-426.

Howe, H. F. & Brown, J. S. 2001. The ghost of granivory past. *Ecology Letters* 4: 371-378.

Howe, H. F., Schupp, E. W. & Westley, L. C. 1985. Early consequences of seed dispersal for a Neotropical tree (*Virola surinamensis). Ecology* 66: 781-791.

Howe, H. F. & Smallwood, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201-228.

Howe, H. F. & vande Kerckhove, G. A. 1981. Removal of wild nutmeg *Virola surinamensis* crops by birds. *Ecology* 62: 1093-1106.

Hubbell, S. P. 1980. Seed predation and the coexistence of tree species in tropical forests. *Oikos* 35: 214-229.

Hulme, P. E. & Benkman, C. W. 2002. Granivory. Pp. 132-154 In Herrera, C. M. & Pellmyr, O. (eds.). *Plant-animal interactions. An evolutionary approach.* Blackwell, Oxford.

Idani, G. 1986. Seed dispersal by pygmy chimpanzees *Pan paniscus*. A preliminary report. *Primates* 27: 441-448.

IUCN. 2007. Red List of Threatened Species. <www.iucnredlist.org>. Downloaded on 29 September 2008.

Izhaki, I. & Safriel, U. N. 1990. The effect of some Mediterranean scrubland frugivores upon germination patterns. *Journal of Ecology* 78: 56-65.

Izhaki, I., Walton, P. B. & Safriel, U. N. 1991. Seed shadows generated by frugivorous birds in an eastern Mediterranean scrub. *Journal of Ecology* 79: 575-590.

Jansen, P. A., Bartholomeus, M., Bongers, F., Elzinga, J. A., den Ouden, J. & van Wien, S. E. 2002. The role of seed size in dispersal by a scatter-hoarding rodent. Pp. 209-225 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation.* CABI, Wallingford.

Jansen, P. A., Bongers, F. & Hemerik, L. 2004. Seed mass and mast seeding enhance dispersal by a Neotropical scatter-hoarding rodent. *Ecological Monographs* 74: 569-589.

Jansen, P. A., Bongers, F. & van der Meer, P. J. 2008. Is farther seed dispersal better? Spatial patterns of offspring mortality in three rainforest tree species with different dispersal abilities. *Ecography* 31: 43-52.

Janson, C. H. 1983. Adaptation of fruit morphology to dispersal agents in a Neotropical forest. *Science* 219: 187-189.

Janson, C. H., Stiles, E. W. & White, D. W. 1986. Selection on plant fruit traits by brown capuchin monkeys: a multivariate approach. Pp. 83-92 In Estrada, A. & Fleming, T. H. (eds.). *Frugivores and seed dispersal.* Dr. W. Junk Publishers, Dordrecht.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *The American Naturalist* 104: 501-528.

Janzen, D. H. 1986. Mice, big mammals, and seeds: it matters who defecates what where. Pp. 251-271 In Estrada, A. & Fleming, T. H. (eds.). *Frugivores and seed dispersal.* Dr. W. Junk Publishers, Dordrecht.

Jolly, C. J. 1998. Baboon nomenclature. *African Primates* 3: 47-48.

Jordano, P. 1995a. Angiosperm fleshy fruits and seed dispersers: a comparative anaysis of adaptation and constraints in plant-animal interactions. *The American Naturalist* 145: 163-191.

Jordano, P. 1995b. Frugivore-mediated selection on fruit and seed size: birds and St. Lucie's cherry, *Prunus mahaleb*. *Ecology* 76: 2627-2639.

Jordano, P. 2000. Fruits and frugivory. Pp. 125-165 In Fenner, M. (ed.). *Seeds. The ecology of regeneration in plant communities.* CABI, Wallingford.

Jordano, P. & Godoy, J. A. 2002. Frugivore-mediated seed shadows: a landscape view of demographic and genetic effects. Pp. 305-321 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seeds dispersal and frugivory.* CABI, Wallingford.

Julliot, C. 1996a. Fruit choice by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest. *American Journal of Primatology* 40: 261-282.

Julliot, C. 1996b. Seed dispersal by red howler monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. *International Journal of Primatology* 17: 239-258.

Kaplin, B. A. & Moermond, T. C. 1998. Variation in seed handling by two species of forest monkeys in Rwanda. *American Journal of Primatology* 45: 83-101.

Kaspari, M. 1993. Removal of seeds from Neotropical frugivore droppings: ant responses to seed number. *Oecologia* 95: 81-88.

Kinnaird, M. F. 1998. Evidence for effective seed dispersal by the Sulawesi red-knobbed hornbill, *Aceros cassidix*. *Biotropica* 30: 50-55.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T. & Noma, N. 2002. Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia* 133: 559-572.

Knight, R. S. & Siegfried, W. R. 1983. Interrelationships between type, size and color of fruits and dispersal in southern African trees. *Oecologia* 56: 405-412.

Knogge, C. & Heymann, E. W. 2003. Seed dispersal by sympatric tamarins, *Saguinus mystax* and *Saguinus fuscicollis*: diversity and characteristics of plant species. *Folia Primatologica* 74: 33-47.

Krell, F. T., Korb, J. & Walther, P. 2003. The beetle fauna of hyaena latrines: coprocenoses consisting of necrophagus beetles (Coleptera: Trogidae, Scarabaeidae). *Tropical Zoology* 16: 145-152.

Krell-Westerwalbesloh, S., Krell, F. T. & Linsenmair, K. E. 2004. Diel separation of Afrotropical dung beetle guilds - avoiding competition and neglecting resources (Coleptera: Scarabaeidae). *Journal of Natural History* 38: 2225-2249.

Lambert, J. E. 1998. Primate frugivory in Kibale National Park, Uganda, and its implications for human use of forest resources. *African Journal of Ecology* 36: 234-240.

Lambert, J. E. 2002. Exploring the link between animal frugivory and plant strategies: the case of primate fruit processing and post-dispersal seed fate. Pp. 365-380 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation*. CABI, Wallingford.

Lambert, J. E. & Garber, P. A. 1998. Evolutionary and ecological implications of primate seed dispersal. *American Journal of Primatology* 45: 9-28.

Lauginie, F. 1995. Problèmes liés a la conservation de la grande faune en Afrique. L'exemple des grans mammifères du Parc National de la Comoé. PhD thesis. University of Orleans, France.

Lawson, G. W. 1986. Vegetation and environment in West Africa. Pp. 111 In Lawson, G. W. (ed.). *Plant Ecology in West Africa*. John Wiley & Sons, Chichester.

Leishman, M. R., Wright, I. J., Moles, A. T. & Westoby, M. 2000. The evolutionary ecology of seed size. Pp. 31-56 In Fenner, M. (ed.). *Seeds. The ecology of regeneration in plant communities*. CABI, Wallingford.

Levey, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. *The American Naturalist* 129: 471-485.

Levey, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology* 69: 1076-1089.

Levey, D. J. & Byrne, M. M. 1993. Complex ant-plant interactions: Rain forest ants as secondary dispersers and post-dispersal seed predators. *Ecology* 74: 1802-1812.

Levin, S. A., Muller-Landau, H. C., Nathan, R. & Chave, J. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology, Evolution, & Systematics* 34: 575-604.

Lieberman, D., Hall, J. B., Swaine, M. D. & Lieberman, M. 1979. Seed dispersal by baboons in the Shai Hills, Ghana. *Ecology* 60: 65-75.

Lieberman, M. & Lieberman, D. 1986. An experimental study of seed ingestion and germination in a plant-animal assemblage in Ghana. *Journal of Tropical Ecology* 2: 113-126.

Link, A. & Di-Fiore, A. 2006. Seed dispersal by spider monkeys and its importance in the maintenance of Neotropical rain-forest diversity. *Journal of Tropical Ecology* 22: 235-246.

Loiselle, B. A. 1990. Seeds in droppings of tropical fruit-eating birds: importance of considering seed composition. *Oecologia* 82: 494-500.

Loiselle, B. A. & Blake, J. G. 2002. Potential consequences of extinction of frugivorous birds for shrubs of a tropical wet forest. Pp. 397-406 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation*. CABI, Wallingford.

Lykke, A. M. 2000. Local perceptions of vegetation change and priorities for conservation of woody-savanna vegetation in Senegal. *Journal of Environmental Management* 59: 107-120.

Mack, A. L. 1993. The sizes of vertebrate dispersed fruits: a Neotropical-Paleotropical comparison. *The American Naturalist* 142: 840-856.

McConkey, K. R. 2000. Primary seed shadow generated by gibbons in the rain forests of Barito Ulu, Central Borneo. *American Journal of Primatology*. 52: 13-29.

McConkey, K. R. & Chivers, D. J. 2007. Influence of gibbon ranging patterns on seed dispersal distance and deposition site in a Bornean forest. *Journal of Tropical Ecology* 23: 269-275.

McPherson, J. M. 1988. Preference of cedar waxwings in the laboratory for fruit species, colour and size: a comparison with field observations. *Animal Behaviour* 36: 961-969.

Medellin, R. A. & Gaona, O. 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, México. *Biotropica* 31: 478-485.

Melnick, D. J. & Pearl, M. C. 1987. Cercopithecines in multimale groups: genetic diversity and population structure. Pp. 121-134 In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsacker, T. T. (eds.). *Primate societies*. University of Chicago Press, Chicago.

Mess, A. & Krell, F. T. 1999. Preliminary list of rodents and shrews living in the Comoé National Park, Ivory Coast (Mammalia: Rodentia, Insectivora: Soricidae). *Stuttgarter Beiträge zur Naturkunde Serie A*: 1-11.

Michaels, H. J., Benner, B., Hartgerink, A. P., Lee, T. D., Rice, S., Willson, M. F. & Betin, R. I. 1988. Seed size variation: magnitude distribution and ecological correlates. *Evolutionary Ecology* 2: 157-166.

Mizutani, F. 1999. Impact of leopards on a working ranch in Laikipia, Kenya. *African Journal of Ecology* 37: 211-225.

Moermond, T. C. & Denslow, J. S. 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. *Ornithological Monographs* 36: 865-896.

Mühlenberg, M., Galat-Luong, A., Poilecot, P., Steinhauer-Burkart, B. & Kühn, I. 1990. L' importance des ilôts forestièrs de la savane humide pour la conservation de la faune de forêt dense en Côte d'Ivoire. *Revue d'Ecologie: La Terre et la Vie* 45: 197-214.

Muller-Landau, H. C., Wright, S. J., Calderón, O., Hubbell, S. P. & Foster, R. B. 2002. Assessing recruitment limitation: concepts, methods and case-studies from a tropical forest. Pp. 35-53 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation*. CABI, Wallingford.

Murray, K. G. 1988. Avian seed dispersal of three Neotropical gap-dependent plants. *Ecological Monographs* 58: 271-298.

Nagel, U. 1973. A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. *Folia Primatologica* 19: 104-165.

Nathan, R. & Muller-Landau, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* 15: 278-285.

Nchanji, A. C. & Plumptre, A. J. 2003. Seed germination and early seedling establishment of some elephant-dispersed species in Banyang-Mbo Wildlife Sanctuary, south-western Cameroon. *Journal of Tropical Ecology* 19: 229-237.

Newman, T. K., Jolly, C. J. & Rogers, J. 2004. Mitochondrial phylogeny and systematics of baboons (*Papio*). *American Journal of Physical Anthropology* 124: 17-27.

Norconk, M. A. & Conklin-Brittain, N. L. 2004. Variation on frugivory: the diet of Venezuelan white-faced sakis. *International Journal of Primatology* 25: 1-26.

Norconk, M. A., Grafton, B. W. & Conklin-Brittain, N. L. 1998. Seed dispersal by Neotropical seed predators. *American Journal of Primatology* 45: 103-126.

Nuñez-Iturri, G. & Howe, H. F. 2007. Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rain forest in western Amazonia. *Biotropica* 39: 348-354.

Ogutu, J. O. & Dublin, H. T. 1998. The response of lions and spotted hyaenas to sound playbacks as a technique for estimating population size. *African Journal of Ecology* 36: 83-95.

Otani, T. & Shibata, E. 2000. Seed dispersal and predation by Yakushima macaques, *Macaca fuscata yakui*, in a warm temperate forest of Yakushima Island, southern Japan. *Ecological Research* 15: 133-144.

Ouborg, N. J., Piquot, Y. & Van Groenendael, J. M. 1999. Population genetics, molecular markers and the study of dispersal in plants. *Journal of Ecology* 87: 551-568.

Pacala, S. W. & Crawley, M. J. 1992. Herbivores and plant density. *American Nauralist* 140: 243-260.

Packer, C. 1979. Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Animal Behavior* 27: 1-36.

Peck, S. B. & Howden, H. F. 1984. Response of a dung beetle guild to different sizes of dung bait in a Panamian rainforest. *Biotropica* 16: 235-238.

Peres, C. A. 1991. Seed predation of *Cariniana micrantha* (Lecythidaceae) by brown capuchin monkeys in Central Amazonia. *Biotropica* 23: 262-270.

Peres, C. A. & van Roosmalen, M. 2002. Primate frugivory in two species-rich Neotropical forests: implications for the demography of large-seeded plants in overhunted areas. Pp. 407-421 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation*. CABI, Wallingford.

Pigozzi, G. 1992. Frugivory and seed dispersal by the European badger in a Mediterranean habitat. *Journal of Mammalogy* 73: 630-639.

Poilecot, P. 1991. *Un écosystème de savane soudanienne: le Parc National de la Comoé (Côte d'Ivoire)*. UNESCO, Paris.

Pomeroy, D. E. & Service, M. W. 1986. *Tropical ecology*. Longman, Harlow.

Ponce-Santizo, G., Andresen, E., Cano, E. & Cuaron, A. D. 2006. Primary dispersal of seeds by primates and secondary dispersal by dung beetles in Tikal, Guatemala. *Biotropica* 38: 390-397.

Poorter, L., Bongers, F., Kouamé, F. N. & Hawthorne, W. D. (eds.). 2004. *Biodiversity of West African forests. An ecological atlas of woody plant species*. CABI, Wallingford.

Porembski, S. 1991. Beiträge zur Pflanzenwelt des Comoé-Nationalparks (Elfenbeinküste). *Natur und Museum* 121: 61-82.

Porembski, S. 2001. Phytodiversity and structure of the Comoé river gallery forest (NE Ivory Coast). Pp. 1-10 In Gottsberger, G. & Liede, S. (eds.). *Life forms and dynamics in tropical forests*. Dissertationes Botanicae. Borntraeger, Berlin.

Portnoy, S. & Willson, M. F. 1993. Seed dispersal curves: behavior of the tail of the distribution. *Evolutionary Ecology* 7: 25-44.

Post, D. G. 1981. Activity patterns of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya. *Animal Behaviour* 29: 357-374.

Poulsen, J. R., Clark, C. J. & Smith, T. B. 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *Journal of Tropical Ecology* 17: 787-808.

Pratt, T. K. & Stiles, E. W. 1985. The influence of fruit size and structure on composition of frugivore assemblages in New-Guinea. *Biotropica* 17: 314-321.

Price, M. V. & Correll, R. A. 2001. Depletion of seed patches by Merriam's kangaroo rats: are GUD assumptions met? *Ecology Letters* 4: 334-343.

Refisch, J. 1995. Samenverbreitung durch Paviane im Parc National de la Comoé, Elfenbeinküste. Diploma thesis. University of Bayreuth, Germany.

Reid, N. 1991. Coevolution of misteltoes and frugivorous birds? *Australian Journal of Ecology* 16: 457-469.

Rheindt, F. E., Grafe, T. U. & Linsenmair, K. E. 2002. New bird records in Comoé National Park, Ivory Coast. *Malimbus* 24: 38-40.

Rhine, R. J. & Westlund, B. J. 1978. The nature of a primary feeding habit in different age-sex classes of yellow baboons (*Papio cynocephalus*). *Folia Primatologica* 30: 64-79.

Rose, M. D. 1977. Positional behaviour of olive baboons (*Papio anubis*) and its relationship to maintenance and social activities. *Primates* 18: 59-116.

Rowe, N. 1996. *The pictorial guide to the living primates*. Pogonias Press, New York.

Rowell, T. E. 1966. Forest living baboons in Uganda. *Journal of Zoology* 149: 344-364.

Rowell, T. E. & Mitchell, B. J. 1991. Comparison of seed dispersal by guenons in Kenya and capuchins in Panama. *Journal of Tropical Ecology* 7: 269-274.

Russo, S. E. 2003. Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia* 136: 80-87.

Salewski, V. 2000. The birds of Comoé National Park, Ivory Coast. *Malimbus* 22: 55-76.

Salewski, V. & Göken, F. 2001. Black-and-white mannakin *Lonchura bicolor*, new for Comoé National Park, Ivory Coast. *Malimbus* 23: 56.

Sambrook, T. D., Whiten, A. & Strum, S. C. 1995. Priority of access and grooming patterns of females in a large and a small group of olive baboons. *Animal Behaviour* 50: 1667-1682.

Sanders, M. J., Owen-Smith, R. N. & Pillay, N. 1997. Fruit selection in the olive thrush: the importance of colour. *South African Journal of Zoology* 32: 21-23.

Sanford, W. W. & Isichei, A. O. 1986. Savanna. Pp. 95-149 In Lawson, G. W. (ed.). *Plant Ecology in West Africa*. John Wiley & Sons, Chichester.

Sapolsky, R. M. 1996. Why should an aged male baboon ever transfer troops? *American Journal of Primatology* 39: 149-157.

Sarmiento, E. 1998. Current problems with *Papio* taxonomies. *African Primates* 3: 48-52.

Schaefer, H. M. & Schaefer, V. 2006. The fruits of selectivity: how birds forage on *Goupia glabra* fruits of different ripeness. *Journal of Ornithology* 47: 638-643.

Schaefer, H. M., Schaefer, V. & Levey, D. J. 2004. How plant-animal interactions signal new insights in communication. *Trends in Ecology & Evolution* 19: 577-584.

Schmidt, V., Schaefer, H. M. & Winkler, H. 2004. Conspicuousness, not colour as foraging cue in plant-animal signalling. *Oikos* 106: 551-557.

Schupp, E. W. 1988a. Factors affecting post-dispersal seed survival in a tropical forest. *Oecologia* 76: 525-530.

Schupp, E. W. 1988b. Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos* 51: 71-78.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108: 15-29.

Shepherd, V. E. & Chapman, C. A. 1998. Dung beetles as secondary seed dispersers: impact on seed predation and germination. *Journal of Tropical Ecology* 14: 199-215.

Shilton, L. A., Altringham, J. D., Compton, S. G. & Wittaker, R. J. 1999. Old world fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. *Proceedings of the Royal Society of London Series B* 266: 219-223.

Snow, D. W. 1971. Evolutionary aspects of fruit-eating by birds. *Ibis* 113: 194-202.

Stacey, P. B. 1986. Group size and foraging efficiency in yellow baboons. *Behavioral Ecology and Sociobiology* 18: 175-187.

Stanley, M. C. & Lill, A. 2002. Importance of seed ingestion to an avian frugivore: an experimental approach to fruit choice based on seed load. *The Auk* 119: 175-184.

Stevenson, P. R., Pineda, M. & Samper, T. 2005. Influence of seed size on dispersal patterns of woolly monkeys (*Lagothrix lagothricha*) at Tinigua Park. *Oikos* 110: 435-440.

Stiles, E. W. 2000. Animals as seed dispersers. Pp. 111-124 In Fenner, M. (ed.). *Seeds: The ecology of regeneration in plant communities*. CABI, Wallingford.

Strasburger, E., Nol, F., Schenk, H. & Schimper, A. F. W. 1991. *Lehrbuch der Botanik für Hochschulen*. Gustav Fischer, Stuttgart.

Strum, S. C. 1981. Processes and products of change: baboon predatory behavior at Gilgil, Kenya. Pp. 255-302 In Harding, R. S. O. & Teleki, G. (eds.). *Omnivorous primates. Gathering and hunting in human evolution*. Columbia Press, New York.

Tewksbury, J. J. & Lloyd, J. D. 2001. Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia* 127: 425-434.

Théry, M., Stevens, A. D., Hoppe, J. R., Charles-Dominique, P. & Schuchmann, K. L. 1998. Angiosperm pollination and seed dispersal, a review. *Ecotropica* 4: 69-91.

Tischler, W. 1993. *Einführung in die Ökologie.* Fischer, Stuttgart.

Traveset, A. 1995. Seed dispersal of *Cneorum triococcon* L. (Cneoraceae) by lizards and mammals in the Balearic islands. *Botanical Journal of the Linnean Society* 117: 221-232.

Traveset, A. & Verdú, M. 2002. A meta-analysis of the effect of gut treatment on seed germination. Pp. 339-351 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation.* CABI, Wallingford.

Tutin, C. E. G., Parnell, R. J. & White, F. 1996. Protecting seeds from primates: examples from *Diospyros* spp. in the Lopé Reserve, Gabon. *Journal of Tropical Ecology* 12: 371-384.

Tutin, C. E. G., Williamson, M. E. & Fernandez, M. 1991. A case study of a plant-animal relationship: *Cola lizae* and lowland gorillas in the Lopé Reserve, Gabon. *Journal of Tropical Ecology* 7: 181-199.

UNEP. 2007. Global environment outlook (GEO-4). Technical Report. United Nations, New York.

UNESCO. 1992-2008. World Heritage List. <<http://whc.unesco.org>> Downloaded on 29 September 2008.

Urbani, B. 2002. A field observation on color selection by new world sympatric primates, *Pithecia pithecia* and *Alouatta seniculus*. *Primates* 43: 95-101.

Van der Pijl, L. 1982. *Principles of dispersal in higher plants.* Springer, Berlin.

Vander Wall, S. B. 1994. Seed fate pathways of antelope bitterbrush: dispersal by seed-caching yellow pine chipmunks. *Ecology* 75: 1911-1926.

Vander Wall, S. B. & Longland, W. S. 2004. Diplochory: are two seed dispersers better than one? *Trends in Ecology & Evolution* 19: 155-161.

VanderWall, S. B., Kuhn, K. M. & Beck, M. J. 2005. Seed removal, seed predation, and secondary dispersal. *Ecology* 86: 801-806.

Varela, F. J., Palacios, A. G. & Goldsmith, T. H. 1993. Color vision of birds. Pp. 77-98 In Zeigler, H. P. & Bischof, H. (eds.). *Vision, brain, and behavior in birds.* MIT Press, Cambridge.

Voysey, B. C., McDonald, K. E., Rogers, M. E., Tutin, C. E. G. & Parnell, R. J. 1999a. Gorillas and seed dispersal in the Lopé Reserve, Gabon. I: gorilla acquisition by trees. *Journal of Tropical Ecology* 15: 23-38.

Voysey, B. C., McDonald, K. E., Rogers, M. E., Tutin, C. E. G. & Parnell, R. J. 1999b. Gorillas and seed dispersal in the Lopé Reserve, Gabon. II: survival and growth by seedlings. *Journal of Tropical Ecology* 15: 39-60.

Wang, B. C., Sork, V. L., Leong, M. T. & Smith, T. B. 2007. Hunting of mammals reduces seed removal and dispersal of the Afrotropical tree *Antrocaryon klaineanum* (Anacardiaceae). *Biotropica* 39: 340-347.

Warren, Y. 2003. Olive baboons (*Papio cynocephalus anubis*): behaviour, ecology and human conflict in Gashaka Gumti National Park, Nigeria. PhD thesis. University of Surrey, Roehampton, UK.

Weir, J. E. S. & Corlett, R. T. 2006. How far do birds disperse seeds in the degraded tropical landscape of Hong Kong, China? *Landscape Ecology* 22: 131-140.

Wenny, D. G. 2000. Seed dispersal, seed predation, and seedling recruitment of a Neotropical montane tree. *Ecological Monographs* 70: 331–351.

Wenny, D. G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research* 3: 51-74.

Wenny, D. G. & Levey, D. J. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences* 95: 6204-6207.

Westoby, M. & Rice, B. 1981. A note on combining two methods of dispersal-for-distance. *Australian Journal of Ecology* 6: 189-192.

Wheelwright, N. T. 1985. Fruit size, gape width and the diets of fruit-eating birds. *Ecology* 66: 808-818.

Wheelwright, N. T. 1988. Fruit-eating birds and bird dispersed plants in the tropics and the temperate zone. *Trends in Ecology & Evolution* 3: 270-274.

White, F. 1979. The Guinean-Congolian region and its relation to other phytocoria. *Bulletin du Jardin National Botanique de Belgique* 49: 11-55.

White, F. 1983. *The vegetation of Africa*. UNESCO, Paris.

Whiten, A., Byrne, R. W., Barton, R. A., Waterman, P. G. & Henzi, S. P. 1991. Dietary and foraging strategies of baboons. *Philosophical Transactions of the Royal Society of London Series B* 334: 187-197.

Whiten, A., Byrne, R. W. & Henzi, S. P. 1987. The behavioral ecology of mountain baboons. *International Journal of Primatology* 8: 367-388.

Whitmore, T. C. 1998. *An introduction to tropical rain forests*. Oxford University Press, Oxford.

Wilkinson, D. M. 1997. The role of seed dispersal in the evolution of mycorrhizae. *Oikos* 78: 394-396.

Willson, M. F. 1993. Dispersal mode, seed shadows, and colonization patterns. *Vegetatio* 107: 261-280.

Willson, M. F., Hoppes, W. C., Goldman, D. A. & Thomas, P. A. 1987. Sibling competition in plants: an experimental study. *The American Naturalist* 129: 304-311.

Willson, M. F., Rice, B. L. & Westoby, M. 1990. Seed dispersal spectra: a comparison of temperate plant communities. *Journal of Vegetation Science* 1: 547-562.

Willson, M. F. & Traveset, A. 2000. The ecology of seed dispersal. Pp. 85-110 In Fenner, M. (ed.). *Seeds. The ecology of regeneration in plant communities.* CABI, Wallingford.

Willson, M. F. & Whelan, C. J. 1990a. The evolution of fruit color in fleshy-fruited plants. *The American Naturalist* 136: 790-809.

Willson, M. F. & Whelan, C. J. 1990b. Variation in postdispersal survival of vertebrate-dispersed seeds: effects of density, habitat, location, season, and species. *Oikos* 57: 191-198.

Witmer, M. C. 1991. The dodo and the tambalacoque tree: an obligate mutualism reconsidered. *Oikos* 61: 133-137.

Wolfheim, J. H. 1983. *Primates of the world. Distribution, abundance, and conservation.* University of Washington Press, Seattle.

Wrangham, R. W., Chapman, C. A. & Chapman, L. J. 1994. Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology* 10: 355-368.

Wright, S. J., Zeballos, H., Domínguez, I., Gallardo, M. M., Moreno, M. C. & Ibáñez, R. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conservation Biology* 14: 227-239.

Yagihashi, T., Hayashida, M. & Miyamota, T. 1999. Effects of bird ingestion on seed germination of two *Prunus* species with different fruit-ripening seasons. *Ecological Research* 14: 71-76.

Yumoto, T., Maruhashi, T., Yamagiwa, J. & Mwanza, N. 1995. Seed dispersal by elephants in a tropical rain forest in Kahuzi-Biega National Park, Zaire. *Biotropica* 27: 526-530.

Zhang, S. Y. & Wang, L. X. 1995. Fruit consumption and seed dispersal of *Ziziphus cinnamomum* (Rhamnaceae) by two sympatric primates (*Cebus apella* and *Ateles paniscus*) in French Guiana. *Biotropica* 27: 397-401.

Zinner, D. & Deschner, T. 2000. Sexual swellings in female hamadryas baboons after male take-overs: "deceptive" swellings as a possible female counter-strategy against infanticide. *American Journal of Primatology* 52: 157-168.

Chapter 2

Diet and Behavioural Ecology of Olive Baboons in the Comoé National Park

with K. E. Linsenmair

Published in *Folia Primatologica* (2008) 79: 31-51
http://www.karger.com/fpr, DOI 10.1159/000108384

Abstract Despite living under environmental conditions considerably distinct from those of savanna baboons (*Papio* spp.) in East and southern Africa, very little is known about western *Papio* populations. We monitored the abundance and group sizes of olive baboons (*P. anubis*) in the savanna-forest mosaic of northern Ivory Coast, and observed two habituated groups of different sizes. Against expectations for the kind of habitat, the individual density in the study area was low, yielding only 1.2 baboons/km^2. The groups were small and the proportion of one-male groups was remarkably high (50-63%). One-male groups were more female biased than multi-male groups. The baboons were highly frugivorous, spending about 50% of their feeding time on fruits and seeds of at least 79 plant species. The two habituated groups had large home ranges compared to other study sites in West Africa, and used forests more often than expected by random. We argue that regular subgrouping of the larger focal group and different habitat quality countervailed inter-group variations in our study area. Differences to other study sites, however, are not completely explained by current models on baboon (socio)ecology. It appears that the social organization of olive baboons is more flexible than assumed from data on East African populations.

2. 1 INTRODUCTION

Due to their wide distribution and ecological flexibility, baboons (*Papio* spp.) are focal targets in studies on behavioural and ecological plasticity in primates (Hill & Dunbar 2002; Henzi & Barrett 2005). As the phylogeny and taxonomy of the genus *Papio* is still disputed, we follow Groves (2001) and distinguish five different species (*P. ursinus*, *P. cynocephalus*, *P. anubis*, *P. papio, P. hamadryas*). Henceforth, we refer to the first four species as 'savanna baboons', a term that separates the 'desert baboon' *P. hamadryas* by differences in habitat occupancy and socio-ecology (Estes 1991). Savanna baboons are typically organized in multi-male-multi-female groups of several dozens to a hundred individuals. One-male groups have been recorded less frequently (e.g. Altmann & Altmann 1970; Hamilton & Bulger 1992; Barton & Whiten 1993). Females are generally philopatric, whereas males emigrate with sexual maturity (Henzi & Barrett 2005).

Savanna baboons are widespread throughout sub-Saharan Africa and occupy habitats from thorn scrub to rain forest, coastal areas and high mountain sites (Wolfheim 1983). The habitat can affect baboon group size and composition, home range size and use, and time budgets through the availability and dispersion of essential resources and the risk of predation (Henzi *et al.* 1992; Barton *et al.* 1996; Cowlishaw 1997). Baboon group size has also been correlated to day length, ambient temperature and rainfall (Dunbar 1994; Hill *et al.* 2003). Group size, in turn, can affect baboon home range size and time budgets (Stacey 1986; Barton *et al.* 1992).

Though diet as well as socio- and behavioural ecology of savanna baboons show considerable variation across different sites (Whiten *et al.* 1991; Hill & Dunbar 2002), field research up to date has focused on populations in East and southern Africa. Dunbar (1992) listed 31 *Papio* studies, of which only three were carried out on western populations. Although *P. anubis* is the most widespread of all *Papio* species, ranging from Mali to Ethiopia, Kenya, and northwest Tanzania (Groves 2001), merely one of these studies (by Depew 1983) investigated its behavioural ecology in West Africa. Yet, olive baboons in West Africa live under different environmental conditions than their conspecifics in East Africa. West and East Africa are distinct phytogeographic regions (White 1983). The aboveground forest biomass per area unit is higher in West than in East Africa (FAO 2001). Two floras intervene in the latitudinal belt of the Guineo-Congolia / Sudania transition zone, forming the species-rich savanna-forest-mosaic of West Africa (White 1979), where the abundance of woody fruit plant species can be high (Hovestadt 1997). By contrast, (*Acacia*) wooded grassland and grassland dominate large areas at many baboon study sites in East Africa (but see Norton *et al.* 1987). Furthermore, the density of nonhuman predators presumably has been historically lower in West than in East Africa (e.g. Bauer *et al.* 2003).

Since Dunbar's review (1992), only one extensive study has been reported on the behavioural ecology of olive baboons in West Africa (Nigeria, Warren 2003). Data from Ghana (Depew 1983) and Nigeria (Warren 2003) suggest that western populations form smaller groups, occupy smaller home ranges and spend more time feeding on fruit and seeds than their conspecifics in East Africa. Due to the small number of studies however, knowledge on olive baboons in West Africa is still very fragmentary. With the present study we aim to add to the ongoing discussion of the formative role of the environment on baboon ecology by focusing on population density, group size, and group composition in the savanna-forest mosaic of the Comoé National Park (CNP), northern Ivory Coast. Moreover, we present results from a comparative study in the CNP on home range, activity and diet of two olive baboon groups of different size. Due to habitat variations across sites, we predicted olive baboons in the CNP not only to deviate in their diet and behavioural ecology from populations in East Africa but also to some extent from populations studied in Ghana and Nigeria.Following current models in baboon socioecology, we assumed that the study area would support a relatively high density of largely frugivorous baboons living in small groups. These groups, however, should occupy comparatively large home ranges due to the patchy distribution of essential resources. The diet and resource distribution would be reflected by a low proportion of feeding time and a high proportion of moving time in the baboons' time budget. We also expected variation in the time budget between the focal groups due to differences in group size.

2. 2 METHODS

2.2.1 STUDY AREA

The Comoé National Park (CNP), north-eastern Ivory Coast (08°30-09°36' N, 003°07'-004°25' W), covers 11,500 km^2 at an average altitude of 250-300 m above sea level (Poilecot 1991). The park stretches across two vegetation zones: the southern area is situated within the 'Guinea-Congolia / Sudania regional transition zone' whereas the northern part belongs to the 'Sudanian regional centre of endemism' (following White 1983). The data presented here were collected by the first author over a period of 24 months (November 1997 to July 2000). The study period covered each month of the year at least once. Research focused on an area of approximately 145 km^2 in the southern part of the national park, where the vegetation consists of a mosaic of different savanna formations (~91 %), forest islands (7 %), and gallery forest (2 %) (FGU-Kronberg 1979). We use the term 'savanna' throughout this paper to summarize different vegetation types in the CNP with a percent cover of woody plants ranging from 20-70% (Hovestadt 1997). We also use 'savanna' as a general term referring to open habitats elsewhere whenever this habitat is not particularly specified (e.g. 'forest versus savanna'). Otherwise, we will apply the vegetation classification of White (1983).

In the study area, 292 woody plant species have been recorded, of which about 70% produce fleshy fruits available for consumption by animals (Hovestadt 1997). The vegetation is described in more detail in Poilecot (1991) and Porembski (1991). Savanna and gallery forests are separated by a band of grass vegetation with few woody species (Porembski 1991), henceforth referred to as 'plains'. Large areas of open grassland are lacking at the study site (FGU-Kronberg 1979).

The climate is characterized by a dry season from November to March/April, during which up to 95% of the savanna may be burned (Poilecot 1991). The mean annual precipitation from January 1994 to December 1999 was 1,053 mm and the mean annual temperature was 26.3°C. Only the river Comoé and the lower part of its tributary Iringou reliably provide water the whole year round.

The density of baboons' chief predators, leopards (*Panthera pardus*), lions (*P. leo*) and hyenas (in the CNP: *Crocuta crocuta*) (Cowlishaw 1994) is low in the CNP (FGU-Kronberg 1979; Fischer *et al.* 2002).

2.2.2 INDIVIDUAL DENSITY AND GROUP SIZES

At least twice per month, we crossed an area of approximately 145 km^2 in search of baboon groups by slowly driving along dirt roads (~10 km/h). The locations were recorded where we sighted or heard a group or found fresh evidence of baboons like tracks and/or faeces. We noted the number of visible individuals, their identity or age-sex-classes (following Altmann *et al.* 1977), and evidence for individuals out of sight (e.g. vocalization, movement in dense vegetation). In addition, we frequently crossed the area or large parts of it by car or foot in the course of supplemental tasks (e.g. sampling of plant phenology, fruit collection) and thereby encountered baboon groups *ad libitum*, which we likewise noted. Moreover, at least every other day, we recorded the presence of other groups in a core area of about 20 km^2 within the study area that included most of the home ranges of two focal groups. Due to individually recognizable baboons, different sizes and compositions of neighbouring groups and relatively little overlap in their home ranges we were able to distinguish reliably between groups. We estimated each group's annual size by adding the maximum number of individuals recorded in each age-sex-class during the respective year. The mean size per group was calculated across the annual sizes (1998-2000). The overall mean group size in the study area was calculated from all group means. Group means were summed to obtain the total number of individuals in the study area.

We determined the overall median number of adult males and adult females from their maximum number recorded per group.

2.2.3 BEHAVIOURAL OBSERVATIONS OF FOCAL GROUPS

We habituated and observed two groups of different size. The GP-group comprised 9-13 individuals (one to two adult males, two to three adult females (one reaching sexual maturity during the study) plus offspring, and one juvenile male immigrating together with an adult male during the study). We observed the GP-group over 140 days (20 months) between January 1998 and June 2000. The 1S-group comprised of 36-44 individuals (five to six adult males, one subadult male, nine adult females plus offspring), and was observed over 70 days (14 months) between January 1999 and July 2000. Observation distance to single individuals ranged from two to about 50 meters. We used binoculars (Leica 8 x 42) whenever appropriate.

Observations were not evenly distributed over time between months and in 1999 and 2000 between groups, due to difficulties in locating and tracking the animals in the dense vegetation. However, the number of scans did not differ significantly across groups in 1999 and 2000, neither within hours nor months. Records between 6:00 and 7:00 (seasonal variation in day length), as well as between 14:00 and 16:00 are slightly underrepresented in both groups.

Habitat sight restrictions, group spread, and frequent subgrouping of the 1S-group meant that observations were generally on a subset of group members only (median number of individuals visible: four of the GP-group, N = 1,779 scans; five individuals of the 1S-group, N = 932 scans). We refer to the term 'subgroup' when a part of a larger troop temporarily ranged and foraged independently and out of sight of the rest of the group.

For statistical analysis across groups, only data from 1999 and 2000 were considered.

2.2.3.1 Ranging

While following a group or subgroup, we recorded its geographic position at 20-minute intervals using a handheld GPS (864 GPS records of the GP-group, and 332 of the 1S-group). We analysed the home range data using the Geographic Information System (GIS) ESRI ArcView® (version 3.2a) plus the extension 'Animal Movement' (version 2.0). One hundred percent minimum convex polygons (100%MCP) were calculated for comparability with other baboon studies. Kernel density estimators (70%) were applied to determine centres of activity (Rodgers & Carr 1998). We used fixed kernel density estimation and least square cross validation (LSCV) to calculate the smoothing factor (H) (Seaman & Powell 1996).

We recorded the habitat (plain, savanna, forest) in which groups were found during scan sampling (see below). Forest habitats included gallery forest as well as the forest islands. For the analysis of habitat selection we considered only habitat records that were at least ten minutes apart to allow for group movements between habitats. Effectual habitat records were not constraint by a minimum number of individuals in sight since otherwise results would have been biased towards open habitats with more favourable sight conditions. Following Cowlishaw (1997) data were excluded when a group was in a mixture of habitats. To account for potential temporal and seasonal trends, we averaged the proportion of habitat records per time of day, season and year in each group. Daytime was divided into three periods: 6:00 to 9:59 h, 10:00: to 13:59 h, and 14:00 to 18:00 h. We calculated the overall time spent by a group in each habitat from all means. We used the χ^2-test with Yates correction to compare the time spent per habitat across groups.

Due to clear-cut forest boundaries, we were able to estimate the proportion of forest habitat within the home range of each group from a georeferenced map (as in Figure 1), using the area function in ArcView®. We calculated Ivlev's electivity index $(r-n)/(r+n)$ as an indicator of forest habitat selectivity (Ivlev 1961) where r is the proportion of observations in forests, and n is the proportion of forest in the home range. An index of -1 indicates avoidance, +1 selection.

2.2.3.2 Time Budget

We used Scan sampling to record group members' activities (Altmann 1974a). In 1998, when only the GP-group was habituated for observations, we carried out scans at 20-minute intervals. From January 1999, observation of two groups required a schedule modification to increase the number of scans per hour. Two-minute intervals are often used as the minimum time between consecutive sampling of baboon activity that is assumed not to be auto-correlated (e.g. Stacey 1986; Altmann 1998). Other tasks in the course of our study on seed dispersal by olive baboons, however, frequently required different time intervals and did not allow for continuous sampling of baboon activities at short time intervals. Therefore, we randomly chose two time points per hour at which we started a sequence of five consecutive two-minute scans each. In between these sequences, we collected baboon activities at 10-minute time intervals.

To represent individual behaviour adequately within a group, we restricted behavioural data analysis to scans comprising of at least three individuals older than one year. According to GP-group size variation during the study period three individuals correspond to a minimum of a third to one quarter of the older GP-group members. A total of 1,235 group scans comprising of three or more individuals were accomplished for the GP-group, and 682 for the 1S-group.

During scan-sampling, we attributed individual behaviour to one out of six mutually exclusive categories: (f) feeding (including picking and processing of food and hand-to-mouth movements), (u) foraging (searching for food on the ground or in feeding trees, sweeping through leaf litter), (d) drinking, (m) moving (locomotion not directly connected to feeding or social behaviour), (r) resting (including sleeping and self-grooming), and (O) social (including allo-grooming, playing with others, and rarely occurring sexual and agonistic behaviour) (adapted from Post 1981). We collected a total of 5,957 (GP-group) and 4,270 (1S-group) individual records. To adjust for the varying number of individuals in sight, we calculated a ratio per scan and behavioural category (number of individuals performing a given behaviour during the scan divided by the total number of individuals recorded during the scan) for further analyses. For each group, we averaged the proportions of behaviour per hour, month and year. Since the study period included repeats of several months, we first calculated the hourly means across the same months, before averaging the total hourly means. A group's time budget was then averaged from all total hourly means (adapted from Post 1981; Dunbar 1992).

For time budget comparisons across groups we applied Wilcoxon’s exact matched-pairs signed-rank test. For that purpose, we calculated means for each activity per daily observation and group (following van Schaik *et al.* 1983). Days were paired across groups according to their chronology. To eliminate potential temporal trends, we only considered observations that had been conducted during the same hours of the day within each pair of days, and of pairs that were at most ten days apart (average 4.6 ± 3.2 days, $n = 10$) (see van Schaik *et al.* 1983).

2.2.4 DIET

We categorized food items as listed in Table 3. The consumption of seed arils was attributed to seed eating, because baboons often consumed seed and aril together, and it was sometimes difficult to distinguish which part was eaten.

For each food type and food species, we calculated the mean percentage of feeding records across repeated months investigated between 1998 and 2000, prior to the calculation of the overall mean per group. Plant species accounting for more than 1% of all feeding observations were defined as core food (Norton *et al.* 1987). To complete the food list, we also considered *ad libitum* observations from groups other than the focal ones. In addition, we collected a total of 396 faecal samples throughout the study period from all baboon groups in the study area. The faeces were rinsed through sieves with decreasing mesh width (minimum 1 mm), and checked for plant and animal material. Food plants were identified from the following sources: Hutchinson *et al.* (1954-1968), von Maydell (1990), Arbonnier (2000), Kasparek (2000), a seed reference collection established in previous years by T. Hovestadt and P. Poilecot, and comparison with seeds taken from fresh fruits of identified plants. S. Porembski (University of Rostock, Germany) and E. Robbrecht (National Botanic Garden of Belgium) verified the plant material in question. Habitat preference of food plant species is following Hovestadt (1997) and Hutchinson *et al.* (1954-1968).

2.2.5 GENERAL STATISTICS

The median (x_{md}) and 25%- and 75%-percentiles (q_1, q_3) are given, when the data were not normally distributed. We applied non-parametric tests whenever assumptions for parametric testing were violated. We used exact tests for small sample sizes (SPSS Exact Extension, version 12.0, 13.0). Tests were run with the SPSS for Windows statistical package (version 12.0 or 13.0) or the SsS package (Rubisoft software 1.0e) with confidence limits set at 95%. All tests were two-tailed. We adjusted the level of significance for multiple comparisons using the sequential Bonferroni correction (Rice 1989).

2. 3 RESULTS

2.3.1 INDIVIDUAL DENSITY AND GROUP SIZES

We identified ten different groups (Table 1) with a total of 167 individuals in an area of 145 km^2, resulting in an individual density of 1.2/km^2. The groups consisted of 4-44 individuals (x = 14.1 ± 10.2). It is possible that there were two groups of intermediate size that were never recorded completely. When these are excluded, mean group size was 15.3 ± 11.1 individuals.

Table 1 Size and composition of the ten olive baboon groups recorded between 1998 and 2000 in the study area in the Comoé National Park, Ivory Coast

Only direct observations are included. (fc): focal group, regularly observed from 1998-2000 (GP-group) and from 1999-2000 (1S-group), see methods for detailed information. *: I-group and Z-group probably were never recorded completely.

	Group									
	3N	**K**	**1N**	**D**	**3S**	**GP**	**2S**	**1S**	**Z***	**I***
N°. of group observations	6	19	19	5	26	(fc)	34	(fc)	5	10
Mean group size	3.3	11	14	7.5	19.5	12	15	40	7	11.7
Max. n°. of										
adult males	1	1	1	1	4	2	2	6	2	1
subadult males	0	1	2	2	2	0	1	1	1	0
adult females	1	2	3	3	6	3	4	9	2	2

Between one and six adult males (x_{md} = 1.5, q_1 = 1, q_3 = 2.5) and one and nine adult females (x_{md} = 3, q_1 = 2.75, q_3 = 4.5,) were present per group (n = 8). In four of these groups, no more than one male was ever recorded. Moreover, the GP-group persisted as a one-male group for at least 14 months, before a second male and an older juvenile male immigrated. Between nine and twelve months later, during a short interruption in the observations, the first male disappeared and yet another adult male immigrated. Thus, 50% to 62.5 % of the groups were one-male groups during the study period.

One relatively stable one-male unit, comprising of eleven to 13 individuals, frequently separated from the 1S-group and often foraged and slept alone. In 1999, we also found that the second biggest group (26 individuals) split, at least temporarily, into two subgroups (including a one-male unit).

The overall adult-sex-ratio (calculated from the mean number of adult males = 2.25, and females = 3.88) was 1 male : 1.72 females per group. One-male groups (including temporary ones) were more female biased (1:2.25) than multi-male groups (1:1.57).

2.3.2 RANGING

The 100%MCP calculation revealed a home range area of 414 ha for the GP-group, and 1,657 ha for the 1S-group (Figure 1).

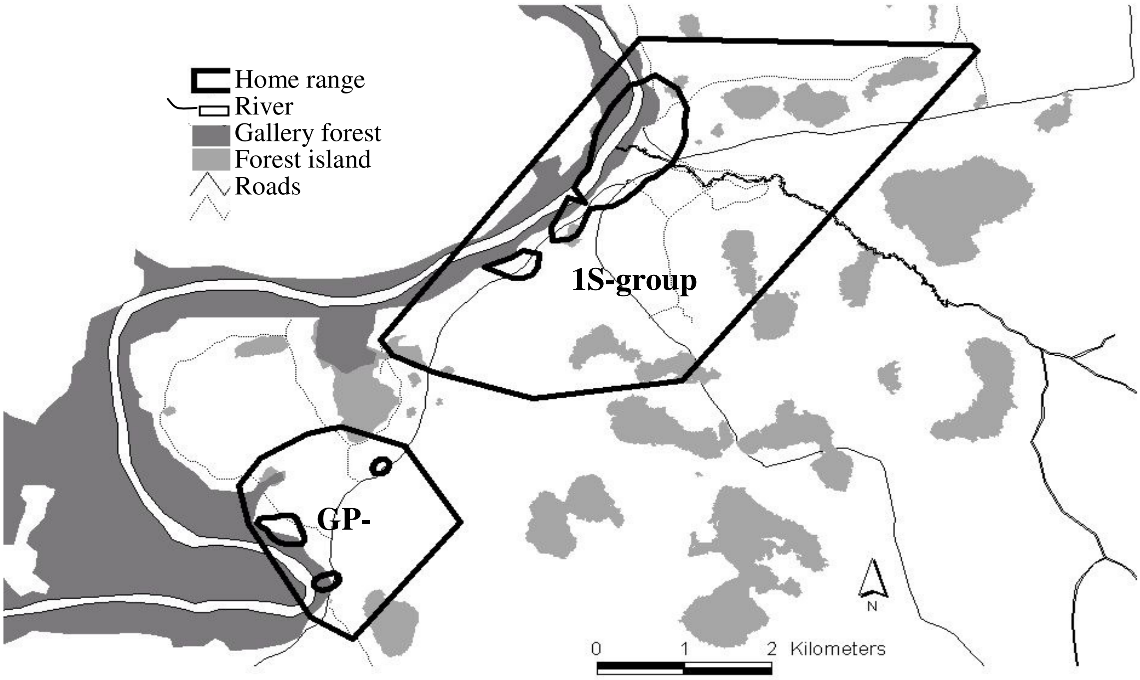


Figure 1 Home ranges of the two focal baboon groups (GP-group and 1S-group) in the Comoé National Park

The 100% Minimum Convex Polygons (angled black outline) and 70% kernels are given for each group.

Another group occupied the area in between the home ranges of the two focal groups, slightly overlapping with each group's home range. However, neither focal groups, nor other groups in the study area, were observed in inter-group encounters.

The 70% kernel density estimation for the GP-group resulted in three core areas amounting to 20 ha in total. The 1S-group spent 70% of its daytime in two core areas covering 157 ha. All but one of these core areas included gallery forests and baboon sleeping sites.

Both focal groups regularly used all three habitat types (plains, savanna, and forest). The GP-group (1998-2000) spent twice as much time under observation in the savanna (54.6%, *N* = 1,049 habitat records) than in either forest (25.9%) or on plains (19.6%). The 1S-group (1999-2000) spent considerably more time in the savanna (51.9%) and forest (32.7%), than on plains (15.4%) (*N* = 417 habitat records). Forests made up 10.9 % of the GP-group's, and 11.9 % of the 1S-group's home range. Ivlev's electivity index for forest habitats was 0.41 for the GP-group and 0.47 for the 1S-group, indicating a non-random use of this habitat.

If the data from 1999-2000 are compared across groups (GP = 706 habitat records, 1S as above), differences between the groups are significant, except for plains. The 1S-group was recorded more often in forest habitats and less often in savanna than the GP-group ($\chi^2 = 31.179$, $df = 1$; $p < 0.001$ and $\chi^2 = 13.586$, $df = 1$, $p < 0.01$, respectively; both tests with Yates correction).

2.3.3 TIME BUDGET

Both groups spent about a third of the observed daytime feeding (see Table 2). Foraging and feeding accounted for more than 40% of their time budget. Moving and resting were the second and third most frequent activities. Drinking was rarely recorded and thus excluded from further analyses. When compared on a daily basis, groups differed significantly only in one category: the 1S-group spent more time resting than the GP-group ($Z = -2.80$, $p < 0.01$, $n = 10$ pairs of days).

Table 2 Time budgets (%) of the two habituated baboon groups (GP- and 1S-group) in the CNP
GP-group: 1,229 group scans comprising of 5,923 individual records (1998-2000); 1S-group (1999-2000): 672 group scans with 4,215 individual records. Mean proportions of activity were calculated from mean ratios (number of animals recorded in each activity related to the number of animals visible per scan) per hour and month.

% of records	GP-group	1S-group
Feeding	32.6	30.1
Foraging	9.1	11.2
Drinking	0.1	0.5
Moving	26.0	25.2
Resting	18.1	19.5
Socializing	14.3	13.5

2.3.4 DIET

The food items consumed by baboons in the CNP are given in Table 3. Half of the feeding observations on the two focal groups were on flowers, fruits, and seeds from woody plants. The GP-group spent a higher proportion feeding on these items than the 1S-group ($\chi^2 = 33.172$, $df = 2$, $p < 0.001$, data from 1999-2000). Flowers (mainly *Daniellia* *oliveri*, Caesalpiniaceae) and leaves were eaten occasionally, and all other food items, except grass, were rarely included in the diet. Animal matter mostly consisted of caterpillars (Noctuidae) during short periods of outbreaks, termites (Nasutitermitinae) from knocked-off mounds, galls, and ants collected from stems or leaves. We never observed baboons in the CNP hunting large vertebrate prey, and hairs and bones of small vertebrates were found in only 1.8% of all faeces examined (*N* = 396).

Direct feeding records (*N* = 3,649) of all groups in the study area and faecal analysis (*N* = 396) provided evidence for 84 food plant species (exclusive of grasses and sedges). We were able to identify the habitat preference for 70 food plant species. Eight species were habitat generalists, 24 species were growing in the savanna and in forest islands, and 25 can be found in forest islands and in the gallery forest. Thirteen species were habitat specialists, growing either in the savanna (7), or in the gallery forest (1), or in forest islands (5).

Baboons consumed the fruits and/or seeds of 79 out of the 84 food plant species (including eleven yet unidentified species which were recorded rarely and by faecal analysis only). Eighteen woody plant species were core foods for at least one of the focal groups (GP-group = 13, 1S-group = 12) (Appendix 1).

Table 3 Mean proportions of different food types consumed by the two habituated baboon groups (1S-group and GP-group) in the Comoé National Park

Scan sampling data only. GP-group (1998-2000), feeding records: *N* = 2,116; 1S-group (1999-2000), *N* = 1,355. If 1998 feeding data were excluded from GP-group's analysis, figures changed only slightly (mean difference = 0.4% ± 0.5%, range 1.6-2.0%), except for time spent feeding on grass (30.1% for 1999-2000).

* including grass blades, grass seeds, and subterranean parts

	% feeding records		
food type	**GP-group**	**1S-group**	**total**
Flowers	4.43	7.63	6.03
Fruit	31.87	26.56	29.21
Seeds	22.52	13.54	18.03
Leaves	3.99	5.64	4.81
Bark	0.15	0.06	0.10
Exudate	1.85	0.95	1.40
Grass*	25.23	32.99	29.11
Mushrooms	0.06	0.00	0.03
Soil	1.85	2.31	2.08
Arthropods	0.20	1.43	0.82
Unidentified items	8.30	9.84	9.07

2. 4 DISCUSSION

2.4.1 INDIVIDUAL DENSITY AND GROUP SIZES

Olive baboons in the CNP seem to differ in several ways from conspecifics at other study sites. However, considering the various methodologies applied in different studies and the variation in study length and intensity, comparisons across sites have to be made cautiously.

Variation in individual densities of primates across sites is often related to habitat-specific food availability. Generally, baboon densities tend to be lower in open habitats, where baboons depend mostly on grass and roots, and higher in forest habitats, where fruit generally constitutes the largest part of baboon diet (Melnick & Pearl 1987; Dunbar 1994). The olive baboons in the study area in the CNP deviate from this pattern: their individual density is extremely low (Table 4) despite intensively using the species rich fruit supply in the savanna-forest-mosaic. The value of 1.2 baboons/km^2 in the study area may be an underestimation, as we possibly never recorded two groups completely. However, there was no evidence (e.g. vocalization, traces) for higher individual numbers in these groups and thus for any remarkably higher individual density in the area. We assume that the density across the whole area of the CNP is even lower. The study area was situated within the more humid southern part of the national park and extended along the eastern side of the river Comoé. As baboons need to drink every to every other day (Altmann & Altmann 1970), groups are likely to concentrate their home ranges along the two main rivers and a few pools. Roughly two-thirds of the park area (7,667 km^2) might be within one to two days walking distance of permanent water sources during the dry season. We thus estimate the total baboon population in the CNP to be 9,200 individuals, yielding an overall individual density of 0.8/km^2. This number is consistent with estimates resulting from aerial surveys in the CNP between 1977 and 1990 (0.3-0.9 individuals/km^2, Poilecot 1991). Previous estimates from road-strip counts along main roads in February and March 1977 and April 1978 yielded a density of 1.4 baboons/km^2 (FGU-Kronberg 1979), but did not take into account the spatial distribution of available water.

While olive baboon densities seem to be lower in West Africa (x = 2.1 individuals/km^2, Table 4) than in East Africa (x = 13.6 individuals/km^2), the baboon density in the CNP is low even for western populations. Periods of food (fruit) scarcity in a highly seasonal habitat like the CNP may account for a lower baboon density than in more forested areas across Africa that receive higher amounts of rainfall and have less pronounced dry seasons (e.g. Chapman *et al.* 1999). However, this explanation is not supported by the fact that in drier habitats higher densities of olive baboons are found (e.g. Awash valley: 5.6 individuals/km^2 and 639 mm/year; see Dunbar 1992, and Table 4). A population decline due to recent vegetation changes or ecological catastrophes as elsewhere (Altmann *et al.* 1985;

Tutin *et al.* 1997) is unlikely for the CNP. The savanna- forest pattern has been remarkably stable in the CNP, at least during the last 50 years (Goetze *et al.* 2006). Baboon density in the CNP has been low at least since the late 1970s (see above). It seems therefore unlikely that poaching is responsible for the low baboon abundance, as hunting intensity has only increased in the CNP since the 1990s (Poilecot 1991; Fischer & Linsenmair 2001). Moreover, the group sizes apparently have been small at least since 1979. During a north-south transition of the park along the river Comoé, Balzamo *et al.* (1980) recorded groups ranging from eight to 32 individuals (x = 18.4). In an extensive study on the flora and fauna of the national park, Poilecot (1991) reported an average group size of 15 individuals.
The mean group size across Africa as listed in Table 4 is 45.5 (excluding data from the CNP). Reviews by Wolfheim (1983) and Dunbar (1988) revealed a mean group size of 36.1 and 41.2 individuals, respectively.

Besides low population density, the density and distribution of essential resources, predation risk and anti-predator behaviour can mediate group size in primates (Dunbar 1994; Barton *et al.* 1996). Large groups should fission when food patches are often too small for the whole group and increased travel costs to visit more food patches are not repaid of by an increase in energy gain or some other fitness advantage (Chapman *et al.* 1995; Barton *et al.* 1996). Concordantly, all members of the small GP-group were generally feeding together in a fruiting tree, whereas the 1S-group either foraged in dispersed formation or split up into subgroups for one or several days. Dunbar (1996) developed a model of habitat-specific minimum and maximum group sizes for baboons. Groups should split when exceeding the maximum tolerable group size defined by ecological (and cognitive) constraints.
The two largest groups in our study area (the focal 1S-group, and another group of 26 individuals) were small compared to predictions made by the model. Yet, they regularly formed independent subgroups that supposedly were in transition to permanent fissioning. The average group size of 15 individuals in the CNP was smaller than the predicted minimum permissible group size (19-20 individuals, Dunbar 1996) and even groups below the mean persisted at least during the entire study period.

Small groups (or subgroups) can be monopolized by a single adult male (Byrne *et al.* 1993; Hill & Lee 1998). Accordingly, the proportion of one-male groups in our study area (≥ 50%) was exceptionally high for savanna baboons. Low group encounter rates at low population densities may have facilitated the long persistence of these one-male groups (Byrne *et al.* 1987). We never observed inter-group encounters, despite overlapping home ranges of the two focal groups with other groups. One-male groups may try to reduce the risk of male intrusion by avoiding encounters with multi-male groups. The GP-group's single adult male regularly monitored the vicinity from a tree top at dawn and subsequently led the group silently away from where other groups had been heard (see also Stacey 1986; Hamilton & Bulger 1992). Finally, however, two other adult males succeeded in immigrating into the formerly one-male GP-group. As the adult sex ratio was more favourable for males in one-male than in multi-male groups and one male-groups may be easier to take over, they are likely the preferred targets of male invaders.

Small group sizes and a large proportion of one-male groups are also seen as an indication for low predation risk (Barton *et al.* 1996; Hill & Lee 1998). Primary baboon predators are leopards, lions, and hyenas (Cowlishaw 1994). Lions (*Panthera leo*) have been historically rare in West Africa (Bauer *et al.* 2003), and are nowadays nearly extinct in the CNP. Individual densities of leopards (*P. pardus*) (0.69-0.87 individuals/100 km^2, FGU-Kronberg 1979; 0.35-0.43/100 km^2 in the nineties, M. Groß, pers. comm.) and the spotted hyena (*Crocuta crocuta*) (0.87/100 km^2, FGU-Kronberg 1979) are very low in the CNP, compared to East Africa (e.g. ~10 leopards/100 km^2 at Laikipia (Kenya), Mizutani & Jewell 1998). Baboons are not leopards' preferred prey (Hayward *et al.* 2006). Only 2.87% of 209 leopard scats contained baboon remains in the CNP (M. Groß, pers. comm.). Spotted hyenas in the CNP live and hunt solitarily (Korb 2000) and the CNP-baboons may thus be less vulnerable to hyena attacks than in East Africa. This suggests that the predation risk for baboons in the CNP may be lower than predicted by Dunbar's model (1996) for this kind of habitat and could thus be a possible reason for the smaller than predicted group sizes found in the CNP. If the density of large carnivores in similar baboon habitats (according to the level of vegetation cover) is generally lower in West than in East Africa, Dunbar's model may regularly overestimate minimum permissible group size in western baboon populations.

2.4.2 RANGING, TIME BUDGET, AND DIET

Home range size in baboons is often positively correlated to group size (Stacey 1986; Barton *et al.* 1992; but see Hamilton *et al.* 1975), and negatively to vegetation cover from savanna to forest (Dunbar 1988; see also Melnick & Pearl 1987). Despite comparable group sizes at all three West African study sites, olive baboons in the CNP had larger home ranges than in Nigeria and Ghana (Table 4). This is true even so the 100%MCPs slightly overestimate the total size of the focal groups' home ranges in the CNP. By connecting the outermost location points, 100%MCPs comprise areas West of the river Comoé where we never observed the groups (see Figure 1). Corrected values excluding these areas are 407 ha for the GP-group and 1,540 ha for the 1S-group.

Larger home ranges of CNP baboons could be explained by the lower population density compared to the Shai Hills in Ghana (no population density estimates are available from the Nigerian study site) and a thinner and more patchy distribution of important foods, water, refuges and sleeping sites (following Altmann 1974b; Stacey 1986). Areas in which several (critical) resources co-occur tend to be favoured by baboons (Harding 1976; Barton *et al.* 1992). The 70% kernels encompass only 5-10% of each focal group's total home range. Both core areas of the 1S-group and two out of the three core areas of the GP-group included sleeping sites in the gallery forest, areas of (midday) resting periods, areas in close vicinity to sleeping sites where the baboons generally spent part of the morning (1S-group) and/or evening hours (1S-group, GP-group), and were close to the only permanent water source (river Comoé). Water was believed not to be a limiting factor at the Nigerian study site and core areas (70% kernels) were more evenly distributed over the total home range of the groups (Warren 2003). Furthermore, home ranges at the Nigerian study site are likely to be more productive, comprising of 80% forest, and/or agricultural areas from which crops were fed on (Warren 2003). Olive baboons seem to show a general preference for forest habitats when available (Rowell 1966; Nagel 1973; Warren 2003) and both CNP-groups spent more time in forest habitats than would be expected on a random basis. Though the proportion of forest area in the home ranges of both groups was similar (12% and 11 %, respectively), the 1S-group spent significantly more time in forest habitats than did the GP-group. Different habitat utilization may partly result from variation in habitat quality. In the study area, gallery forest is constantly dominated by *Cynometra megalophylla* (Caesalpiniaceae) (Porembski 2001) which baboons eat only occasionally (Appendix 1). Forest islands, however, differ significantly in species composition and the abundance of animal-dispersed plant species (Hovestadt *et al.* 1999). The home range of the 1S-group encompasses large forest islands of the dry, species rich vegetation type (following Hovestadt 1997). In contrast, the GP-group's home range encompasses only the humid type, which is similar in species composition to the gallery forest (see Hovestadt 1997). While fruit availability is generally higher in forests than savannas (e.g. Hill & Dunbar 2002) the Guinea-savanna in the CNP is not a poor habitat in terms of baboons food (see Hovestadt 1997). It comprises many woody plant species bearing fleshy fruits and legume species with protein rich seeds (Hovestadt 1997; Kunz & Linsenmair 2007). More than half of the identified food plant species of the baboons are growing in the savanna, including 14 out of the 18 woody core food species (following Hovestadt 1997).

Time spent feeding and foraging in baboons reflects the richness and distribution of food sources and food processing time, and thus tends to decrease with vegetation cover and the amount of fruit in the diet (Post 1981; Hill & Dunbar 2002). Consequently, baboons may spend more time resting and/or socializing in richer than in poorer habitats (Eley *et al.* 1989; Dunbar 1992). Group size can confound these habitat/environmental effects. For example, time spent moving and feeding may increase with baboon group size, and resting time may decrease (Stacey 1986; Hill & Dunbar 2002; but see Bronikowski and Altmann 1996). In the CNP, however, the larger 1S-group spent more time resting than the smaller GP-group, while time spent in other behavioural categories did not vary significantly between groups. Time-compensating counterstrategies like speeding up travelling and limiting the number of grooming partners can be at work in large groups (Dunbar 1992; Sambrook *et al.* 1995). We suppose, however, that different habitat quality across home ranges and frequent subgrouping of the larger 1S-group are likely to having countervailed size-dependent differences in the time budget between groups. Probably, large savanna ponds retaining water long into the dry season and a greater number of suitable sleeping sites in the home range of the 1S-group reduced their need to travel to access these resources in comparison with the GP-group (*c.f.*, Altmann 1974b; see also Hill *et al.* 2003).

Given the habitat and the high amount of fruits and seeds in the baboon diet in the CNP, time spent feeding and foraging by both groups seems comparatively high (*cf.* Dunbar 1992; Hill & Dunbar 2002, see also Table 5). Bearing in mind the differences that may derive from different study methods, the variation in time budget across baboons in the CNP and at the Shai Hills in Ghana still is striking. The Shai Hills seem ecologically more similar to the CNP (regarding annual rainfall, mean annual temperature, plant composition, predation risk) than any other study site of olive baboons, and both populations consist of relatively small groups (Table 4). Olive baboons in Ghana also spent a high amount of their feeding and foraging time on fruits and seeds, but feeding and foraging accounted for only half of their time budget compared to CNP-baboons (Table 5).

As expected, CNP-baboons differed to some extend from other populations in East Africa, as well as in West Africa. The reason for their extremely low density in the CNP is not clear, as the Guinea-savanna and forest islands are not poor habitats in terms of baboon food, and direct human influence seems marginal. We suppose that the patchy nature of the habitat in combination with the density and distribution of permanent water sources in the CNP could constrain baboon density. The limited availability of permanent water is likely to narrow the total area across which baboons can establish home ranges, i.e. along the main water courses. A patchy and variable distribution of other essential resources (fruiting trees, sleeping sites in forests) should result in comparatively large home ranges. As a likely consequence of the high fruit availability and the relatively low predation risk from nonhuman predators, baboons live in small groups in the CNP, of which an unusual high proportion are relatively stable one-male groups. Differences in CNP-baboons' time budget to other highly frugivorous populations, however, require further investigation. In fact, more ecological studies on western baboon populations are needed to evaluate current models on baboon socio- and behavioural ecology.

Table 4 Summary of olive baboon group sizes, adult sex ratios and home range sizes across field study sites

For reasons of comparability, the classification of vegetation types follows White (1983). Vegetation types are marked in *italics* when descriptions available on a study site could not be clearly transferred to White's classification. ^{x} = mean value; (*) = number of groups; $^{\#}$ = Guinea-Savanna; $^{+}$ = Guinea- and Sudan-Savanna

Country	Study site	Source	Habitat	Individual density/km^{2}	N^{o}. of groups	Group size	Mean group size	Mean/ study site	N$^{o.}$ of adult males	Adult sex ratio	Home range^{x} (ha) (*)
Ethiopia	Awash valley	1	(Wooded / bushed) grassland, bushland, gallery forest	5.6	5	16-71	47.2	47.2	17.3	1.52	-
	Bole valley	2	Grassland, bushland / thicket, gallery forest	26	7	15-24	20	20	-	-	93.7^{x} (3)
Kenya	Kekopey-Gilgil	3	Grassland, *bushland / thicket*, cliffs	-	7	35-121	65	65	3-5	3.2-6	1,968.4 (1)
	Laikipia	4; 5	*Acacia* wooded (bushed) grassland, *woodland*, inselbergs	-	1	103	96.5	64	16	1.63	4,375 (1)
		6			2	40-80	60		-	-	-
		7			1	64-72	68		4-7	2.4-4	-
	Nairobi NP	8	(*Acacia* wooded) grassland	3.9	5	17-76	39	39	3^{x}	2.5	2,325^{x} (5)
		9			2	30-39	34.5		8 & 5	-	-
	Maisai Mara Reserve	10	*Acacia* wooded grassland, *bushland / thicket,* gallery forest	-	2	60-90	75	75	-	-	-
Tanzania	Gombe	11	Grassland, (miombo) woodland, (semi) evergreen forest	-	2	20-34	27	27	8	1.38	-
		12; 13		21.9	3	26-51	38.3		-	-	-
	Lake Manyara	9	Grassland, *Acacia* woodland, *bushland / thicket*, forest	-	2	51-81	66	66	13 & 4	-	-
	Serengeti	9	Grassland, gallery forest, inselbergs	-	2	10-34	22	59.5	4 & 9	-	-

Table 4 (continued)

Country	Study site	Source	Habitat	Individual density/km^2	N^{o}. of groups	Group size	Mean group size	Mean/ study site	N$^{o.}$ of adult males	Adult sex ratio	Home range^x (ha) (*)
Uganda	Murchison Falls	14	(Wooded) grassland, drier semi-evergreen rain forest	-	8	14-48	29.9	29.9	-	-	-
	Queen Elizabeth Park	15	Grassland, bushland, gallery forest	10.8	2	32-58	45	45	5 & 14	1-1.14	530 & 390
Nigeria	Gashaka Gumti NP	16	Wooded (bushed) grassland$^{\#}$, rain forest, gallery forest, (plantations)	-	2	14-28	21	21	4 & 6	1-1.17	148 & 149
Benin	Pendjari NP	17	Sudanian woodland	3.06	-	-	-	-	-	-	-
Ghana	Shai Hills	18; 19	Grassland, thicket, dry forest	3.5 (2.6-4.3)	-	20-36	19.1	19.1	-	-	70 (1)
Ivory Coast	Comoé NP	20	Wooded (bushed) grassland$^+$, woodland, semi-evergreen rain forest, gallery forest	-	14	18	18.4	16.9	3.9^x	1.74	-
		this study		(0.8-) 1.2	8 (10)	4-44	15.3 (14.1)		2.3^x	1.72	407 & 1,540

1 = Nagel (1973); 2 = Dunbar & Dunbar (1974); 3 = Harding (1976); 4 = Barton (1989); 5 = Barton & Whiten (1993); 6 = Sambrook *et al.* (1995); 7 = Castles *et al.* (1999); 8 = DeVore & Hall (1965); 9 = Altmann & Altmann (1970); 10 = Sapolsky (1996); 11 = Nash (1976); 12 = Packer (1979); 13 = J. Oliver pers. comm. to Dunbar (1988); 14 = Hall 1965 cited in Melnick & Pearl (1987) ; 15 = Rowell (1966); 16 = Warren (2003); 17 = Sinsin *et al.* (2002); 18 = Lieberman *et al.* (1979); 19 = Depew (1983); 20 = Balzamo *et al.* (1980).

Table 5 Summary of olive baboon time budgets and time spent feeding on different food items across field study sites

Habitat classification is following White (1983). Vegetation types are marked in *italics* when descriptions available on a study site could not be clearly transferred to White's classification. Subter. = underground plant material; $^{\#}$ = Guinea-Savanna; $^{+}$ = Guinea- and Sudan-Savanna; * = 34.6% if analysis is restricted to data from 1999-2000, as in 1S-group

					% of time spent				% of time spent feeding on				
Country	Study site	Source	Habitat	Group size	feeding/ foraging	moving	resting	social.	flowers	fruits / seeds	leaves, subter.	animal matter	other
Ethiopia	Awash Valley	1; 21	(Wooded / bushed) grassland, bushland, gallery forest	71	30.9	25	30.5	12.2	-	-	-	-	-
	Bole Valley	2; 21	Grassland, bushland / thicket, gallery forest	19	20.5	25.4	35.4	15.9	7.4	54.9	34.5	2.7	0.7
	Mulu	21	?	22	40.8	25	22.4	14.7	-	-	-	-	-
Kenya	Kekopey-Gilgil	3; 22	Grassland, *bushland / thicket*, cliffs	49.5	50.7	30.4	9.6	9.3	2.6	9.5	79.9	1.9	5.7
	Laikipia	4	*Acacia* wooded (bushed) grassland, *woodland*, cliffs	103	40.2	33.1	17.1	7.8	20.6	22.5	56.2	1	0
Tanzania	Gombe	13	Grassland, (miombo) woodland, (semi) evergreen forest	-	-	-	-	-	2.2	48.6	20.5	13.1	14.3
Nigeria	Gashaka Gumti NP	16	Wooded grassland$^{\#}$, rain forest, plantations	14	26.7	25.2	34.5	11	4.8	54	9.6	13.6	17.9
			Wooded (bushed) grassland$^{\#}$, rain forest, gallery forest	28	31.2	29.6	27.8	8.5	4.9	62.8	6.2	8.1	18
Ghana	Shai Hills	19	Grassland, thicket, dry forest	23.7	20.3	18.2	38.7	22.7	4.6	58.8	24	0	12.4
Ivory Coast	Comoé NP	this study	Wooded (bushed) grassland^{+}, woodland, semi-evergreen rain forest, gallery forest	12	41.7	26	18.1	14.3	4.4	54.4	29.2*	0.2	12.2
				40	41.3	25.2	19.5	13.5	7.6	40.1	38.6	1.4	13.2

1 = Nagel (1973); 2 = Dunbar & Dunbar (1974); 3 = Harding (1976); 4 = Barton (1989); 13 = J. Oliver pers. comm. to Dunbar (1988); 16 = Warren (2003); 19 = Depew (1983); 21 = Dunbar (1992); 22 = Eley *et al.* (1989).

2. 5 ACKNOWLEDGEMENTS

We kindly thank K. Kouadio, S. Porembski, and E. Robbrecht who identified plant material. K. Koenig and M. Wegmann provided indispensable help with GIS ArcView. S. Teelen and Y. Warren made helpful comments on an earlier draft of the manuscript. Research permission for the CNP was kindly granted by the "Ministère de l'Agriculture et des Ressources Animales" and the "Ministère de l'Enseignement Supérieure et de la Recherche Scientifique", Abidjan. The study was funded by PhD scholarships from the German Academic Exchange Service (DAAD) and the University of Wuerzburg (HSP III). The research camp in the CNP was constructed with generous funds from the Volkswagen-Foundation.

2. 6 REFERENCES

Altman, J. 1974a. Observational study of behavior: sampling methods. *Behaviour* XLIX: 227-267.

Altmann, J., Altmann, S. A., Hausfater, G. & McCuskey, S. A. 1977. Life history of yellow baboons: physical development, reproductive parameters, and infant mortality. *Primates* 18: 315-330.

Altmann, J., Hausfater, G. & Altmann, S. A. 1985. Demography of Amboseli baboons, 1963-1983. *American Journal of Primatology* 8: 113-125.

Altmann, S. A. 1974b. Baboons, space, time, and energy. *American Zoologist* 14: 221-248.

Altmann, S. A. 1998. *Foraging for survival: yearling baboons in Africa*. University of Chicago Press, Chicago.

Altmann, S. A. & Altmann, J. 1970. *Baboon ecology*. S. Karger, Basel.

Arbonnier, M. 2000. *Arbres, arbustres et lianes des zones sèches d'Afrique de l'Ouest*. Muséum National d'Histoire Naturelle, Paris.

Balzamo, E., Seri, B. & Kouako, K. 1980. Répartition géographique de *Papio anubis* dans le nord-est et le centre-sud de Côte d'Ivoire. *Primates* 21: 524-537.

Barton, R. 1989. Foraging strategies, diet and competition in olive baboons. PhD thesis. University of St. Andrew, UK.

Barton, R. A. & Whiten, A. 1993. Feeding competition among female olive baboons, *Papio anubis*. *Animal Behaviour* 46: 777-789.

Barton, R. A., Byrne, R. W. & Whiten, A. 1996. Ecology, feeding competition and social structure in baboons. *Behavioral Ecology and Sociobiology* 38: 321-329.

Barton, R. A., Whiten, A., Strum, S. C., Byrne, R. W. & Simpson, A. J. 1992. Habitat use and resource availability in baboons. *Animal Behaviour* 43: 831-844.

Bauer, H., DeLongh, H., Princée, F. & Ngantou, D. 2003. Research needs for lion conservation in West and Central Africa. *Comptes Rendus Biologies* 326: 112-118.

Bronikowski, A. M. & Altmann, J. 1996. Foraging in a variable environment: weather patterns and the behavioral ecology of baboons. *Behavioural Ecology and Sociobiology* 39: 11-25.

Byrne, R. W., Whiten, A. & Henzi, S. P. 1987. One-male groups and intergroup interactions of mountain baboons. *International Journal of Primatology* 8: 615-633.

Byrne, R. W., Whiten, A., Henzi, S. P. & McCulloch, F. M. 1993. Nutritional constraints on mountain baboons (*Papio ursinus*): implications for baboon socioecology. *Behavioral Ecology and Sociobiology* 33: 233-246.

Castles, D. L., Whiten, A. & Aureli, F. 1999. Social anxiety, relationships and self-directed behaviour among wild female olive baboons. *Animal Behaviour* 58: 1207-1215.

Chapman, C. A., Gautier-Hion, A., Osates, J. F. & Onderdonk, D. A. 1999. African primate communities: determinants of structure and threats to survival. Pp. 1-37 In Fleagle, J. G., Janson, C. & Reed, K. E. (eds.). *Primate communities*. Cambridge University Press, Cambridge.

Chapman, C. A., Wrangham, R. W. & Chapman, L. J. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology* 36: 59-70.

Cowlishaw, G. 1994. Vulnerability to predation in baboon populations. *Behaviour* 131: 3-4.

Cowlishaw, G. 1997. Trade-offs between foraging and predation risks determine habitat use in a desert baboon population. *Animal Behaviour* 53: 667-686.

Depew, L. A. 1983. Ecology and behaviour of baboons (*Papio anubis*) in the Shai Hills Game Production Reserve, Ghana. MSc thesis. Cape Coast University, Ghana.

DeVore, I. & Hall, K. R. L. 1965. Baboon ecology. Pp. 20-52 In DeVore, I. (ed.). *Primate behaviour. Field studies of monkeys and apes.* Holt, Rinehart & Wilson, New York.

Dunbar, R. I. M. 1988. *Primate social systems*. Cornell University Press, New York.

Dunbar, R. I. M. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology* 31: 35-49.

Dunbar, R. I. M. 1994. Ecological constraints on group size in baboons. *Physiology and Ecology Japan* 29: 221-236.

Dunbar, R. I. M. 1996. Determinants of group size in primates: a general model. Pp. 33-57 In Runciman, W. G., Maynard Smith, J. & Dunbar, R. I. M., (eds.). *Evolution of social behaviour patterns in primates and man*. Oxford University Press, Oxford.

Dunbar, R. I. M. & Dunbar, E. P. 1974. Ecological relations and niche separation between sympatric terestrial primates in Ethiopia. *Folia Primatologica* 21: 36-60.

Eley, R., Strum, S. C., Muchemi, G. & Reid, G. D. F. 1989. Nutrition, body condition, activity patterns, and parasitism of free-ranging troops of olive baboons (*Papio anubis*) in Kenya. *American Journal of Primatology* 18: 209-219.

Estes, R. D. 1991. *The behavior guide to African mammals*. University of California Press, Berkley.

FAO, 2001. *Global forest resources assessment 2000. Main report*. FAO, Rome.

FGU-Kronberg, 1979. Gegenwärtiger Status der Comoé- und Tai-Nationalparks sowie des Azagny-Reservats und Vorschläge zu deren Erhaltung und Entwicklung zur Förderung des Tourismus. Technical Report. Deutsche Gesellschaft für Technische Zusammenarbeit GmbH, Eschborn, Germany.

Fischer, F. & Linsenmair, K. E. 2001. Decreases in ungulate population densities. Examples from the Comoé National Park, Ivory Coast. *Biological Conservation* 101: 131-135.

Fischer, F., Groß, M. & Linsenmair, K. E. 2002. Updated list of the larger mammals of the Comoé National Park, Ivory Coast. *Mammalia* 66: 83-92.

Goetze, D., Hoersch, B. & Porembski, S. 2006. Dynamics of forest-savanna mosaics in north-eastern Ivory Coast from 1954 to 2002. *Journal of Biogeography* 33: 653-664.

Groves, C. P. 2001. *Primate Taxonomy*. Smithsonian Institution Press, Washington.

Hamilton, W. J. I. & Bulger, J. 1992. Facultative expression of behavioral differences between one-male and multi-male savanna baboon groups. *American Journal of Primatology* 28: 61-71.

Hamilton, W. J. I., Buskirk, R. E. & Buskirk, W. H. 1975. Chacma baboon tactics during intertroop encounters. *Journal of Mammalogy* 56: 857-870.

Harding, R. S. O. 1976. Ranging patterns of a troop of baboons (*Papio anubis*) in Kenya. *Folia Primatologica* 25: 143-185.

Hayward, M. W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G. & Kerley, I. H. 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* 270: 298-313.

Henzi, S. P. & Barrett, L. 2005. The historical socioecology of savanna baboons (*Papio hamadryas*). *Journal of Zoology* 265: 215-226.

Henzi, S. P., Byrne, R. W. & Whiten, A. 1992. Patterns of movement by baboons in the Drakensberg mountains: primary response to the environment. *International Journal of Primatology* 13: 601-629.

Hill, R. A., Barrett, L., Gaynor, D., Weingrill, T., Dixon, P., Payne, H. & Henzi, S. P. 2003. Day length, latitude and behavioural (in)flexibility in baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology* 53: 278-286.

Hill, R. A. & Dunbar, R. I. M. 2002. Climatic determinants of diet and foraging behaviour in baboons. *Evolutionary Ecology* 16: 579-593.

Hill, R. A. & Lee, P. C. 1998. Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. *Journal of Zoology* 245: 447-456.

Hovestadt, T. 1997. Fruchtmerkmale, endozoochore Samenausbreitung und ihre Bedeutung für die Zusammensetzung der Pflanzengemeinschaft. Untersuchungen im Wald-Savannenmosaik des Comoé Nationalparks, Elfenbeinküste. PhD thesis. University of Würzburg, Germany.

Hovestadt, T., Yao, P. & Linsenmair, K. E. 1999. Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoé National Park, Ivory Coast). *Plant Ecology* 144: 1-25.

Hutchinson, J., Dalziel, J. M. & Keay, R. W. J. 1954-1968. *Flora of West Tropical Africa*. Vols. I-III. London, Crown Agents for Oversea Governments and Administrations.

Ivlev, V. 1961. *Experimental ecology of the feeding of fishes*. Yale University Press, New Haven.

Kasparek, M. (ed.). 2000. *Flore du Parc National de Tai (Côte d'Ivoire)*. Kasparek, Heidelberg.

Korb, J. 2000. Methods to study elusive spotted hyenas in the Comoé National Park, Côte d'Ivoire. *IUCN Hyaena Specialist Group Newsletter* 7: 3-12.

Kunz, B. K. & Linsenmair, K. E. 2007. Changes in baboon feeding behavior: maturity dependent fruit and seed size selection within a food plant species. *International Journal of Primatology* 28: 819-835.

Lieberman, D., Hall, J. B., Swaine, M. D. & Lieberman, M. 1979. Seed dispersal by baboons in the Shai Hills, Ghana. *Ecology* 60: 65-75.

Melnick, D. J. & Pearl, M. C. 1987. Cercopithecines in multimale groups: genetic diversity and population structure. Pp. 121-134 In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsacker, T. T. (eds.). *Primate societies*. University of Chicago Press, Chicago.

Mizutani, F. & Jewell, P. A. 1998. Home range and movements of leopards (*Panthera pardus*) on a lifestock ranch in Kenya. *Journal of Zoology* 244: 269-286.

Nagel, U. 1973. A comparison of anubis baboons, hamadryas baboons and their hybrids at a species border in Ethiopia. *Folia Primatologica* 19: 104-165.

Nash, L. T. 1976. Troop fissioning in free-ranging baboons in the Gombe Stream National Park, Tanzania. *American Journal of Physical Anthropology* 44: 63-78.

Newman, T. K., Jolly, C. J. & Rogers, J. 2004. Mitochondrial phylogeny and systematics of baboons (*Papio*). *American Journal of Physical Anthropology* 124: 17-27.

Norton, G. W., Rhine, R. J., Wynn, G. W. & Wynn, R. D. 1987. Baboon diet: a five-year study of stability and variability in plant feeding and habitat of the yellow baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. *Folia Primatologica* 48: 78-120.

Packer, C. 1979. Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Animal Behavior* 27: 1-36.

Poilecot, P. 1991. *Un écosystème de savane soudanienne: le Parc National de la Comoé (Côte d'Ivoire)*. UNESCO, Paris.

Porembski, S. 1991. Beiträge zur Pflanzenwelt des Comoé-Nationalparks (Elfenbeinküste). *Natur und Museum* 121: 61-82.

Porembski, S. 2001. Phytodiversity and structure of the Comoé river gallery forest (NE Ivory Coast). Pp. 1-10 In Gottsberger, G. & Liede, S. (eds.). *Life forms and dynamics in tropical forests*. Borntraeger, Berlin.

Post, D. G. 1981. Activity patterns of yellow baboons (*Papio cynocephalus*) in the Amboseli National Park, Kenya. *Animal Behaviour* 29: 357-374.

Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223-225.

Rodgers, A. R. & Carr, A. P. 1998. *HRE: The Home Range Extension for ArcView. User's Manual.* Ministry of Natural Resources, Ontario.

Rowell, T. E. 1966. Forest living baboons in Uganda. *Journal of Zoology* 149: 344-364.

Sambrook, T. D., Whiten, A. & Strum, S. C. 1995. Priority of access and grooming patterns of females in a large and a small group of olive baboons. *Animal Behaviour* 50: 1667-1682.

Sapolsky, R. M. 1996. Why should an aged male baboon ever transfer troops? *American Journal of Primatology* 39: 149-157.

Seaman, D. E. & Powell, R. A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77: 2075-2085.

Sinsin, B., Tehou, A. C., Daouda, I. & Saidou, A. 2002. Abundance and species richness of larger mammals in Pendjari National Park in Benin. *Mammalia* 66: 369-380.

Stacey, P. B. 1986. Group size and foraging efficiency in yellow baboons. *Behavioral Ecology and Sociobiology* 18: 175-187.

Tutin, C. E. G., Ham, R. M., White, L. T. J. & Harrison, M. J. S. 1997. The primate community of the Lopé Reserve, Gabon: diets, responses to fruit scarcity, and effects on biomass. *American Journal of Primatology* 42: 1-24.

van Schaik, C. P., van Norwijk, M. A., de Boer, R. J. & den Tonkelaar, I. 1983. The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behavioral Ecology and Sociobiology* 13: 173-181.

von Maydell, H. J. 1990. *Trees and shrubs of the Sahel. Their characteristics and uses.* Weikersheim, Josef Margraf.

Warren, Y. 2003. Olive baboons (*Papio cynocephalus anubis*): behaviour, ecology and human conflict in Gashaka Gumti National Park, Nigeria. PhD thesis. University of Surrey, Roehampton, UK.

White, F. 1979. The Guinean-Congolian region and its relation to other phytocoria. *Bulletin du Jardin Botanique National de Belgique* 49: 11-55.

White, F. 1983. *The vegetation of Africa*. UNESCO, Paris.

Whiten, A., Byrne, R. W., Barton, R. A., Waterman, P. G. & Henzi, S. P. 1991. Dietary and foraging strategies of baboons. *Philosophical Transactions of the Royal Society of London Series B* 334: 187-197.

Wolfheim, J. H. 1983. *Primates of the world. Distribution, abundance, and conservation.* University of Washington Press, Seattle.

Appendix 1 Proportion of baboon feeding time on identified plant species

Data obtained from direct observations of GP- and 1S-group. The average of the monthly proportion for each food plant is given. The figures in parentheses ( ) indicate the number of food species of the same genus matched together for this analysis, when species could not always be distinguished reliably during field observations. Total number of feeding records $N = 3{,}589$ (data for GP-group from 1998-2000, 1S-group from 1999 & 2000).

Plant species	**Family**	**Mean % of feeding records / month** **GP-group**	 **1S-group**
Cissus sp.	Ampelidaceae		2.10
Lannea spp.(3)	Anacardiaceae	1.72	4.30
Saba senegalensis	Apocynaceae	3.66	0.34
Kigelia africana	Bignoniaceae	0.03	
Afzelia africana	Caesalpiniaceae	1.79	0.28
Cynometra megalophylla			0.30
Daniellia oliveri		13.49	11.96
Detarium microcarpum		0.73	
Dialium guineense		1.16	4.53
Erythrophleum guineense		0.48	3.13
Piliostigma thonningii		5.20	1.51
Tamarindus indica		2.52	
Tapura fischeri	Chailletiacea		10.26
Anogeissus leiocarpa	Combretaceae	0.03	
Combretum spp.(2)		1.50	2.56
Terminalia macroptera		0.20	
Diospyros mespiliformis	Ebenaceae	10.37	3.85
Bridelia ferruginea	Euphorbiaceae	2.47	
Pseudocedrela kotschyi	Meliaceae	0.85	
Acacia cf. sieberiana	Mimosaceae	0.22	0.07
Albizia sp.		0.37	
Parkia biglobosa		1.98	15.53
Ficus spp.(3)	Moraceae	14.56	
Syzygium guineense	Myrthaceae	1.03	
Mitragyna inermis	Rubiaceae	0.54	0.75
Sarcocephalus latifolius		0.23	4.92
Vitellaria paradoxa	Sapotaceae	0.33	0.77
Cola cordifolia	Sterculiaceae		1.02
Vitex doniana	Verbenaceae	0.72	

Chapter 3

Fruit Traits in Baboon Diet: a Comparison with Plant Species' Characteristics in a West African Savanna-Forest Mosaic

with K. E. Linsenmair
(Submitted)

Abstract Primate fruit choice among plant species has been attributed to different morphological plant and fruit characteristics. Despite a high abundance of animal-dispersed plant species in the savanna-forest mosaic of West Africa, few data are available on the interplay between morphological fruit traits and primate fruit consumers in this ecosystem. We tested whether olive baboons (*Papio anubis*) at Comoé National Park, north-eastern Ivory Coast, prefer fruit species with particular characteristics relative to the availability of these traits among the woody plant species at the study site. Specifically we were interested in the suites of traits that best predict fruit choice and seed handling by baboons. The baboons ate fruit/seeds from 74 identified plant species, representing 25% of the regional pool of woody plant species. They preferred trees to shrubs and lianas as fruit sources. Otherwise, baboons seemed to consume whatever fruit type, colour, and size of fruit and seeds available, though they especially included larger fruit into their diet. Against expectations from the African bird-monkey fruit syndrome of brightly coloured drupes and berries, baboons ate mostly species having large, dull-coloured fruit. Fruit type and colour best described whether baboons included a species into their diet, whereas fruit type and seed size best predicted whether baboons predated upon the seeds of their food plant species. As most plant species at the study site had medium-sized to large fruits and seeds, large frugivores like baboons might be particularly important for plant fitness and plant community dynamics in West African savanna-forest ecosystems.

3. 1 INTRODUCTION

Fruit is a regular part of the diet of almost all diurnal primate species (Jordano 2000). Frugivorous primates commonly consume fruits and seeds of a wide range of different plant species (Lieberman *et al.* 1979; Lambert 1998; Otani & Shibata 2000; Poulsen *et al.* 2001; Knogge & Heymann 2003). Primate fruit use can, among other factors, be influenced by several plant and fruit traits, such as temporal and spatial aspects of fruit display, the growth form of plant species (e.g. tree, shrub, climber), morphological fruit characteristics, and chemical and nutrient content of fruit and seeds (e.g. Glander 1982, and references therein; Gautier-Hion *et al.* 1985; Janson *et al.* 1986; Sourd & Gautier-Hion 1986; Barton & Whiten 1994; Russo 2003). Suites of morphological fruit traits, i.e. fruit type, fruit colour, and the size of fruits and seeds, have been related to specific groups of dispersers (van der Pijl 1982). The seeds of large, dull coloured (yellow, brown, green) fruits seem to be predominantly dispersed by mammals, whereas typical 'bird-dispersed fruits' are small and brightly coloured drupes and berries (Janson 1983; Knight & Siegfried 1983). For the Neotropics, Peres & van Roosmalen (2002) defined a large-primate fruit syndrome of indehiscent, thick or hard-husked fruits, that contain one or few large seeds strongly adherent to the fruit pulp (see also Julliot 1996a). African primates, however, seem more similar in their fruit diet to birds than to other mammals, although primates may eat larger fruit than most birds (Gautier-Hion *et al.* 1985). Gautier-Hion *et al.* (1985) thus separated a 'bird-monkey syndrome' of brightly coloured drupes and berries from a 'ruminant-rodent-elephant syndrome' of large, dull-coloured, fibrous fruit in Africa.

Such functional associations do not necessarily reflect strict plant adaptations to frugivores, nor do they imply a close coevolution between plants and their seed dispersers (Jordano 1995). Given the often substantial biomass of many primate species, primate fruit selection may have, however, considerable ecological effects on plant fitness, local plant populations and community dynamics via seed dispersal and seed predation (Chapman & Onderdonk 1998; Lambert & Garber 1998). As analyses on primate-plant interactions to date focused on tropical forests, few data are available on the interplay between morphological fruit traits and primate fruit consumers in savanna ecosystems (Happel 1986; Hovestadt 1997). The West African savanna-forest mosaic is particularly rich in animal dispersed plants. In the Comoé National Park (CNP), north-eastern Ivory Coast, for example, 70% of the 292 woody plant species provide fruit for endozoochorous dispersal (Hovestadt *et al.* 1999). Baboons (*Papio* spp., Cercopithecidae) are commonly associated with savanna habitats in West and East Africa (Wolfheim 1983). Olive baboons (*P. anubis*) inhabiting the CNP are highly frugivorous, spending about half of their feeding time on fruit and seeds (Kunz & Linsenmair 2008a).

The objectives of the study were (a) to identify the fruit species included in baboon diet in a West African savanna ecosystem and (b) to test whether the baboons predominantly use species having particular growth forms and morphological fruit characteristics. As trait use by primates might simply reflect availability among the species in the regional plant pool, we compared the frequency of occurrence of the traits in baboon diet to the entirety of the plant species in CNP. In addition, we analysed (c) which suites of morphological traits best predict fruit choice and (d) seed dispersal by baboons.

3. 2 METHODS

3.2.1 STUDY SITE

The first author conducted field research during 24 months from November 1997 to July 2000 in the Comoé National Park (CNP) (08°30'-09°36' N, 003°07'-004°25' W), north-eastern Ivory Coast. The study period included each month of the year at least once. The national park covers about 11,500 km^2 at an altitude of about 250-300 m a.s.l. (Poilecot 1991). The northern part of the CNP belongs to the 'Sudanian regional centre of endemism', whereas the southern sub area is situated within the 'Guinea-Congolia / Sudania regional transition zone' (White 1983). The study area (~145 km^2) is located in the Southwest, where the vegetation consists of a mosaic of different savanna formations (approximately 91 %), forest islands (7 %), and gallery forest (2 %) along the two main rivers (FGU-Kronberg 1979). The vegetation is described in detail elsewhere (Poilecot 1991; Porembski 1991, 2001; Hovestadt *et al.* 1999).

The climate in the study area is characterized by a dry season from November to March/April. The mean annual precipitation from January 1994 to December 1999 was 1,053 mm per year, and the mean annual temperature was 26.3°C.

Among the nine recently recorded diurnal primate species in CNP, the olive baboon is the most abundant (Fischer *et al.* 2000). Ten different groups of olive baboons lived within the study area, ranging in size from 4-44 individuals (mean 15) (Kunz & Linsenmair 2008a).

3.2.2 BABOON DIET

We recorded baboon diet during scan sampling (Altmann 1974) of two habituated groups as well as during incidental encounters of other groups in the study area. The habituated groups comprised 9-13 individuals (1-2 adult males, 2-3 adult females plus juveniles), and 36-44 individuals (5-6 adult males, 1 subadult male, 9 adult females plus offspring), respectively. A detailed description on how the baboons were studied is given in (Kunz & Linsenmair 2008a).

During a total of 3,649 feeding records of all baboon groups in the study area we classified the plant food items consumed as fruit (unripe, ripe), seed, seed aril, or other. In addition, we identified seeds retrieved from a total of 396 baboon faecal samples, collected throughout the study period from all baboon groups in the study area. The faeces were rinsed through sieves with decreasing mesh width (minimum 1 mm), and checked for plant material. Food plants were identified using the following sources: Hutchinson *et al.* (1954-1968), von Maydell (1990), Arbonnier (2000), Kasparek (2000), a seed reference collection established in previous years by T. Hovestadt and P. Poilecot, and comparison with seeds taken from fresh fruits of identified plants. S. Porembski (University of Rostock, Germany) and E. Robbrecht (National Botanic Garden of Belgium) verified plant material in question.
To complete the list of baboon fruit plants, we included additional species that had been recorded during previous studies in CNP by Refisch (1995) and Hovestadt (1997).

We identified baboons as pre-dispersal seed predators for a given species when one of the following conditions was met: (a) all the seeds in faecal samples were destroyed (> 25% damage of the testa and/or > 5% damage of the endosperm/cotyledons) (Kunz & Linsenmair 2008b), (b) direct observations revealed that baboons only consumed unripe fruit from the species, or (c) baboons directly fed on (chewed) ripe seeds instead of fruit pulp (Kunz & Linsenmair 2008a).

3.2.3 PLANT AND FRUIT TRAITS

Fruit use by baboons was almost exclusively from woody plants (Kunz & Linsenmair 2008a, b). We therefore confined analyses of plant and fruit traits in baboon diet to woody plant species. We first compared the frequency of the traits among the plant species consumed by baboons to the frequency among the species in regional plant pool. We then analysed the significance of the traits for fruit use by baboons at the plant species level in a binary logistic regression model.

3.2.3.1 Growth Forms

Unlike otherwise stated, we followed growth form given in Hovestadt (1997), who classified the woody plant species in CNP as either 'tree', 'shrub', or 'climber'. 'Shrub' species included typical shrubs that start branching at the base, but also small trees with a maximum height of 5 m. 'Climbers' comprise all species needing structural support for height growth (Hovestadt 1997). In a few exceptional cases (e.g. when data were missing in Hovestadt 1997) we followed Hutchinson *et al.* (1954-1968).

3.2.3.2 Fruit Types

We assigned fruit pulp texture as either fleshy or dry as listed in Hovestadt (1997), except *Cynometra megalophylla* the pulp of which we classified as dry. Information on the pulp texture of four species came from Hutchinson *et al.* (1954-1968).

Species' botanical fruit types follow Hutchinson *et al.* (1954-1968), Arbonnier (2000), and Kasparek (2000). Botanical fruit types were classified as either *achene* (a dry, indehiscent single-seeded fruit formed from a superior ovary of one carpel, in which the testa of the seed is connected to the pericarp), *baccate* (indehiscent berry like fruit, pericarp usually fleshy, containing one or many seeds), *capsular* (a fleshy or dry dehiscent fruit that develops from several carpels, containing several seeds), *drupaceous* (indehiscent fruit with a thin exocarp and generally a fleshy mesocarp, containing one or several seeds surrounded by a woody or stony layer), *fig* (a hollow and fleshy indehiscent fruit formed from an inflorescence, containing many very small seeds), *follicle* (a dry dehiscent fruit that is formed from a single carpel and splits along one side and contains a single or many seeds), *indehiscent fruit*: fruit not opening upon maturity to release seeds (including compound indehiscent fruits), *nut/nutlet* (a usually single-seeded fruit, with a hard pericarp, indehiscent), (legume) *pod* (develops from one carpel, dry or fleshy, either dehiscent along both sides, or indehiscent), *samara* (a dry single-seeded indehiscent fruit with a hard periocarp that forms a membranous wing-like structure) (following Strasburger *et al.* 1991; Wagenitz 2003).

3.2.3.3 Fruit Sizes

We took a random sample of fruits per species upon availability, yet at least from two different individuals per species. Fruit numbers are displayed in Appendix 1. Priority was given to fruit species included in baboon diet. We measured fruit length using a sliding calliper (accuracy 0.01 mm), but used a ruler for large, elongated fruit. We calculated the mean fruit size per species.

Data on mean fruit size of species not measured by the first author were taken from Hovestadt (1997), Arbonnier (2000), and Kasparek (2000).

For statistical analyses, we assigned each species into one of three fruit size classes: small (mean fruit length ≤ 10 mm), medium (> 10 and ≤ 30 mm long), large (> 30 mm) (following Lambert & Garber 1998) (Appendix 1).
Across all fruit plant species in baboon diet, we calculated the median (x_{md}) and first ($q1$) and third ($q3$) percentiles.

3.2.3.4 Seed Sizes

We likewise measured the maximum dimension of seeds retrieved from 396 faecal samples of baboons. Seeds measured were fully turgescent and undamaged along the largest diameter. Very small seeds (< 2 mm), were difficult to measure accurately, hence we used a value of 2 mm for all calculations.

Baboons directly feed on and thereby destroy the seeds of some species. We randomly collected fruits of these species from at least two different plant individuals and extracted the seeds mechanically. Numbers of seeds measured per species are given in Appendix 1.
Otherwise, we used seed size data provided by Hovestadt (1997). We classified each seed species into one seed size class: small (seed size ≤ 5 mm), medium (> 5 mm and < 20 mm), large (≥ 20 mm) (following Wrangham *et al.* 1994; Lambert & Garber 1998).

3.2.3.5 Fruit Colours

Fruit colour classification of species' ripe fruits followed Hovestadt (1997): green, white, yellow, orange, red, blue-violet, grey-brown, or black (including deep brown, deep blue and deep violet). Irrespective of fruit colour at maturity, we classified a fruit species in baboon diet as 'green', when baboons exclusively consumed the fruit of the species while unripe and green.

3.2.4 STATISTICS

We tested for variation in the frequency distribution of each trait between species in baboon diet and in the regional plant pool applying χ^2-test with Yates correction. We used Mann-Whitney *U*-test to compare mean fruit lengths and seed sizes, respectively, between the species included and those not included in baboon diet. Mann-Whitney *U*-test was also used to compare the mean fruit size of species across particular fruit types.
Variation in mean fruit length across growth forms was analysed using the Kruskal-Wallis test. We tested for correlation between mean fruit length and mean seed size using Spearman's rank correlation.

We analysed the applicability of the plant and fruit traits as predictors for baboon fruit choice in a logistic regression model with backward stepwise selection of variables (based on log-likelihood ratio test, -2log LR). Occurrence of a fruit species in baboon diet was used as binominal dependent variables (0 = not eaten, 1 = eaten). Nagelkerke's R^2 indicates calibration and refinement of the model. To predict the discriminatory accuracy of the model, we used *ROC* curve statistics. The 'area under curve value' (*AUC*) is given as a validation of the model and a quality criterion of the prognosis. Likewise, we tested which traits best predict whether or not baboons predate on the seeds of a food plant species.

Tests were run in SPSS version 15.0 or ssS version 1.0. Confidence limits were set at 95% and all tests were two-tailed. We corrected the level of significance for multiple comparisons using the sequential Bonferroni technique (Rice 1989).

3. 3 RESULTS

3.3.1 BABOON DIET

During our study, baboons consumed fruits and/or seeds from 79 species (67 identified woody plant species). Adding seven species from previous studies in CNP to the list (Refisch 1995; Hovestadt 1997) totals 74 identified woody plant species out of 29 families (Appendix 1). The 74 species represent 25 % of the woody plant species in CNP (*N* = 292) and 45% of the families (*N* = 64).
More than half of the woody plant species consumed by baboons belonged to the five families Rubiaceae, Euphorbiaceae, Caesalpiniaceae, Moraceae and Mimosaceae (Figure 1). The first four families also comprise the highest number of species in the regional plant pool.

Baboons fed on the pulp of 58 of the identified species (Appendix 1). They directly ate (chewed) the seeds from six additional species. In six other species they fed on fruit pulp as well as on the seeds, or seeds retrieved from faecal samples were always destroyed. From two species, seed arils as well as seeds were eaten. (In two other species it remained unclear, which part was consumed.)

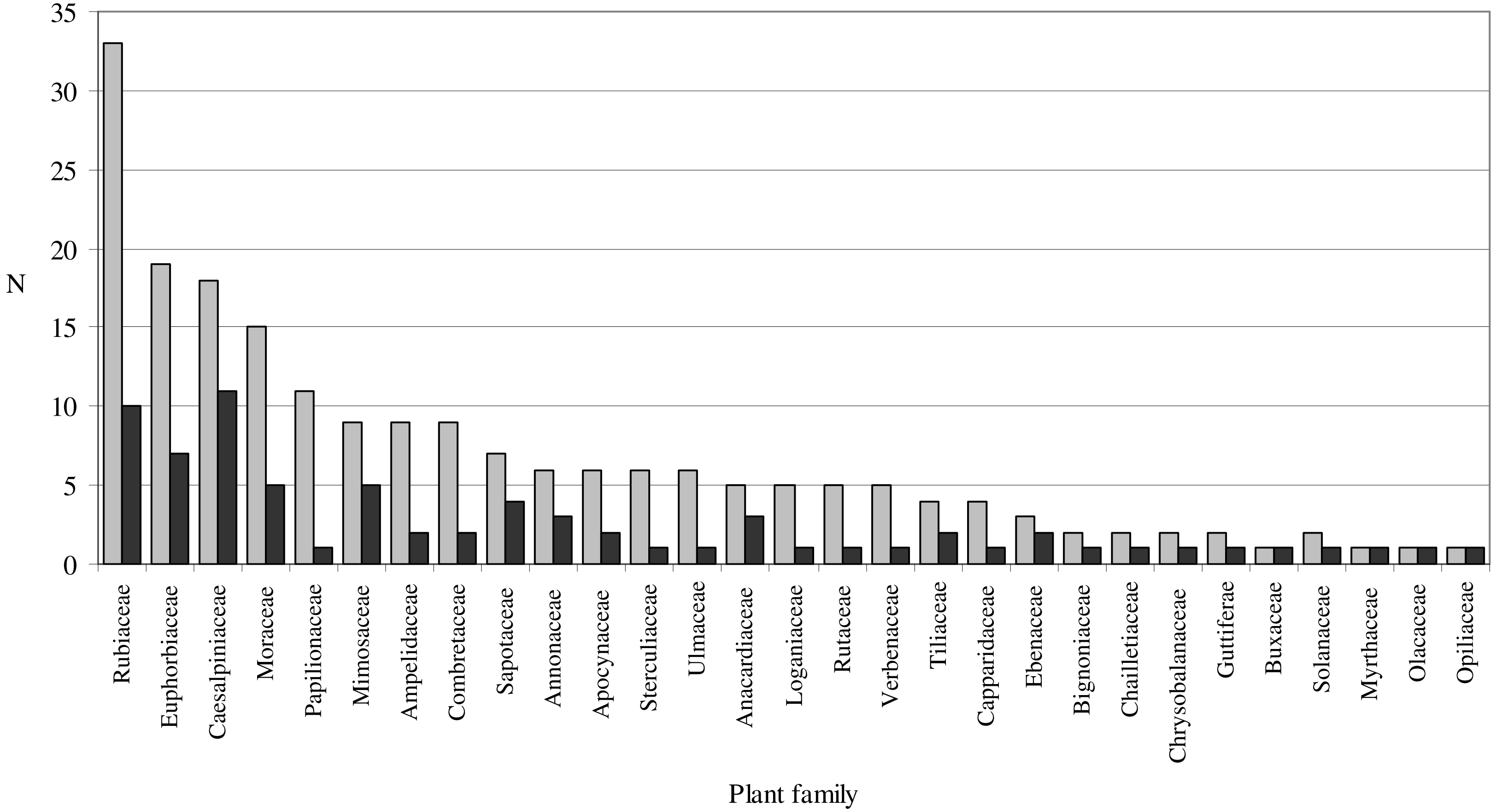


Figure 1 Number of woody plant species per family in the regional plant pool (grey columns) (following Hovestadt 1997) and in baboon diet (black columns) in CNP

Only plant families of which baboons consume fruit and/or seeds from at least one species are included.

3.3.2 GROWTH FORMS

Information on the growth form was available for 99.7% of the woody plant species in CNP (*N* = 292) and for 94.6% of the identified fruit plant species in baboon diet (*N* = 74). Most species in the regional plant pool as well as in baboon diet were trees, followed by shrubs, and climbers (Figure 2).

Variation in the distribution of growth forms between woody plant species in CNP and in baboon diet was statistically significant ($\chi^2 = 8.115$, $df = 2$, $p < 0.05$). Tree species accounted for a significantly higher proportion in baboon diet (61.4%) than in the regional plant pool (43.6%) ($\chi^2 = 6.468$, $df = 1$, $p = 0.05$ after applying sequential Bonferroni technique).

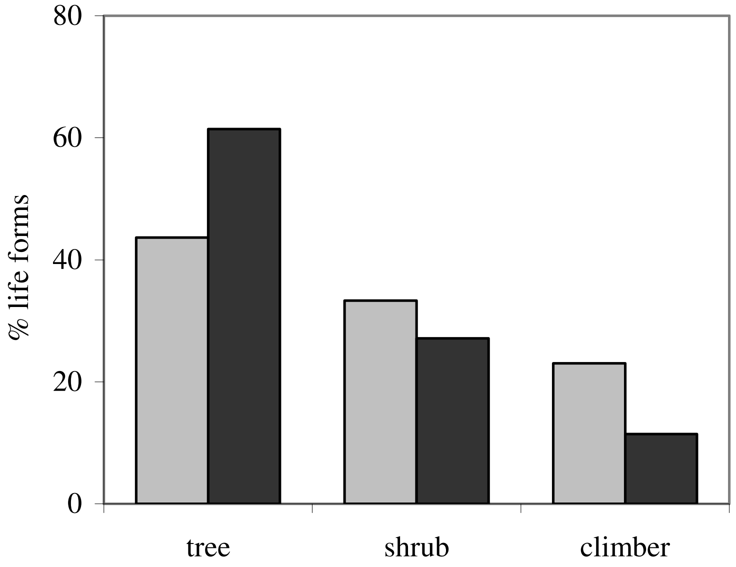


Figure 2 Distribution of growth forms in the regional plant pool of woody species (grey columns, *n* = 291) (following Hovestadt 1997) and in baboon diet in CNP (black columns, *n* = 70)

3.3.3 FRUIT TYPES

Fruit pulp texture was classified for 89% of the woody plant species in CNP and for all identified woody fruit plant species in baboon diet. Seventy percent of the fruit species consumed by baboons had fleshy fruit. However, most woody plant species (61%) in CNP also have fleshy fruit, and variation between the frequency of this trait in baboon diet and in the regional plant pool was statistically not significant (χ^2 with Yates correction = 1.839, $df = 1$, $p > 0.05$).

Data on botanical fruit types were available for 84.6% of the woody plant species in CNP and for 94.6% of the species in baboon diet. Fruit types most frequently represented among the woody plant species in CNP are baccate fruit (26%), followed by drupaceous fruit (18%), capsules and pods (17 and 14%, respectively) (Figure 3). Most species consumed by baboons also had baccate fruit 29%. Species with drupaceous fruit and pods were included about equally into baboon diet (20% and 21%, respectively). Pods and indehiscent fruit were overrepresented when compared to the regional plant pool, while capsular fruit and follicles were underrepresented.

For statistical analysis, we pooled data from 'indehiscent', 'samara', 'achene', and 'nut/nutlet' into one category ('other'). Fruit types in baboon diet did not vary significantly compared to availability in the regional plant pool ($\chi^2 = 6.126$, $df = 6$, $p > 0.05$).

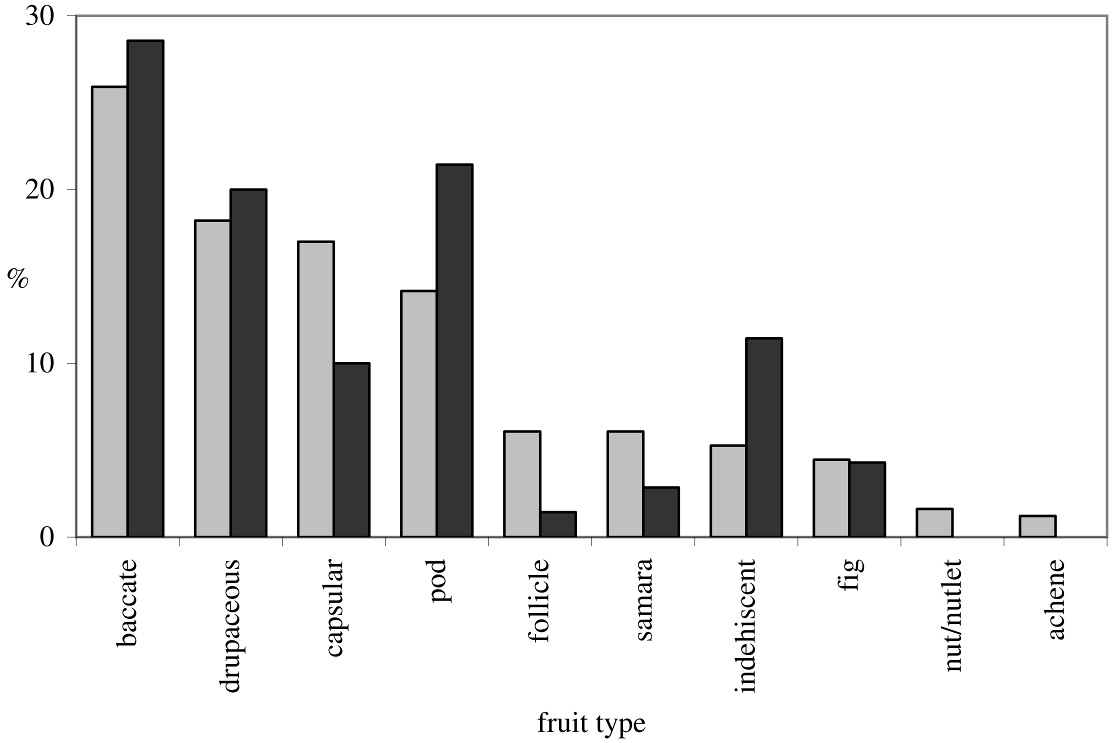


Figure 3 Distribution of fruit types among woody plant species in the regional plant pool (grey columns, $n = 247$) and in baboon diet in CNP (black columns, $n = 70$)

Fruit plant species in the regional plant pool follow Hovestadt (1997). Fruit types of species follow Hutchinson *et al.* (1954-1968), Arbonnier (2000), Kasparek (2000). See 'Methods' for definition of fruit types.

3.3.4 FRUIT SIZES

Baboons exploited fruits as small as *Tapura fischeri* (4.6 mm fruit length) and as large as *Kigelia africana* (about 450 mm long). Eighty-two percent of the woody plant species in baboon diet ($n = 65$), however, had medium to large fruits (Figure 4). The median size of fruit exploited by baboons was 24.9 mm ($q1 = 12.4$ mm, $q3 = 51.4$ mm, $n = 63$). If pods are excluded, the median fruit length was 18.2 mm ($q1 = 10.3$ mm, $q3 = 34.7$ mm, $n = 48$). For comparison with other studies, the average size and standard deviation of fruit species is also given: 59.2 ± 99.6 mm (35.0 ± 65.8 mm if pods are excluded). Species eaten had significantly larger fruit than species not included into baboon diet (Mann-Whitney U = 11406.5, $p < 0.05$).

The vast majority of woody plant species in CNP for which we have data on fruit size ($n = 182$) also have medium to large fruits. Baboon included about 12% more species with large fruits into their diet, compared to the proportion of large fruited species in the regional plant pool, but variation between fruit size classes was statistically not significant ($\chi^2 = 2.322$, $df = 2$, $p > 0.05$).

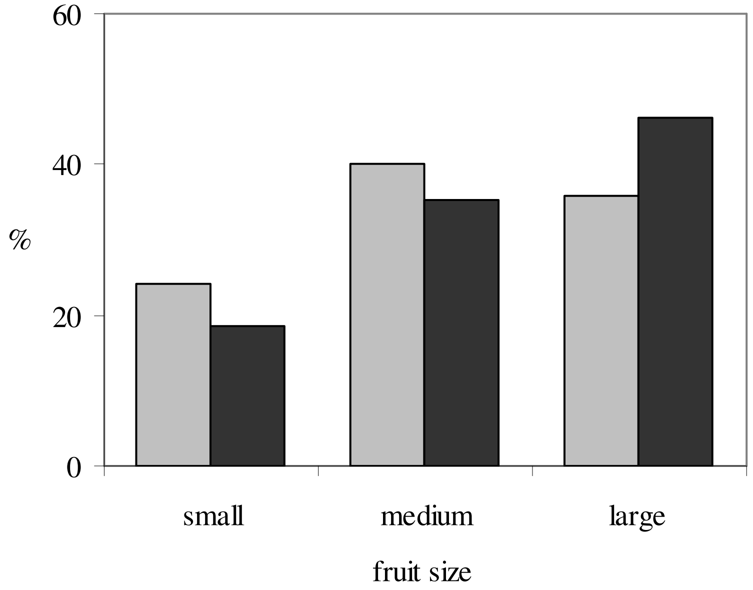


Figure 4 Distribution of fruit size classes among woody plants in the regional plant pool (grey columns, $n = 182$) (following Hovestadt 1997, and our own measurements) and in baboon diet (black columns, $n = 65$) in CNP
Small fruits: ≤ 10 mm long, medium-sized fruits > 10 ≤ 30 mm, large fruits > 30 mm.

3.3.5 SEED SIZES

We classified seed size in 50.0% of the woody plant species in the study area, and in 94.6% of the identified fruit plant species in baboon diet. More than 60% of these species had seeds of intermediate size, both in the regional plant species pool and in baboon diet (Figure 5). Variation in the distribution of seed size classes among the woody plant species in baboon diet and in CNP were statistically not significant ($\chi^2 = 1.906$, $df = 2$, $p > 0.05$). The median seed size across woody fruit plant species in baboon diet was 8.2 mm ($q1$ = 5.0 mm, $q3$ = 14.3 mm, n = 62 species). Seed sizes of species included and not included in baboon diet did not vary significantly (Mann-Whitney $U = 1519$, $p > 0.05$).

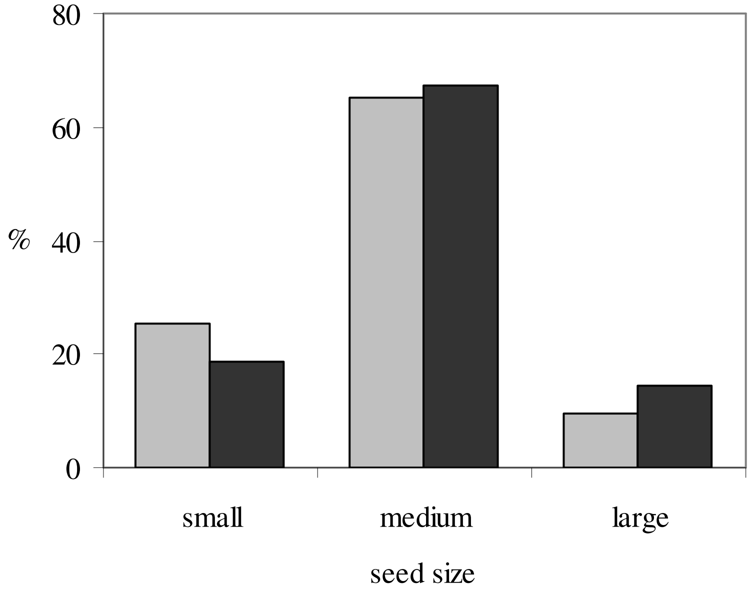


Figure 5 Distribution of seed size classes among woody plants in the regional plant pool (grey columns, n = 146) (following Hovestadt 1997, and our own measurements) and in baboon diet (black columns, n = 70) in CNP
Small seeds: maximum dimension ≤ 5 mm, medium-sized seeds: > 5 mm < 20 mm, large seeds ≥ 20 mm.

3.3.6 FRUIT COLOURS

Information on fruit colour was available for 82.9 % of the woody plant species in CNP and for 93.2% of the fruit plant species in baboon diet. Baboons in CNP exploited fruits of all colours, except white fruits, which, however, were rare in CNP (n = 2) (Figure 6). Most fruit species consumed by the baboons had brown-grey fruit, followed by about equal proportions of species with orange and yellow fruit. We observed the baboons feeding only on unripe (green) and not on ripe fruit in four plant species (*Craibia atlantica*, *Daniellia oliveri*, *Isoberlinia doka*, and *Syzygium guineense*). While the unripe seeds of the former three species were chewed, the seeds of *S. guineense* were spat out during consumption of pulp.

The distribution of fruit colours among the plant species in baboon diet did not differ significantly from the distribution among the species in the regional plant pool ($\chi^2 = 8.76$, $df = 6$, $p > 0.05$; excluding white fruit).

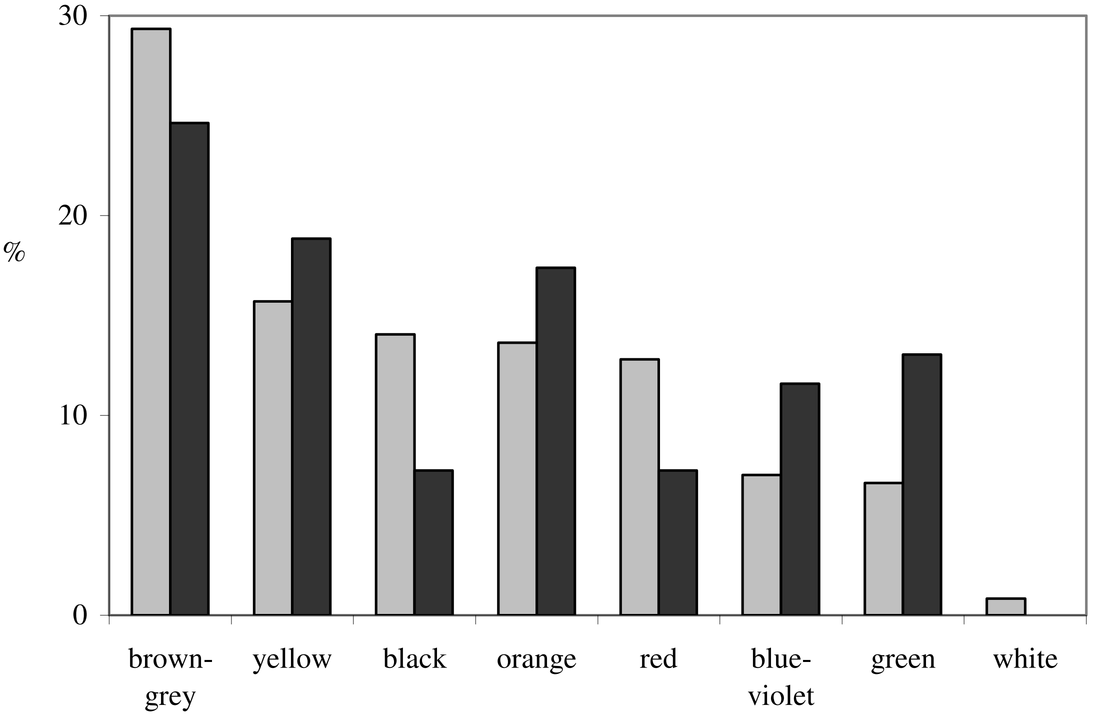


Figure 6 Distribution of fruit colours among woody plant species in CNP (grey columns, $n = 242$) (following Hovestadt 1997) and in baboon diet (black columns, $n = 69$)

3.3.7 RELATIVE IMPORTANCE OF TRAITS FOR BABOON FRUIT CHOICE AND SEED PREDATION

Logistic regression yielded that among the traits tested in this study, fruit type and fruit colour best predict whether or not baboons in CNP included a fruit species into their diet ($R^2_{\text{Nagelkerkes}} = 0.327$, $p < 0.001$, $AUC = 0.778$).

Among the fruit species eaten by the baboons, fruit type and seed size best predict whether or not baboons predate on the seeds of a species ($R^2_{\text{Nagelkerkes}} = 0.822$, $p < 0.001$, $AUC = 0.977$).

3.3.8 INTERDEPENDENCE OF TRAITS

Several traits are not independent from each other. Fruit length and seed size were slightly correlated ($r_s = 0.360$, $p < 0.001$, $n = 119$). Fruit length of species was also correlated to growth form (Kruskal Wallis test, $\chi^2 = 26.24$, $df = 2$, $p < 0.001$, $n = 182$). Climber and tree species, respectively, had larger fruit than shrub species (a posteriori Mann-Whitney U-test trees versus shrubs: $U = 1695.5$, climbers versus shrubs: $U = 573.0$, $p = 0.001$ in each case after applying sequential Bonferroni technique).

Pods and follicles were larger than other fruit types (pooled) (Mann-Whitney $U = 657$, $p = 0.001$), and drupaceous fruit types were smaller than all other fruit types ($U = 1212.5$, $p = 0.001$) (after sequential Bonferroni correction). Capsular fruit and baccate fruit were also small. Other fruit types (indehiscent fruit, samara, achene, nut) had intermediate sizes.

Among large fruits, the colours brown-grey and green were dominant, whereas small fruit were mostly blue-violet, red and black.

3. 4 DISCUSSION

Olive baboons in the savanna-forest mosaic of the CNP exploit fruits of a large number of woody plant species and families. The results conform to outcomes from studies in more forested areas in Africa, where different primate species include fruit/seeds from 57 to 87 plant species into their diet, representing between 28.5% and 40% of the plant species in the respective area (Sourd & Gautier-Hion 1986; Lambert & Garber 1998; Poulsen *et al.* 2001; Warren 2003). Baboons in CNP are not only highly frugivorous, they also act as effective seed dispersers for many of their food plant species (Kunz & Linsenmair 2008b). Seventy-three percent of seeds in baboon dung remained undamaged during ingestion. Intact seeds were from 65 species, including at least 53 woody plant species (Kunz & Linsenmair 2008b).

The baboons preferred tree species as fruit sources to shrubs and climbers. In general, trees in CNP provide larger fruit mass (larger fruit and larger crown volume), enabling all members of a baboon group of average size to feed simultaneously in the same tree (Kunz & Linsenmair 2008a). Surprisingly, however, 35% of the tree species in baboon diet had dry fruit. Compared to other studies on frugivorous primates (Lieberman *et al.* 1979; Gautier-Hion *et al.* 1985; Hovestadt 1997), the baboons included a comparatively large proportion of dry-fruited species into their diet. In Ghana, a higher number of seeds from fleshy fruit were found in olive baboon dung relative to the frequency of the trait in the regional plant pool (Lieberman *et al.* 1979). Dry fruit often have low nutritive value and high fibre content (e.g. Sourd & Gautier-Hion 1986). The existence of protein rich seeds and seeds with arils in 50% of the dry-fruited species (particularly legume pods) could, however, explain why the baboons in CNP used this otherwise nutrient-poor food type so intensively. Legume seeds often are important protein sources and are included in the diet of many primates (Whiten *et al.* 1991; Gathua 2000; Barnes 2001; Norconk & Conklin-Brittain 2004). Because these seeds are generally chewed, faecal analyses alone is likely to underestimate the number of dry fruited species in the diet of primates (Kunz & Linsenmair 2008b).

Baboons in CNP exploited almost all fruit types available, except nuts and achenes, which, however, are rare among the species in the regional plant pool. Primates commonly use a wide range of different fruit sizes and types (Julliot 1996a; Lambert & Garber 1998; Otani & Shibata 2000; Poulsen *et al.* 2002). Some primate species are considered particularly important for the dispersal of seeds from large fruit with a hard and indehiscent fruit husk that many other frugivores cannot handle (Julliot 1996b; Peres & van Roosmalen 2002; Link & Di-Fiore 2006). In contrast, berries and drupes are commonly associated with seed dispersal by birds (Knight & Siegfried 1983; Cooper *et al.* 1986; Balasubramanian 1996; Herrera 2002; Schmidt *et al.* 2004). Following availability in the woody plant species pool, most species eaten by baboons had baccate or drupaceous fruit. In Kibale, Uganda, drupes and berries together also accounted for 51% of the fruit in the diet of four primate species (Lambert & Garber 1998). Gautier-Hion *et al.* (1985) found that the diet of monkeys and birds in Africa can largely overlap regarding morphological fruit characteristics and thus defined a bird-monkey fruit syndrome of brightly coloured, fleshy drupes and berries. Likewise, Hovestadt (1997) described fruit species eaten by birds in CNP as a subset of the species consumed by baboons.

Among the woody plant species in CNP, baccate and drupaceous fruit generally are small. However, 32% of the species with baccate or drupaceous fruit in baboon diet had large fruit of which 92% had medium-sized to large seeds. Several of these larger berries and drupes might be beyond the size most frugivorous birds can handle, with the possible exception of hornbills (Bucerotidae). Fruit and seed size in particular seem to separate bird from mammal fruit (Knight & Siegfried 1983; Gautier-Hion *et al.* 1985; Jordano 1995; Pizo 2002; Bollen *et al.* 2004). Although baboons fed on small and typical "bird dispersed fruit species" the vast majority of fruit species in baboon diet was medium or large-sized. The mean size of fruit exploited by olive baboons in CNP (35.0 mm) conforms to the average fruit size exploited by primates in Kibale (39.6 mm Lambert & Garber 1998) (pods excluded in both cases). The comparison of fruit sizes between species eaten and those not eaten by baboons in CNP may be weakened because we did not account for potential phylogenetic effects in plant species data. Congeneric pairwise comparison of fruit species consumed and not consumed by olive baboons (following Knogge & Heymann 2003) were too few for statistical analyses. Due to the fact that most genera of which baboons consume fruit are represented in CNP by one species only and that baboons mostly feed on all species within multi-species genera in their diet (e.g. *Lannea* spp.), results are rather conservative and phylogenetic effects, at least on the genus level, may be marginal.

Among several Neotropical and Paleotropical primate species red, yellow and orange fruit species seem to be consumed most frequently (Gautier-Hion *et al.* 1985; Sourd & Gautier-Hion 1986; Julliot 1996a; Lambert & Garber 1998; but see Poulsen *et al.* 2002). In CNP, red fruits (as well as 'black' fruits) were rare among the fruit plant species in baboon diet, although the fruit colour was about equally represented among the woody plant species in the regional plant pool as orange. Unlike several other African primates (Gautier-Hion *et al.* 1985; Happel 1986; Sourd & Gautier-Hion 1986) olive baboons in CNP did not avoid green and brown fruit and also exploited the seeds of four additional species while fruits were green and unripe. Fruit colour among woody plant species in CNP is associated with fruit type and fruit size: red, black and violet fruit in CNP are commonly small, whereas yellow, brown and green fruit are often large (pods, follicles or indehiscent fruit) (Hovestadt 1997). When feeding on seeds, West African monkeys seem to prefer (unripe) green and/or brown-black fruit, particularly legume pods (Happel 1986; Davies *et al.* 1999).

Among the morphological traits investigated, fruit type and fruit colour best predicted whether or not a fruit species was included into baboon diet. Other studies commonly highlighted fruit colour and pulp texture as important characteristics for fruit choice in primates (Gautier-Hion *et al.* 1985; Sourd & Gautier-Hion 1986; Julliot 1996a). Seed size and fruit type on the other hand, best predicted if baboons were pre-dispersal seed predators or potential seed dispersers for a food plant species. Most species the seeds of which baboons feed on have large seeds. When feeding on pulp, however, large seeds (e.g. *Vitellaria paradoxa*, *Detarium* spp.) are dropped rather than chewed (Kunz & Linsenmair 2008b, Kunz, pers. observ.). Likewise, Hovestadt (1997) found a significant negative effect of seed size upon the occurrence of seeds in baboon dung in CNP.

Foraging strategies of primates, however, are complex and morphological fruit characteristics are not the only factors influencing fruit choice in primates. Analyses of fruit trait selection at the species level do not take into account, for example, the density of plant species and (varying) fruit availability, which is known to affect foraging in primates (Howe 1980; Barton & Whiten 1994). Moreover, nutritive values of fruit and seeds as well as the content of water, fibre, and the nature and quantity of secondary compounds can also affect primate fruit choice (e.g. Glander 1982, and references therein; Janson *et al.* 1986; Barton & Whiten 1994). Nonetheless, the results emphasise some underlying pattern in the interactions between olive baboons and their fruit plants that likely affect plant populations and community dynamics in the savanna-forest mosaic of West Africa. Overall, olive baboons exploit fruit having all kinds of morphological traits. With few exceptions, they seem to consume whatever fruit type, colour and size available. If fruit consumption is regarded irrespective of seed treatment, olive baboons in CNP do not strictly suit the dichotomy of fruit syndromes in Africa (Gautier-Hion *et al.* 1985) as they feed on many large, dull-coloured species that are typical for the ruminant-rodent-elephant syndrome (see also Happel 1986; Barton & Whiten 1994). In CNP, olive baboons showed a preference for tree species as fruit sources and for species with large fruit. As most woody plant species in the study area have medium-sized to large fruit, and medium sized seeds, olive baboons might be particularly important for seed dispersal and natural plant regeneration of fleshy fruited tree species. Olive baboons act, however, as pre-dispersal seed predators, rather than as seed dispersers for many of the large seeded legume species that have dry pods.

3. 5 ACKNOWLEDGEMENTS

We thank T. Hovestadt and E. Obermaier for helpful comments on the manuscript. The "Ministère de l'Agriculture et des Ressources Animales" and the "Ministère de l'Enseignement Supérieure et de la Recherche Scientifique", Abidjan, granted research permission for the CNP. PhD scholarships from the German Academic Exchange Service (DAAD) and the University of Wuerzburg (HSP III) funded the study. Generous funds from the Volkswagen-Foundation facilitated the construction of the research camp in CNP.

3. 6 REFERENCES

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227-267.

Arbonnier, M. 2000. *Arbres, arbustres et lianes des zones sèches d'Afrique de l'Ouest*. Muséum National d'Histoire Naturelle, Paris.

Balasubramanian, P. 1996. Interactions between fruit-eating birds and bird-dispersed plants in the tropical dry evergreen forest of point Calimere, South India. *Journal of the Bombay Natural History Society* 93: 428-441.

Barnes, M. E. 2001. Seed predation, germination and seedling establishment of *Acacia erioloba* in northern Botswana. *Journal of Arid Environments* 49: 541-554.

Barton, R. A. & Whiten, A. 1994. Reducing complex diets to simple rules: food selection by olive baboons. *Behavioural Ecology and Sociobiology* 35: 283-293.

Bollen, A., Van Elsacker, L. & Ganzhorn, J. U. 2004. Tree dispersal strategies in the littoral forest of Sainte Luce (SE-Madagascar). *Oecologia* 139: 604-616.

Chapman, C. A. & Onderdonk, D. A. 1998. Forests without primates: primate/plant codependency. *American Journal of Primatology* 45: 127-141.

Cooper, H. M., Charles-Dominique, P. & Vienot, F. 1986. The significance of the color of fruits as a function of the vision of the vertebrates that consume them. *Memoires du Museum National d'Histoire Naturelle Serie A Zoologie* 132: 131-144.

Davies, A. G., Oates, J. F. & Dasilva, G. L. 1999. Patterns of frugivory in three West African colobine monkeys. *International Journal of Primatology* 20: 327-357.

FGU-Kronberg. 1979. Gegenwärtiger Status der Comoé- und Tai-Nationalparks sowie des Azagny-Reservats und Vorschläge zu deren Erhaltung und Entwicklung zur Förderung des Tourismus. Technical Report. Deutsche Gesellschaft für Technische Zusammenarbeit GmbH, Eschborn.

Fischer, F., Groß, M. & Kunz, B. 2000. Primates of the Comoé National Park, Ivory Coast. *African Primates* 4: 10-15.

Gathua, M. 2000. The effects of primates and squirrels on seed survival of a canopy tree, *Afzelia quanzensis*, in Arabuko-Sokoke Forest, Kenya. *Biotropica* 32: 127-132.

Gautier-Hion, A., Duplantier, J. M., Quris, R., Feer, F., Sourd, C., Decoux, J. P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C. & Thiollay, J. M. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65: 324-337.

Glander, K. E. 1982. The impact of plant secondary compounds on primate feeding behavior. *Yearbook of Physical Anthropology* 25: 1-18.

Happel, R. E. 1986. The role of fruit characters determining preferences by West African monkeys. *American Journal of Primatology* 10: 406.

Herrera, C. M. 2002. Seed dispersal by vertebrates. Pp. 185-208 In Herrera, C. M. & Pellmyr, O. (eds.). *Plant-animal interactions. An evolutionary approach*. Blackwell, Oxford.

Hovestadt, T. 1997. Fruchtmerkmale, endozoochore Samenausbreitung und ihre Bedeutung für die Zusammensetzung der Pflanzengemeinschaft. Untersuchungen im Wald-Savannenmosaik des Comoé Nationalparks, Elfenbeinküste. PhD thesis. University of Würzburg, Germany.

Hovestadt, T., Yao, P. & Linsenmair, K. E. 1999. Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoé National Park, Ivory Coast). *Plant Ecology* 144: 1-25.

Howe, H. F. 1980. Monkey dispersal and waste of a Neotropical fruit. *Ecology* 61: 944-959.

Hutchinson, J., Dalziel, J. M. & Keay, R. W. J. 1954-1968. *Flora of West Tropical Africa.* Vols. I-III. Crown Agents for Oversea Governments and Administrations, London.

Janson, C. H. 1983. Adaptation of fruit morphology to dispersal agents in a Neotropical forest. *Science* 219: 187-189.

Janson, C. H., Stiles, E. W. & White, D. W. 1986. Selection on plant fruit traits by brown capuchin monkeys: a multivariate approach. Pp. 83-92 In Estrada, A. & Fleming, T. H. (eds.). *Frugivores and seed dispersal.* Dr. W. Junk Publishers, Dordrecht.

Jordano, P. 1995. Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions. *The American Naturalist* 145: 163-191.

Jordano, P. 2000. Fruits and frugivory. Pp. 125-165 In Fenner, M. (ed.). *Seeds. The ecology of regeneration in plant communities*. CABI, Wallingford.

Julliot, C. 1996a. Fruit choice by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest. *American Journal of Primatology* 40: 261-282.

Julliot, C. 1996b. Seed dispersal by red howler monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. *International Journal of Primatology* 17: 239-258.

Kasparek, M. 2000. *Flore du Parc National de Tai (Côte d'Ivoire).* Kasparek, Heidelberg.

Knight, R. S. & Siegfried, W. R. 1983. Interrelationships between type, size and color of fruits and dispersal in Southern African trees. *Oecologia* 56: 405-412.

Knogge, C. & Heymann, E. W. 2003. Seed dispersal by sympatric tamarins, *Saguinus mystax* and *Saguinus fuscicollis*: diversity and characteristics of plant species. *Folia Primatologica* 74: 33-47.

Kunz, B. K. & Linsenmair, K. E. 2008a. The disregarded West: diet and behavioural ecology of olive baboons in the Ivory Coast. *Folia Primatologica* 79: 31-51.

Kunz, B. K. & Linsenmair, K. E. 2008b. The role of the olive baboon (*Papio anubis*, Cercopithecidae) as seed disperser in a savanna-forest mosaic of West Africa. *Journal of Tropical Ecology* 24: 235-246.

Lambert, J. E. 1998. Primate frugivory in Kibale National Park, Uganda, and its implications for human use of forest resources. *African Journal of Ecology* 36: 234-240.

Lambert, J. E. & Garber, P. A. 1998. Evolutionary and ecological implications of primate seed dispersal. *American Journal of Primatology* 45: 9-28.

Lieberman, D., Hall, J. B., Swaine, M. D. & Lieberman, M. 1979. Seed dispersal by baboons in the Shai Hills, Ghana. *Ecology* 60: 65-75.

Link, A. & Di-Fiore, A. 2006. Seed dispersal by spider monkeys and its importance in the maintenance of Neotropical rain-forest diversity. *Journal of Tropical Ecology* 22: 235-246.

Norconk, M. A. & Conklin-Brittain, N. L. 2004. Variation on frugivory: the diet of Venezuelan white-faced sakis. *International Journal of Primatology* 25: 1-26.

Otani, T. & Shibata, E. 2000. Seed dispersal and predation by Yakushima macaques, *Macaca fuscata yakui*, in a warm temperate forest of Yakushima Island, southern Japan. *Ecological Research* 15: 133-144.

Peres, C. A. & van Roosmalen, M. 2002. Primate frugivory in two species-rich Neotropical forests: implications for the demography of large-seeded plants in overhunted areas. Pp. 407-421 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation*. CABI, Wallingford.

Pizo, M. A. 2002. The seed-dispersers and fruit syndromes of Myrthaceae in the Brazilian Atlantic forest. Pp. 129-143 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation*. CABI, Wallingford.

Poilecot, P. 1991. *Un écosystème de savane soudanienne: le Parc National de la Comoé (Côte d'Ivoire).* UNESCO, Paris.

Porembski, S. 1991. Beiträge zur Pflanzenwelt des Comoé-Nationalparks (Elfenbeinküste). *Natur und Museum* 121: 61-82.

Porembski, S. 2001. Phytodiversity and structure of the Comoé river gallery forest (NE Ivory Coast). Pp. 1-10 In Gottsberger, G. & Liede, S. (eds.). *Life forms and dynamics in tropical forests*. Dissertationes Botanicae. Borntraeger, Berlin.

Poulsen, J. R., Clark, C. J., Connor, E. F. & Smith, T. B. 2002. Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology* 83: 228-240.

Poulsen, J. R., Clark, C. J. & Smith, T. B. 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *Journal of Tropical Ecology* 17: 787-808.

Refisch, J. 1995. Samenverbreitung durch Paviane im Parc National de la Comoé, Elfenbeinküste. Diploma thesis. University of Bayreuth, Germany.

Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223-225.

Russo, S. E. 2003. Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia* 136: 80-87.

Schmidt, V., Schaefer, H. M. & Winkler, H. 2004. Conspicuousness, not colour as foraging cue in plant-animal signalling. *Oikos* 106: 551-557.

Sourd, C. & Gautier-Hion, A. 1986. Fruit selection by a forest guenon *Cercopithecus cephus*. *Journal of Animal Ecology* 55: 235-244.

Strasburger, E., Nol, F., Schenk, H. & Schimper, A. F. W. 1991. *Lehrbuch der Botanik für Hochschulen*. Gustav Fischer, Stuttgart.

van der Pijl, L. 1982. *Principles of dispersal in higher plants*. Springer, Berlin.

von Maydell, H. J. 1990. *Trees and shrubs of the Sahel. Their characteristics and uses.* Josef Margraf, Weikersheim.

Wagenitz, G. 2003. *Wörterbuch der Botanik*. Spektrum, Heidelberg.

Warren, Y. 2003. Olive baboons (*Papio cynocephalus anubis*): behaviour, ecology and human conflict in Gashaka Gumti National Park, Nigeria. PhD thesis. University of Surrey, Roehampton, UK.

White, F. 1983. *The vegetation of Africa*. UNESCO, Paris.

Whiten, A., Byrne, R. W., Barton, R. A., Waterman, P. G. & Henzi, S. P. 1991. Dietary and foraging strategies of baboons. *Philosophical Transactions of the Royal Society of London Series B* 334: 187-197.

Wolfheim, J. H. 1983. *Primates of the world. Distribution, abundance, and conservation.* University of Washington Press, Seattle.

Wrangham, R. W., Chapman, C. A. & Chapman, L. J. 1994. Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology* 10: 355-368.

Appendix 1 Plant and fruit traits of identified fruit plant species in the diet of olive baboons at Comoé National Park

Species: [a] = identified by Hovestadt (1997), [b] = by Refisch (1995). Baboons feed on: 'fruit (seed)' indicates that baboons feed on fruits of the species but the seeds are destroyed during consumption. Classification of growth forms follows Hovestadt (1997), otherwise (1) Hutchinson *et al.* (1954-1968). Where two growth forms occur, the less dominant in CNP is marked in parentheses and was excluded from further analyses. **Fruit type**: ach = achene, bac = baccate, cap = capsular, com = composed, drup = drupaceous, fig, fol = follicle, in = indehiscent, pod (dehiscent, if not otherwise stated), sam = samara, ar = with seed aril, bac/drup: information available is ambiguous, fruit either baccate or drupaceous; ? = not known. **Mes**. = Mesocarp; fleshy (fl) or dry, following Hovestadt (1997). **Fruit colour** of ripe fruits: b = brown-grey, g = green, l = black, o = orange, r = red, v = blue-violet, y = yellow. Fruit colour follows Hovestadt (1997). [ ] indicates differing fruit colour as consumed by baboons. **Fruit size**: s = small (≤ 10 mm length), m = medium ($> 10 \leq 30$ mm), l = large (> 30 mm). **Seed size**: s = small (maximum seed dimension ≤ 5 mm), m = medium ($> 5 \leq 20$ mm), l = large (> 20 mm). **N** = number of fruits or seeds measured. Fruit and seed size were measured by the first author, otherwise data are from [a] = (Hovestadt 1997), [b] = (Refisch 1995), [1] = (Hutchinson *et al.* 1954-1968), [2] = (Kasparek 2000), [3] = (Arbonnier 2000). #: a total of 49 *Ficus* spp. seeds were measured from presumably three different species.

Species	Baboons feed on	Growth form	Fruit type	Mes.	Fruit colour	Fruit size class	N (fruits)	Seed size class	N (seeds)
Ampelidaceae									
Cissus populnea	fruit	climber	bac[1]	fl	v	m	12	m	33
Cissus sp.	fruit	climber	bac[1]	fl	-	-	-	m	3
Anacardiaceae									
Lannea acida	fruit	tree	drup[1]	fl	v	s	154	m	241
Lannea barteri	fruit	tree	drup[1]	fl	v	m	112	m	31
Lannea welwitschii	fruit	tree	drup[1]	fl	v	s	121	m	30
Annonaceae									
Annona senegalensis	fruit	shrub	com-in[1,3]	fl	g	l[a]	5	m[a]	-
Enneastemon barteri [a,b]	fruit	climber	?	fl	y	m[a]	10	m[a]	-
Uvaria chamae	fruit	shrub	in[1,3]	fl	y	l	22	m	238
Apocynaceae									
Landolphia (Ancylobotrys) amoena [a,b]	fruit	climber	bac[3]	fl	o	l[a]	2	m[b]	-
Saba senegalensis	fruit	climber	bac[1,3]	fl	o	l	70	m	190
Bignoniaceae									
Kigelia africana	fruit	tree	in[1]	fl	g	l[2]	-	m	1
Buxaceae									
Notobuxus acuminata	fruit, (seed)	shrub	cap[1]	dry	b	s[a]	12	m[a]	-
Caesalpiniaceae									
Afzelia africana	aril, seed	tree	pod-ar[1]	dry	l	l	63	l	101
Cassia sieberiana [a]	seed?	tree	pod	dry	l	l[a]	4	m[a]	-
Cynometra megalophylla	fruit, seed	tree	pod-in[1,2]	dry	b [g]	l	60	l	60
Daniellia oliveri	seed	tree	pod[1]	dry	b [g]	l	14	l	78
Detarium microcarpum	fruit	tree	drup[1,3]	fl	b	l	55	l[a]	-
Detarium senegalense	fruit	tree	drup[1,2,3]	fl	b	l	11	l[a]	-
Dialium guineense	fruit	tree	pod-in[3]	dry	l	m	122	m	509
Erythrophleum guineense	seed	tree	pod[1]	dry	l	l	10	m	169

Appendix 1 (continued)

Species	Baboons feed on	Growth form	Fruit type	Mes.	Fruit colour	Fruit size class	N (fruits)	Seed size class	N (seeds)
Isoberlinia doka	seed	tree	pod[1]	dry	b [g,b]	l	97	l	97
Piliostigma thonningii	seed	(tree) shrub[1]	pod-in[1]	dry	b	l	125	m	24
Tamarindus indica	fruit	tree	pod-in[1]	fl	b	l	57	m	191
Capparidaceae									
Ritchiea capparoides [a]	fruit	climber	bac/drup[1]	fl	o	-	-	-	-
Chailletiaceae									
Tapura fischeri	fruit	tree[1]	drup[1]	fl	r [g]	s	41	s	55
Chrysobalanaceae									
Parinari curatellifolia	?	tree	drup[1]	fl	y	l[a]	41	l[a]	-
Combretaceae									
Anogeissus leiocarpa	fruit	tree	ach[1]	dry	l	m[a]	2	m[a]	-
Combretum spp.	fruit (seed)	tree, climber	sam[2]	dry	b [g,b]	-	-	-	-
Ebenaceae									
Diospyros abyssinica	fruit	tree	bac[1]	fl	r	m[a]	10	m[a]	-
Diospyros mespiliformis	fruit	tree	bac[1,2]	fl	o	m	100	m	298
Euphorbiaceae									
Bridelia ferruginea	fruit	shrub	drup[1]	fl	v	s	30	m[a]	-
Drypetes floribunda	fruit	shrub	in[1]	fl	y	m	84	m	294
Drypetes gilgiana	fruit	shrub	in[1]	fl	y	m[a]	10	m[a]	-
Mallotus oppositifolius	fruit	shrub	cap[1]	dry	b	s[a]	10	s[a]	-
Phyllanthus sp.	fruit	tree, shrub	cap[1]	-	-	-	-	s	51
Ricinodendron heudelotii	fruit	tree	drup[2]	fl	y	l[a]	10	m[a]	-
Uapaca togoensis	fruit	tree	cap-in[1]	fl	y	m[a]	6	m	27
Guttiferae									
Garcinia afzelii [a]	fruit	tree	bac	fl	y	m[a]	12	m[a]	3
Loganiaceae									
Strychnos sp.	fruit	climber	bac[1]	fl	o	l[a]	8	m	10
Mimosaceae									
Albizia sp.	seed	tree	pod-in[1]	dry	b	-	-	-	-
Dichrostachys glomerata	fruit	tree	pod-in[3]	dry	b	l[3]	-	s[a]	-
Leucaena glauca	fruit	shrub	pod[1]	dry	b	-	-	m[a]	-
Parkia biglobosa	fruit, seed	tree	pod-in[1]	dry	b [g,b]	l	53	m	86
Tetrapleura tetraptera	fruit (seed)	tree	pod-in[1,2]	dry	b	l[a]	10	m[a]	
Moraceae									
Antiaris africana	fruit	tree	drup[1]	fl	r	l[a]	10	m[a]	
Chlorophora excelsa	fruit	tree	cap[2]	fl	g	l[2]	-	s	1
Ficus glumosa	fruit	tree	fig[1]	fl	r	s[a]	10	s	(49)[#]
Ficus ingens	fruit	tree	fig[1]	fl	r	m[a]	10	s	#

Appendix 1 (continued)

Species	Baboons feed on	Growth form	Fruit type	Mes.	Fruit colour	Fruit size class	n (fruits)	Seed size class	n (seeds)
Ficus platyphylla	fruit	tree	fig[1]	fl	v	m[a]	6	s	#
Myrthaceae									
Syzygium guineense	fruit	tree	in[1]	fl	l [g]	m	45	m	29
Olacaceae									
Ximenia americana	fruit	shrub	drup[1]	fl	o	m	35	m	1
Opiliaceae									
Opilia celtidifolia [a]	fruit	climber[1]	drup[3]	-	o*	m	-	-	
Papilionaceae									
Craibia atlantica	seed	tree	pod[1]	dry	b [g]	l	35	m	34
Rubiaceae									
Canthium venosum	fruit	shrub	bac[1,3]	fl	b	m[a]	10	m[a]	
Canthium sp.	fruit	-	bac[1,3]	-	-	-	-	m	151
Cremaspora triflora	fruit	shrub	bac/drup[1]	fl	v	s[a]	10	m[a]	
Crossopteryx febrifuga	fruit	tree	cap[1,3]	dry	b	s	24	m	4
Gardenia aqualla	fruit	shrub	bac[1]	dry	y	l[a]	4	s[a]	
Oxyanthus racemosus	fruit	shrub	bac[1]	fl	o	m	49	s	111
Psychotria vogeliana	fruit	shrub	bac[1,3]	fl	v	s[a]	10	s[a]	
Sarcocephalus latifolius	fruit	shrub	com[1]	fl	r	l	20	s	45
Sarcocephalus cf. *xanthoxylon*	fruit	tree	com[1]	fl	y	l	8	s	10
Tricalysia sp.	fruit	-	bac[3]	fl	-	-	-	m	6
Rutaceae									
Afraegle paniculata [a,b]	fruit	(tree) shrub(1)	bac[1]	fl	g	l[a]	10	m	14
Sapotaceae									
Malacantha alnifolia	fruit	tree	bac[1]	fl	o	m	10	m	21
Manilkara multinervis	fruit	tree	bac[1,3]	fl	o	m	66	m	55
Mimusops kummel	fruit	tree	bac[1,3]	fl	o	m	33	m	26
Vitellaria paradoxa	fruit, seed	tree	bac[1]	fl	y	l	80	l	130
Solanaceae									
Solanum incanum	fruit	shrub	bac[1]	fl	y	m[a]	10	m	3
Sterculiaceae									
Cola cordifolia	aril, seed	tree	fol[1,2]	fl	o	l[3]	-	l	2
Tiliaceae									
Christiana africa	fruit	tree	cap[2]	dry	b	s[a]	6	s	2
Grewia cf. bicolor	fruit	shrub	bac/drup[1,3]	fl	y	s[a]	8	m	2
Ulmaceae									
Celtis sp.	fruit	tree	drup[1]	fl	-	-	-	m	1
Verbenaceae									
Vitex doniana	fruit	tree	drup[1]	fl	l	m	22	m	45

Chapter 4

The Role of Olive Baboons as Seed Dispersers in the Savanna-Forest Mosaic of West Africa

with K. E. Linsenmair

Published in *Journal of Tropical Ecology* (2008) 24: 235-246
http://journals.cambridge.org/action/displayIssue?jid=TRO&volumeId=24&issueId=03&iid=1871996,

Abstract Primates are among the major groups of frugivores in the tropics, but little is known about their role in natural regeneration of African savanna ecosystems. In the savanna-forest mosaic of north-eastern Ivory Coast the olive baboon (*Papio anubi*s Lesson 1827) harvests fruit from at least 79 plant species. Over a 24 month study period, 396 faecal samples from 10 groups of baboons were analysed in terms of quantitative and qualitative aspects of seed handling and dispersal (excluding grasses and sedges). Seventy-three percent of seeds in faecal samples were undamaged. Intact seeds were from 65 species. On average, defecations contained intact seeds from 2.0 species (range = 0-10). Seed size varied between 1 and 27 mm, and 77% of the species had medium-sized to large seeds. No linear correlation between mean seed size and seed damage was found. Eighteen out of 19 species tested were viable after ingestion, but effects of gut passage upon germination varied widely. The baboon population in the study area (145 km^2) dispersed an estimated 1,483 intact seeds d^{-1} km^{-2} (129 seeds > 2 mm in size). The results suggest that the olive baboon is an important seed disperser in the savanna-forest ecosystem of West Africa.

4. 1 INTRODUCTION

Frugivory and seed dispersal are crucial for maintaining the structural and dynamic properties of diverse tropical ecosystems (Howe & Miriti 2000; Jordano 2000). Primates are among the major groups of frugivores in the tropics (Lambert & Garber 1998; Stiles 2000); almost all diurnal primate species include fruit and seeds in their diet (Hladik 1981; Stiles 2000). With their often high biomass and relatively large home ranges, primates are able to harvest considerable proportions of fruit crops (Peres 1991; Chapman & Chapman 1996; Kunz & Linsenmair 2007). They may disperse high numbers of seeds over wide areas (Wrangham *et al.* 1994; Link & Di-Fiore 2006; McConkey 2007), thereby influencing the spatial and genetic structure of plant populations and contributing to plant community dynamics (Chapman & Onderdonk 1998; Pacheco & Simonetti 2000; Nuñez-Iturri & Howe 2007). Some species are considered particularly important for the dispersal of large-seeded fruit, that many other frugivores cannot swallow, at least not without serious damage of the seeds (Chapman & Onderdonk 1998; Peres & van Roosmalen 2002; Nuñez-Iturri & Howe 2007; but see Dominy & Duncan 2005).

Primates vary in their effectiveness (*sensu* Schupp 1993) as seed dispersers due to differences in morphology, physiology, feeding and ranging behaviour (Rowell & Mitchel 1991; Kaplin & Moermond 1998). As most primate species inhabit forests, studies to date on the interplay between primates and their fruit plants focused mainly on forest ecosystems. Several primate species, however, range within drier and more open habitats, such as the savannas of Africa. These ecosystems cover about 65% of the African continent (Tischler 1993). Africa's savannas are highly vulnerable to land degradation with considerable impacts on land cover and biodiversity (UNEP 2007). The Guinea savanna-forest mosaic of West Africa is particularly rich in plant species the seeds of which are dispersed by animals. In the Comoé National Park (CNP) in north-eastern Ivory Coast, 70% of the woody plant species provide fleshy fruit for dispersal by animals (Hovestadt *et al.*1999). At least nine diurnal nonhuman primate species inhabit the area (Fischer *et al.* 2000). The role of primates for natural plant regeneration and biodiversity in West African savanna systems, however, remains largely unexplored (but see Lieberman *et al.* 1979; Refisch 1995; Hovestadt 1997).

The most widely distributed nonhuman primate in sub-Saharan Africa is the olive baboon (*Papio anubis* Lesson 1827) (Wolfheim 1983; Rowe 1996). Its range extends from Mali to Ethiopia, Kenya, and north-western Tanzania (Groves 2001). Groups comprise one or several males, and several females with their offspring. Group size across African study sites averages 42 individuals, yet tends to be smaller in West Africa than elsewhere (Kunz & Linsenmair 2008). Groups occupy home ranges of about 100 to over 2000 ha (reviewed in Kunz & Linsenmair 2008). In West Africa the olive baboon spends 40-60% of feeding time eating fruit and seeds (Depew 1983; Warren 2003; Kunz & Linsenmair 2008) and disperses seeds of 31 to 51 dicotyledonous species per study site (Lieberman *et al.* 1979; Hovestadt 1997). Fruit of both forest and savanna species are consumed (Warren 2003; Kunz & Linsenmair 2008). Due to the high abundance of fruit species and the baboon's high degree of frugivory in West Africa, we presumed previous lists totalling 31 plant species (Refisch 1995; Hovestadt 1997) dispersed by the olive baboon in the CNP to be incomplete. We hypothesized that the olive baboon is an effective seed disperser in the savanna-forest mosaic of the CNP, both quantitatively and qualitatively, dispersing intact seeds of a higher number of woody plant species than previously recorded. We expected that a large frugivore like the olive baboon disperses seeds of a wide range of sizes undamaged, including large ones. The specific aims of the study were to (1) identify the species and number of intact seeds dispersed by the olive baboon in CNP, (2) determine whether the olive baboon disperses particularly seeds of a certain range of sizes, (3) analyse whether seed size and seed damage during ingestion are correlated, and (4) test for effects of baboon gut passage upon viability of dispersed seeds. We compare the data to other studies on primate seed dispersal, notably in Africa, and discuss the baboon's potential role for plant regeneration in the savanna-forest mosaic of West Africa.

4. 2 METHODS

4.2.1 STUDY SITE

The first author conducted field research over 24 month from November 1997 to July 2000. The study period included each month of the year at least once. The Comoé National Park (CNP) (08°30-09°36' N, 003°07'-004°25' W) comprises an area of 11,500 km^2 at an average altitude of 250-300 m asl (Poilecot 1991). The southern part of the CNP, where research took place in an area of approximately 145 km^2, is situated within the Guinea-Congolia / Sudania regional transition zone (*sensu* White 1983). The climate in the study area is characterized by a dry season from November to March/April. The mean annual precipitation from January 1994 to December 1999 was 1,053 mm, and the mean annual temperature was 26.3°C. The vegetation consists of a mosaic of different savanna formations (~91 %), forest islands (7 %), and gallery forest (2 %) (FGU-Kronberg 1979) and is described in more detail elsewhere (Poilecot 1991; Porembski 1991, 2001; Hovestadt *et al.* 1999). Seventy percent of the 292 woody plant species recorded in the study area produce fleshy fruit for consumption by animals (Hovestadt 1997). So far, 498 bird species (Salewski 2000; Salewski & Göken 2001; Rheindt *et al.* 2002) and 152 mammal species have been recorded (Poilecot 1991; Mess & Krell 1999; Fischer *et al.* 2002). Among the nine recently recorded diurnal primate species, the olive baboon is the most abundant (Fischer *et al.* 2000). Ten different baboon groups inhabited the study area, comprising on average 15 individuals per group (range = 4-44) (Kunz & Linsenmair 2008).

4.2.2 ANALYSIS OF FAECAL SAMPLES

Faecal samples were collected opportunistically from the 10 baboon groups in the study area. Two of these groups were habituated to the presence of the first author and were observed regularly. Faeces of the other groups were collected during fortnightly monitoring of the baboon population, and when crossing varying parts of the area by foot or car (about every other day). A detailed description on how the baboon population was studied is given in Kunz & Linsenmair (2008).

Faeces were only collected when they were whole. Samples were bagged and stored at the field station in a dry place at ambient temperature, until analysed within three days of collection. To extract seeds, we thoroughly mixed each sample with water and rinsed it through sieves with decreasing mesh width (4, 2, 1 mm). All seeds remaining in the first two sieves were counted. To estimate the number of very small seeds (< 2 mm) we evenly stirred the material remaining in the sieve with the smallest mesh width and counted the number of seeds in subsamples. We identified seed species using a reference collection established in previous years by T. Hovestadt and P. Poilecot, supplemented by seeds taken from fresh fruits of identified plants during the present study. Plant nomenclature follows the African Flowering Plants Database (Conservatoire et Jardin Botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria, <http://www.ville-ge.ch/cjb/bd/africa/index.php>).

We were unable to distinguish seeds of different *Ficus* species and pooled them for further analyses. The focus of the study was on woody plant species; hence we only collected presence-absence data on pooled seeds of grasses and sedges and did not include them into further analyses.

To avoid a bias towards small seeds, which are usually dispersed in greater quantities than large seeds, we calculated the number of dispersal events (DE) for each plant species (following Knogge & Heymann 2003). A dispersal event for a given species was defined as the occurrence of one or more ripe intact seed of the species in a sample. Because plant species have different fruiting periods and we did not retrieve faecal samples in equal quantities across all months of the year (mean ± *sd* = 33 ± 13.5 samples per month of year, range = 6-54), we calculated a monthly DE-ratio (DE_r) for each species: for each month in which one or more seeds of the species occurred in one or more faecal sample we divided the number of DE of the species by the number of faecal samples collected in that month. Subsequently, we calculated the 'mean monthly DE_r ' for each species by dividing the sum of DE_r by the number of months of the year in which the seeds of the species appeared in faecal samples. Instead of DE_r, other studies often quote separately the seed number that includes only seeds larger than a certain minimum size (e.g. > 2 mm, Wrangham *et al.* 1994; > 3 mm Link & Di-Fiore 2006). For reasons of comparison we also provide figures of seed numbers with and without very small seeds (> 2 mm).

We examined the seeds visually for damage, using a lens (10× magnification) for small seeds. Each seed checked for damage was classified into one damage category: (0) = 'intact seed' (completely undamaged or ≤ 5% of the testa damaged); (1) = 'medium damage' (seed with > 5% to ≤ 25% damage of the testa and/or ≤ 5% damage of the endosperm and cotyledons); (2) = 'heavy damage' (> 25% damage of the testa and/or > 5% damage of the endosperm/cotyledons). Generally, we checked more than 90% of the seeds from each species, except species with very small seeds (e.g. *Ficus* spp., *Sarcocephalus* spp.). For each identified species that occurred in six or more faecal samples, we calculated the percentage of seeds in each damage category, referring to the number of seeds checked per species as 100%. For statistical analyses we calculated the mean seed damage per species.

To identify whether the olive baboon predominantly disperses seeds of a certain range of size we measured length and width of fresh, fully turgescent seeds in damage category 0 (and 1 when dimensions of the seed were undamaged), using a sliding calliper (0.1 mm accuracy). Seeds ≤ 2 mm size were difficult to measure accurately, hence for these species we used a value of 2 mm in all calculations. We classified seed species according to their mean maximum diameter (length or width, whichever larger) into different size categories: small (≤ 5 mm), medium (> 5 - < 20 mm), and large (≥ 20 mm) (following Wrangham *et al.* 1994; Lambert & Garber1998). We compared the frequency of occurrence of the three size classes among the seed species dispersed by the olive baboon to the frequency of occurrence of the size classes among the woody plant species in CNP. Data on seed sizes of species that did not occur in faecal samples were taken from Hovestadt (1997).

4.2.3 GERMINATION EXPERIMENTS

At the field station, we undertook germination viability experiments on the ingested seeds from 19 plant species. The species were a regular part in baboon diet, as judged from direct observations and/or seeds retrieved from dung. In 14 out of the 19 species we conducted comparative experiments between seeds from faecal samples and from fresh ripe fruits. Generally, we obtained fresh seeds from six or more fruits from each of four to ten individuals per plant species. Most crops of *Lannea acida* trees (Anacardiaceae) were depleted before maturity (Kunz, unpubl. data); hence we sampled only two trees. We cleaned fresh seeds from pulp mechanically and briefly rinsed the seeds with water.

An important benefit of ingestion, however, might be the removal of fruit pulp, which otherwise can delay or inhibit germination (Barnea *et al.* 1991; Yagihashi *et al.* 1998; Engel 2000). Seeds of *Tamarindus indica* (Fabaceae) occur with and without the glutinous pulp in baboon faeces, hence we tested germination of fresh and ingested seeds, both with and without pulp. In contrast, the coat of dry pulp around *Dialium guineense* (Fabaceae) seeds is removed during ingestion. We compared germination of fresh *D. guineense* seeds with pulp, fresh seeds without pulp, and ingested seeds without pulp.

We stored undamaged seeds from baboon faeces and from fresh ripe fruit in a dark, dry place at ambient temperature until we obtained sufficient seeds for the trials. For germination, we placed the seeds in Petri dishes on a double layer of filter paper. Based on the number of seeds available in a given species, we tested germination under one to three different light conditions: shade (provided by a dense reed coverage), semi-shade (loose, translucent reed coverage), sun (no coverage). When seeds of a species were sparse, or the species had already been tested during this study for effects of light upon seed germination, priority was given to trials in semi-shade and shade, as these conditions had proved the most promising. We watered seeds as necessary, checked them daily for penetration of the seed coat by the radicle, and removed germinating seeds. When experiments extended throughout and beyond the dry season, we stopped watering of the seeds as long as rains ceased, and restarted with the onset of the next rainy season. We repeated germination experiments upon availability of fresh and ingested seeds.

4.2.4 STATISTICAL ANALYSES

We calculated the median (x_{md}) and 25% (*q1*) and 75% (*q3*) percentiles instead of the mean and standard deviation when data were not normally distributed, but for reasons of comparison with other studies, the mean and standard deviation (*sd*) may also be given. We used mean seed size and mean seed damage per species in a linear regression model. Values of mean seed damage were fitted to the normal distribution using a Box-Cox-transformation. We tested for variation in the frequency distribution of seed size classes between woody plant species dispersed by the olive baboon and woody plant species in the local plant pool of the CNP, using χ^2 test with Yates correction. We analysed germination data using non-parametric life-time analysis which takes into account germination ratios as well as times to germination and considers seeds that did not germinate until the end of the experiment as right-censored data points (Fox 1993). We focused on variation across fresh and ingested seeds. We performed all tests in SPSS version 15.0 or ssS version 1.0. Tests were two-tailed and the level of significance set at 95%. We adjusted the level of significance for multiple testing following the sequential Bonferroni technique (Rice 1989).

4. 3 RESULTS

4.3.1 ANALYSIS OF FAECAL SAMPLES

In 99.0 % of the faecal samples ($N = 396$) we were able to determine the number of seed species. Seeds from grasses and/or sedges, which are henceforth excluded from further analyses, were present in 14.7% of the faecal samples. Dispersal events occurred in 88.9% of all faecal samples, and in 91.9% of all samples that contained seeds.
Seventy-three percent of the seeds in faecal samples ($N = 171,736$) were intact and 26.6% were damaged. In addition, 13% of the faecal samples contained an indeterminate number of seed fragments. The median number of intact seeds per sample was 20.5 ($q1 = 5$, $q3 = 115.3$, mean ± $sd = 322 \pm 1188$, max = 13,258, $n = 392$). If very small seeds (≤ 2 mm) are excluded, the median seed number is 7 ($q1 = 1$, $q3 = 22$, mean ± $sd = 28.2 \pm 70.5$, range = 0-734). Figure 1 displays the frequency distribution of seed numbers in faecal samples.

We extracted a total of 69 species, of which 58 species from 23 families were identified (Appendix 1). On average (mean ± *sd*), a sample comprised intact seeds from 2.0 ± 1.5 species (range = 0-10, $n = 392$) (Figure 2). The five taxa with the highest mean DE_r were *Sarcocephalus xanthoxylon* (Rubiaceae), *Uvaria chamae* (Annonaceae), *T. indica* (Fabaceae), *Ficus* spp. (Moraceae) and *D. guineense* (Fabaceae) (Appendix 1). However, dispersal events for most other plant species were rare. Species with no recorded dispersal of intact seeds were *Afzelia toxicaria* and *Tetrapleura tetraptera* (Fabaceae), *Combretum* sp. (Combretaceae), and *Buxus acutata* (Buxaceae). The mean (± *sd*) monthly DE_r across all identified species was 0.08 ± 0.10.

In 19 out of the 21 taxa occurring in six or more faecal samples at least 85% of the seeds checked for damage were intact (mean ± $sd = 88.8\% \pm 21.7\%$) (Table 1). Across species, there was no linear correlation between seed size and damage of seeds ($r^2_{\text{length}} = 0.049$, $F = 0.974$, $p > 0.05$; $r^2_{\text{width}} = 0.017$, $F = 0.321$, $p > 0.05$).

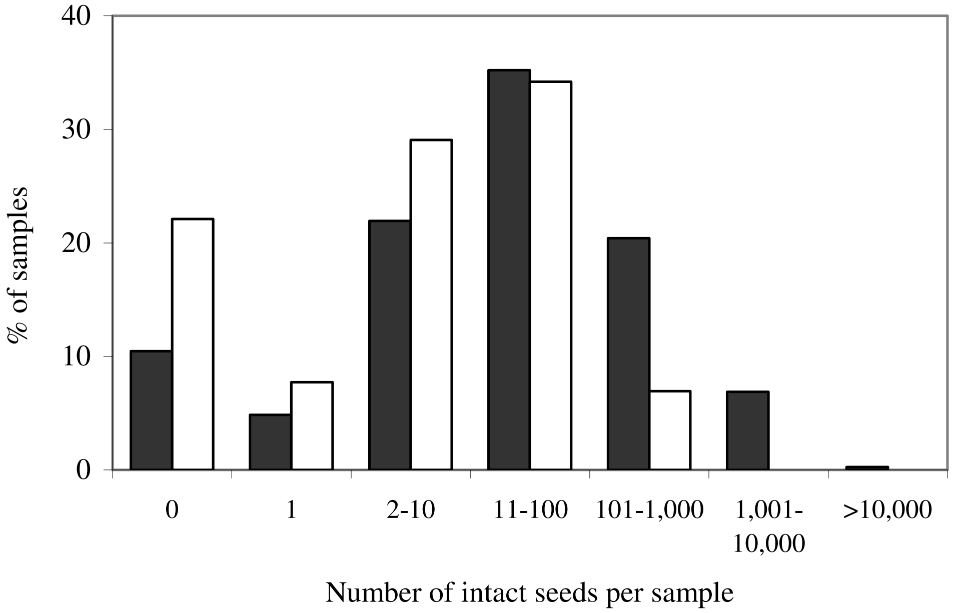


Figure 1 Distribution of the number of intact seeds in faecal samples ($N = 396$)
Dark columns represent the frequency distribution of seed numbers in faecal samples when seeds of all sizes are included. White columns represent the frequency distribution of seed numbers in faecal samples when very small seeds (< 2 mm) are excluded.

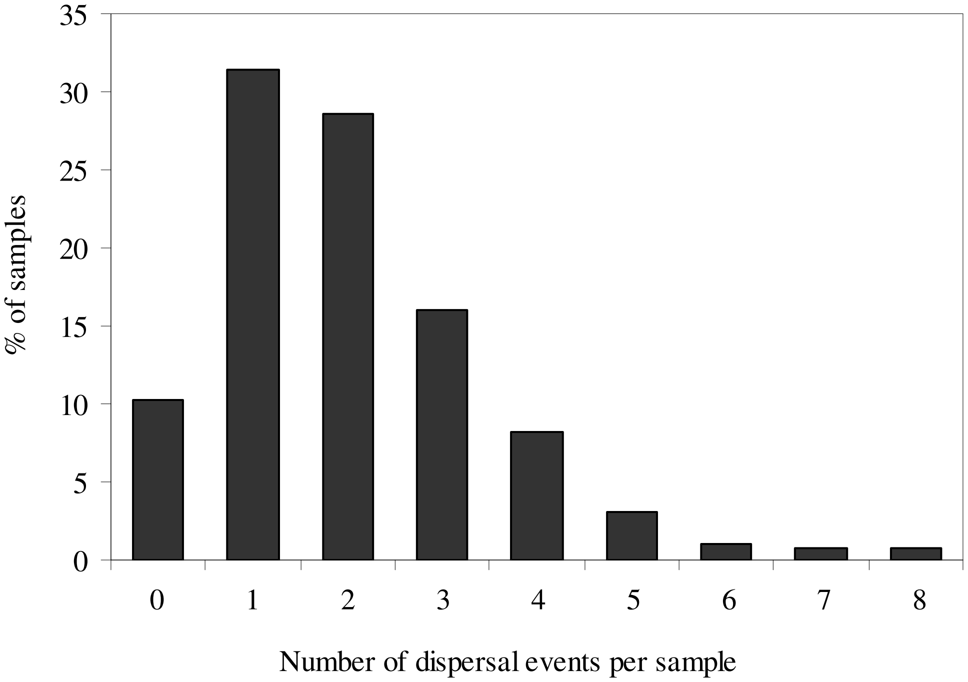


Figure 2 Distribution of the number of dispersal events in faecal samples ($N = 396$)
A dispersal event is defined as the occurrence of one or more ripe intact seed of a given species in the sample.

Table 1 Damage and size of seeds extracted from faeces of olive baboons at Comoé National Park (*N* = 396 faecal samples)

Only identified taxa with seeds occurring in ≥ 6 faecal samples are presented. Fs_n = total number of faecal samples (fs) containing a given species; x = indicates an indeterminate number of seed fragments. Seed size classes: s = (small) mean maximum diameter ≤ 5 mm, m = (medium) > 5 - ≤ 20 mm. DC (damage category), DC0 = intact seeds, DC1 = medium damage, DC2 = heavy damage. % of seeds in damage categories: in each species 100% correspond to the total number of seeds checked for damage.

Plant species	fs_n	∑ of seeds in fs_n	Seed size class	% checked for damage	% in damage categories			
					DC0	DC1	DC2	mean DC
Ficus spp. (3 species)	91	99,150	s	3.8	66.9	0.1	33.1	0.662
Sarcocephalus cf. *xanthoxylon*	79	33,943	s	4.8	99.6	0.1	0.3	0.007
Dialium guineense	72	2,841	m	98.1	94.7	1.7	3.6	0.088
Tamarindus indica	57	304	m	100	90.5	3.0	6.6	0.161
Diospyros mespiliformis	46	362	m	95.6	88.2	5.2	6.6	0.185
Drypetes floribunda	38	1,230	m	100	99.8	0.2	0.0	0.002
Saba senegalensis	35	257	m	100	98.4	0.0	1.6	0.031
Sarcocephalus latifolius	35	13,864	s	4.1	95.4	2.3	2.3	0.068
Parkia biglobosa	21	159	m	100	88.7	6.9	4.4	0.157
Uvaria chamae	18	1,172	m	100	99.5	0.4	0.1	0.006
Oxyanthus racemosus	17	125	s	100	93.6	2.4	4.0	0.104
Keetia sp.	15	155	m	100	95.5	2.6	1.9	0.065
Aframomum exscapum	14	2,167	s	91.9	99.4	0.2	0.4	0.010
Erythrophleum suaveolens	14	338	m	100	93.8	4.7	1.5	0.077
Tetrapleura tetraptera	13	164+x	m	(100)	0.0	0.0	100	2.000
Vitex doniana	12	46	m	100	97.8	2.2	0.0	0.043
Cissus populnea	8	33	m	100	100	0.0	0.0	0.000
Lannea welwitschii	8	127+x	m	(100)	(98.4)	(1.6)	x	0.016
Tapura fischeri	8	504	s	95.9	85.0	1.2	13.8	0.289
Milicia excelsa	6	46	s	26.1	91.7	0.00	8.30	0.167
Strychnos sp.	6	33	m	93.9	87.9	12.1	0	0.065

The seeds of species in baboon faeces ranged in size from ~1 mm (*Ficus* spp. and *Sarcocephalus* spp.) to 24.6 mm (mean length of *Cola cordifolia* (Sterculiaceae) seeds). The longest intact seed was 27.0 mm (*Parinari curatellifolia*, Chrysobalanaceae), and the largest intact seed regarding both length and width was 24.8 × 21.8 mm (*Vitex doniana*, Verbenaceae). Overall, 5.7% of the dispersed species had large seeds (≥ 20 mm), 71.7% were of intermediate seed size (> 5 - < 20 mm), and 22.6% had small seeds (≤ 5 mm)

(Appendix 1). Data on seed size classes were available for 48.6% (*n* = 142) of the woody plant species in CNP. Ten percent had large seeds, 64.8% medium-sized seeds, and 25.0% small seeds. Variation in the distribution of seed size classes between the local plant pool of woody species and the faecal samples of the baboons were statistically not significant ($\chi^2 = 1.04$, $df = 2$, $p > 0.05$).

4.3.2 GERMINATION EXPERIMENTS

Germination of seeds was highly variable (Table 2). Only in *D. guineense* did seeds also germinate in the second rainy season (~ 65 % of the germinating seeds). All 18 species tested under different light conditions generally performed better in the shade or semi-shade than in the sun. Only six species germinated in the sun, of which five species had < 10% of seeds germinating. Of five species that were each tested in the shade and semi-shade simultaneously, germination was improved in the semi-shade in three species. In *Diospyros mespiliformis*, however, only ingested but not fresh seeds performed better in the semi-shade. Due to the low germination success in the sun, statistical comparisons focus on variation across ingested and fresh seeds under semi-shaded and shaded conditions.

Baboons dispersed viable seeds of all species tested except *Drypetes floribunda*. In five of the 14 species for which we compared germination of fresh and ingested seeds (Table 2), gut passage enhanced germination significantly. In three additional species, germination of ingested seeds was improved in one out of two experiments under the same light conditions. Fresh seeds germinated better than ingested seeds in three species, and in one species, differences in germination between fresh and ingested seeds were not statistically significant. Two species were not compared statistically, due to low germination in both ingested and fresh seeds.

The effect of pulp upon seed germination varied among species. In *D. guineense*, differences in germination between ingested seeds without pulp, fresh seeds without pulp, and fresh seeds with pulp were not significant (Table 2). In *T. indica*, ingested seeds without pulp performed significantly better than ingested seeds with pulp (Wilcoxon-Gehan = 10.9, $p = 0.01$), better than fresh seeds without pulp (Wilcoxon-Gehan = 10.2, $p = 0.01$) and better than fresh seeds with pulp (Wilcoxon-Gehan = 18.4, $p = 0.01$). However, ingested seeds with pulp did not germinate better than fresh seeds without pulp (Wilcoxon-Gehan = 0.139, $p > 0.05$) ($df = 1$, p values after applying sequential Bonferroni technique, $n = 25$ seeds in each treatment). Germination success of *T. indica* seeds with pulp, whether ingested or from fresh fruit, was too low for statistical comparisons of these two classes.

Table 2 Germination of seeds from olive baboon faeces and from fresh fruits

Light conditions were: shade, semi-shade, sun. Ing: ingested; wp: with pulp (*D. guineense* and *T. indica* only); percent germination of seeds with pulp is given in parentheses. WG: Wilcoxon-Gehan statistics; *df* = 1 in all tests except for *D. guineense* under shaded conditions, where *df* = 2. (1): test statistics are given for the comparison of fresh and ingested seeds, both without pulp. (Bf): level of significance after applying sequential Bonferroni technique. When a varying number of seeds were used under different light conditions, numbers are given separately for shade/semi-shade/sun. Otherwise, seed numbers were similar in each light condition. (+) indicates that experiments included the following dry season during which watering of seeds ceased.

Plant species	Duration [d]	Seeds per ing.	treatment fresh	% Germination									
				Shade				Semi-shade				Sun	
				ing.	fresh (wp)	*WG*	*p*	ing. (wp)	fresh (wp)	*WG*	*p*	ing.	fresh (wp)
Aframomum excarpum	266$^{(+)}$	100	-	89.0								0	
Cynometra megalophylla	21	3	-					100					
Dialium guineense	455$^{(+)}$	30	30	73.8	73.8 (43.3)	2.98	ns					0	0 (0)
	362$^{(+)}$	60	60	78.3	56.7	5.15	*						
Diospyros mespiliformis	91	60	60	78.3	85.0	0.25	ns	85.0	71.7	6.95	**	0	0
	126	30	30	93.3	30.0	21.41	***					3.3	0
Drypetes floribunda	357$^{(+)}$	30	-					0					
	56	60	-	0								0	
Keetia sp.	91	10	-	0								0	
	126	10	-	10.0				40.0				0	
Lannea acida	70	60	60	83.3	3.3	70.77	***					0	0
L. barteri	70	25/10/10	25/10/10	52	0	16.77	***	70.0	0	9.72	**	0	0
L. welwitschii	70	30/20/20	30/20/20	23.3	0	7.76	**	5.0	0			0	0
Manilkara obovata	91	30	30	16.7	30.0	8.96	***					0	20.0
Oxyanthus racemosus	257$^{(+)}$	50	50	66.0	46.0	3.60	ns					0	0
Parkia biglobosa	91	50	-	10.0								6.0	
	455$^{(+)}$	10	40					60.0	17.5	5.74	*		

Table 2 (continued)

				% Germination									
				Shade				Semi-shade				Sun	
Plant species	Duration [d]	Seeds per ing.	treatment fresh	ing.	fresh (wp)	*WG*	*p*	ing. (wp)	fresh (wp)	*WG*	*p*	ing.	fresh (wp)
Pouteria alnifolia	70	10	10	20.0	70.0	6.60	*					0	1
Saba senegalensis	91	16	16	50.0	0	10.08	**					0	6.25
	70	42/36	42/36	47.6	0	25.32	***					2.8	0
Sarcocephalus latifolius	210	50	50	14.0	66	23.67	***					0	0
Tamarindus indica	91	55	-	47.3								9.1	
	126	25	25					56.0 (12.0)	16.0 (0)	10.89(1) (-)	**(Bf)		
	70	20/10/10	20/10/10	45.0	35.0	0.54	ns	20.0	20.0	0.19	ns	0	0
Tapura fischeri	336(+)	60	60	3.3	0							0	0
Uapaca togoensis	91	5	-	40.0								0	
Uvaria chamae	336(+)	60	60	6.7	0							0	0

4. 4 DISCUSSION

The study corroborates the hypothesis that the olive baboon is an effective seed disperser, both quantitatively and qualitatively, for a large number of woody plant species in the savanna-forest mosaic of West Africa. Noteworthy is the fact that the results from this study are similar to outcomes of studies in tropical forests where the proportion of primate faeces that contain intact seeds often seem to be high, e.g. 78.5% in the chimpanzee (*Pan troglodytes*) and 33.7% to 100% in several Cercopithecidae (Kaplin & Moermond 1998; Poulsen *et al.* 2001). Intact seeds of at least 85% of the species of which baboons consumed fruits and/or seeds (*N* = 79, Kunz & Linsenmair 2008) occurred in the faecal samples. Assuming that *Ficus* seeds pooled in faecal analyses represented the three species (*F. glumosa*, *F. ingens, F. platyphylla*) on which we observed baboons feeding (Kunz & Linsenmair 2008, Kunz unpubl. data), at least 19% of the woody plant species in the local plant pool (*N* = 292, Hovestadt 1997) had one or more dispersal event (unidentified species not included). Two previous studies in CNP (Refisch 1995; Hovestadt 1997), add seven species to the list (Table 3).

Table 3 Woody plant species occurring in the Comoé National Park the seeds of which were found in faecal samples of the olive baboon in Ghana and during previous studies in CNP, but not during the present study
Site: CNP = Comoé National Park (Ivory Coast), SH = Shai Hills (Ghana).
References: 1 = Refisch (1995), 2 = Hovestadt (1997), 3 = Lieberman *et al.* (1979).
Synonyms are given in parentheses when names of species deviate form the nomenclature in the original articles.

Plant species	Family	Site and references
Monanthotaxis (*Enneastemon*) *barteri*	Annonaceae	CNP [1, 2]
Ancylobotrys amoena	Apocynaceae	CNP [1, 2]
Adansonia digitata	Bombacaceae	SH [3]
Cordia guineensis	Boraginaceae	SH [3]
Crateva adansonii	Capparaceae	SH [3]
Ritchiea capparoides		CNP [2]
Garcinia afzelii	Clusiaceae	CNP [2]
Flueggea (*Securinega*) *virosa*	Euphorbiaceae	SH [3]
Desmodium velutinum	Fabaceae	SH [3]
Cassia sieberiana		CNP [2]
Flacourtia indica (syn. *flavescens*)	Flacourtiaceae	SH [3]
Opilia amentacea (syn. *celtidifolia*)	Opiliaceae	CNP [2], SH [3]
Afraegle paniculata	Rutaceae	CNP [1, 2]

In the Shai Hills in Ghana, the olive baboon dispersed viable seeds from at least 51 dicotyledonous species (Lieberman *et al.* 1979), including six woody plant species that can be found in CNP but for which evidence for consumption by baboons is lacking (Table 3) (Refisch 1995; Hovestadt 1997; Kunz & Linsenmair 2008). The number of plant species dispersed by the olive baboon in CNP corresponds to findings from studies on great apes in Africa: chimpanzees and gorillas (*Gorilla gorilla*) dispersed 59 and 65 species, respectively (Tutin *et al.* 1991; Wrangham *et al.* 1994).

Following Hovestadt (1997), 40% of the species dispersed by the olive baboon in CNP were restricted to gallery forest, forest islands, or both. Thirty-one percent can be found in forest islands and savanna, 7.3% only in savanna, and 12.7% are habitat generalists. (Habitat preference for five dispersed taxa remained unidentified). However, the olive baboon dispersed most species infrequently (low mean monthly DE_r values). Species with the highest mean monthly DE_r produce large fruit crops and/or are common in CNP. Most of these species have extended fruiting periods (e.g. *D. guineense*, *D. mespiliformis*) or fruit that persist over a long time on the tree (e.g. *T. indica*) (Hovestadt 1997; Kunz unpubl. data).

Mean numbers of species occurring in faecal samples of the olive baboon in CNP conform to numbers in faecal samples of Cercopithecidae elsewhere (1.0–3.0, Kaplin *et al.* 1998; Poulsen *et al.* 2001). Similar values were also found for chimpanzees (1.7) and gorillas (2.8) (Wrangham *et al.* 1994; Poulsen *et al.* 2001), as well as for several primate species outside Africa (1.9-2.4; McConkey 2000; Otani 2003; Wehncke *et al.* 2003; Link & Di-Fiore 2006).

To estimate the number of seeds dispersed d^{-1} per baboon, data on baboon defecation rate is required. In the literature only an anecdotal remark on an infant that defecated four times d^{-1} is available (Rhine *et al.* 1980). Defecation rates of other Cercopithecinae and the chimpanzee range between 3-7 d^{-1} per individual (Wrangham *et al.* 1994; Poulsen *et al.* 2001). Taking four defecations d^{-1} per baboon as an estimate and the mean number of seeds per faecal samples, each baboon would disperse 1,288 seeds d^{-1} (112 seeds > 2 mm). Based on a total of 167 baboon individuals inhabiting the study area of 145 km^2 (Kunz & Linsenmair 2008), the baboon population dispersed 1,483 seeds d^{-1} km^{-2} (129 seeds > 2 mm).

Mean seed numbers per baboon faecal sample seem high compared to other frugivorous primates (Wrangham *et al.* 1994; Poulsen *et al.* 2001; Link & Di-Fiore 2006), though Yakushima macaques might on average have similar seed quantities per faeces (Otani & Shibata 2000). Comparisons with other studies, however, are hampered by different methods applied in faecal analyses, e.g. different cut-offs of seed sizes below which seed numbers are estimated or seeds are excluded from analyses, and whether or not seed numbers include only undamaged seeds.

In our study, the vast majority of seeds in faecal samples seemed intact. Yet, the proportion of seeds damaged heavily by baboons inevitably is an underestimate, because completely digested seeds do not turn up in faeces. In particular, legumes whose large, soft, unripe seeds are part of baboon diet in CNP (i.e. *Daniellia oliveri*, *Craibia atlantica*, *Isoberlinia doka*, Kunz & Linsenmair 2008, Kunz pers. observ.) were not retrieved during faecal analyses. Likewise, ripe seeds of *Piliostigma thonningii* and *Erythrophleum suaveolens* seem to escape chewing only occasionally. Contrary to findings by Gautier-Hion (1984) for five African monkey species, seed size and seed damage during ingestion by baboons were not positively correlated, whether or not large legume seeds were included in the analyses. As expected, the olive baboon in CNP dispersed seeds of a wide range of sizes. The largest seed (27 mm) was of similar maximum size as dispersed by the chimpanzee (Wrangham *et al.* 1994). Seeds larger than this size were generally discarded by the olive baboon while feeding on the pulp (Kunz pers. observ.). The proportion of species with medium-sized to large seeds (77% ≥ 5 mm) dispersed by the olive baboon is high in comparison with other Cercopithecinae (30-40% > 2 mm, Kaplin *et al.* 1998) and chimpanzees (51% ≥ 5 mm, Wrangham *et al.* 1994) and does not confirm that baboons swallow particularly small seeds (Lambert 2002). Gorillas and tamarins (*Saguinus* spp.) may disperse similar and higher proportions, respectively, of seeds ≥ 5 mm (gorilla: 71%, Tutin *et al.* 1991; tamarins up to 100%, Garber 1986; Oliveira & Ferrari 2000). Yet, the frequency of occurrence of species with different seed sizes in faecal samples of a primate might - below a maximum threshold - simply reflect seed size distribution of plant species at the study site.

The olive baboon in CNP dispersed viable seeds from all but one of the plant species tested in germination experiments. Like in other studies on primate seed dispersal, effects of gut passage upon germination varied widely across plant species (Lieberman *et al.* 1979; Idani 1986; Julliot 1996; Otani & Shibata 2000). The results show that effects can vary across study sites and experiments within the same plant species. *Drypetes floribunda* did not germinate in our study, but baboons dispersed viable seeds in Ghana (Lieberman *et al.* 1979). Fresh seeds of *Sarcocephalus latifolius* (Rubiaceae) germinated better than seeds dispersed by the olive baboon in CNP, whereas in Ghana seeds had improved germination after baboon gut passage (Lieberman *et al.* 1979). Like Lieberman *et al.* (1979) and Refisch (1995), we did not find significant differences between ingested and fresh *D. mespiliformis* seeds in one experiment. However, germination of ingested seeds was enhanced when trials were repeated. Results from repeated trials of two other species also varied. Variation in the number of seeds used in successive trials of the same species cannot always account for the different outcomes, since fewer seeds sometimes revealed significant results while larger numbers did not. Slight changes in experimental conditions (e.g. light regime, humidity) might reveal differences that otherwise remain undetected (Engel 2000). Moreover, fruit 'choice' in both primates and researchers could influence outcomes of experiments. As a result of a variable overall fruit availability, primates might predominantly feed on some species prior to full maturation in one season, while otherwise ripe fruits of the species might be preferred. Fruit that researchers consider ripe may still not have reached full maturity. We suggest that experiments designed to compare germination of ingested and fresh seeds should be repeated when possible, or otherwise interpreted cautiously as results from just one fruiting season might yield an incomplete picture of disperser effectiveness (Engel 2000).

The results emphasise that the olive baboon is likely to play a major role in seed dispersal in the savanna-forest mosaic of West Africa. In CNP, the olive baboon is the most abundant primate (Fischer *et al.* 2000). It depletes entire fruit crops of individual plants (Kunz & Linsenmair 2007), and disperses large quantities of undamaged seeds from a high number of different plant species. Quantitatively, baboon seed dispersal potential seems comparable to that of great apes in African forests. The long gut retention time of the olive baboon (> 24 h for seeds of wild fruits fed to captive individuals, Kunz, unpubl. data) in combination with the use of all kinds of habitats in its relatively large home ranges (Kunz & Linsenmair 2008) enables this species to transport seeds over wide distances within and between habitats. As the olive baboon in CNP dispersed many woody plant species that grow only in forests, it might be particularly important for seed transfer between distant forest islands (Hovestadt 1997). All other diurnal primate species in CNP occur in much lower densities, and most are more restricted to forest habitats (Poilecot 1991; Fischer *et al.* 2000; Kunz, unpubl. data). Other large, long-distance seed dispersers like the African elephant (*Loxodonta africana*) and species of hornbill (Bucerotidae) (Lieberman *et al.* 1987; Hovestadt 1997) have become rare in CNP (Lauginie 1995, Fischer *et al.* 2002; Kunz pers. observ.). Baboons (*Papio* spp.) are widely distributed across sub-Saharan Africa and are still relatively abundant in many areas. Considering the large extent of African savannas, the effect of baboons on natural plant regeneration and population dynamics of these ecosystems merits further study.

4. 5 ACKNOWLEDGEMENTS

We thank J. Korb, K. Kouadio, and N. Reintjes for their help with faecal sample collection and germination experiments. Y. Warren and two anonymous reviewers made helpful comments on the manuscript. The Ministère de l'Agriculture et des Ressources Animales and the Ministère de l'Enseignement Supérieure et de la Recherche Scientifique, Abidjan, kindly granted research permission for the CNP. PhD scholarships from the German Academic Exchange Service (DAAD) and the University of Wuerzburg (HSP III) funded this study. The research camp in CNP was constructed with generous funds from the Volkswagen-Foundation.

4. 6 REFERENCES

Barnea, A., Yom-Tov, Y. & Friedman, J. 1991. Does ingestion by birds affect seed germination. *Functional Ecology* 5: 394-402.

Chapman, C. A. & Chapman, L. J. 1996. Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. *Journal of Tropical Ecology* 12: 491-504.

Chapman, C. A. & Onderdonk, D. A. 1998. Forests without primates: primate/plant codependency. *American Journal of Primatology* 45: 127-141.

Depew, L. A. 1983. Ecology and behaviour of baboons (*Papio anubis*) in the Shai Hills Game Production Reserve, Ghana. MSc thesis. Cape Coast University, Ghana.

Dominy, N. J. & Duncan, B. W. 2005. Seed-spitting primates and the conservation and dispersion of large-seeded trees. *International Journal of Primatology* 26: 631-649.

Engel, T. R. 2000. *Seed dispersal and forest regeneration in a tropical lowland biocoenosis (Shimba Hills, Kenya)*. Logos, Berlin.

FGU-Kronberg. 1979. Gegenwärtiger Status der Comoé- und Tai-Nationalparks sowie des Azagny-Reservats und Vorschläge zu deren Erhaltung und Entwicklung zur Förderung des Tourismus. Technical Report. Deutsche Gesellschaft für Technische Zusammenarbeit GmbH, Eschborn.

Fischer, F., Groß, M. & Kunz, B. 2000. Primates of the Comoé National Park, Ivory Coast. *African Primates* 4: 10-15.

Fischer, F., Groß, M. & Linsenmair, K. E. 2002. Updated list of the larger mammals of the Comoé National Park, Ivory Coast. *Mammalia* 66: 83-92.

Fox, G. A. 1993. Failure-time analysis: emergence, flowering, survivorship, and other waiting times. Pp. 253-290 In Scheiner, S. M. & Gurevitch, J. (eds.). *Design and analysis of ecological experiments*. Chapman & Hall, New York.

Garber, P. A. 1986. The ecology of seed dispersal in two species of callitrichid primates (*Saguinus mystax* and *Saguinus fuscicollis*). *American Journal of Primatology* 10: 155-170.

Gautier-Hion, A. 1984. La dissemination des graines par les Cercopithecides forestiers africains. *La Terre et la Vie* 39: 159-165.

Groves, C. P. 2001. *Primate taxonomy*. Smithsonian Institution Press, Washington.

Hladik, M. C. 1981. Diet and the evolution of feeding strategies among forest primates. Pp. 215-254 In Harding, R. S. O. & Teleki, G. (eds.). *Omnivorous primates. Gathering and hunting in human evolution*. Columbia Press, New York.

Hovestadt, T. 1997. Fruchtmerkmale, endozoochore Samenausbreitung und ihre Bedeutung für die Zusammensetzung der Pflanzengemeinschaft. Untersuchungen im Wald-Savannenmosaik des

Comoé Nationalparks, Elfenbeinküste. PhD thesis. University of Würzburg, Germany.

Hovestadt, T., Yao, P. & Linsenmair, K. E. 1999. Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoé National Park, Ivory Coast). *Plant Ecology* 144: 1-25.

Howe, H. F. & Miriti, M. N. 2000. No question: seed dispersal matters. *Trends in Ecology & Evolution* 15: 434-436.

Idani, G. 1986. Seed dispersal by pygmy chimpanzees *Pan paniscus*. A preliminary report. *Primates* 27: 441-448.

Jordano, P. 2000. Fruits and frugivory. Pp. 125-165 In Fenner, M. (ed.). *Seeds. The ecology of regeneration in plant communities*. CABI, Wallingford.

Julliot, C. 1996. Seed dispersal by red howler monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. *International Journal of Primatology* 17: 239-258.

Kaplin, B. A. & Moermond, T. C. 1998. Variation in seed handling by two species of forest monkeys in Rwanda. *American Journal of Primatology* 45: 83-101.

Kaplin, B. A., Munyaligoga, V. & Moermond, T. C. 1998. The influence of temporal changes in fruit availability on diet composition and seed handling in blue monkeys (*Cercopithecus mitis doggetti*). *Biotropica* 30: 56-71.

Knogge, C. & Heymann, E. W. 2003. Seed dispersal by sympatric tamarins, *Saguinus mystax* and *Saguinus fuscicollis*: diversity and characteristics of plant species. *Folia Primatologica* 74: 33-47.

Kunz, B. K. & Linsenmair, K. E. 2007. Changes in baboon feeding behavior: maturity dependent fruit and seed size selection within a food plant species. *International Journal of Primatology* 28: 819-835.

Kunz, B. K. & Linsenmair, K. E. 2008. The disregarded West: diet and behavioural ecology of olive baboons in the Ivory Coast. *Folia Primatologica* 79: 31-51.

Lambert, J. E. 2002. Exploring the link between animal frugivory and plant strategies: the case of primate fruit processing and post-dispersal seed fate. Pp. 365-380 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation*. CABI, Wallingford.

Lambert, J. E. & Garber, P. A. 1998. Evolutionary and ecological implications of primate seed dispersal. *American Journal of Primatology* 45: 9-28.

Lauginie, F. 1995. Problèmes liés a la conservation de la grande faune en Afrique. L'exemple des grans mammifères du Parc National de la Comoé. PhD thesis. University of Orleans, France.

Lieberman, D., Hall, J. B., Swaine, M. D. & Lieberman, M. 1979. Seed dispersal by baboons in the Shai Hills, Ghana. *Ecology* 60: 65-75.

Lieberman, D., Lieberman, M. & Martin, C. 1987. Notes on seeds in elephant dung from Bia National Park Ghana. *Journal of Tropical Ecology* 19: 365-369.

Link, A. & Di-Fiore, A. 2006. Seed dispersal by spider monkeys and its importance in the maintenance of Neotropical rain-forest diversity. *Journal of Tropical Ecology* 22: 235-246.

McConkey, K. R. 2007. Influence of gibbon ranging patterns on seed dispersal distance and deposition site in a Bornean forest. *Journal of Tropical Ecology* 23: 269-275.

Mess, A. & Krell, F. T. 1999. Preliminary list of rodents and shrews living in the Comoé National Park, Ivory Coast (Mammalia: Rodentia, Insectivora: Soricidae). *Stuttgarter Beiträge zur Naturkunde Serie A* 586: 1-11.

Nuñez-Iturri, G. & Howe, H. F. 2007. Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rain forest in western Amazonia. *Biotropica* 39: 348-354.

Oliveira, A. C. M. & Ferrari, S. F. 2000. Seed dispersal by black-handed tamarins, *Saguinus midas niger* (Callithrichinae, Primates): implications for the regeneration of degraded forest habitats in eastern Amazonia. *Ecology* 16: 709-716.

Otani, T. 2003. Seed dispersal and predation of fleshy-fruited plants by Japanese macaques in the cool temperate zone of northern Japan. *Mammal Study* 28: 153-156.

Otani, T. & Shibata, E. 2000. Seed dispersal and predation by Yakushima macaques, *Macaca fuscata yakui*, in a warm temperate forest of Yakushima Island, southern Japan. *Ecological Research* 15: 133-144.

Pacheco, L. F. & Simonetti, J. A. 2000. Genetic structure of a mimosoid tree deprived of its seed dispersers, the spider monkey. *Conservation Biology* 14: 1766-1775.

Peres, C. A. 1991. Seed predation of *Cariniana micrantha* (Lecythidaceae) by brown capuchin monkeys in central Amazonia. *Biotropica* 23: 262-270.

Peres, C. A. & van Roosmalen, M. 2002. Primate frugivory in two species-rich Neotropical forests: implications for the demography of large-seeded plants in overhunted areas. Pp. 407-421 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation*. CABI, Wallingford.

Poilecot, P. 1991. *Un écosystème de savane soudanienne: le Parc National de la Comoé (Côte d'Ivoire)*. UNESCO, Paris.

Porembski, S. 1991. Beiträge zur Pflanzenwelt des Comoé-Nationalparks (Elfenbeinküste). *Natur und Museum* 121: 61-82.

Porembski, S. 2001. Phytodiversity and structure of the Comoé river gallery forest (NE Ivory Coast). Pp. 1-10 In Gottsberger, G. & Liede, S. (eds.). *Life forms and dynamics in tropical forests*. Dissertationes Botanicae. Borntraeger, Berlin.

Poulsen, J. R., Clark, C. J. & Smith, T. B. 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *Journal of Tropical Ecology* 17: 787-808.

Refisch, J. 1995. *Samenverbreitung durch Paviane im Parc National de la Comoé, Elfenbeinküste*. Diploma thesis. University of Bayreuth, Germany.

Rheindt, F. E., Grafe, T. U. & Linsenmair, K. E. 2002. New bird records in Comoé National Park, Ivory Coast. *Malimbus* 24: 38-40.

Rhine, J. R., Norton, G. W., Roertgen, J. W. & Klein, H. D. 1980. The brief survival of free-ranging baboon infants (*Papio cynocephalus*) after separation from their mothers. *International Journal of Primatology* 1: 401-409.

Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223-225.

Rowe, N. 1996. *The pictorial guide to the living primates*. Pogonias Press, New York.

Rowell, T. E. & Mitchel, B. J. 1991. Comparison of seed dispersal by guenons in Kenya and capuchins in Panama. *Journal of Tropical Ecology* 7: 269-274.

Salewski, V. 2001. The birds of Comoé National Park, Ivory Coast. *Malimbus* 22: 55-76.

Salewski, V. & Göken, F. 2001. Black-and-white mannikin *Lonchura bicolor*, new for Comoé National Park, Ivory Coast. *Malimbus* 23: 56.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108: 15-29.

Stiles, E. W. 2000. Animals as seed dispersers. Pp. 111-124 In Fenner, M. (ed.). *Seeds: the ecology of regeneration in plant communities*. CABI, Wallingford.

Tischler, W. 1993. *Einführung in die Ökologie*. Fischer, Stuttgart.

Tutin, C. E. G., Williamson, M. E. & Fernandez, M. 1991. A case study of a plant-animal relationship: *Cola lizae* and lowland gorillas in the Lopé Reserve, Gabon. *Journal of Tropical Ecology* 7: 181-199.

UNEP. 2007. Global environment outlook (GEO-4). Technical Report. http://www.unep.org/geo/geo4/media/

Warren, Y. 2003. Olive baboons (*Papio cynocephalus anubis*): behaviour, ecology and human conflict in Gashaka Gumti National Park, Nigeria. PhD thesis. University of Surrey Roehampton, UK.

Wehncke, E. V., Hubbell, S. P., Foster, R. B. & Dalling, J. W. 2003. Seed dispersal patterns produced by white-faced monkeys: implications for the dispersal limitation of Neotropical tree species. *Journal of Ecology* 91: 677-685.

White, F. 1983. *The vegetation of Africa*. UNESCO, Paris.

Wolfheim, J. H. 1983. *Primates of the world. Distribution, abundance, and conservation*. University of Washington Press, Seattle.

Wrangham, R. W., Chapman, C. A. & Chapman, L. J. 1994. Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology* 10: 355-368.

Yagihashi, T., Hayashida, M. & Miyamota, T. 1998. Effects of bird ingestion on seed germination of *Sorbus commixta*. *Oecologia* 114: 201-212.

Appendix 1 Dispersal events of identified seed species in faecal samples of the olive baboon in the Comoé National Park.

Seed size classes: s = (small) mean maximum diameter ≤ 5 mm, m = (medium) > 5 - ≤ 20 mm, l = (large) > 20 mm. Seed size taken from seeds extracted from baboon faeces, otherwise from fresh seeds or data taken from Hovestadt (1997). N = 396 faecal samples. Fs_n= total number of faecal samples (fs) containing a given species; DE_n = total number of dispersal events (≥ 1 ripe intact seed in a faecal sample) for a given species across all samples; DE_r = monthly ratio of dispersal events in a given species; Mean monthly DE_r = all DE_r of the species were added and divided by the number of months of the year in which the seeds of the species appeared in faecal samples.

Food plant species	Baboons feed on	Seed size	DE_n	DE_n/ fs_n	Months of year in fs	Mean monthly DE_r
Anacardiaceae						
Lannea acida	fruit	m	4	1.00	2	0.05
Lannea barteri	fruit	m	1	1.00	1	0.03
Lannea welwitschii	fruit	m	7	0.88	3	0.06
Annonaceae						
Annona senegalensis	fruit	m	2	1.00	2	0.03
Uvaria chamae	fruit	m	18	1.00	3	0.33
Apocynaceae						
Saba senegalensis	fruit	m	34	0.97	5	0.16
Bignoniaceae						
Kigelia africana	fruit	m	1	1.00	1	0.03
Buxaceae						
Buxus acutata	fruit	m	0	0.00	1	0.00
Chrysobalanaceae						
Parinari curatellifolia	?	l	2	0.50	4	0.01
Combretaceae						
Anogeissus leiocarpa	fruit	m	1	1.00	1	0.04
Combretum sp.	fruit	m	0	0.00	1	0.00
Dichapetalaceae						
Tapura fischeri	fruit	s	6	0.75	3	0.09
Ebenaceae						
Diospyros abyssinica	fruit	m	1	1.00	1	0.02
Diospyros mespiliformis	fruit	m	37	0.80	9	0.15
Euphorbiaceae						
Bridelia ferruginea	fruit	m	3	1.00	1	0.09
Drypetes floribunda	fruit	m	38	1.00	4	0.19
Drypetes gilgiana	fruit	m	1	1.00	1	0.03
Mallotus oppositifolius	fruit	s	4	1.00	3	0.04
Phyllanthus sp.	fruit	s	3	1.00	2	0.04
Ricinodendron heudelotii	fruit	m	1	1.00	1	0.03
Uapaca togoensis	fruit	m	2	0.67	3	0.02
Fabaceae						
Afzelia africana	aril/seed	l	0	0.00	1	0.00
Cynometra megalophylla	fruit/seed	l	2	1.00	1	0.04
Dialium guineense	fruit	m	70	0.97	9	0.22
Dichrostachys cinerea	fruit	s	2	1.00	1	0.04
Erythrophleum suaveolens	seed	m	11	0.79	3	0.08
Leucaena leucocephala	fruit	m	1	1.00	1	0.04

Appendix 1 (continued)

Food plant species	Baboons feed on	Seed size	DE_n	DE_n/fs_n	Months of year in fs	Mean monthly DE_r
Parkia biglobosa	fruit/seed	m	15	0.71	3	0.12
Piliostigma thonningii	seed	m	4	1.00	2	0.08
Tamarindus indica	fruit	m	52	0.91	6	0.30
Tetrapleura tetraptera	fruit	m	0	0.00	5	0.00
Moraceae						
Antiaris toxicaria	fruit	m	1	1.00	1	0.04
Ficus spp.	fruit	s	85	0.93	12	0.24
Milicia excelsa	fruit	s	6	1.00	3	0.06
Olacaceae						
Ximenia americana	fruit	m	3	0.60	3	0.02
Rubiaceae						
Cremaspora triflora	fruit	m	2	1.00	2	0.03
Crossopteryx febrifuga	fruit	m	1	1.00	1	0.02
Gardenia cf. *aqualla*	fruit	s	2	1.00	2	0.03
Keetia venosa	fruit	m	4	0.80	3	0.04
Keetia sp.	fruit	m	13	0.87	5	0.10
Oxyanthus racemosus	fruit	s	16	0.94	3	0.15
Psychotria vogeliana	fruit	s	4	0.80	2	0.06
Sarcocephalus latifolius	fruit	s	30	0.86	7	0.18
Sarcocephalus cf. *xanthoxylon*	fruit	s	79	1.00	5	0.55
Tricalysia sp.	fruit	m	2	1.00	2	0.02
Sapotaceae						
Manilkara obovata	fruit	m	5	1.00	2	0.05
Mimusops kummel	fruit	m	1	1.00	1	0.03
Pouteria alnifolia	fruit	m	3	1.00	2	0.04
Solanaceae						
Solanum incanum	fruit	m	4	0.80	4	0.03
Sterculiaceae						
Cola cordifolia	aril/seed	l	1	1.00	1	0.02
Strychnaceae						
Strychnos sp.	fruit	m	6	1.00	2	0.07
Tiliaceae						
Christiana africana	fruit	s	1	1.00	1	0.03
Grewia cf. *bicolor*	fruit	m	1	0.50	1	0.05
Ulmaceae						
Celtis sp.	fruit	m	1	1.00	1	0.02
Verbenaceae						
Vitex doniana	fruit	m	11	0.92	3	0.14
Vitaceae						
Cissus populnea	fruit	m	8	1.00	3	0.06
Cissus sp.	fruit	m	1	1.00	1	0.03
Zingiberaceae						
Aframomum exscapum	fruit	s	14	1.00	2	0.14

Chapter 5

Changes in Baboon Feeding Behaviour: Maturity-Dependent Fruit and Seed Size Selection within a Food Plant Species

with K. E. Linsenmair

Published in *International Journal of Primatology* (2007) 28: 819-835
The original article is available at http://www.springerlink.com/fpr, DOI 10.1007/s10764-007-9160-6.

Abstract Despite considerable inter- and intra-individual variation in fruit and seed size in many plant species, the relevance of these traits for primate fruit choice within a food plant species and its implications for tree regeneration have received little attention. We studied feeding behaviour and selectivity of olive baboons (*Papio anubis*, Cercopithecidae) in the African locust bean (*Parkia biglobosa,* Mimosaceae), using direct observations of habituated groups and indirect evidence from leftovers of pods after feeding events. Olive baboons acted as both pre-dispersal seed predators and seed dispersers for *Parkia biglobosa*. They fed on and destroyed unripe seeds, and swallowed intact ripe seeds when consuming mature fruit pulp. Predation rate was high, and only 10% of the seeds were dispersed. Predation and dispersal of seeds was linked to seed number and size. Digestible unripe seeds accounted for 10% of the unripe fruit mass, while indigestible ripe seeds made up 28% of the mature fruit mass. With these constraints, olive baboons increased food gain per fruit by selecting unripe pods containing a high number of large and heavy seeds. Consequently, only pods with fewer and smaller seeds remained for maturation. Thereafter, baboons fed on mature pods containing the smallest seeds, and exploited pods with more seeds to a greater extent than those with fewer seeds. Thus, fruits with small seeds and an intermediate seed number contributed the most to dispersal by baboons.

5. 1 INTRODUCTION

Fruit and seeds constitute much of the diet of many primate species (e.g. Chapman & Onderdonk 1998; Norconk *et al.* 1998). Several studies have shown that the feeding behaviour of fruit- and seed-eating primates is not completely random, and can be influenced by different plant and fruit traits. Relevant plant traits include spatial and temporal properties of entire fruit crops, such as plant density, distribution, fruit abundance, and crop sizes of individual plants (e.g. Howe 1980; Janson *et al.* 1986; Russo 2003). Chemical fruit and seed traits take into account the level of macronutrients, amount of fibre, nature and quantity of minerals and secondary compounds (Glander 1982, and references therein; Wrangham & Waterman 1983; Janson *et al.* 1986; Sourd & Gautier-Hion 1986; Barton & Whiten 1994; Altmann 1998; Dominy *et al.* 2001; Norconk & Conklin-Brittain 2004). Important physical fruit traits include colour, fruit type, fruit and seed size, and seed-pulp-ratio (Gautier-Hion *et al.* 1985; Julliot 1996; Dominy *et al.* 2001; Parrado-Rosselli *et al.* 2002; Knogge & Heymann 2003; Stevenson *et al.* 2005).

Studies of fruit choice frequently address the relevance of these traits on the community level, and emphasize primate preferences for plant species or fruit types (e.g. Gautier-Hion *et al.* 1985; Happel 1986; Julliot 1996; Parrado-Rosselli *et al.* 2002; Knogge & Heymann 2003). However, there are few studies that concentrate on a primate's choice of food among plants of the same species as well as within individual plants. Still, fruit and seed size (alternatively seed mass) often vary considerably within and among individuals of the same plant species (e.g. Howe & vande Kerckhove 1981; Ouédraogo 1995; see also Michaels *et al.* 1988). When this variation is heritable, it provides a mechanism for natural selection (Howe & Richter 1982; Mack 1993; Herrera 2002; Alcantara & Rey 2003), though some authors argue that environmental factors cause intraspecific variation (Leishman *et al.* 2000; Hulme & Benkman 2002). In any case, fruit size and seed mass, which are typically correlated (e.g. Mack 1993; Leishman *et al.* 2000), are important traits for plant fitness, because they affect several steps between the end of the reproductive cycle of an adult plant and the establishment of its offspring. A seed-predating primate that favours seeds of a given size not only reduces the quantity of seeds available for dispersal, but it can also affect the seed shadow of its food plant qualitatively if the disperser also prefers seeds of a certain size (Dirzo & Domínguez 1986). Size selection by primate seed dispersers may also influence post dispersal seed fate. Secondary seed dispersal by dung beetles, ants and rodents as well as post-dispersal predation by rodents and ants, can depend on seed size (Jansen *et al.* 2002; Rey *et al.* 2002; Andresen & Levey 2004). Furthermore, seedling survival often varies with seed size, because seedlings emerging from large seeds generally have better competitive abilities and increased survival rates under harsh external conditions than seedlings from small seeds (reviewed in Leishman *et* *al.* 2000). Primates often harvest considerable amounts of a tree's fruit crop (Peres 1991; Chapman & Chapman 1996; Tutin *et al.* 1996; Voysey *et al.* 1999). By choosing among and within fruiting individuals, they may thus be able to shift the overall fruit production toward a distinct subset of dispersed seeds (see also Jordano 1995). Nonetheless, studies on primate seed size selection within a food plant species are rare (but see Garber & Kitron 1997; Russo 2003; Stevenson *et al.* 2005; see also Howe & vande Kerckhove 1981). Data indicate that New World primates select smaller and larger seeds of some plant species, respectively, than available, when feeding on pulp or seed-arils (Howe & vande Kerckhove 1981; Garber & Kitron 1997; Stevenson *et al.* 2005). Smaller seeds reduce indigestible load (Corlett & Lucas 1990). Large seeds with high pulp or aril reward may be ingested to minimize handling time during feeding (Garber & Kitron 1997). This may be especially important for New World primates which lack cheek pouches. Alternatively, large seeds may be swallowed to expel gut parasites (Garber & Kitron 1997; but see Stevenson *et al.* 2005). However, seeds of other plants are ingested irrespective of available size within the plant species (Russo 2003; Stevenson *et al.* 2005).

Because research on primate seed size selection within a plant species has focused on the Neotropics, there is a lack of data on seed size selectivity in Old World monkeys. Furthermore, when primates feed on seeds instead of pulp or seed arils, they may select for different sizes. Baboons (*Papio* spp., Cercopithecidae) are known as eclectic omnivores (e.g. Altmann 1998). We investigated the effects of plant use, feeding behaviour, and fruit and seed size selection by olive baboons (*Papio anubis*) on the African locust bean (*Parkia biglobosa*, Mimosaceae). In the study area in Comoé National Park (CNP), northern Ivory Coast, olive baboons are the most abundant primates (Fischer *et al.* 2000). Compared to most other baboon populations (as listed in Hill & Dunbar 2002) baboons in CNP are highly frugivorous, spending on average 54.4% of their annual feeding time on fruits and seeds (Kunz, unpubl. data). In CNP, baboons feed on unripe seeds as well as on ripe fruit pulp of *Parkia biglobosa*. The tree is also one of the most important wild food plants for humans in West and Central Africa (e.g. Mertz *et al.* 2001; Adeyeye *et al.* 2002). However, little is known of the quantitative and qualitative dimensions of fruit choice and seed dispersal by its nonhuman consumers, and on the consequences of seed predation for regeneration of the tree (Hall *et al.* 1997). To understand the importance of *Parkia biglobosa* for olive baboons, we first describe density and fruiting pattern of the tree in the study area. We then assess the following questions: (1) To what extent do olive baboons harvest fruits from individual trees? (2) What proportion of seeds is dispersed and what proportion of seeds is predated? (3) Are olive baboons selective in fruit choice according to seed number and seed size? (4) Are there differences in selection criteria for unripe and ripe fruits? We discuss potential reasons for differential feeding strategies, and consider the implications of size selection by baboons during seed predation and dispersal for tree regeneration.

5. 2 METHODS

5.2.1 STUDY AREA

B. Kunz conducted field research in the Comoé National Park (CNP) (08°30-09°36' N, 003°07'-004°25' W), northern Ivory Coast, during 24 months between November, 1997 and July, 2000, including three fruiting periods of *Parkia biglobosa.* The park covers approximately 11,500 km^2 at an altitude of about 250-300 m a.s.l., and comprises different vegetation zones from Guinea-Savanna in the South to Sudan-Savanna in the North (FGU-Kronberg 1979). Data presented are from an area of about 145 km^2 in the southwest. The vegetation there consists of a mosaic of different savanna formations (~91%), forest islands (7%), and gallery forest (2%) along the two main rivers (FGU-Kronberg 1979), and is described in detail elsewhere (Poilecot 1991; Porembski 1991).

Between January, 1994 and December, 1999 mean annual temperature was 26.3 °C, and mean annual rainfall was 1,053 mm - with a pronounced dry season from November to March.

Despite its conservation status, local people frequently enter park areas adjacent to villages for firewood and honey collection. Fruits are not intensively collected inside CNP. Poaching has become increasingly damaging in recent years (Hovestadt *et al.* 1999), diminishing the population of *Loxodonta africana* Blumenbach (African elephant) and other big mammals (Poilecot 1991; Fischer & Linsenmair 2001). Although olive baboons, like other primates, are hunted for their meat and the fetish market, poaching did not notably affect their abundance in the study area between 1977 and 2000 (Poilecot 1991, Kunz, unpubl. data).

5.2.2 FOCAL SPECIES

5.2.2.1 Olive Baboon (*Papio anubis* LESSON 1827)

The phylogeny and taxonomy of the genus *Papio* (Cercopithecidae) still is disputed. We follow Groves (2001) and consider *P. anubis* as a valid species. Its range extends from Mali to Ethiopia, Kenya, and northwestern Tanzania (Groves 2001), and overlaps largely with the distribution of *Parkia biglobosa*.

In CNP, individuals live in relatively small groups with one or more males, several females and their offspring, averaging 15.3 +/- 11.1 members (range 4-44) (Kunz, unpubl. data).

5.2.2.2 African Locust Bean (*Parkia biglobosa* (Jacq.) R. Br. ex G. Don., Mimosaceae)

The African locust bean is a large savanna tree of 10-20 m in height (Hall *et al.* 1997). The fruit is a pod, 12-35 cm long and 1.5-2.5 cm wide. The thin exocarp is soft and green when unripe, becoming brown and slightly leathery during maturation. Each pod contains 5-20 seeds in a row. Seeds are about 1.5 cm large (Hall *et al.* 1997). Unripe seeds are soft and green, but ripe seeds have a hard, black testa. Ripe seeds represent a significant source of protein (~30-40% dry mass), fatty acids, and minerals (Campbell-Platt 1980; Cook *et al.* 2000; Lockett *et al.* 2000) (no data for unripe seeds available). The yellow ripe fruit pulp is soft and dry and provides a high amount of carbohydrates (~70-85% dry mass) and vitamins (Nordeide *et al.* 1996; Cook *et al.* 2000; Lockett *et al.* 2000). The fruiting period in CNP starts in March, and pods mature at the end of March/beginning of April. Pods do not dehisce upon maturity and remain on the trees for several months if not harvested (Kunz, unpubl. data).

Parkia biglobosa is distributed from The Gambia to Sudan and Uganda, and also occurs on the islands Sao Tomé and Principe (Hall *et al.* 1997). The species is declining in some areas as a result of general degradation of woody species in the savanna and over-harvesting of fruits (Gijsbers *et al.* 1994; Lykke 2000).

Other species in CNP that both predate on and disperse seeds of *Parkia biglobosa* elsewhere are *Loxodonta africana* (African elephant) and *Pan troglodytes verus* Schwarz (western chimpanzee) (Hovestadt 1997; Matsumoto-Oda & Hayashi 1999). We suppose that several other primate species are also potential consumers of *Parkia biglobosa*. In CNP, they include *Chlorocebus aethiops* Linnaeus (vervet monkey), *Cercocebus torquatus lunulatus* Temmink (white-crowned mangabey), *Erythrocebus patas* Schreber (patas monkey), and, if trees are growing at a forest edge, also the more forest-restricted primate species *Cercopithecus petaurista* Schreber (lesser spot-nosed monkey) and *Cercopithecus lowei* Thomas (Lowe's monkey). Birds may also potentially consume seeds or fruit pulp (Hopkins 1983). However, we believe olive baboons are the most important consumers of *Parkia biglobosa* in the study area. *Loxodonta africana*, which mostly destroys ripe seeds through mastication (Engel T., pers. comm.), has become extremely rare and was not observed during our research. *Pan t. verus* seems to be restricted to the national park's area west of the river Comoé, whereas our study was undertaken east of the river. Compared to other monkeys, the olive baboon is the biggest and most common species of monkey in the national park (Fischer *et al.* 2000, Kunz, unpubl. data). We spent 24 additional hours observing two fruiting trees when olive baboons were not present (Kunz, unpubl. data), and observed only one starling species (*Lamprotornis* sp.) and one unidentified bird species occasionally visiting the trees for feeding. The birds were pecking on the pulp and did not swallow seeds. We once observed a single individual of *Cercocebus t. lunulatus* feeding on *Parkia biglobosa* together with baboons. Camera trapping (192 hours) and experiments we conducted on fruit and seed consumption under three fruiting trees yielded no indication of terrestrial consumers (Kunz, unpubl. data).

5.2.3 FRUIT PRODUCTION, AND FRUIT HARVEST BY OLIVE BABOONS

5.2.3.1 Fruiting Pattern, Crop Size, and Tree Density of *Parkia biglobosa*

In order to assess the relative importance of *Parkia biglobosa* for olive baboons, we collected basic data on tree abundance and phenology. At the beginning of the study, we randomly selected five focal trees within the home range of two habituated baboon groups for phenological monitoring. We indexed fruit abundance per tree once per month on a quasi-logarithmic scale from 1 (1-10 fruits) to 10 (5,001-10,000 fruits) (following Levey 1988). Likewise, we monitored the fruiting pattern of four additional trees since March 1999.

To estimate tree density of *Parkia biglobosa*, we carefully conducted transect counts in 2000 along two small dirt roads of 17,400 m length in total. Strip width was 20 m on both sides of the road, resulting in a sampled area of 69.6 ha. Other density estimation methods like the point-quarter method and t-square sampling are inappropriate or extremely time consuming for rare species (e.g. James & Shugart 1970; Krebs 1989).

We observed flowering and/or fruiting in 1998 and 1999 only in *Parkia biglobosa* trees of 8 m height or more, and thus considered trees of at least this height in the transects in 2000. Because of the readily identifiable tree shape, we are confident in having detected all adult individuals along the transects.

5.2.3.2 Direct Observations on Plant Use and Fruit Selection by Olive Baboons

We applied two different approaches to illustrate feeding activity and selectivity of olive baboons: (a) direct observation of the two habituated baboon groups, and (b) gathering of indirect evidence from leftovers of pods after feeding events.

We observed GP-group, comprising of 9-13 individuals, between January 1998 and June 2000 (140 days; 20 months). Behavioural observations of 1S-group (up to 44 individuals) were conducted between January 1999 and July 2000 (70 day; 14 months).
During the fruiting peak of *Parkia biglobosa* from March to April, we followed GP-group

at 58 days and 1S-group on 22 days, resulting in 135 hours of scan-sampling (Altmann 1974). Due to habitat sight restrictions, spreading, and frequent subgrouping of the large 1S-group, we could simultaneously observe only individuals within a subgroup. At the beginning of the study in 1998, when only GP-group was habituated and observed, we carried out scans at 20-minute time intervals. Since January 1999, however, we had to split observation time between GP- and 1S-group. We thus modified the schedule in a way that increased the number of scan-sampling points per hour and group but still allowed us to carry out other tasks in between scans. These tasks (e.g. mapping, tagging and measuring of food plants, collection of food items and faeces) were part of a more general study on seed dispersal and seed predation by olive baboons in CNP and required different time intervals. Since January 1999, we therefore conducted scans at 10-minute intervals. In addition, at two randomized times during each hour, we made four consecutive scans at 2-minute intervals, so that we obtained 14 scan-samples per complete sampling hour in 1999 and 2000. As the duration of most bouts of baboon activity is less than two minutes, data collected at 2-minute intervals are probably not auto-correlated (Stacey 1986; Byrne *et al.* 1993; Altmann 1998). Overall, we accomplished a total of 2,711 behavioural scans, of which 1,143 were conducted during the fruiting seasons of *Parkia biglobosa*. During scan sampling, we recorded the behaviour, including feeding, of individuals older than one year. From these feeding records, we calculated the proportion baboons spent feeding on *Parkia biglobosa* over the entire study period (January, 1998 to July, 2000) from the monthly means. We averaged the proportion of time spent feeding on *Parkia biglobosa* during the months of fruiting across fruiting seasons.

5.2.3.3 Predation and Dispersal Rates per Tree

Olive baboons generally harvest and feed on unripe and ripe pods of *Parkia biglobosa* directly in the tree, and drop the more or less exploited fruits beneath the crown. Thus, leftovers can be collected for analysis after feeding sessions. The term 'leftover' in this paper refers to pods of *Parkia biglobosa*, that are harvested and dropped by baboons, irrespective of fruit maturity.

We checked seven feeding trees located within the home ranges of the two habituated groups once a week from the beginning of the fruiting season in March 2000, until we found the first leftovers of fruits. Subsequently, we checked trees every second to third day until May, or until completely harvested. To determine the harvesting rate for each tree, we counted all unripe and ripe leftovers as well as fruits remaining on the tree at the end of the observation in May. When pods were torn into pieces, we considered only the piece attached to the peduncle. To calculate the total number of seeds produced by each tree, we multiplied the overall median number of seeds in unripe and ripe pods (see below) with the number of unripe and ripe fruits, respectively, of each tree.

Olive baboons did not always remove all seeds from a pod. Unripe seeds collected at the time of consumption were not able to germinate, neither directly nor after maturation in the harvested pods (Kunz, unpubl. data). Thus, we equated the predation rate for each tree to the number of unripe fruits harvested per tree. To estimate the number and proportion of dispersed seeds (dispersal rate), we took into account only the seeds removed from ripe pods. Therefore, we used the median degree of ripe fruit exploitation - as described below in the section "Fruit Exploitation of Ripe and Unripe Fruits" - for the calculation.

5.2.4 FRUIT AND SEED CHARACTERISTICS

5.2.4.1 Fruit Exploitation of Ripe and Unripe Fruits

Baboons exploited pods of *Parkia biglobosa* to different degrees (0-100%). In 1998 and 1999, we gathered fresh leftovers of a total of 20 feeding visits from under seven trees. We calculated the degree of baboon fruit exploitation per pod by comparing the number of seeds removed to the original number of seeds. In most cases, imprints in the fruit husk indicated the number of removed seeds. Some fruits were squashed from baboon handling or had weak imprints so that we were unable to determine the original seed number precisely. We included these pods in the analysis only if all (100% exploitation) or no seeds (0% exploitation) were missing. Torn fruits (8.5%), however, were discarded for this analysis, because neither their degree of exploitation nor their original number of seeds was identifiable.

To investigate whether olive baboons are selective in fruit choice according to the number of seeds per pod and the state of maturation, we compared:

1. the number of seeds in unripe and ripe pods harvested by baboons
2. the degree of fruit exploitation (= number of seeds removed) of unripe and ripe pods
3. the number of seeds per pod in poorly exploited (0-25%) pods to the number of seeds in highly exploited (≥ 75%) pods, both for unripe and ripe fruits.

5.2.4.2 Seed Characteristics of Exploited and Unexploited Fruits

We used different approaches to examine the role of seed size and seed mass for fruit selection in unripe and ripe pods due to differences in seed treatment by olive baboons. Baboons masticated and destroyed unripe seeds completely. Therefore, it was impossible to measure unripe ingested seeds directly. Hence, we applied an indirect method to compare seed sizes of unripe exploited (≥ 1 seed removed) and unexploited (= no seed removed) pods. In 1999, we collected all leftovers from one feeding session each from the ground beneath the crown of two feeding trees. For each tree, we separated unexploited and exploited fruits into two piles. For randomized sampling, we mixed each pile and laid out pods in a row. We chose exploited pods according to a list of random numbers, and measured the seed remaining nearest to the middle of each of these pods. For every exploited unripe fruit, we took an unexploited unripe fruit from the same feeding session accordingly, and measured the seed at the corresponding position. Seed imprints in the fruit husk were not suitable for exact measurements instead of unripe seeds, because fruit margins of exploited pods were often broken. We took possible water loss of soft unripe seeds during measuring into account by comparing dry instead of fresh seed mass. Seeds were dried at 60°C until two successive weighing revealed less than 0.004 g deviation.

Of ripe pods, baboons usually swallowed the entire hard, ripe seeds embedded in the fruit pulp, and most of the seeds could thus be found intact in their faeces. Only 4.3% of seeds extracted from faeces were destroyed (Kunz, unpubl. data). We measured and weighed only completely undamaged seeds. Fresh mass of ripe ingested seeds was taken only of seeds that had been extracted from fresh faeces. As baboons often fed on several *Parkia biglobosa* trees each day, source trees of dispersed seeds could not be allocated without a molecular tool. Thus, we compared ingested ripe seeds to seeds from fresh unexploited ripe pods, collected randomly from four feeding trees within the home ranges of the baboon groups. Because olive baboons start feeding in the middle section of the elongated pod, leaving seeds on both ends when fruits are not depleted completely (Kunz, pers. observ.), we randomly extracted one seed per collected fruit from the middle section of about 50% of the pod length. We cleaned all seeds, ripe and unripe, from pulp or faeces before measuring them.

5.2.4.3 Seed-Pulp-Ratio

To estimate the median seed-pulp-ratio in unripe and ripe pods, we collected fresh fruits, stored them in plastic bags, and weighed each fruit directly after returning to the field station. From the median fresh mass of unripe pods, we subtracted the total median mass of unripe seeds per pod (calculated from the median number of unripe seeds per pod multiplied by the median seed mass of unripe seeds, see above). Likewise, we estimated seed-pulp ratio in ripe pods, considering the median seed number in ripe fruits and the median mass of mature seeds. We were unable to separate the thin fruit husk from the pulp in unripe fruits, and thus included it in the pulp mass of unripe and ripe fruits.

5.2.5 DATA ANALYSIS

We give the median (x_{md}), 1st (q_1) and 3rd (q_3) percentiles when data are not normally distributed. All tests were run with the SPSS for Windows statistical package (version 11.5) or the SsS package (Rubisoft Software, version 1.0e). Confidence limits were set at 95%. All tests were two-tailed. We adjusted the level of significance for multiple testing using the sequential Bonferroni technique (Rice 1989).

5. 3 RESULTS

5.3.1 FRUIT PRODUCTION, AND FRUIT HARVEST BY OLIVE BABOONS

5.3.1.1 Fruiting Pattern, Crop Size, and Tree Density of *Parkia biglobosa*

The fruiting pattern across individual trees was irregular. While three trees fruited in two or three consecutive years, others produced no fruit for at least one (n = 4) or two years (n = 2). Moreover, tree crop size can be very variable across years (Figure 1). Only one focal tree monitored since the beginning of the study (Tree 2, see Figure 1) reliably produced high fruit quantities (1,000-2,000 pods) each year. Tree density was 0.29 adult *Parkia biglobosa* per hectare.

5.3.1.2 Direct Observations on Plant Use and Fruit Treatment by Olive Baboons

Parkia biglobosa fruits made up an important part of baboon diet. During the fruiting seasons in March and April, 1998-2000, we obtained 1,262 feeding records from 36 baboon individuals. The mean seasonal proportion of feeding on *Parkia biglobosa* was 22.06% ± 13.74%. Over the entire observation period (January, 1998 to July, 2000), *Parkia biglobosa* accounted for 5.1% of all feeding records (N = 3,589).

The baboons visited all known fruiting trees within their home ranges in a given fruiting season. Groups returned about every day to every third day to the same feeding trees. Trees not visited for feeding bore no fruits in any of the study year.

Baboons fed on both ripe and unripe pods. They did not consume unripe pods until fruit length and seed number seemed to be fully developed (see also below). Fruit husk at the time of first consumption was completely green, fruit pulp white, and seeds were still green and soft, but well developed in size. Baboons fed directly on the unripe seeds, spitting out fruit husk and the bitter pulp. In contrast, they peeled mature pods and swallowed the sweet and soft pulp, including the seeds.

Baboons have cheek pouches in which they can store fruits for later processing. However, we observed no intensive cheek pouch use when baboons fed on ripe *Parkia biglobosa* fruits. Likewise, we found no piles of spat out *Parkia biglobosa* seeds. Baboons stayed for extended feeding sessions (up to 56 minutes; mean = 26 min, *n* = 14 baboon individuals, 1-4 recorded feeding visits/baboon) in *Parkia biglobosa* trees and swallowed bites directly.

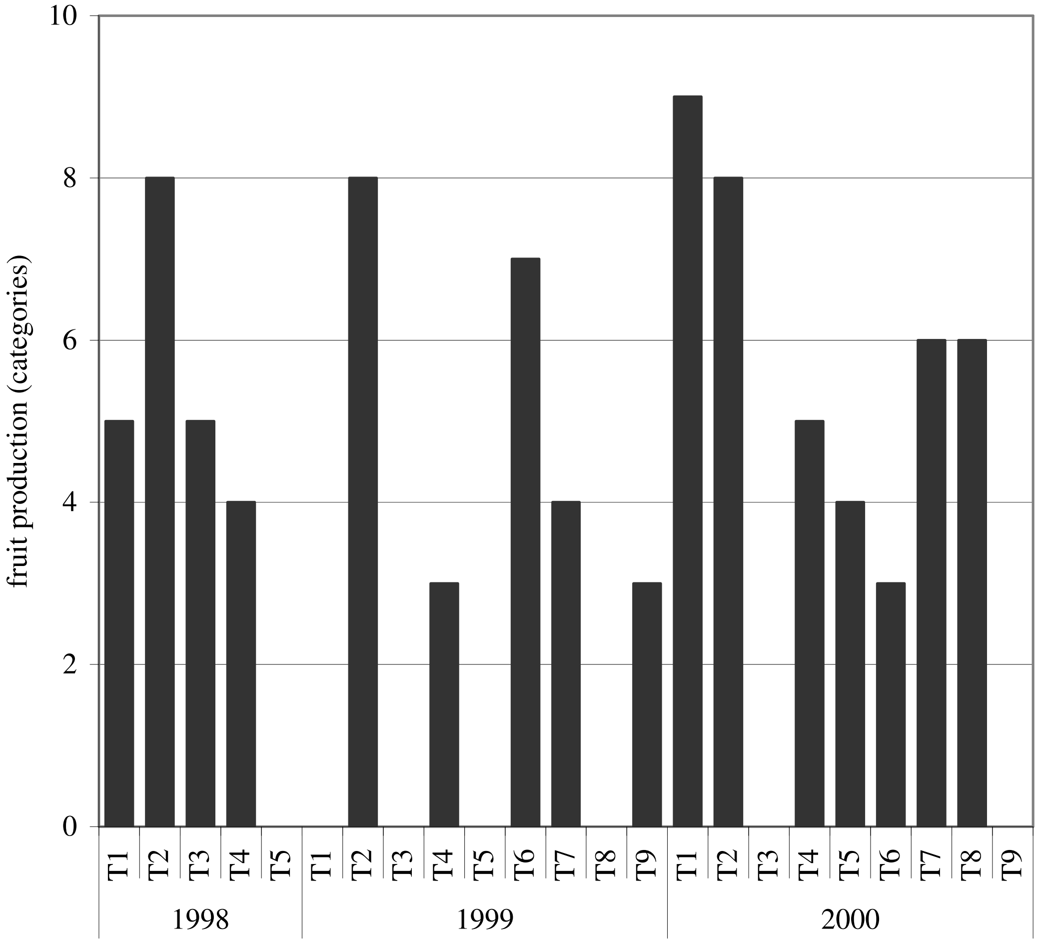


Figure 1 Fruit production of *Parkia biglobosa* focal trees

Trees T1-T5 monitored during the fruiting seasons 1998 to 2000, trees T6-T9 monitored from 1999-2000. Fruit production was estimated in categories: 1 = 1-10; 2 = 11-25; 3 = 26-50; 4 = 51-100; 5 = 101-200; 6 = 201-500; 7 = 501-1,000; 8 = 1,001-2,000; 9 = 2,001-5,000; 10 = 5,001-10,000 fruits per tree.

5.3.1.3 Predation and Dispersal Rates per Tree

The median crop size was 1,398 pods per feeding tree (q_1 = 539.5, q_3 = 2,636.5, range = 171-3,266, N = 7) (Table 1). All trees had well developed unripe but no mature fruits at the beginning of the observation. Olive baboons depleted the crop of all but two trees completely (Figure 2). Of these two, only 0.3% and 3.9%, respectively, of the pods were not harvested. Predation rate of unripe pods per tree was x_{md} = 82.6% (q_1 = 69.1%, q_3 = 89.6%, range = 16.4-90.9%), and did not depend on crop size (geometric mean regression, t = 2.242, df = 5, $p > 0.05$). Despite the high predation rate, baboons consumed some ripe fruits of every tree. The percentage of unripe and ripe fruits harvested varied considerably across trees (Figure 2).

Total seed production per tree can be estimated from the number of unripe and ripe leftovers collected and the number of ripe fruits remaining on the tree, multiplied by the median seed number per unripe (x_{md} = 16) and ripe fruit (x_{md} = 13) (see below in "Fruit and Seed Characteristics"). Because baboons depleted ripe pods only to a degree of 72.7%, the number of dispersed seeds was lower than the total number of seeds in harvested ripe pods (Table 1). Thus, the median value of seeds dispersed from a tree's original seed crop was 10.4% (q_1 = 6.3%, q_3 = 18.2%).

Table 1 Estimation of seeds dispersed per *Parkia biglobosa* feeding tree
Total number of fruits and number of ripe fruits harvested was counted for each of the seven feeding trees in 2000. Total number of seeds was calculated according to the percentage of unripe and ripe fruits collected per tree as shown in Figure 2 and the median number of seeds calculated for unripe (x_{md} = 16) and ripe fruits (x_{md} = 13) (see results "Fruit Exploitation of Ripe and Unripe Seeds"). Because ripe fruits are generally depleted to only 72.7%, the number of seeds dispersed is smaller than the total number of seeds in harvested ripe fruits.

Tree n^o.	Total n^o. of fruits	Total n^o. of seeds	N^o. of ripe fruits harvested	N^o. of ripe seeds harvested	N^o. of seeds dispersed	% of seeds dispersed
1	3,266	51,365	297	3,861	2,807	5.5
4	3,002	46,469	511	6,643	4,830	10.4
7	2,271	30,642	1,898	24,674	17,938	58.5
2	1,398	21,939	143	1,859	1,352	6.2
3	615	9,177	197	2,561	1,862	20.3
6	464	7,064	120	1,560	1,134	16.1
5	171	2,682	18	234	170	6.3

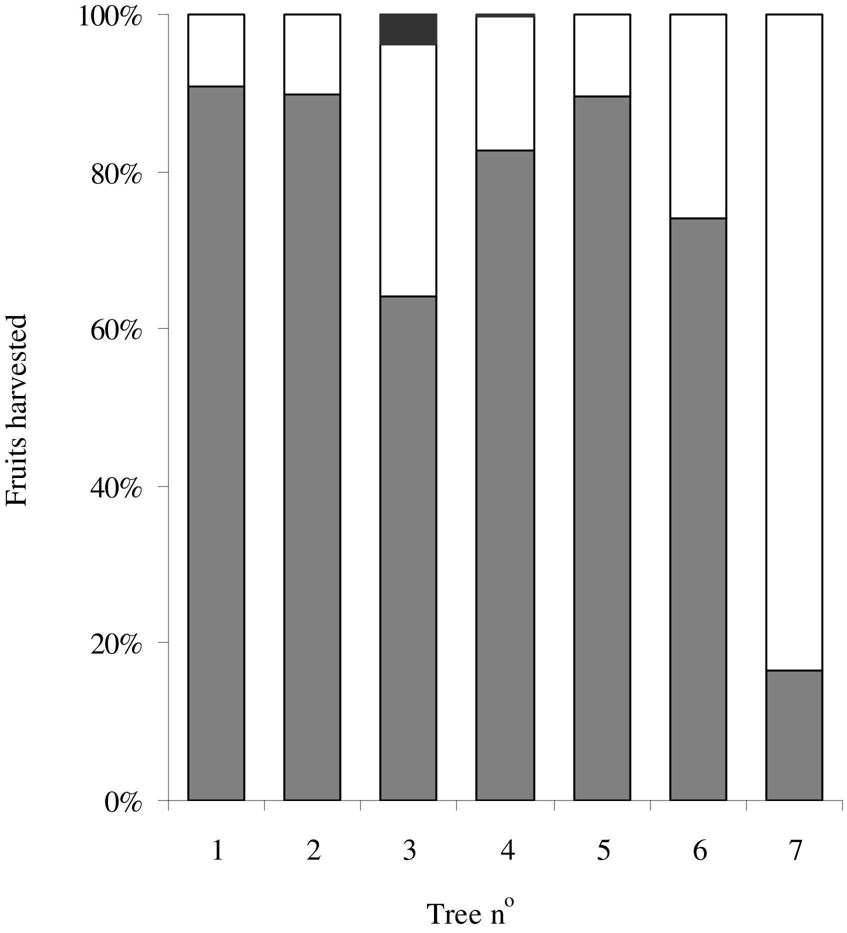


Figure 2 Proportion of fruits harvested by baboons from seven *Parkia biglobosa* feeding trees between March and May, 2000
Gray bar section: harvested unripe fruits; white: harvested ripe fruits; black: fruits remaining on the tree at the end of the observation period. Note: trees do not correspond to Figure 1, except tree n°. 1 (= T1) & tree n°. 2 (= T2).

5.3.2 FRUIT AND SEED CHARACTERISTICS

5.3.2.1 Fruit Exploitation of Ripe and Unripe Fruits

We were able to determine the degree to which baboons exploited single unripe and ripe pods (0%-100%) in 80.68% of all leftovers collected (N = 1,837 pods). While 0% or 100% exploited pods were easily identifiable, the exact number of seeds or seed imprints in a pod sometimes was not, due to destruction caused by baboons during fruit handling. Thus, we could quantify the original number of seeds per fruit for 68.21% of the pods. Unripe pods contained significantly more seeds (x_{md} = 16, q_1 = 13, q_3 = 18, n = 1,006 fruits) than ripe ones (x_{md} = 13, q_1 = 10, q_3 = 1, n = 247 fruits) (Mann-Whitney U = 84,997.50, $p < 0.001$). The significance remains when only ripe and unripe pods collected from the same trees in the same year are compared ($U = 38{,}526.50$, $p < 0.001$, $n = 654$). However, the degree to which baboons removed seeds from unripe and ripe pods did not differ significantly ($\chi^2 = 0.222$, $df = 1$, $p > 0.05$, $n = 1{,}482$). They extracted a median proportion of 71.4% of the seeds from unripe pods ($q_1 = 26.3\%$, $q_3 = 91.7\%$, $n = 1{,}142$) and 72.7% from ripe pods ($q_1 = 28.5\%$, $q_3 = 100\%$, $n = 340$).

The baboons were selective in food choice, feeding on unripe and ripe pods that contained the most seeds. Unripe pods exploited to ≥ 75% had significantly more seeds per fruit ($x_{md} = 17$, $q_1 = 15$, $q_3 = 19$, $n = 392$) than unripe pods exploited only by 0-25% ($x_{md} = 14$, $q_1 = 11$, $q_3 = 17$, $n = 276$) (Mann-Whitney $U = 34{,}821.50$, $p < 0.001$). The same was true for ripe pods (≥ 75%-exploited: $x_{md} = 14$, $q_1 = 11.5$, $q_3 = 17$, $n = 75$; 0-25%-exploited: $x_{md} = 11$, $q_1 = 8$, $q_3 = 14$, $n = 77$) ($U = 1{,}752.50$, $p < 0.001$).

5.3.2.2 Seed Characteristics of Exploited and Unexploited Fruits

Seed size and mass also played a role in fruit selection by baboons, both within unripe and ripe pods. Unripe seeds in exploited unripe pods (of which ≥ 1 seed was removed by baboons) were significantly larger (Mann-Whitney $U_{length} = 715.5$, $U_{width} = 781.5$), thicker (t-test $T = 5.79$, $df = 97.20$) and heavier (dry mass) ($U = 2{,}041.5$) than those in unexploited unripe pods ($p < 0.001$) ($N = 68$ seeds of exploited and unexploited fruits each, except for dry mass: $N = 54$ seeds each).

In contrast, ripe seeds in faeces were significantly smaller and thinner than those extracted directly from ripe unexploited fruits ($N_{faeces} = 86$, $N_{fresh} = 47$, Mann-Whitney $U_{length} = 341$, $U_{width} = 502.\ 5$, $U_{gauge} = 1{,}080.5$; $p < 0.001$). The result holds true if only ripe seeds collected in the same month and year are considered ($n_{faeces} = 75$, $n_{fresh} = 47$, $U_{length} = 244$, $U_{width} = 363$, $U_{gauge} = 929$; $p < 0.01$).

5.3.2.3 Seed-Pulp-Ratio

Unripe fruits had a median fresh mass of 22.6 g ($q_1 = 18.5$ g, $q_3 = 30.5$ g, $N = 31$). Ripe fruits were significantly lighter, with a median mass of 14.0 g ($q_1 = 12.6$ g, $q_3 = 23$ g, $N = 23$) (Mann-Whitney $U = 199.5$, $p < 0.01$). Taking the median number of seeds per fruit (see results "Fruit Exploitation of Ripe and Unripe Seeds") and the median fresh mass of seeds (unripe = 0.144 g, $N = 153$; ripe = 0.300 g, $N = 98$) and fruits into account, seeds in unripe pods make up 10.2%, and pulp and the thin fruit husk 89.8% of the total fruit mass. In ripe pods, total seed mass accounts for 27.9% and pulp and husk for 72.1% (Figure 3).

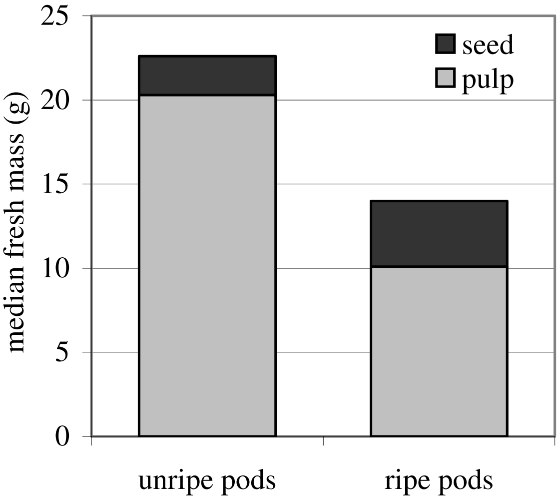


Figure 3 Median seed-pulp ratio in fresh unripe and ripe pods of *Parkia biglobosa*
'Pulp' refers to the pulp plus the thin exocarp. See methods "Fruit and Seed Characteristics" for calculation.

5. 4 DISCUSSION

As group-living animals with a relatively high body mass and food intake, olive baboons were effective harvesters and regular visitors (*sensu* Schupp 1993) of *Parkia biglobosa* in CNP. *Parkia biglobosa* was a core food species in the diet of the baboons, accounting for 5% of all feeding records during the entire study period. During the months of fruiting, feeding on *Parkia biglobosa* fruits and seeds accounted for more than 20% of baboons' feeding records. However, given the low tree density (compare to Nikièma 1993; Ouédraogo 1995) and the irregular individual fruiting pattern, we do not consider *Parkia biglobosa* to be a keystone resource (*sensu* Peres 2000) for baboons in CNP. Moreover, seed and fruit availability of *Parkia biglobosa* falls within the fruiting period of several other baboon core food species when fruit do not seem to be limited (Kunz, unpubl. data). This is further supported by the fact that baboons feed on *Parkia biglobosa* fruits and seeds in a wasteful manner, because most pods are not depleted completely.

Fruits of the Neotropical *Parkia panurensis* are an important food source for tamarins (*Saguinus* spp.) (Feldmann 2000). But whereas tamarins are dispersers of *P. panurensis* Knogge & Heymann 2003), olive baboons act as both seed dispersers and seed predators for *Parkia biglobosa*, by consuming ripe fruits as well as unripe seeds. The viability of dispersed ripe seeds was verified in germination experiments (Kunz, unpubl. data). Food selection in primates can be positively affected by protein content of food items (e.g. Ganzhorn 1988; Barton & Whiten 1994). Fruit pulp often is low in protein. Unlike in other areas (e.g. Strum 1981; Rhine *et al.* 1986), olive baboons in CNP did not hunt larger animal prey (Kunz, unpubl. data), but presumably fulfilled part of their protein demands by eating protein-rich, unripe *Parkia* seeds (see also Rowell 1966). Protein-rich legume seeds are part of the diet of many primate species (Whiten *et al.* 1991; Gathua 2000; Barnes 2001; Norconk & Conklin-Brittain 2004). For example, *Papio papio* (Guinea baboon) and *Pan troglodytes* also consume unripe seeds of *Parkia spp.* (Matsumoto-Oda & Hayashi 1999; Culot 2003). Ripe seeds of *Parkia biglobosa* are harder to break and are attached very tightly to the fruit pulp. Less than 5% of ripe *Parkia biglobosa* seeds in faeces were heavily to completely destroyed, ascribing the nutritional value of ripe fruits to the pulp (particularly carbohydrates and vitamins, e.g. Nordeide *et al.* 1996; Lockett *et al.* 2000). Ripe *Parkia biglobosa* seeds contain a variety of secondary compounds and anti-nutritional factors such as tannins, trypsin inhibitor and phytic acid (e.g. Addy *et al.* 1995; see also Hopkins 1983), reducing the efficiency of the nitrogen uptake (e.g. Whiten *et al.* 1991). No datum on the concentration of these metabolites in unripe *Parkia biglobosa* seeds is available. However, an increase in the concentration of secondary compounds during maturation would explain why baboons confined seed eating of *Parkia biglobosa* to unripe seeds. Likewise, seed-eating by *Chiropotes satanas* (bearded sakis) shifted to consumption of mesocarp in a plant species, when handling time and condensed tannin levels increased with seed maturity, even though seeds had the highest macronutrient content when ripe (Norconk *et al.* 1998). Tannin distribution was also negatively related to food selection by *Chlorocebus aethiops* (Wrangham & Waterman 1981). Accordingly, the fruit husk of ripe pods of *Parkia biglobosa* has a very high tannin concentration (Culot 2003) and was likewise discarded by *Papio anubis* (this study) and *P. papio* (Culot 2003). As reviewed by Dominy *et al.* (2001) catarrhine primates are able to perceive tannins by taste.

Even though feeding trees showed a wide range in crop size, olive baboons removed at least 95% of the total crop per tree. Comparable proportions were documented for *Gorilla gorilla* (lowland gorillas) feeding on *Diospyros zenkeri* (Ebenaceae) (up to 100%) (Tutin *et al.* 1996) and *Cebus apella* (brown capuchins) harvesting *Cariniana micrantha* (Lecythidaceae) (99.6%) (Peres 1991), but less intensive crop removal has also been found (Chapman & Chapman 1996; Voysey *et al.* 1999). Pre-dispersal fruit loss accounted for more than 80%, which is not unusual for primate seed predators and their food plants (e.g. Peres 1991; Tutin *et al.* 1996; Barnes 2001). In CNP, the low abundance of (fruiting) *Parkia biglobosa* trees might have prevented saturation of seed-predating baboons. Nevertheless, each of the seven feeding trees for which we recorded harvesting rates had some seeds dispersed, though there was a large difference in the proportion of dispersed seeds among trees. A staggered onset of fruiting cannot account for the variation, because all trees had well-developed unripe and no ripe fruits at the beginning of the observations. We found no linear relationship between crop size and predation rate, which may be due to small sample size. Tree 7 had a relatively large crop, but also the lowest predation rate and most seeds dispersed, both in absolute and relative numbers. This might have been a consequence of the attraction of olive baboons to its nearest neighbour (Tree 1), which had the largest crop size and the highest predation rate. Compared to tamarins, which dispersed on average 68% of all seeds of *Parkia panurensis* per crop (Feldmann 2000), olive baboons were relatively ineffective dispersers in terms of quantity for *Parkia biglobosa*, dispersing only 10% of the original seed crop per tree. Higher dispersal rates by primates have also been reported for other tree species (Voysey *et al.* 1999; Gathua 2000), but were attributed to more than one primate species.

Which *Parkia biglobosa* seeds baboons are likely to predate on and disperse seems to be largely determined by the number and size of seeds. As in other plant species, these parameters are highly variable within *Parkia biglobosa* trees (e.g. Michaels *et al.* 1988; Ouédraogo 1995), offering the possibility for selection by frugivores. Fruit size and seed mass are two key traits in the plant-frugivore interaction (Jordano 1995). Some bird species select preferred fruit sizes within a plant species (e.g. McPherson 1988; Stanley & Lill 2002), and may thereby reduce seed load (Stanley & Lill 2002). Post-dispersal seed predation by rodents can increase (e.g. Brewer 2001) or decrease (e.g. Hulme & Benkman 2002) with seed size in a given plant species. Seed size selectivity has also been documented for New World primates. Stevenson *et al.* (2005) found evidence for seed size selection by woolly monkeys (*Lagothrix lagothricha*) in five out of eleven plant species, with a tendency to swallow relatively smaller seeds from the three large-seeded plant species, but not from the medium- and small-seeded ones. Spider monkeys (*Ateles paniscus*) ingest smaller seeds than available in *Virola surinamensis* (Howe & vande Kerckhove 1981), but not in *V. calophylla* (Russo 2003). By contrast, tamarins (*Sagiunus mystax* and *S. geoffroyi*) ingest the larger seeds from *Inga* sp., which offer high pulp reward (Garber & Kitron 1997).

We demonstrated that olive baboons can be highly selective in fruit and seed size choice within a plant species. Furthermore, they are able to select seeds in unripe and ripe *Parkia biglobosa* fruits differentially. In unripe pods, of which baboons consumed only the unripe seeds but not the fruit pulp, the seeds accounted for only 10% of the median unripe fruit mass. In ripe pods, of which baboons fed on the pulp, the indigestible ripe seeds made up 28% of the median ripe fruit mass. Within these constraints, olive baboons increased their food gain per fruit by selecting unripe pods containing a high number of large and heavy seeds. Consequently, only pods with fewer and smaller seeds remained for maturation. Indigestible seed load (here: ripe seeds) decreases further intake of pulp (Sorensen 1984; Corlett & Lucas 1990). Baboons selected ripe pods of *Parkia biglobosa* containing the smallest seeds, and exploited the pods with more seeds to a greater extent than those with fewer seeds. Consequently, fruits with an intermediate seed number and small seeds contributed most to seed dispersal by baboons. While large seeds often have advantages over small seeds for plant establishment in a variable environment (Moles & Westoby 2004), further research is needed to assess the consequences of seed size selection by olive baboons for plant fitness, comparing secondary seed dispersal, germination success, and seedling growth between small and large seeds of *Parkia biglobosa*.

5. 5 ACKNOWLEDGEMENTS

We kindly thank S.M. Berghoff, E.W. Heymann, N. Reintjes, and F. Walravens for their helpful comments on the manuscript. Research permission for CNP was kindly granted by the "Ministère de l'Agriculture et des Ressources Animales" and the "Ministère de l'Enseignement Supérieure et de la Recherche Scientifique", Abidjan. This study was funded by PhD scholarships from the German Academic Exchange Service (DAAD) and the University of Wuerzburg (HSP III). The research camp in CNP was constructed with generous funds from the Volkswagen-Foundation.

5. 6 REFERENCES

Addy, E. O. H., Salami, L. I., Igboeli, L. C. & Remawa, H. S. 1995. Effect of processing on nutrient composition and anti-nutritive substances of African locust bean (*Parkia filicoidea*) and baobab seed (*Adansonia digitata*). *Plant Foods for Human Nutrition* 48: 113-117.

Adeyeye, E. I., Ipinmoroti, K. O. & Oguntokun, M. O. 2002. Chemical composition and functional properties of the African locust bean (*Parkia biglobosa*) seeds. *Pakistan Journal of Scientific and Industrial Research* 45: 29-33.

Alcantara, J. M. & Rey, P. J. 2003. Conflicting selection pressures on seed size: Evolutionary ecology of fruit size in a bird-dispersed tree, *Olea europaea*. *Journal of Evolutionary Biology* 16: 1168-1176.

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour.* 49: 227-267.

Altmann, S. A. 1998. *Foraging for survival: yearling baboons in Africa.* University of Chicago Press, Chicago.

Andresen, E. & Levey, D. 2004. Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. *Oecologia* 139: 45-54.

Barnes, M. E. 2001. Seed predation, germination and seedling establishment of *Acacia erioloba* in northern Botswana. *Journal of Arid Environments* 49: 541-554.

Barton, R. A. & Whiten, A. 1994. Reducing complex diets to simple rules: food selection by olive baboons. *Behavioural Ecology and Sociobiology* 35: 283-293.

Brewer, S. W. 2001. Predation and dispersal of large and small seeds of a tropical palm. *Oikos* 92: 245-255.

Byrne, R. W., Whiten, A., Henzi, S. P. & McCulloch, F. M. 1993. Nutritional constraints on mountain baboons (*Papio ursinus*): implications for baboon socioecology. *Behavioural Ecology* *and Sociobiology* 33: 233-246.

Campbell-Platt, G. 1980. African locust bean (*Parkia* species) and its West African fermented food product, Dawadawa. *Ecology of Food and Nutrition* 9: 123-132.

Chapman, C. A. & Chapman, L. J. 1996. Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. *Journal of Tropical Ecology* 12: 491-504.

Chapman, C. A. & Onderdonk, D. A. 1998. Forests without primates: Primate/plant codependency. *American Journal of Primatology* 45: 127-141.

Cook, J. A., vander Jagt, D. V., Pastuszyn, A., Mounkaila, G., Glew, R. S., Millson, M. & Glew, R. H. 2000. Nutrient and chemical composition of 13 wild plant foods of Niger. *Journal of Food Composition and Analysis* 13: 83-92.

Corlett, R. T. & Lucas, P. W. 1990. Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaque *Macaca fascicularis*. *Oecologia* 82: 166-171.

Culot, L. 2003. Contribution à l'étude de l'écologie alimentaire du babouin de Guinée, *Papio cynocephalus papio*, dans le Parc National du Haute Niger (Republique de Guinée). MSc thesis. University of Liège, Belgium.

Dirzo, R. & Domínguez, C. A. 1986. Seed shadows, seed predation and the advantages of dispersal. Pp. 237-249 In Estrada, A. & Fleming, T. H. (eds.). *Frugivores and seed dispersal*. Dr. W. Junk Publishers, Dordrecht.

Dominy, N. J., Lucas, P. W., Osorio, D. & Yamashita, N. 2001. The sensory ecology of primate food perception. *Evolutionary Anthropology* 10: 171-186.

Feldmann, M. 2000. Samenökologie von Parkia im Amazonas-Regenwald. Samenausbreitung durch Krallenaffen (Callitrichidae), sekundäre Samenausbreitung von Samen und Samenprädation. Diploma thesis. University of Göttingen, Germany.

FGU-Kronberg. 1979. Gegenwärtiger Status der Comoé- und Tai-Nationalparks sowie des Azagny-Reservats und Vorschläge zu deren Erhaltung und Entwicklung zur Förderung des Tourismus. Technical Report. Deutsche Gesellschaft für Technische Zusammenarbeit GmbH, Eschborn.

Fischer, F., Groß, M. & Kunz, B. 2000. Primates of the Comoé National Park, Ivory Coast. *African Primates.* 4: 10-15.

Fischer, F. & Linsenmair, K. E. 2001. Decreases in ungulate population densities. Examples from the Comoé National Park, Ivory Coast. *Biological Conservation* 101: 131-135.

Ganzhorn, J. U. 1988. Food partitioning among Malagasy primates. *Oecologia* 75: 436-450.

Garber, P. A. & Kitron, U. 1997. Seed swallowing in tamarins: evidence of a curative function or enhanced foraging efficiency? *International Journal of Primatology* 18: 523-538.

Gathua, M. 2000. The effects of primates and squirrels on seed survival of a canopy tree, *Afzelia quanzensis*, in Arabuko-Sokoke Forest, Kenya. *Biotropica* 32: 127-132.

Gautier-Hion, A., Duplantier, J. M., Quris, R., Feer, F., Sourd, C., Decoux, J. P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C. & Thiollay, J. M. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65: 324-337.

Gijsbers, H. J. M., Kessler, J. J. & Knevel, M. K. 1994. Dynamics and natural regeneration of woody species in farmed parklands in the Sahel region (Province of Passore, Burkina Faso). *Forest Ecology and Management* 64: 1-12.

Glander, K. E. 1982. The impact of plant secondary compounds on primate feeding behavior. *Yearbook of Physical Anthropology* 25: 1-18.

Groves, C. P. 2001. *Primate Taxonomy.* Smithsonian Institution Press, Washington.

Hall, J. B., Tomlinson, H. F., Oni, P. I., Buchy, M. & Aebischer, D. P. 1997. *Parkia biglobosa*: *a monograph*. University of Wales, Bangor.

Happel, R. E. 1986. The role of fruit characters determining preferences by West African monkeys. *American Journal of Primatology* 10: 406.

Herrera, C. M. 2002. Seed dispersal by vertebrates. Pp. 185-208 In Herrera, C. M. & Pellmyr, O. (eds.). *Plant-animal interactions. An evolutionary approach*. Blackwell, Oxford.

Hill, R. A. & Dunbar, R. I. M. 2002. Climatic determinants of diet and foraging behaviour in baboons. *Evolutionary Ecology* 16: 579-593.

Hopkins, H. C. 1983. The taxonomy, reproductive biology and economic potential of *Parkia* (Leguminosae: Mimosoideae) in Africa and Madagascar. *Botanical Journal of the Linnean Society* 87: 137-167.

Hovestadt, T. 1997. Fruchtmerkmale, endozoochore Samenausbreitung und ihre Bedeutung für die Zusammensetzung der Pflanzengemeinschaft. Untersuchungen im Wald-Savannenmosaik des Comoé Nationalparks, Elfenbeinküste. PhD thesis. University of Würzburg, Germany.

Hovestadt, T., Yao, P. & Linsenmair, K. E. 1999. Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoé National Park, Ivory Coast). *Plant Ecology* 144: 1-25.

Howe, H. F. 1980. Monkey dispersal and waste of a Neotropical fruit *Tetragastris panamensis*. *Ecology* 61: 944-959.

Howe, H. F. & Richter, W. M. 1982. Effects of seed size on seedling size in *Virola surinamensis*: a within and between tree analysis. *Oecologia* 53: 347-351.

Howe, H. F. & vande Kerckhove, G. A. 1981. Removal of wild nutmeg *Virola surinamensis* crops by birds. *Ecology* 62: 1093-1106.

Hulme, P. E. & Benkman, C. W. 2002. Granivory. Pp. 132-154 In Herrera, C. M. & Pellmyr, O. (eds.). *Plant-animal interactions. An evolutionary approach.* Blackwell, Oxford.

James, F. C. & Shugart, H. H. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24: 727-736.

Jansen, P. A., Bartholomeus, M., Bongers, F., Elzinga, J. A., den Ouden, J. & van Wien, S. E. 2002. The role of seed size in dispersal by a scatter-hoarding rodent. Pp. 209-225 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation.* CABI, Wallingford.

Janson, C. H., Stiles, E. W. & White, D. W. 1986. Selection on plant fruit traits by brown capuchin monkeys: a multivariate approach. Pp. 83-92 In Estrada, A. & Fleming, T. H. (eds.). *Frugivores and seed dispersal.* Dr. W. Junk Publishers, Dordrecht.

Jordano, P. 1995. Frugivore-mediated selection on fruit and seed size: birds and St. Lucie's cherry, *Prunus mahaleb*. *Ecology* 76: 2627-2639.

Julliot, C. 1996. Fruit choice by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest. *American Journal of Primatology* 40: 261-282.

Knogge, C. & Heymann, E. W. 2003. Seed dispersal by sympatric tamarins, *Saguinus mystax* and *Saguinus fuscicollis*: diversity and characteristics of plant species. *Folia Primatologica* 74: 33-47.

Krebs, C. J. 1989. *Ecological Methodology*. Harper Collins, New York.

Leishman, M. R., Wright, I. J., Moles, A. T. & Westoby, M. 2000. The evolutionary ecology of seed size. Pp. 31-56 In Fenner, M. (ed.). *Seeds. The ecology of regeneration in plant communities.* CABI, Wallingford.

Levey, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology* 69: 1076-1089.

Lockett, C. T., Calvert, C. C. & Grivetti, L. E. 2000. Energy and micronutrient composition of dietary and medicinal wild plants consumed during drought. Study of rural Fulani, Northeastern Nigeria. *International Journal of Food Science and Nutrition* 51: 195-208.

Lykke, A. M. 2000. Local perceptions of vegetation change and priorities for conservation of woody-savanna vegetation in Senegal. *Journal of Environmental Management* 59: 107-120.

Mack, A. L. 1993. The sizes of vertebrate dispersed fruits: a Neotropical-Paleotropical comparison. *The American Naturalist* 142: 840-856.

Matsumoto-Oda, A. & Hayashi, Y. 1999. Nutritional aspects of fruit choice by chimpanzees. *Folia Primatologica* 70: 154-162.

McPherson, J. M. 1988. Preference of cedar waxwings in the laboratory for fruit species, colour and size: a comparison with field observations. *Animal Behaviour* 36: 961-969.

Mertz, O., Lykke, A. M. & Reenberg, A. 2001. Importance and seasonality of vegetable consumption and marketing in Burkina Faso. *Economic Botany* 55: 276-289.

Michaels, H. J., Benner, B., Hartgerink, A. P., Lee, T. D., Rice, S., Willson, M. F. & Betin, R. I. 1988. Seed size variation: magnitude distribution and ecological correlates. *Evolutionary Ecology* 2: 157-166.

Moles, A. T. & Westoby, M. 2004. Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* 92: 372-383.

Nikièma, A. 1993. Regeneration of *Parkia biglobosa* (Jacq.) R. Br. ex G. Don. in an agroforestry system. A pilot study in Burkina Faso. MSc thesis. Wageningen Agricultural University, Netherlands.

Norconk, M. A. & Conklin-Brittain, N. L. 2004. Variation on frugivory: the diet of Venezuelan white-faced sakis. *International Journal of Primatology* 25: 1-26.

Norconk, M. A., Grafton, B. W. & Conklin-Brittain, N. L. 1998. Seed dispersal by Neotropical seed predators. *American Journal of Primatology* 45: 103-126.

Nordeide, M. B., Hatloy, A., Folling, M., Lied, E. & Oshaug, A. 1996. Nutrient composition and nutritional importance of green leaves and wild food resources in an agricultural district, Koutiala, in southern Mali. *International Journal of Food Science and Nutrition* 57: 455-468.

Ouédraogo, A. S. 1995. *Parkia biglobosa* (Leguminosae) en Afrique de l'Ouest: biosystématique et amélioration. PhD thesis. Wageningen Agricultural University, Netherlands.

Parrado-Rosselli, A., Cavelier, J. & van Dulmen, A. 2002. Effect of fruit size on primary seed dispersal of five canopy tree species of the Colombian Amazon. *Selbyana* 23: 245-257.

Peres, C. A. 2000. Identifying keystone plant resources in tropical forests: the case of gums from *Parkia* pods. *Journal of Tropical Ecology* 16: 287-317.

Peres, C. A. 1991. Seed predation of *Cariniana micrantha* (Lecythidaceae) by brown capuchin monkeys in central Amazonia. *Biotropica* 23: 262-270.

Poilecot, P. 1991. *Un écosystème de savane soudanienne: le Parc National de la Comoé (Côte d'Ivoire).* UNESCO, Paris.

Porembski, S. 1991. Beiträge zur Pflanzenwelt des Comoé-Nationalparks (Elfenbeinküste). *Natur und Museum* 121: 61-82.

Rey, P. J., Garrido, J. L., Alcantara, J. M., Ramirez, J. M., Aguilera, A., Garcia, L., Manzaneda, A. J. & Fernandez, R. 2002. Spatial variation in ant and rodent post-dispersal predation of vertebrate-dispersed seeds. *Functional Ecology* 16: 773-781.

Rhine, R. M., Norton, G. W., Wynn, G. M., Wynn, R. D. & Rhine, H. B. 1986. Insect and meet eating among infant and adult baboons (*Papio cynocephalus*) in Mikumi National Park, Tanzania. *American Journal of Physical Anthropology* 70: 105-118.

Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223-225.

Rowell, T. E. 1966. Forest living baboons in Uganda. *Journal of Zoology* 149: 344-364.

Russo, S. E. 2003. Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia* 136: 80-87.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108: 15-29.

Sorensen, A. E. 1984. Nutrition, energy and passage time: experiments with fruit preference in European blackbirds (*Turdus merula*). *Journal of Animal Ecology* 53: 545-557.

Sourd, C. & Gautier-Hion, A. 1986. Fruit selection by a forest guenon *Cercopithecus cephus*. *Journal of Animal Ecology* 55: 235-244.

Stacey, P. B. 1986. Group size and foraging efficiency in yellow baboons. *Behavioural Ecology and Sociobiology* 18: 175-187.

Stanley, M. C. & Lill, A. 2002. Importance of seed ingestion to an avian frugivore: an experimental approach to fruit choice based on seed load. *The Auk* 119: 175-184.

Stevenson, P. R., Pineda, M. & Samper, T. 2005. Influence of seed size on dispersal patterns of woolly monkeys (*Lagothrix lagothricha*) at Tinigua Park. *Oikos* 110: 435-440.

Strum, S. C. 1981. Processes and products of change: baboon predatory behavior at Gilgil, Kenya. Pp. 255-302 In Harding, R. S. O. & Teleki, G. (eds.). *Omnivorous primates. Gathering and hunting in human evolution.* Columbian Press, New York.

Tutin, C. E. G., Parnell, R. J. & White, F. 1996. Protecting seeds from primates: examples from *Diospyros* spp. in the Lopé Reserve, Gabon. *Journal of Tropical Ecology* 12: 371-384.

Voysey, B. C., McDonald, K. E., Rogers, M. E., Tutin, C. E. G. & Parnell, R. J. 1999. Gorillas and seed dispersal in the Lopé Reserve, Gabon. I: gorilla acquisition by trees. *Journal of Tropical Ecology* 15: 23-38.

Whiten, A., Byrne, R. W., Barton, R. A., Waterman, P. G. & Henzi, S. P. 1991. Dietary and foraging strategies of baboons. *Philosophical Transactions of the Royal Society of London Series B* 334: 187-197.

Wrangham, R. W. & Waterman, P. G. 1981. Feeding behaviour of vervet monkeys on *Acacia tortilis* and *Acacia xanthophloea* with special reference to reproductive strategies and tannin production. *Journal of Animal Ecology* 50: 715-731.

Wrangham, R. W. & Waterman, P. G. 1983. Condensed tannins in fruits eaten by chimpanzees. *Biotropica* 15: 217-222.

Chapter 6

Seed Size Selection by Olive Baboons

with K. E. Linsenmair

Published in *Primates* (2008) 49: 239-245

The original publication is available at http://www.springerlink.com, DOI 10.1007/s10329-008-0101-6.

Abstract Seed size is an important plant fitness trait that can influence several steps between fruiting and the establishment of a plant's offspring. Seed size varies considerably within many plant species, yet the relevance of the trait for intraspecific fruit choice by primates has received little attention. Primates may select certain seed sizes within a species for a number of reasons, e.g. to decrease indigestible seed load or increase pulp intake per fruit. Olive baboons (*Papio anubis*, Cercopithecidae) are known to select seed size in unripe and mature pods of *Parkia biglobosa* (Mimosaceae) differentially, so that pods with small seeds, and an intermediate seed number, contribute most to dispersal by baboons. We tested whether olive baboons likewise select for smaller ripe seeds within each of nine additional fruit species whose fruit pulp baboons commonly consume, and for larger seeds in one species in which baboons feed on the seeds. Species differed in fruit type and seed number per fruit. For five of these species, baboons dispersed seeds that were significantly smaller than seeds extracted manually from randomly collected fresh fruits. In contrast, for three species, baboons swallowed seeds that were significantly longer and/or wider than seeds from fresh fruits. In two species, sizes of ingested seeds and seeds from fresh fruits did not differ significantly. Baboons frequently spat out seeds of *Drypetes floribunda* (Euphorbiaceae) but not those of other plant species having seeds of equal size. Oral processing of *D. floribunda* seeds depended on seed size: seeds that were spat out were significantly larger and swallowed seeds smaller, than seeds from randomly collected fresh fruits. We argue that seed size selection in baboons is influenced, among other traits, by the amount of pulp rewarded per fruit relative to seed load, which is likely to vary with fruit and seed shape.

6. 1 INTRODUCTION

Frugivorous primates are important seed dispersers and pre-dispersal seed predators for many of their food plant species (e.g. Chapman & Onderdonk 1998; Norconk *et al.* 1998; Nunez-Iturri & Howe 2007), being able to harvest considerable amounts of fruit and to disperse large numbers of seeds over wide areas (Peres 1991; Wrangham *et al.* 1994; McConkey 2005; Link & Di-Fiore 2006; Kunz & Linsenmair 2007). Whether primates disperse the seeds of their food plants depends largely on the mode of oral seed processing during fruit consumption; primates may either swallow seeds, remove pulp and spit or drop the seeds, or chew the seeds. When feeding on fruit pulp or seed arils, primates tend to drop or spit seeds from large-seeded plant species at the feeding site whereas small seeds are more likely to be swallowed (Corlett & Lucas 1990; Kaplin & Moermond 1998; Dominy & Duncan 2005). Seed size varies not only across but also within many plant species (Michaels *et al.* 1988; Leishman *et al.* 2000). Primates may select fruits with certain seed sizes within a plant species to decrease indigestible seed load or increase pulp intake per fruit (Corlett & Lucas 1990; Garber & Kitron 1997; Kunz and Linsenmair 2007). This intraspecific seed size selection at the pre-dispersal stage can affect plant fitness by altering dispersal probabilities by other frugivores as well as post-dispersal seed fate and seedling survival. For example, a primate that favours fruits with seeds of a given size can affect the seed shadow of its food plant qualitatively if other dispersers also prefer fruits and seeds of a certain size (see also Dirzo & Domínguez 1986). Secondary seed dispersal by dung beetles, ants and rodents as well as post-dispersal seed predation by rodents and ants can depend on seed size. Several studies on secondary dispersal of seeds from primate dung found a negative relationship between seed size and the percentage of seeds buried by dung beetles (reviewed in Andresen & Feer 2005). Some ant species rarely remove seeds > 20 mg (Rey *et al.* 2002). The probability of escaping post-dispersal seed predation by seed-eating rodents may decrease (Brewer 2001) or increase with seed size (Jansen *et al.* 2004; Xiao *et al.* 2004). Furthermore, seedling survival often varies with seed size, since seedlings emerging from large seeds generally have better competitive abilities and increased survival rates under harsh external conditions than seedlings from small seeds (reviewed in Leishman *et al.* 2000).

Seed size selection by primates within a plant species has received little attention (Howe & vande Kerckhove 1981; Garber & Kitron 1997; Russo 2003; Stevenson *et al.* 2005; Kunz & Linsenmair 2007). Studies to date have focused on the Neotropics (but see Kunz & Linsenmair 2007), where primates lack the cheek pouches that Old World monkeys use for food stuffing. In a previous study, we have shown that olive baboons (*Papio anubis*, Cercopithecidae) are able to select different seed sizes in unripe and ripe *Parkia biglobosa* pods (Mimosaceae). Baboons predate heavily on immature seeds of *P.*

biglobosa, selecting unripe pods that contain a high number of large and heavy seeds. When consuming mature pulp and thereby swallowing embedded ripe seeds entirely, baboons select pods with the smallest seeds. Thus the seeds from fruits with an intermediate seed number and small seeds are most commonly dispersed by baboons (Kunz & Linsenmair 2007).

In this study, we investigated whether olive baboons also select particular seed sizes in other fruit species and fruit types. We compared sizes of seeds extracted from fresh baboon dung to seeds from fresh ripe fruit in ten additional plant species commonly eaten by olive baboons in Comoé National Park (CNP), north-eastern Ivory Coast. We expected that baboons disperse smaller than average seeds of the plant species whose fruit pulp they eat. Seeds of *Erythrophleum guineense* (Caesalpiniaceae), however, are predated upon by baboons; hence in this plant species baboons should select the largest seeds for feeding. Baboons frequently spit as well as swallow seeds from one of the species (*Drypetes floribunda*, Euphorbiaceae). We expected that the mode of oral processing of *D. floribunda* seeds would depend on seed size: larger seeds would be spat out and smaller seeds swallowed. We discuss the effects of other fruit traits and fruit availability upon seed handling and intraspecific seed size selection by baboons.

6. 2 METHODS

The study took place during 24 months from November 1997 to July 2000, covering each month of the year at least once. The CNP (08°30-09°36' N, 003°07'-004°25' W), comprises about 11,500 km^2 at an average altitude of 250-300 m asl (Poilecot 1991). The study area (~145 km^2) was situated in the southern park area within the 'Guinea-Congolia / Sudania regional transition zone' (following White 1983) where the vegetation consists of a mosaic of different savannah formations (~91 %), forest islands (7 %), and gallery forest (2 %) (FGU-Kronberg 1979). Mean annual precipitation during the rainy season from March/April to October is about 1,000 mm. The park harbours a rich fauna and flora, including nine recently recorded diurnal primate species (Fischer *et al.* 2000). Among them, olive baboons are the most abundant. Ten olive baboon groups, ranging in size from 4 to 44 individuals (mean 15), live within the study area (Kunz & Linsenmair 2008a).

To determine the size of seeds dispersed by baboons, we collected baboon faecal samples opportunistically throughout the entire study period. These were stored in sealed plastic bags in a dry, dark place at ambient temperature until analysed within 3 days of collection. We extracted seeds by briefly placing each sample in water and then rinsing it through sieves with decreasing mesh width (4, 2, 1 mm). We identified seed species using a reference collection established in previous years by T. Hovestadt and P. Poilecot, supplemented by seeds taken from fresh fruits of identified plants. Plant names follow the 'International Plant Names Index' (http://www.ipni.org/).

We included 10 plant species in the analyses (Table 1) from which baboons in CNP commonly eat fruits/seeds, as judged from direct feeding observations of two habituated baboon groups (Kunz & Linsenmair 2008a) and occurrence of the respective seeds in faecal samples (Kunz & Linsenmair 2008b). Analyses focused on seeds < 20 mm in length because the seeds of species with larger average seed size were either completely chewed during ingestion or seeds found in faeces were too few for statistical analyses. We measured length and maximum width of fully turgescent seeds using a sliding calliper (0.1 mm accuracy).

For comparison with the seeds dispersed by baboons, we extracted seeds from fresh fruit of the same ten plant species. Within each species, individual plant were randomly chosen among baboons' feeding plants (Kunz & Linsenmair 2008a). The fruit number collected per plant species followed availability, but we generally obtained ≥ 6 fruits from each of four to ten plant individuals per species. Most tree crops of *Lannea acida*, however, were depleted before maturity (Kunz, unpubl. data); hence we could only sample fruit from two trees.

According to our observations on the two habituated groups, the baboons generally foraged throughout the canopy of trees and scrubs. Thus, in easily accessible scrubs and small understorey trees (*Oxyanthus racemosus*, *Tapura fischeri*, *Uvaria chamae*) we collected fruits from all levels of the crown following a protocol of random numbers according to which branches and fruits were selected. In large trees, we collected fresh fruits from the ground within small quadrants, placed randomly beneath the crown. Fruit collection from the ground often took place soon after baboons had caused an increased fall of fruits and branches of various sizes while moving through the canopy during foraging.

In multi-seeded fruit like berries (e.g. *Diospyros mespiliformis*), one seed per fruit was randomly taken and measured. As regards to the elongated, multi-seeded pods of *Tamarindus indica*, olive baboons generally start feeding on the middle part of the fruit, while the ends of the pod are sometimes discarded (Kunz, pers. observ., see also Kunz & Linsenmair 2007). Consequently, we randomly extracted a seed from the middle part for measuring, discarding about 25% of fruit on each end. We mechanically cleaned the seeds from the pulp, briefly rinsed them with water and measured the seeds as described above.

We collected spat out *D. floribunda* seeds directly after feeding events from the ground around six different fruiting plants for comparison with seeds from fresh fruit and from baboon dung. Spat out seeds were free of pulp.

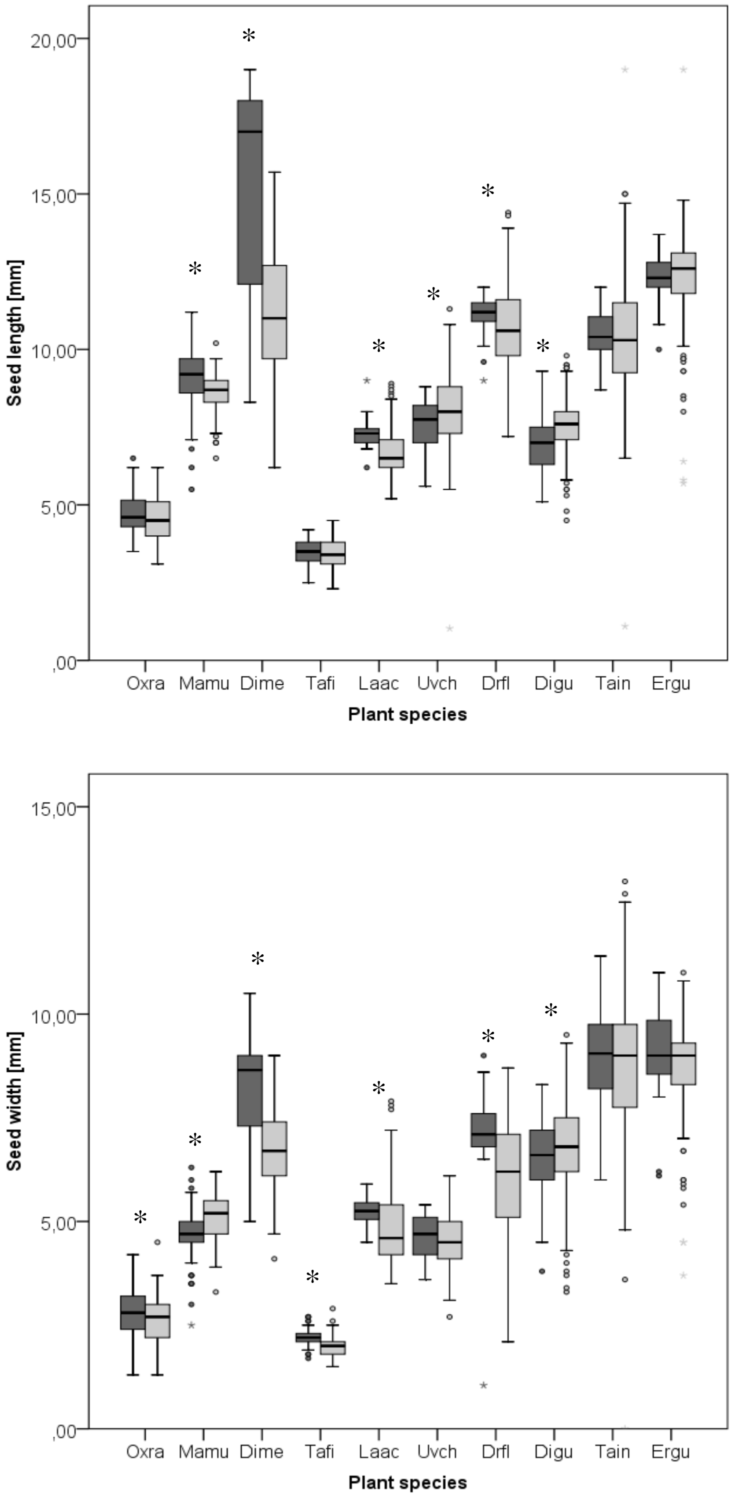
Because seed size in most of the samples was not normally distributed (Kolmogorov-Smirnov test), we used the non-parametric Kruskal-Wallis *H*-test and Mann-Whitney *U*-test to analyse seed size variation across differentially handled seeds (fresh, ingested, spat out).

6. 3 RESULTS

Seed size selection by baboons varied (Figures 1 a, b). Seeds of *L. acida*, *D. mespiliformis*, and *D. floribunda* extracted from baboon faeces were significantly smaller (length and width) than seeds of fresh ripe fruit (Table 1). In the two small-seeded species, *T. fischeri* and *O. racemosus*, ingested seeds were also smaller than seeds from fresh fruits, but length did not vary significantly. In contrast, ingested seeds of *Manilkara multinervis* were significantly shorter and wider than seeds from fresh fruits. *U. chamae* seeds dispersed by baboons were significantly longer than seeds from fresh fruits, but width did not vary.

Dialium guineense was the only species in which baboons selected fruit with larger seeds: ingested seeds were significantly longer and wider than seeds from fresh fruit. We did not find significant differences between fresh and ingested seeds of *T. indica* and *E. guineense* seeds, respectively.

Baboons spat out *D. floribunda* seeds that were on average 11.8 ± 1.1 mm long and 8.0 ± 0.8 mm wide ($N = 61$). Spat seeds were significantly larger than seeds from fresh fruit as well as seeds found in baboon faeces (Table 1) (*H*-test length: $\chi^2 = 42.55$, width: $\chi^2 = 119.59$, df = 2, $p < 0.001$ in each case. A posteriori *U*-test of seeds from fresh fruits versus spat out seeds: $Z_{\text{length}} = -3.944$, $Z_{\text{width}} = -5.240$; seeds from faeces versus spat out seeds: $Z_{\text{length}} = -6.066$, $Z_{\text{width}} = -9.8636$, $p_{\text{length}} = 0.01$, $p_{\text{width}} = 0.001$ in each case, after applying sequential Bonferroni technique).



Figures 1a, b Intraspecific seed size variation between seeds extracted from fresh fruits and seeds found in faecal samples of olive baboons

Figure 1a (above) Variation in seed length, Figure 1 b (below) Variation in seed width. Plant species on the x-axis arranged in order of fruit type and seed size: berries (Oxra, Mamu, Dime), drupes (Tafi, Laac), indehiscent fruits (Uvch, Drfl), pods (Digu, Tain, Ergu). Species' codes and sample sizes are given in Table 1. Dark grey boxes: 25%-75% percentile of the sizes of seeds from fresh fruits, light grey boxes: 25%-75% percentile of the sizes of seeds from faeces. *: significant variation ($p < 0.05$).

Table 1 Size variation between seeds extracted from fresh fruits and from faeces of olive baboons

We classified fruit types following Hutchinson *et al.* (1954-1968), Strasburger *et al.* (1991), Arbonnier (2000), Kasparek (2000), Wagenitz (2003).

*: corrected *p* value after application of sequential Bonferroni technique; ns: not significant. See Figures 1a,b for seed sizes.

					Length		**Width**		**N seeds from**	
Plant species	**Code**	**Family**	**Fruit type**	**Seeds per fruit**	***Z***	***p***	***Z***	***p***	**fresh fruit**	**baboon faeces**
Lannea acida	Laac	Anacardiaceae	Drupe	one	-3.957	<0.001	-3.072	<0.01	20	241
Uvaria chamae	Uvch	Annonaceae	Indehiscent-elongated	many	-2.676	<0.01	-0.975	ns	38	238
Dialium guineense	Digu	Caesalpiniaceae	Pod-indehiscent	one	-7.017	<0.001	-2.597	<0.01	123	509
Erythrophleum guineense	Ergu		Pod-indehiscent	many	-0.973	ns	-1.740	ns	38	169
Tamarindus indica	Tain		Pod-indehiscent	many	-0.095	ns	-0.767	ns	36	191
Tapura fischeri	Tafi	Chailletiaceae	Drupe	many	-0.688	ns	-4.057	<0.001	61	55
Diospyros mespiliformis	Dime	Ebenaceae	Berry	many	-12.027	<0.001	-11.172	<0.001	142	298
Dryptes floribunda	Drfl	Euphorbiaceae	Indehiscent-oval	many	-2.739	0.01*	-5.672	0.001*	43	294
Oxyanthus racemosus	Oxra	Rubiaceae	Berry	many	-1.168	ns	-1.993	<0.05	60	111
Manilkara multinervis	Mamu	Sapotaceae	Berry	one	-3.481	<0.001	-3.644	<0.001	69	55

6. 4 DISCUSSION

Primates may select fruits with regard to a variety of different fruit characteristics, including, for example, the chemical composition of the pulp (e.g. Glander 1982, and references therein; Janson *et al.* 1986; Barton & Whiten 1994), and physical fruit traits such as fruit and seed size (Julliot 1996; Knogge & Heymann 2003; Stevenson *et al.* 2005). Results from studies on intraspecific seed size selection in primates have not, however, revealed a consistent pattern. Stevenson *et al.* (2005) found evidence for seed size selection by woolly monkeys (*Lagothrix lagothricha*) in five out of eleven plant species, with a tendency to swallow relatively smaller seeds from three large-seeded plant species. Spider monkeys (*Ateles paniscus*) ingest smaller seeds than available in *Virola surinamensis* (Howe & vande Kerckhove 1981), but not in *V. calophylla* (Russo 2003). Results from the present study are also inconsistent. The two different methods of fruit collection (fruits taken from the canopy versus from the ground) did not seem to bias the outcome of seed size comparisons. With both methods species' samples from fresh fruits had larger seeds, smaller seeds, and seeds that did not differ significantly in size from seeds found in baboon faeces.

Among species from which baboons consume ripe pulp and thereby swallow entire seeds, we found significant intraspecific differences between dispersed and non-dispersed seeds across all investigated fruit types and the whole range of seed sizes.

However, the pattern of selectivity varied both within fruit types and among species with seeds of similar size. We did not take size-dependent variation of seed-pulp-ratio within each species into account, yet the correlation between pulp and seed size is likely to differ among species according to such traits as fruit type, shape of fruit and seeds, thickness of fruit husk, and the number of seeds per fruit. For example, baboons disperse smaller and shorter seeds than available from *D. mespiliformis* and *D. floribunda*. The fleshy fruits of both plant species are round-oval and the multiple seeds are elongated and acuminated. In the two fleshy-fruited species with oval fruits and small, flat-oval seeds (*O. racemosus* and *T. fischeri*) baboons selected seeds that were smaller in width. Among the medium-sized (seed length $> 5 \leq 10$ mm), oval-seeded species *M. multinervis*, *L. acida*, and *U. chamae* baboons selected seeds differentially, possibly due to different fruit shapes. In contrast to *M. multinervis* (oval berry) and *L. acida* (oval drupe) *U. chamae* has long indehiscent, pod-like fruits. Here, the longer seeds dispersed by baboons probably derived from longer fruits that might offer a relatively higher pulp reward.

D. guineense is the only species with a round and flat fruit that provides a dry and flour-like pulp surrounding a single seed. A strong positive correlation between the amount of pulp and the size of the seed would explain why seeds in baboon faeces were significantly longer and wider than the seeds from a random sample of fresh fruit. That primates may select fruits with large seeds that offer high pulp reward has been shown for female tamarins (*Saguinus mystax* and *S. geoffroyi*) and *Inga* sp. fruits (Garber & Kitron 1997).

In each of two species, *T. indica* and *E. guineense*, sizes of ingested seeds and seeds from fresh fruits did not vary significantly. *T. indica* pods persist for a long period on the trees and baboons continuously exploit fruits until the crops are completely depleted (Kunz, pers. observ.). Our data show that *T. indica* seeds can vary in size by several millimetres. Because we measured only one seed per pod (from the middle part), the data indicate that seed size varies among fruits. It remains to be tested whether baboons start feeding on pods with the most profitable pulp-seed ratio at the beginning of the fruiting period prior to consuming less profitable fruits in terms of the relative amount of pulp rewarded.

The fruit of *E. guineense* is a woody pod, offering no pulp. Against expectations, we could not confirm that baboons select larger *E. guineense* seeds for predation. If, however, only seeds below a certain size accidentally escape chewing and are swallowed intact, faecal analysis cannot reveal selection of large seeds. In a previous study, we have shown that olive baboons selected large unripe *P. biglobosa* seeds for feeding (Kunz & Linsenmair 2007), but evidence came from comparisons between seeds remaining in exploited and unexploited indehiscent pods, an approach that was inapplicable in the dehiscent pods of *E. guineense*.

It remained ambiguous to us which clues baboons used for seed size selection. In long, elongated fruits like *U. chamae* and *T. indica* in which the multiple seeds are arranged in a row, fruit length and width might indicate seed size. In some soft-fruit species seeds are palpable. While adult baboons often appeared to select large fruits like *Saba senegalensis* (Apocynaceae) by sniffing and palpating, we did not notice such behaviour in the fruits included in the present study (Kunz, unpubl. data). Some bird species are able to distinguish between artificial fruits with small and large seeds (e.g. Stanley & Lill 2002), and baboons might also use indicators of seed size that do not require tactile fruit investigation. Alternatively, baboons might select fruits for a trait other than seed size, and 'seed size selection' merely is a consequence of the relation of these two traits.

Instead of swallowing entire seeds embedded in fruit pulp, several primate species separate seeds from pulp during fruit consumption and drop or spit out the seeds (Corlett & Lucas 1990; Kaplin & Moermond 1998; Dominy & Duncan 2005). Kaplin & Moermond (1998) reported that two species of Cercopithecus monkeys (*Cercopithecus mitis* and *C. l'hoesti*) tend to drop seeds greater than 10 mm. Long-tailed macaques (*Macaca fascicularis*) have a smaller threshold of 3-4 mm (Corlett & Lucas 1990). We observed extensive seed spitting/dropping by olive baboons for only two plant species, *Syzygium guineense* (Myrthaceae), and *D. floribunda* (Kunz, unpubl. data). *S. guineense* (mean seed length 17.7 ± 1.9 mm, *N* = 29) did not turn up in faecal samples and are probably rarely, if ever swallowed. *D. floribunda* seeds are either spat out or swallowed, but seeds were handled differently according to size: spat seeds were larger than seeds from randomly collected fresh fruits and larger than seeds found in faecal samples. We did not test spat seeds for germination, but all seeds collected were undamaged according to visual inspection (Kunz, unpubl. data). *D. floribunda* seeds swallowed by olive baboons germinated from dung samples (Lieberman *et al.* 1979). Baboons thus apparently act as dispersers of *D. floribunda* seeds in both ways. Since dispersal distances of spat seeds are generally lower than those of ingested seeds (Lambert 2002) large seeds of *D. floribunda* might be dispersed predominantly singly or in small clumps within the vicinity of the parent plant, whereas small seeds are more likely to be dispersed in faecal clumps over larger distances. Baboons, however, may increase distances of spat seeds by stuffing fruits in their cheek pouches for subsequent processing farther away from the food plant. Other Cercopithecinae (*Cercopithecus mitis, C. ascanius*) are known to carry seeds in their cheek pouches up to 100 m away from the fruit source (Rowell & Mitchell 1991).

In plant species in which post-dispersal fate of seeds and establishment of seedlings vary with seed size, dispersal by baboons of only a subset of the available seed sizes is likely to affect plant fitness through changes in secondary dispersal probabilities of seeds from baboons dung, rates of secondary seed predation, and seedling survival. Regarding evolutionary implications, however, the interactions between baboons and their food plants are probably too weak and spatially and temporally inconsistent to exert a long-term selective pressure on seed size. Feeding behaviour of primates can be highly variable both in space and time, depending for example on the animals' dietary requirements and the overall food availability (Lambert & Garber 1998; Chapman & Chapman 2002). The fruits of the plant species investigated in the present study are likely to attract a variety of different frugivores (including other primate species), all of which might have different fruit and seed size preferences within each plant species. Rather than being an adaptation merely to seed dispersal, seed size represents a trade-off between different (often opposing) requirements during different episodes in the reproductive cycle of a plant including, for example, post-dispersal seed predation, secondary seed dispersal and the need for adequate seedling provisioning (Lambert & Garber 1998; Leishman *et al.* 2000). Moreover, seed size can vary considerably within plant individuals, infructescences and within multi-seeded fruits (reviewed in Harper *et al.* 1970). Rather than being heritable, environmental factors seem to cause seed size variation within many plant species (Leishman *et al.* 2000; Hulme & Benkman 2002). All these factors limit the evolutionary potential of the selection pressure exerted by baboons on the seed size of their food plants. In general, the relationship between plants and their dispersers is of a diffuse, non-species specific nature and does not represent a tight co-evolution between species pairs (Howe 1984; Herrera 1985). Given the implications for natural plant regeneration, however, intraspecific seed size selection by primates requires further research, particularly to identify interrelations with other plant and fruit traits and to understand effects on post-dispersal processes and seedling survival in detail.

6. 5 ACKNOWLEDGEMENTS

We thank S. Berghoff and F. Walravens for helpful comments on the manuscript. The "Ministère de l'Agriculture et des Ressources Animales" and the "Ministère de l'Enseignement Supérieure et de la Recherche Scientifique", Abidjan, kindly granted research permission for the CNP. PhD scholarships from the German Academic Exchange Service (DAAD) and the University of Wuerzburg (HSP III) funded the study. The research camp in CNP was constructed with generous funds from the Volkswagen-Foundation.

6. 6 REFERENCES

Andresen, E. & Feer, F. 2005. The role of dung beetles as secondary dispersers and their effect on plant regeneration in tropical rain forests. Pp. 331-349 In Forget, P. M., Lambert, J. E., Hulme, P. E. & van der Wall, S. B. (eds.). *Seed fate: predation, dispersal and seedling establishment.* CABI, Wallingford.

Arbonnier, M. 2000. *Arbres, arbustres et lianes des zones sèches d'Afrique de l'Ouest.* Muséum National d'Histoire Naturelle, Paris.

Barton, R. A. & Whiten A. 1994. Reducing complex diets to simple rules: food selection by olive baboons. *Behavioural Ecology and Sociobiology* 35: 283-293.

Brewer, S. W. 2001. Predation and dispersal of large and small seeds of a tropical palm. *Oikos* 92: 245-255.

Chapman, C. A. & Chapman, L. J. 2002. Plant-animal coevolution: is it thwarted by spatial and temporal variation in animal foraging? Pp. 275-290 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation.* CABI, Wallingford.

Chapman, C. A. & Onderdonk, D. A. 1998. Forests without primates: primate/plant codependency. *American Journal of Primatology* 45: 127-141.

Corlett, R. T. & Lucas, P. W. 1990. Alternative seed-handling strategies in primates: seed-spitting by long-tailed macaque *Macaca fascicularis*. *Oecologia* 82: 166-171.

Dirzo, R. & Domínguez, C. A. 1986. Seed shadows, seed predation and the advantages of dispersal. Pp. 237-249 In Estrada A. & Fleming, T. H. (eds.). *Frugivores and seed dispersal.* Dr. W. Junk Publishers, Dordrecht.

Dominy, N. J. & Duncan, B. W. 2005. Seed-spitting primates and the conservation and dispersion of large-seeded trees. *International Journal of Primatology* 26: 631-649.

FGU-Kronberg 1979. Gegenwärtiger Status der Comoé- und Tai-Nationalparks sowie des Azagny-Reservats und Vorschläge zu deren Erhaltung und Entwicklung zur Förderung des Tourismus. Technical Report. Deutsche Gesellschaft für Technische Zusammenarbeit GmbH, Eschborn.

Fischer, F., Groß, M. & Kunz, B. 2000. Primates of the Comoé National Park, Ivory Coast. *African Primates* 4: 10-15.

Garber, P. A. & Kitron, U. 1997. Seed swallowing in tamarins: evidence of a curative function or enhanced foraging efficiency? *International Journal of Primatology* 18: 523-538.

Glander, K. E. 1982. The impact of plant secondary compounds on primate feeding behavior. *Yearbook Physical Anthropology* 25: 1-18.

Harper, J. L., Lovell, P. H. & Moore, K. G. 1970. The shape and size of seeds. *Annual Review of Ecology and Systematics* 70: 327-356.

Herrera, C. M. 1985. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos* 44: 132-141.

Howe, H. F. 1984. Constraints on the evolution of mutualism. *The American Naturalist* 123: 764-777.

Howe, H. F. & vande Kerckhove, G. A. 1981. Removal of wild nutmeg *Virola surinamensis* crops by birds. *Ecology* 62: 1093-1106.

Hulme, P. E. & Benkman, C. W. 2002. Granivory. Pp. 132-154 In Herrera C. M. & Pellmyr, O. (eds.). *Plant-animal interactions. An evolutionary approach.* Blackwell, Oxford.

Hutchinson, J., Dalziel, J. M. & Keay, R. W. J. 1954-1968. *Flora of West tropical Africa.* Vols. I-III. Crown Agents for Oversea Governments and Administrations, London.

Jansen, P. A., Bongers, F. & Hemerik, L. 2004. Seed mass and mast seeding enhance dispersal by a Neotropical scatter-hoarding rodent. *Ecological Monographs* 74: 569-589.

Janson, C. H., Stiles, E. W. & White, D. W. 1986. Selection on plant fruit traits by brown capuchin monkeys: a multivariate approach. Pp. 83-92 In Estrada, A. & Fleming, T. H. (eds.). *Frugivores and seed dispersal.* Dr. W. Junk Publishers, Dordrecht.

Julliot, C. 1996. Fruit choice by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest. *American Journal of Primatology* 40: 261-282.

Kaplin, B. A. & Moermond T. C. 1998. Variation in seed handling by two species of forest monkeys in Rwanda. *American Journal of Primatology* 45: 83-101.

Kasparek, M. 2000. *Flore du Parc National de Tai (Côte d'Ivoire).* Kasparek, Heidelberg.

Knogge, C. & Heymann, E. W. 2003. Seed dispersal by sympatric tamarins, *Saguinus mystax* and *Saguinus fuscicollis*: diversity and characteristics of plant species. *Folia Primatologica* 74: 33-47.

Kunz, B. K. & Linsenmair, K. E. 2007. Changes in baboon feeding behavior: maturity dependent fruit and seed size selection within a food plant species. *International Journal of Primatology* 28: 819-835.

Kunz, B. K. & Linsenmair, K. E. 2008a. The disregarded West: diet and behavioural ecology of olive baboons in the Ivory Coast. *Folia Primatologica* 79: 31-51.

Kunz, B. K. & Linsenmair, K. E. 2008b. The role of the olive baboon (*Papio anubis*, Cercopithecidae) as seed disperser in a savanna-forest mosaic of West Africa. *Journal of Tropical Ecology* 24: 235-246.

Lambert, J. E. 2002. Exploring the link between animal frugivory and plant strategies: the case of primate fruit processing and post-dispersal seed fate. Pp. 365-380 In Levey, D. J., Silva, W. R., Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation.* CABI, Wallingford.

Lambert, J. E. & Garber, P. A. 1998. Evolutionary and ecological implications of primate seed dispersal. *American Journal of Primatology* 45: 9-28.

Leishman, M. R., Wright, I. J., Moles, A. T. & Westoby, M. 2000. The evolutionary ecology of seed size. Pp. 31-56 In Fenner, M. (ed.). *Seeds. The ecology of regeneration in plant communities.* CABI, Wallingford.

Lieberman, D., Hall, J. B., Swaine, M. D. & Lieberman M. 1979. Seed dispersal by baboons in the Shai Hills, Ghana. *Ecology* 60: 65-75.

Link, A. & Di-Fiore, A. 2006. Seed dispersal by spider monkeys and its importance in the maintenance of Neotropical rain-forest diversity. *Journal of Tropical Ecology* 22: 235-246.

McConkey, K. R. 2005. The influence of gibbon primary seed shadows on post-dispersal seed fate in a lowland dipterocarp forest in central Borneo. *Journal of Tropical Ecology* 21: 255-262.

Michaels, H. J., Benner, B., Hartgerink, A. P., Lee, T. D., Rice, S., Willson, M. F. & Betin, R. I. 1988. Seed size variation: magnitude distribution and ecological correlates. *Evolutionary Ecology* 2: 157-166.

Norconk, M. A., Grafton, B. W. & Conklin-Brittain, N. L. 1998. Seed dispersal by Neotropical seed predators. *American Journal of Primatology* 45: 103-126.

Nuňez-Iturri, G. & Howe, H. F. 2007. Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rain forest in western Amazonia. *Biotropica* 39: 348-354.

Peres, C. A. 1991. Seed predation of *Cariniana micrantha* (Lecythidaceae) by brown capuchin monkeys in central Amazonia. *Biotropica* 23: 262-270.

Poilecot, P. 1991. *Un écosystème de savane soudanienne: le Parc National de la Comoé (Côte d'Ivoire).* UNESCO, Paris.

Rey, P. J., Garrido, J. L., Alcantara, J. M., Ramirez, J. M., Aguilera, A., Garcia L., Manzaneda, A. J. & Fernandez, R. 2002. Spatial variation in ant and rodent post-dispersal predation of vertebrate-dispersed seeds. *Functional Ecology* 16: 773-781.

Rowell, T. E. & Mitchel, B. J. 1991. Comparison of seed dispersal by guenons in Kenya and capuchins in Panama. *Journal of Tropical Ecology* 7: 269-274.

Russo, S. E. 2003. Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia* 136: 80-87.

Stanley, M. C. & Lill, A. 2002. Importance of seed ingestion to an avian frugivore: an experimental approach to fruit choice based on seed load. *The Auk* 119: 175-184.

Stevenson, P. R., Pineda, M. & Samper, T. 2005. Influence of seed size on dispersal patterns of woolly monkeys (*Lagothrix lagothricha*) at Tinigua Park. *Oikos* 110: 435-440.

Strasburger, E., Nol, F., Schenk, H. & Schimper, A. F. W. 1991. *Lehrbuch der Botanik für Hochschulen.* Gustav Fischer, Stuttgart.

Wagenitz, G. 2003. *Wörterbuch der Botanik.* Spektrum, Heidelberg.

White, F. 1983. *The vegetation of Africa.* UNESCO, Paris.

Wrangham, R. W., Chapman, C. A. & Chapman, L. J. 1994. Seed dispersal by forest chimpanzees in Uganda. *Journal of Tropical Ecology* 10: 355-368.

Xiao, Z., Zhang, Z. & Wang, Y. 2004. Dispersal and germination of big and small nuts of *Quercus serrata* in a subtropical broad-leaved evergreen forest. *Forest Ecology and Management* 195: 141-150.

Chapter 7

Olive Baboons as Seed Dispersers of Typical 'Bird-Dispersed' Trees:

7. 1 Variation of Dispersal Agents? Frugivore Assemblages and Fruit Handling in *Lannea acida* (Anacardiaceae)

with T. Hovestadt and K. E. Linsenmair

In press (*Ecotropica*)

Abstract Particular combinations of traits related to the consumption of fruits and dispersal of seeds by specific groups of frugivores have led to the postulation of 'dispersal syndromes'. *Lannea acida* (Anacardiaceae) is a West African tree with small purple drupes characteristic of the bird-dispersal syndrome. Given the fruit type and size, however, the fruits should be attractive to a wider range of arboreal frugivores. To test this, we monitored frugivore assemblages, feeding activity during crop maturation, and fruit handling by frugivores. Fruits were harvested by 22 bird and five mammal species. Birds were the most common frugivores in the canopy of *L. acida* but fed predominantly on unripe, green fruits, and therefore probably acted as seed predators. Primates tended to visit trees after the onset of fruit maturation. Nearly all seeds found in faeces of olive baboons (*Papio anubis*) were undamaged and had a significantly higher germination success compared to undispersed seeds from fresh ripe fruits. Non-granivorous birds that otherwise may be legitimate seed dispersers can become quantitatively important seed predators when consuming unripe fruits, for example during times of fruit scarcity. The role of birds in predispersal seed predation for plant fitness requires further investigation. On the other hand, primates are often considered crucial dispersers for large-seeded tree species, but their importance for plants with small fruit should not be underrated.

7.1.1 INTRODUCTION

Plant-frugivore interactions can, among other factors, be influenced by different fruit traits (Jordano 2000; Herrera 2002). For example, fruit type (e.g. berry, drupe, nut) and the size of fruits and seeds may constrain fruit handling and seed dispersal by animals. Hence, small fruit and large fruit with small seeds are generally consumed and dispersed by a greater number of frugivores than large fruit with large seeds (reviewed by Jordano 2000). Frugivores may also differ in their effectiveness as seed dispersers (reviewed in Schupp 1993). One prerequisite for high-quality dispersal is that a frugivore neither consumes fruits before seed maturity nor destroys the seeds during fruit handling. Most fruits undergo dramatic biochemical changes during maturation, making ripe fruits more attractive to frugivores than unripe fruits (Steentoft 1988; Schaefer *et al.* 2003). Fruit maturity can be indicated through fruit colour (Schaefer *et al.* 2004). 'Green' often signals unripeness and unpalability (Herrera 2002; but see Knight & Siegfried 1983). Many frugivorous birds seem to avoid green and unripe fruit (Knight & Siegfried 1983; Sanders *et al.* 1997; Schaefer & Schaefer 2006). In fruit choice experiments, birds generally preferred ripe over unripe, and brightly coloured (red, orange, and black) as well as UV-reflecting fruit over white and dull (green and yellow) fruit (McPherson 1988; Sanders *et al.* 1997; Honkavaara *et al.* 2004). Red and black are globally the most common fruit colours of bird-dispersed plant species (Willson & Whelan 1990; Herrera 2002). Red and black exhibit stronger contrasts against foliage than other colours, making fruit more conspicuous for avian frugivores (Giles & Lill 1999; Schmidt *et al.* 2004; but see Honkavaara *et al.* 2004).

Fruit colour in combination with other morphological fruit traits has been related to fruit consumption by specific groups of dispersers, and has led to the postulation of 'dispersal syndromes' (van der Pijl 1982; Charles-Dominique 1993). Fruits typically dispersed by birds are small, brightly coloured drupes or berries (Knight & Siegfried 1983; Balasubramanian 1996; Herrera 2002). Fruits associated with seed dispersal by mammals tend to be larger and dull coloured (brown, yellow, or green) (Knight & Siegfried 1983; Herrera 2002; but see Gautier-Hion *et al.* 1985).

Lannea acida A. Rich. (Anacardiaceae) is a tree of up to 14 meters in height that is relatively common in West African savannas and along forest edges. Female trees produce small (~ 10 mm long), single-seeded, ellipsoid drupes, which appear green to the human eye when unripe and dark purple when ripe. Several dozens are clustered in infructescences. Fruiting starts at the end of the dry season/beginning of the wet season and lasts one to two months (von Maydell 1990; Arbonnier 2000; Kunz pers. observ.). Trees are completely leafless during most of the fruiting period, providing excellent observation conditions.

According to the dispersal-syndrome hypothesis, we expected birds to play the major role as seed dispersers for the tree by regularly feeding on ripe crops. Given the fruit type and size, however, *L. acida* fruits should also be attractive to a wide range of arboreal frugivores. The aim of our study was thus twofold: to survey the frugivore assemblage of *L. acida* and to identify effective seed dispersers for the tree. Specifically, we were interested in the qualitative component of seed dispersal: the timing of frugivore feeding visits in relation to crop maturity and their treatment of fruits and seeds.

7.1.2 STUDY SITE

The study took place in the Comoé National Park (CNP) (08°30-09°36' N, 003°07'-004°25' W), north-eastern Ivory Coast. The park covers approximately 11,500 km^2 at an altitude of about 250-300 m asl. The southern park area is situated within the 'Guinea-Congolia / Sudania regional transition zone', whereas the northern part belongs to the 'Sudanian regional centre of endemism' (White 1983). We collected data in the south-western section of CNP where the vegetation consists of a mosaic of different savanna formations (approximately 91 %), forest islands (7 %), and gallery forest (2 %) along the two main rivers (FGU-Kronberg 1979). Savanna and gallery forest are separated by a band of grass vegetation with few woody species, henceforth referred to as 'plain'. The vegetation is described in detail elsewhere (Poilecot 1991; Porembski 1991, 2001; Hovestadt *et al.* 1999).

The climate in the study area is characterized by a dry season from November to March/April. The mean annual precipitation from January 1994 to December 1999 was 1,053 mm year, and the mean annual temperature was 26.3°C.

The CNP harbours a rich flora and fauna. So far, 498 bird species (Salewski 2000; Salewski & Göken 2001; Rheindt *et al.* 2002) and 152 mammal species have been recorded (Poilecot 1991; Mess & Krell 1999; Fischer *et al.* 2002), including recent observations of nine diurnal nonhuman primate species (Fischer *et al.* 2000). Seventy percent of the 292 woody plant species produce fleshy fruit for consumption by animals (Hovestadt 1997).

7.1.3 METHODS

The study had two parts. To identify the seed disperser assemblage of *L. acida*, we first recorded frugivores feeding in different trees (10 trees in 1991 to 1993 monitored by T. Hovestadt, and four in 1998 to 1999 monitored by B. Kunz). B. Kunz then observed two focal trees in 1999 and 2000 in more detail to obtain data on fruit and seed handling by frugivores and the frugivores' timing of feeding visits to *L. acida* trees in relation to crop maturity.

7.1.3.1 Vertebrate Fruit Consumers in *L. acida* Trees

To determine frugivore assemblage feeding in *L. acida*, we randomly selected and consecutively observed trees bearing ripe fruits (as judged from the dark fruit colour) in 1991 to 1993. We observed each tree for one to two days between 06:00 h and 10:00 h. During this time of day bird feeding activity is highest and primates in the study area are also foraging. Observation distance was 20-100 m from a focal tree. We hid behind artificial blinds of dark-green fabric where natural coverage was sparse. All vertebrates feeding on fruit were noted. Trees were discarded from the study when no frugivores were recorded during the first morning, presuming that fruits were not yet attractive. Total observation time of the 10 remaining trees was 17.5 hours (60-150 minutes per tree). Because the Shinozaki curve (Figure 1), calculated using BIODIV (Messner 1996), showed no saturation in the number of bird species recorded as a function of the number of trees observed, we continued sampling frugivores in 1998 to 1999, adding four other trees, including our two focal trees, for 7.25 hours of observations.

Species feeding in the two *L. acida* focal trees that we monitored for details on fruit handling (see below) are also included in the species list. Identification of bird and mammal species was verified using Mackworth-Praed & Grant (1970-1973), Serle & Morel (1977), Brown *et al.* (1982-1992). Bird names follow Borrow & Demey (2001).

7.1.3.2 Fruit Handling

In 1999 and 2000, we concentrated observations on two fruiting focal trees (Laac1, Laac2) to determine the timing of the feeding visits relative to crop maturation, and to record fruit treatment by different frugivores. We selected the focal trees with respect to good visibility of the crown and the fact that they were about equal in height (estimated 13 and 14 m). The trees were situated within 30 m of each other at the forest edge in the vicinity of the former field station of the University of Würzburg, Germany (08° 45.056' N and 003° 49.029' W). In this area, diurnal nonhuman primates (white-crowned mangabey *Cercocebus atys lunulatus* Temminck, Lowe's monkey *Cercopithecus campbelli lowei*

Thomas, lesser white-nosed monkey *C. petaurista* von Schreber, olive baboon *Papio anubis* Lesson) were habituated to the presence of researchers, and were thus more likely to visit a tree under observation than elsewhere in the park.

At the onset of the study, fruit crops of the two focal trees were unripe (green). Crop maturity was visually estimated once a week using binoculars. We multiplied the average number of fruits of 16 randomly-chosen infructescences by the mean number of infructescences of four randomly-selected branches of similar size. We then extrapolated the average fruit number per branch to the total number of similar-sized branches of the crown.
A single maturity state of the crop was noted when ≥ 90% of the visible fruits had the same fruit colouration (green = unripe, greenish-purple = ripening, purple to dark purple = ripe). When > 10% of the crop had a different colouration, a second maturity state was listed, with the dominant state being listed first. For example, the overall crop maturity was defined as 'ripening-ripe' when > 50% to < 90% of the fruits were ripening (greenish-purple) while > 10% to < 50% were ripe (purple to dark purple).

Monitoring of a tree terminated when the crop was reduced by ≥ 95 % compared to the first visual estimation, or when the remaining fruits were withered and seemed no longer attractive to frugivores. Consequently, we observed Laac1 from 21 March to 21 April 1999 (63 hours) and from 21 March to 5 April 2000 (53 hours). Monitoring of Laac2 took place from 21 March to 11 April 1999 (45 hours), whereas the tree's crop was depleted soon after study onset in 2000 (6 observation hours).

We monitored each focal tree from a distance of about 20 m using binoculars. Observations were undertaken for three to five hours a day and were about evenly distributed between 06:00 h to 19:00 h. When both focal trees were fruiting and attractive to frugivores, we alternated observations between the two focal trees (within a day or over consecutive days).
Lannea spp. fruits were not reported to be eaten by bats at Lamto reserve, Ivory Coast (Thomas 1982), although three *Lannea* species are present in the area (Schmidt 1973), yet *L. microcarpa* fruits are consumed by flying foxes in northern Benin (Djossa *et al.* 2008). We checked for the activity of bats and other nocturnal frugivores and observed both focal trees in 1999, and Laac1 again in 2000, during early night hours (between 20:00 h and 23:00 h) at the beginning and peak of fruiting. Night vision gear was used, and four nights of observations totalling five hours in Laac1 and four hours in Laac2 were undertaken.
During daytime and nighttime observations we scanned the tree every five minutes for one minute and recorded the individual number and identity to species level of all birds and mammals foraging in the crown. Each foraging individual seen in a given scan was assessed as one record. We ascribed fruit handling by birds to either pecking of pulp

(peckers/fruit thieves), crushing of fruits and dropping of seeds (mashers/fruit thieves), or swallowing of whole fruits (swallowers) (following Levey 1987). After squirrel feeding events we checked fresh leftovers on the ground for signs of treatment (tooth marks, gnawed seeds). In primates, we observed whether fruits were swallowed entirely, or seeds were spat out during feeding in the tree.

We calculated the mean number of hourly records of swallower birds, squirrels, and primates, respectively, per tree and year. Wilcoxon's signed-rank test and Friedman's ANOVA, respectively, were applied to test for differences in visitation rates within and across groups of frugivores (SPSS version 15.0, confidence limits set at 95%). We used exact tests for small sample sizes (SPSS Exact Extension). The level of significance of *a posteriori* comparisons was adjusted using the sequential Bonferroni technique (Rice 1989).

7.1.3.3 Fruit Availability in the Vicinity of the Focal Trees

In March and April 1999 and 2000, between day 10 and 20 of each month, we checked a 400-m strip for the presence of other fruiting tree and shrub species in the direct vicinity of the focal trees in each of the following habitats: gallery forest (strip width 10 m), savanna (width 20 m), plain (width 50 m). Strip width followed visibility and tree density. We used binoculars when necessary. In addition, we recorded fruit availability along the forest edge (400 m, width about 2-3 m) where the two focal trees were located. When we recorded fruit species potentially suitable for consumption by birds (species with small fruit, or with larger fruit having soft husk and pulp) we noted whether mature fruits were present at the plant. Food plants were identified from the following sources: Hutchinson *et al.* (1954-1968), von Maydell (1990), Arbonnier (2000), Kasparek (2000), and a seed reference collection established in previous years by T. Hovestadt and P. Poilecot. S. Porembski (University of Rostock, Germany) and E. Robbrecht (National Botanic Garden of Belgium) verified plant material in question. Plant nomenclature follows the African Flowering Plants Database (<http://www.ville-ge.ch/cjb/bd/africa/index.php>).

7.1.3.4 Seed Germination

Even though seed traps were installed below the canopy of Laac1 in 1999 and 2000, seeds dropped by birds were not available in adequate quantities for germination experiments and statistical analyses. We thus used seeds from fresh fruits to test for seed germination ability at different stages of maturity. Between the end of March and mid-April 1999 we randomly collected 60 unripe (green) and 60 ripe (dark purple) fresh fruits from each of two *L. acida* trees. Seeds were cleaned from pulp by hand to simulate pulp removal during ingestion and were briefly rinsed with water.

Data on dispersal of *L. acida* seeds by primates were obtained from faecal samples of olive baboons (Kunz & Linsenmair 2008a). During the fruiting period of *L. acida* in 1998 to 2000 we collected baboon faeces opportunistically. Each sample was washed through 1-mm sieves and the extracted seeds were visually examined for damage. In 1999, undamaged seeds from baboon faeces were stored for up to four days in a dark, dry place at ambient temperature until 120 seeds were obtained for germination experiments.

All seeds were placed on a double layer of filter paper in groups of 10 per Petri dish. We exposed half the number of the Petri dishes per maturity state or treatment (undispersed or dispersed by baboons) to full sunlight and the other half to shade (provided by a reed covering). We watered seeds *ad libitum* and checked them daily for penetration of the seed coat by the radicle. Germinating seeds were removed.

Experiments with undispersed ripe seeds and seeds from baboon faeces were conducted from 9 April to 23 June 1999. Experiments with unripe seeds started two days later and lasted until 25 June 1999.

Differences in germination success were tested using the χ^2-test with Yates correction.

7.1.4 RESULTS

7.1.4.1 Vertebrate Fruit Consumers in *L. acida* Trees

Fourteen bird species, the red-legged sun squirrel (*Heliosciurus rufobrachium* Waterhouse) and the olive baboon were observed feeding on fruits of *L. acida* trees in 1991-1993 (Appendix 1). Observations of four additional trees in 1998-1999 yielded two more bird species.

Including frugivores feeding in Laac1 and Laac2 during observations of fruit handling totals 22 bird species and five mammal species (Appendix 1). Bird species noted most often were the village weaver (*Ploceus cucullatus*), violet-backed starling (*Cinnyricinclus leucogaste*r), common bulbul (*Pycnonotus barbatus*), and the African thrush (*Turdus pelios*). There was no evidence of nocturnal visitors.

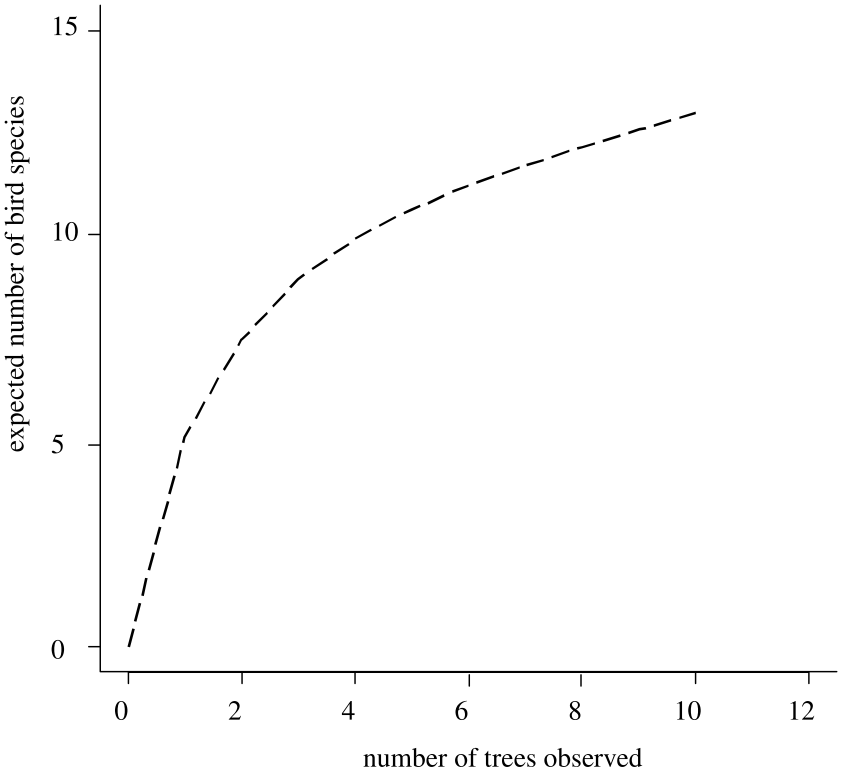


Figure 1 Shinozaki curve showing the total number of bird species recorded as a function of the number of *L. acida* trees observed in 1991-1993

7.1.4.2 Fruit Handling

We classified six of the 22 bird species as pulp peckers, while at least 13 species swallowed entire fruits (Appendix 1). Fruit treatment by three species was not reliably identified. Fruit crushing in the bill (Levey 1987) was not observed, nor did we see birds regurgitating seeds. The four most common bird species visiting the trees (as above) were all fruit swallowers.

The sun squirrel preyed upon seeds by gnawing small holes in the pulp and testa to feed on the cotyledons and embryo. Primates swallowed *L. acida* fruits entirely. Olive baboons and white-crowned mangabeys sometimes also stuffed *L. acida* fruits in their cheek pouches, possibly for later fruit processing, though we never observed intensive seed spitting during or after consumption of *L. acida* fruits.

Altogether, variation in visitation rates per week, year, and tree were high (Figure 2, Table 1). Sun squirrels were not recorded in Laac1 in 1999 and were otherwise rarely observed. Primates were recorded irregularly. Mean records per week in Laac1 in 1999 were six times higher than in 2000. Primate species feeding in Laac1 included *C. a. lunulatus* and *P. anubis* in 1999, and *C. a. lunulatus*, *C. c. lowei*, *C. petaurista* in 2000.

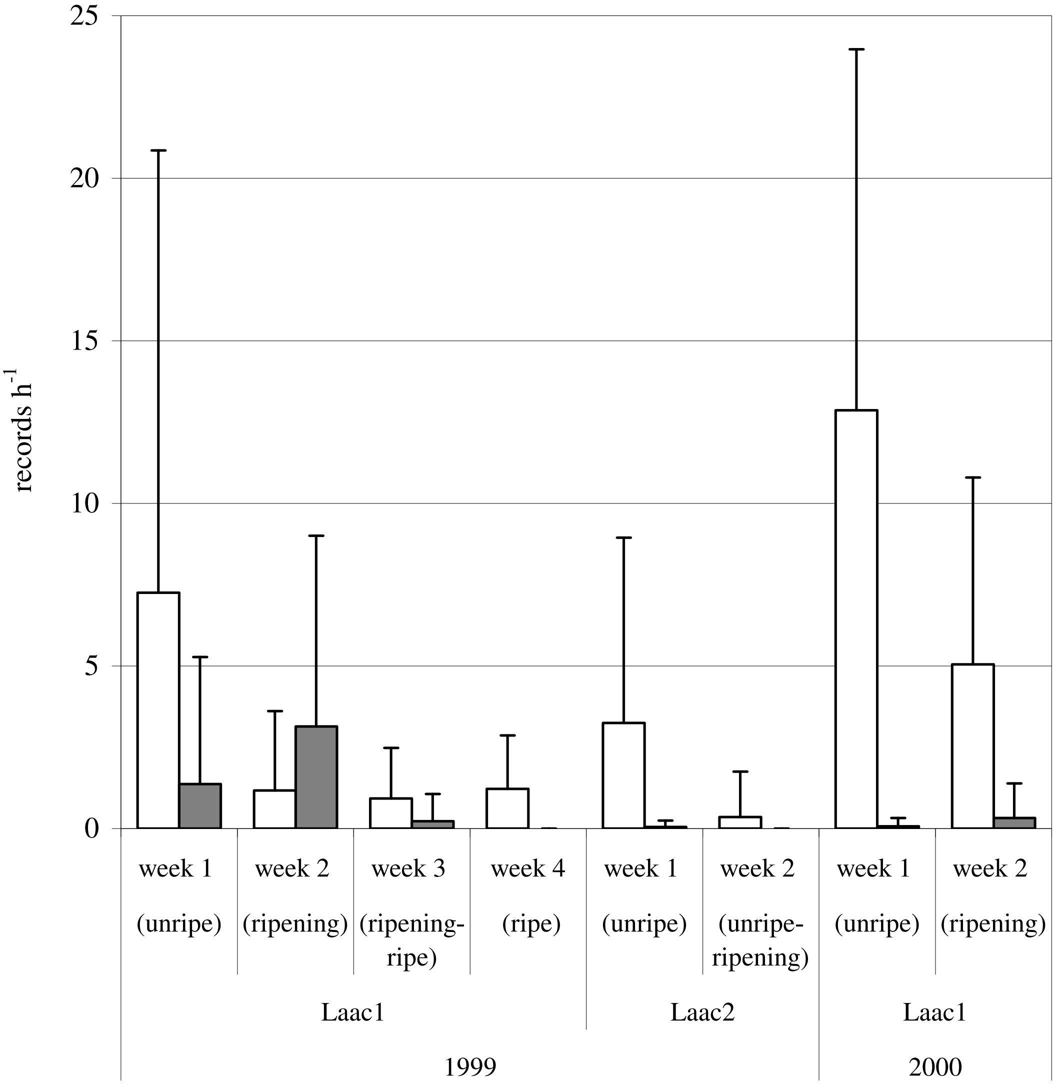


Figure 2 Mean hourly records of birds and primates in *L. acida* focal trees Laac1 and Laac2 during fruiting periods in 1999 and 2000

White columns represent birds, grey columns primates. Crop maturity (unripe, ripening, ripe) is given for each observation week. Observation periods of Laac1: 21 March - 21 April 1999, and 21 March - 5 April 2000. In 2000, fruits dried before full maturation and no birds and mammals were recorded after week 2. Observations of Laac2: 21 March - 11 April 1999. No visitors were recorded after week 2. In 2000 (not displayed), the tree was depleted shortly after study onset.

Table 1 Records of frugivores in *L. acida* focal trees in 1999 and 2000
sd = standard deviation

	Birds				**Mammals**				
	P. barbatus	***T. pelios***	***C. leucogaster***	***P. cucullatus***	***H. rufobrachium***	***C. a. lunulatus***	***C. c. lowei***	***C. petaurista***	***P. anubis***
Laac1									
1999									
N^o. of records in focal tree (63 hrs)	43	24	48	80	0	44	0	0	54
Mean records h^{-1} ± *sd*	0.89 ± 1.45	0.37 ± 0.59	0.72 ± 1.24	1.73 ± 4.24	0	0.76 ± 1.62	0	0	0.70 ± 1.40
2000									
N^o. of records in focal tree (53 hrs)	193	62	47	41	10	7	5	2	0
Mean records h^{-1} ± *sd*	3.70 ± 1.90	1.20 ± 1.10	0.90 ± 0.90	0.80 ± 0.90	0.18 ± 0.32	0.12 ± 0.21	0.09 ± 0.23	0.03 ± 0.09	0
Mean records h^{-1} (1999 & 2000)	2.30	0.79	0.81	1.27	0.09	0.44	0.05	0.02	0.35
Laac2									
1999									
N^o. of records in focal tree (45 hrs)	4	10	4	54	6	1	0	0	0
Mean records h^{-1} ± *sd*	0.06 ± 0.17	0.15 ± 0.34	0.06 ± 0.17	1.75 ± 3.23	0.12 ± 0.31	0.01 ± 0.04	0	0	0

Records of primates in Laac2 were rare, and the only primate species observed feeding was *C. a. lunulatus*. Overall, birds were recorded most often and most regularly (Table 1, Figure 2). However, bird visits h^{-1} were only significantly higher than that of primates and sun squirrels, respectively, in Laac1 and in 2000 (Friedman's ANOVA $\chi^2 = 68.21$, $df = 2$, $p < 0.001$, $n = 36$ hours in which at least one individual in one taxon was recorded, *a posteriori*: birds versus squirrels $Z = -5.2354$, $p = 0.001$; birds versus primates $Z = -5.2368$; $p = 0.001$; p-values in both cases were obtained after applying sequential Bonferroni technique). Visitation rates of primates and sun squirrels to Laac2 were too low for statistical analyses.

Table 2 Wilcoxon's signed-rank test of mean bird records h^{-1} in focal trees during different stages of crop maturity

*No visitors recorded after week 2 in Laac1 in 2000 and Laac2 in 1999. In Laac1 in 1999, results remain significant when only week 1 and week 2 are compared ($Z = -2.201$, $p_{exact} = 0.031$).

	Laac 1 (1999)	**Laac1** (2000)	**Laac2** (1999)
Weeks tested	1 vs. 2-4	1 vs. 2*	1 vs. 2*
Crop maturity	unripe vs. ripening–ripe	unripe vs. ripening	unripe vs. unripe-ripening
Z	-2.243	-3.041	-2.226
p_{exact}	0.023	0.001	0.031

Birds were recorded visiting trees for feeding significantly more often when crops were unripe than when crops were ripening/ripe (Figure 2, Table 2). In Laac1 in 1999, the number of primate feeding records increased in week two with the onset of maturation, though the difference in the mean number of hourly records was not significant between the two time periods ($Z = -0.507$, $p > 0.05$). However, while white-crowned mangabeys were recorded only in week 1 (unripe crop, three times observed) and on the first day of week 2, olive baboons were first observed in week 2 (crop ripening) and revisited the tree until the end of week 3 (six times observed).

7.1.4.3 Fruit Availability

Most woody plant species recorded fruiting in the gallery forest, savanna, and plain around the two focal trees in March and April 1999 and 2000 had fruit not characteristic of the 'bird-dispersal syndrome' (gallery forest: *Cynometra megalophylla, Dialium guineense* Fabaceae; savanna / plain: *Anogeissus leiocarpa, Combretum* sp. Combretaceae, *Parkia biglobosa, Piliostigma thonningii, Tamarindus indica* Fabaceae; *Khaya senegalensis, Pseudocedrela kotschyi* Meliaceae; S*ecuridaca longipedunculata* Polygalaceae; *Crossopteryx febrifuga*, *Mitragyna inermis* Rubiaceae; *Afraegle paniculata* Rutaceae).

Yet two fig trees (*Ficus* spp. Moraceae) in the savanna had unripe or withered fruit in March and April, and in the gallery forest the climber *Canthium* sp. had unripe fruits in April. Only the bird-dispersed climber species *Arbus precatorius* (Fabaceae), in which seeds mimic fruits and are displayed in a dry dehiscent pod, had ripe fruits. Along the forest edge, one additional small *L. acida* tree and five (1999) to four (2000) *L. welwitschii* trees were fruiting. Mature *L. welwitschii* fruits, however, were not available until April.

7.1.4.4 Seed Germination

Four (2.9 %) of the 139 olive baboon faeces collected during the fruiting periods of *L. acida* in 1998 to 2000 contained *L. acida* seeds (range 4-185). Most *L. acida* seeds were undamaged to the human eye (n = 244), or only had shallow scratches on the testa (n = 2). No seed pieces indicating baboons chewed on *L. acida* seeds turned up in faecal samples. All seeds exposed to full sunlight failed to germinate, irrespective of maturity state or treatment (fresh unripe $N = 60$, fresh ripe $N = 60$, or ingested by baboons $N = 60$). Unripe seeds from fresh fruits did not germinate in the shade ($N = 60$). Germination rate of ripe *L. acida* seeds from baboon faeces in the shade (83.3 %, $N = 60$) was significantly increased compared to seeds extracted from fresh ripe fruits (3.3 %, $N = 60$) under the same light condition ($\chi^2 = 78.190$, $df = 1$, $p < 0.001$). Germination of ripe seeds in the shade was rapid (range 4-22 days).

7.1.5 DISCUSSION

The small drupes of *L. acida* provided food for a high number of bird (at least 22) and mammal (a minimum of five) species in the Comoé National Park (CNP). Elephants and chimpanzees, which also consume *L. acida* fruits (McGrew *et al.* 1988; Hovestadt 1997), were not recorded feeding in our study although they were present in the park at the time. The number of species potentially dispersing seeds of *L. acida* in CNP as well as the overall number of frugivorous species observed in the tree is comparable to other studies in Africa. For example, in forest fragments in Kenya 21 frugivorous bird species were recorded in 11 tree species the fruits of which were characteristic of the bird-dispersal syndrome (Githiru *et al.* 2002). In Tanzania, 11 bird species were observed removing seeds of *Leptonychia usambarensis* (Sterculiaceae) (Cordeiro & Howe 2003). In South Africa, the maximum number of frugivorous species in a single fig species was 13 (Bleher *et al.* 2003). However, higher numbers of frugivorous bird species in a single tree species were also observed (36 species in *Prunus africana* (Rosaceae), Farwig *et al.* 2006).

As hypothesized, birds were the most common vertebrate group consuming *L. acida* fruits in CNP. Birds ranged in size from small tinker birds (Capitonidae), of about 10 cm, to large hornbills (Bucerotidae) (80 cm bill tip to tail tip), and included species that are generally considered as insectivorous as well as some granivorous (-insectivorous) species. Most birds swallowed the fruits entirely and thus can potentially act as seed dispersers for the tree. However, only four fruit-swallowing bird species regularly visited the focal trees *(P. barbatus*, *T. pelios, C. leucogaster*, *P. cucullatus*). Among them, *P. barbatus*, *T. pelios* and starlings (*C. leucogaste*r, *Lamprotornis* spp.) are major seed disperser for many woody plant species in CNP (Hovestadt 1997). Bulbuls, in general, play an important role in seed dispersal in many tropical regions of the world (Lieberman & Lieberman 1986; Barnea *et al.* 1990; Kitamura *et al.* 2002; Cordeiro & Howe 2003; Weir & Corlett 2006). In the present study, however, birds visited the two focal trees predominantly during the first week when crops were still unripe. When fruit crops were not depleted before full maturity (Laac1 in 1999), *P. barbatus* was the only bird observed feeding after week 2, when ripe fruits were available (except one record of *T. pelios* and *P. cucullatus* each during this time). *P. barbatus* is the bird with the smallest gape width among the four most often recorded swallower species (measurements of 3-4 specimens per species in the Natural History Museum Berlin; M. Abs, pers. comm.), making it thus unlikely that birds are constrained by the larger size of ripe *L. acida* fruits (mean width of 120 unripe fruits = 8.1 ± 0.6 mm and 8.5 ± 0.6 mm in 20 ripe fruits, B. Kunz unpubl. data).

Ripe *L. acida* fruits are dark purple, a colour strongly preferred by many birds (Willson & Whelan 1990; Herrera 2002; Schmidt *et al.* 2004), whereas unripe, green fruits are often avoided (Knight & Siegfried 1983; Sanders *et al.* 1997; Schaefer & Schaefer 2006). In *L. acida*, however, fruit colour does not seem to be crucial for fruit choice by birds. Other factors, such as time of fruiting, fruit abundance, and overall fruit supply (Foster 1990; Hasui & Hofling 1998; Giles & Lill 1999; Izhaki 2002; Schaefer & Schaefer 2006) may also affect fruit choice in birds. Feeding on unripe fruit can be a way of dealing with seasonal food scarcity (Foster 1977; Schaefer & Schaefer 2006). Our data suggest that ripe fleshy fruit suitable for consumption by birds like bulbuls and thrushes might be locally scarce in March and April in CNP, as apparently was the case in the vicinity of the focal trees. Monthly phenology data from savanna and forest transects in a wider area in the southern part of the CNP support this assumption (Kunz, unpubl. data). *L. acida* trees, on the other hand, are relatively common in CNP (one adult individual ha^{-1}, Hovestadt 1997). In 2000 we had difficulties finding *L. acida* trees with ripe fruit for fruit size measurements, and empty infructescences indicated that crops of *L. acida* trees other than the focal ones were also heavily used while unripe (B. Kunz, unpubl. data).

In some plant species, seeds from apparently unripe fruit may be able to germinate without any treatment (e.g. Broschat & Donselman 1987), but unripe *L. acida* seeds failed to germinate. We thus presume that birds mainly acted as seed predators for the two focal trees during the study period, given the early stage of fruit production at which birds consumed the fruits. However, ingestion by birds can have variable effects on seed germination of *ripe* seeds (Lieberman & Lieberman 1986; Barnea *et al.* 1990). We were unable to find data on the effects of gut passage by birds upon germination ability of *unripe* seeds. Further studies are required in which different bird species are exposed to unripe and ripe *L. acida* fruits under controlled conditions, and in which seeds ingested by birds are tested for viability.

Lannea fruits seem to be included in the diets of African primates where available (Lieberman *et al.* 1979; Norton *et al.* 1987; Kasparek 2000; Poulsen *et al.* 2001; Warren 2003). Given the short fruiting period, *Lannea* fruits make up an important part of baboon diet in CNP relative to other fruit species, accounting for 3 % of baboon feeding observations across a 24-month study period (see Kunz & Linsenmair 2008b). In contrast to most birds, primates were recorded infrequently in *L. acida* trees. However, whenever a group of primates visits a tree it consumes a comparatively large quantity of fruits. A baboon group of mean size in CNP (15 individuals, Kunz & Linsenmair 2008b), eats 5,200 *L. acida* fruits on average per feeding visit, representing 9% of all fruits removed from an average crop (Kunz, unpubl. data). Because we have no evidence that baboons chewed *L. acida* seeds (i.e. no seed fragments turned up in faecal samples) we suppose that baboons disperse the vast majority of *L. acida* seeds they consume. The fact that we found only a relatively small number of *L. acida* seeds in baboon faecal samples, despite the high estimated number of seeds consumed per group per visit to a fruiting tree, might be the consequence of the infrequent and irregular feeding visits to *L. acida* trees, different amounts of fruit consumed by different baboon individuals on different days and, naturally, incomplete sampling of all the faeces deposited by the baboons, rather than indicating generally low dispersal rates by baboons.

Feeding visits by baboons to fruiting *L. acida* individuals are not frequent enough to deplete entire tree crops. Thus it seems unlikely that feeding competition with primates is leading to changes in bird fruit choice. Further, primates, i.e. baboons, seem to visit trees more often after the onset of maturation. Germination success of *L. acida* seeds dispersed by olive baboons was high and enhanced in comparison with seeds from fresh ripe fruits. This could, however, be an artefact of differences in fruit choice between primates and researchers. Many frugivorous primates do not take fruits at random (Howe & vande Kerckhove 1981; Garber & Kitron 1997; Stevenson *et al.* 2005; Kunz & Linsenmair 2007). If baboons predominantly consume fruits that are at the very peak of (seed) maturation, germination success of ingested seeds should be higher than those of seeds from randomly selected ripe fruits.

Most species of Anacardiaceae have drupaceous fruit and are mainly distributed within the tropics and subtropics (Hutchinson *et al.* 1954-1968). In accordance with the concept of the 'dispersal syndrome' (Charles-Dominique 1993; Herrera 2002), smaller fruited-species of the Anacardiaceae with red-coloured drupes seem to be commonly dispersed by birds, e.g. *Pistacia* spp. (Jordano 1989; Izhaki *et al.* 1991; Traveset 1994), *Rhus trichocarpa* (Nishi & Tsuyuzaki 2004; Osada 2005), or *Schinus terebinthifolius* (Hasui & Hofling 1998), though consumption of these fruits by mammals is not excluded. Larger fruits of this family seem to be frequently consumed by mammals including elephants, primates, and bats, e.g. *Spondidas* spp. (Galindo-Gonzalez 1998; Stevenson *et al.* 2005), *Antrocaryon* spp. (Nchanji & Plumptre 2003; Wang *et al.* 2007), or *Trichoscypha* spp. (Nchanji & Plumptre 2003). *L. acida* has fruit characteristic of the bird-dispersal syndrome and in fact many bird species consume its fruits. Although the sample size of focal trees was small, the study showed that birds, which otherwise may be legitimate seed dispersers, can predominantly consume green, unripe fruits from individual plants at least in certain years, thereby potentially acting as pre-dispersal seed predators. So far, pre-dispersal seed predation by birds has mainly been considered in terms of seed-eating species, e.g. parrots (Galetti & Rodrigues 1992; Norconk *et al.* 1997). Though many birds tend to avoid green and unripe fruit in choice experiments, the effect of these traits on fruit choice by birds may change with varying natural conditions. The role of non-granivorous birds as seed predators for the fitness of fleshy-fruited plants thus requires more careful investigation in long-term studies. On the other hand, primates are often considered crucial dispersers for large-seeded tree species (e.g. Howe 1984; Kitamura *et al.* 2002), but their importance for plants with small fruit should not be overlooked.

7.1.6 ACKNOWLEDGEMENTS

We thank S. Berger and S. Luedemann who helped in collecting field data. M. Abs measured bill widths from bird specimens in the Natural History Museum, Berlin. Y. Warren made helpful comments on an earlier draft of the manuscript. Research permission for the CNP was kindly granted by the Ministère de l'Agriculture et des Ressources Animales and the Ministère de l'Enseignement Supérieure et de la Recherche Scientifique, Abidjan. The study was funded by PhD scholarships from the German Academic Exchange Service (DAAD) and the University of Würzburg (HSP III). The research camp in CNP was constructed with generous funds from the Volkswagen-Foundation.

7.1.7 REFERENCES

Arbonnier, M. 2000. *Arbres, arbustres et lianes des zones sèches d'Afrique de l'Ouest.* Muséum National d'Histoire Naturelle, Paris.

Balasubramanian, P. 1996. Interactions between fruit-eating birds and bird-dispersed plants in the tropical dry evergreen forest of point Calimere, South India. *Journal of the Bombay Natural History Society* 93: 428-441.

Barnea, A., Yom, T. Y. & Friedman, J. 1990. Differential germination of two closely related species of *Solanum* in response to bird ingestion. *Oikos* 57: 222-228.

Bleher, B., Potgieter, C. J., Johnson, D. N. & Böhning-Gaese, K. 2003. The importance of figs in a South African coastal forest. *Journal of Tropical Ecology* 19: 375-386.

Borrow, N. & Demey, R. 2001. *The guide to the birds of Western Africa.* Princeton University Press, Princeton.

Broschat, T. K. & Donselman, H. 1987. Effects of fruit maturity, storage, presoaking, and seed cleaning on germination in three species of palms. *Journal of Environmental Horticulture* 5: 6-9.

Brown, L. H., Urban, E. K., Newman, K., Fry, C. H. & Keiths, S. 1982-1992. *The birds of Africa.* Vol. I-IV. Academic Press, London.

Charles-Dominique, P. 1993. Speciation and coevolution: an interpretation of frugivory phenomena. *Vegetatio* 107: 75-84.

Cordeiro, N. J. & Howe, H. F. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences of the United States of America* 100: 14052-14056.

Djossa, B. A., Fahr, J., Kalko, E. K. V. & Sinsin, B. A. 2008. Fruit selection and effects of seed handling by flying foxes on germination rates of shea trees, a key resource in northern Benin, West Africa. *Ecotropica* 14: 37-48.

Farwig, N., Böhning-Gaese, K. & Bleher, B. 2006. Enhanced seed dispersal of *Prunus africana* in fragmented and disturbed forests? *Oecologia* 147: 238-252.

FGU-Kronberg. 1979. Gegenwärtiger Status der Comoé- und Tai-Nationalparks sowie des Azagny-Reservats und Vorschläge zu deren Erhaltung und Entwicklung zur Förderung des Tourismus. Technical Report. Deutsche Gesellschaft für Technische Zusammenarbeit GmbH, Eschborn.

Fischer, F., Groß, M. & Kunz, B. 2000. Primates of the Comoé National Park, Ivory Coast. *African Primates* 4: 10-15.

Fischer, F., Groß, M. & Linsenmair, K. E. 2002. Updated list of the larger mammals of the Comoé National Park, Ivory Coast. *Mammalia* 66: 83-92.

Foster, M. S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* 58: 73-85.

Foster, M. S. 1990. Factors influencing bird foraging preferences among conspecific fruit trees. *The Condor* 92: 844-854.

Galetti, M. & Rodrigues, M. 1992. Comparative seed predation on pods by parrots in Brazil. *Biotropica* 24: 222-224.

Galindo-Gonzalez, J. 1998. Seed dispersion by fruit bats: its importance in the conservation and regeneration of tropical forests. *Acta Zoológica Mexicana (n.s.)* 73: 57-74.

Garber, P. A. & Kitron, U. 1997. Seed swallowing in tamarins: evidence of a curative function or enhanced foraging efficiency? *International Journal of Primatology* 18: 523-538.

Gautier-Hion, A., Duplantier, J. M., Quris, R., Feer, F., Sourd, C., Decoux, J. P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C. & Thiollay, J. M. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65: 324-337.

Giles, S. & Lill, A. 1999. The effect of fruit abundance, conspicuousness and sugar concentration on fruit colour choice by captive silvereyes. *Ethology, Ecology & Evolution* 11: 229-242.

Githiru, M., Lens, L., Bennur, L. A. & Ogol, C. P. K. O. 2002. Effects of site and fruit size on the composition of avian frugivore assemblages in a fragmented Afrotropical forest. *Oikos* 96: 320-330.

Hasui, E. & Hofling, E. 1998. Food preference of the frugivorous birds in a fragment of semideciduous forest, Sao Paulo, Brazil. *Iheringia Série Zoologia* 84: 43-64.

Herrera, C. M. 2002. Seed dispersal by vertebrates. Pp. 185-208 In Herrera, C. M. & Pellmyr, O. (eds.). *Plant-animal interactions. An evolutionary approach.* Blackwell, Oxford.

Honkavaara, J., Siitari, H. & Viitala, J. 2004. Fruit colour preferences of redwings (*Turdus iliacus*): experiments with hand-raised juveniles and wild-caught adults. *Ethology* 110: 445-457.

Hovestadt, T. 1997. Fruchtmerkmale, endozoochore Samenausbreitung und ihre Bedeutung für die Zusammensetzung der Pflanzengemeinschaft. Untersuchungen im Wald-Savannenmosaik des Comoé Nationalparks, Elfenbeinküste. PhD thesis. University of Würzburg, Germany.

Hovestadt, T., Yao, P. & Linsenmair, K. E. 1999. Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoé National Park, Ivory Coast). *Plant Ecology* 144: 1-25.

Howe, H. F. 1984. Implications of seed dispersal by animals for tropical reserve management. *Biological Conservation* 30: 261-281.

Howe, H. F. & vande Kerckhove, G. A. 1981. Removal of wild nutmeg *Virola surinamensis* crops by birds. *Ecology* 62: 1093-1106.

Hutchinson, J., Dalziel, J. M. & Keay, R. W. J. 1954-1968. *Flora of West Tropical Africa.* Vols. I-III. Crown Agents for Oversea Governments and Administrations, London.

Izhaki, I., Walton, P. B. & Safriel, U. N. 1991. Seed shadows generated by frugivorous birds in an eastern Mediterranean scrub. *Journal of Ecology* 79: 575-590.

Izhaki, I. 2002. The role of fruit traits in determining fruit removal in an East Mediterranean ecosystem. Pp. 161-176 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution, and conservation.* CABI, Wallingford.

Jordano, P. 2000. Fruits and frugivory. Pp. 125-165 In Fenner, M. (ed.). *Seeds. The ecology of regeneration in plant communities.* CABI, Wallingford.

Jordano, P. 1989. Pre-dispersal biology of *Pistacia lentiscus* Anacardiaceae: cumulative effects on seed removal by birds. *Oikos* 55: 375-386.

Kasparek, M. 2000. *Flore du Parc National de Tai (Côte d'Ivoire).* Kasparek, Heidelberg.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T. & Noma., N. 2002. Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia* 133: 559-572.

Knight, R. S. & Siegfried, W. R. 1983. Interrelationships between type, size and color of fruits and dispersal in Southern African trees. *Oecologia* 56: 405-412.

Kunz, B. K. & Linsenmair, K. E. 2007. Changes in baboon feeding behavior: maturity dependent fruit and seed size selection within a food plant species. *International Journal of Primatology* 28: 819-835.

Kunz, B. K. & Linsenmair, K. E. 2008a. The role of the olive baboon (*Papio anubis*, Cercopithecidae) as seed disperser in a savanna-forest mosaic of West Africa. *Journal of Tropical Ecology* 24: 235-246.

Kunz, B. K. & Linsenmair, K. E. 2008b. The disregarded West: diet and behavioural ecology of olive baboons in the Ivory Coast. *Folia Primatologica* 79: 31-51.

Levey, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. *The American Naturalist* 129: 471-485.

Lieberman, D., Hall, J. B., Swaine, M. D. & Lieberman, M. 1979. Seed dispersal by baboons in the Shai Hills, Ghana. *Ecology* 60: 65-75.

Lieberman, M. & Lieberman, D. 1986. An experimental study of seed ingestion and germination in a plant-animal assemblage in Ghana. *Journal of Tropical Ecology* 2: 113-126.

Mackworth-Praed, C. W. & Grant, C. H. B. 1970-1973. *Birds of West Central and Western Africa*. Vols. I-II. Longman, London.

McGrew, W. C., Baldwin, P. J. & Tutin, C. E. G. 1988. Diet of wild chimpanzees (*Pan troglodytes verus*) at Mt. Assirik, Senegal: I. Composition. *American Journal of Primatology* 16: 213-226.

McPherson, J. M. 1988. Preference of cedar waxwings in the laboratory for fruit species, colour and size: a comparison with field observations. *Animal Behaviour* 36: 961-969.

Mess, A. & Krell, F. T. 1999. Preliminary list of rodents and shrews living in the Comoé National Park, Ivory Coast (Mammalia: Rodentia, Insectivora: Soricidae). Stuttgarter Beiträge zur Naturkunde Serie A: 1-11.

Messner, S. 1996. Untersuchungen zur Biodiversität der Myrmecofauna (Formicidae) im Parc National de la Comoé (Elfenbeinküste). Diploma thesis. University of Würzburg, Germany.

Nchanji, A. C. & Plumptre, A. J. 2003. Seed germination and early seedling establishment of some elephant-dispersed species in Banyang-Mbo Wildlife Sanctuary, south-western Cameroon. *Journal of Tropical Ecology* 19: 229-237.

Nishi, H. & Tsuyuzaki, S. 2004. Seed dispersal and seedling establishment of *Rhus trichocarpa* promoted by a crow (*Corvus macrorhynchos*) on a volcano in Japan. *Ecography* 27: 311-322.

Norconk, M. A., Wertis, C. & Kinzey, W. G. 1997. Seed predation by monkeys and macaws in Eastern Venezuela: preliminary findings. *Primates* 38: 177-184.

Norton, G. W., Rhine, R. J., Wynn, G. W. & Wynn, R. D. 1987. Baboon diet: a five-year study of stability and variability in plant feeding and habitat of the yellow baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. *Folia Primatologica* 48: 78-120.

Osada, N. 2005. Influence of between-year variation in the density of *Rhus trichocarpa* fruits on the removal of fruit by birds. *Plant Ecology* 176:195-202.

Poilecot, P. 1991. *Un écosystème de savane soudanienne: le Parc National de la Comoé (Côte d'Ivoire).* UNESCO, Paris, France.

Porembski, S. 1991. Beiträge zur Pflanzenwelt des Comoé-Nationalparks (Elfenbeinküste). *Natur und Museum* 121: 61-82.

Porembski, S. 2001. Phytodiversity and structure of the Comoé river gallery forest (NE Ivory Coast). Pp. 1-10 In Gottsberger, G. & Liede, S. (eds.). *Life forms and dynamics in tropical forests.* Dissertationes Botanicae. Borntraeger, Berlin.

Poulsen, J. R., Clark, C. J. & Smith, T. B. 2001. Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. *Journal of Tropical Ecology* 17: 787-808.

Rheindt, F. E., Grafe, T. U. & Linsenmair, K. E. 2002. New bird records in Comoé National Park, Ivory Coast. *Malimbus* 24: 38-40.

Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223-225.

Salewski, V. 2000. The birds of Comoé National Park, Ivory Coast. *Malimbus* 22: 55-76.

Salewski, V. & Göken, F. 2001. Black-and white mannikin *Lonchura bicolor*, new for Comoé National Park, Ivory Coast. *Malimbus* 23: 56.

Sanders, M. J., Owen-Smith, R. N. & Pillay, N. 1997. Fruit selection in the olive thrush: the importance of colour. *South African Journal of Zoology* 32: 21-23.

Schaefer, H. M. & Schaefer, V. 2006. The fruits of selectivity: how birds forage on *Goupia glabra* fruits of different ripeness. *Journal of Ornithology* 47: 638-643.

Schaefer, H. M., Schaefer, V. & Levey, D. J. 2004. How plant-animal interactions signal new insights in communication. *Trends in Ecology & Evolution* 19: 577-584.

Schaefer, H. M., Schmidt, V. & Winkler, H. 2003. Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. *Oikos* 102: 318-328.

Schmidt, V., Schaefer, H. M. & Winkler, H. 2004. Conspicuousness, not colour as foraging cue in plant-animal signalling. *Oikos* 106: 551-557.

Schmidt, W. 1973. Vegetationskundliche Untersuchungen im Savannenreservat Lamto (Elfenbeinküste). *Plant Ecology* 28: 145-200.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108: 15-29.

Serle, W. & Morel, G. 1977. *Birds of West Africa.* Collins, London.

Steentoft, M. 1988. *Flowering plants in West Africa*. Cambridge University Press, Cambridge.

Stevenson, P. R., Pineda, M. & Samper, T. 2005. Influence of seed size on dispersal patterns of woolly monkeys (*Lagothrix lagothricha*) at Tinigua Park. *Oikos* 110: 435-440.

Thomas D. W. 1982. The ecology of an African savanna fruit bat community: resource partitioning and role in seed dispersal. PhD thesis. University of Aberdeen, UK.

Traveset, A. 1994. Influence of type of avian frugivory on the fitness of *Pistacia terebinthus* L. *Evolutionary Ecology* 8: 618-627.

van der Pijl, L. 1982. *Principles of dispersal in higher plants*. Springer, Berlin, Germany.

von Maydell, H.J. 1990. *Trees and shrubs of the Sahel. Their characteristics and uses.* Josef Margraf, Weikersheim.

Wang, B. C., Sork, V. L., Leong, M. T. & Smith, T.B. 2007. Hunting of mammals reduces seed removal and dispersal of the Afrotropical tree *Antrocaryon klaineanum* (Anacardiaceae). *Biotropica* 39: 340-347.

Warren, Y. 2003. Olive baboons (*Papio cynocephalus anubis*): behaviour, ecology and human conflict in Gashaka Gumti National Park, Nigeria. PhD thesis. University of Surrey, Roehampton, UK.

Weir, J. E. S. & Corlett, R. T. 2006. How far do birds disperse seeds in the degraded tropical landscape of Hong Kong, China? *Landscape Ecology* 22: 131-140.

White, F. 1983. *The vegetation of Africa.* UNESCO, Paris.

Willson, M. F. & Whelan, C. J. 1990. The evolution of fruit color in fleshy-fruited plants. *The American Naturalist* 136: 790-809.

Appendix 1 Species observed feeding on fruits or seeds of *L. acida* in the Comoé National Park, Ivory Coast

Bird names and diets follow Borrow & Demey (2001); Diet: f = fruits, s = seeds, i = insects, n = nectar, o = omnivorous; FT (fruit treatment): W = swallower, K = pulp pecker, SE = seed eater, ? = unclear; Records: [x] = species were observed in 1999-2000 in trees other than the two focal ones.

					Species recorded in	
	Common name	**Scientific name**	**Diet**	**FT**	**1991-93**	**1998-00**
Birds						
Musophagidae	Green Turaco	*Tauraco persa*	f	W		x
	Western grey plantain-eater	*Crinifer piscator*	f	W		x
Phoeniculidae	Black wood-hoopoe	*Rhinopomastus aterrimus*	i	?	x	
Bucerotidae	Piping hornbill	*Bycanistes fistulator*	f, i	W	x	[x]
	Black-and-white-casqued hornbill	*B. subcylindricus*	f, i	W	x	
Capitonidae	Yellow-rumped tinkerbird	*Pogoniulus bilineatus*	f	W		x
	Yellow-fronted tinkerbird	*P. chrysoconus*	f	W	x	x
	Vieillot's barbet	*Lybius vieilloti*	f		x	
Pycnonotidae	Western bearded greenbul	*Criniger barbatus*	f, i	W	x	
	Common bulbul	*Pycnonotus barbatus*	f, i	W	x	x
Turdidae	African thrush	*Turdus pelios*	f, i	W	x	x
Platysteiridae	Senegal batis	*Batis senegalensis*	i	W?		x
Nectariniidae	Splendid sunbird	*Cinnyris coccinigaster*	n, i	K	x	
Zosteropidae	Yellow white-eye	*Zosterops senegalensis*	i, n, f	K	x	
Sturnidae	Bronze-tailed glossy starling	*Lamprotornis cf. chalcurus*	o	W		[x]
	Lesser blue-eared starling	*L. chloropterus*	o	W		[x]
	Violet-backed starling	*Cinnyricinclus leucogaster*	o	W	x	x
Ploceidae	Black-necked weaver	*Ploceus nigricollis*	s, i	K	x	
	Heuglin's masked weaver	*P. heuglini*	s, i	K	x	
	Village weaver	*P. cucullatus*	s, i	W		x
Fringillidae	Yellow-fronted canary	*Serinus mozambicus*	s	K	x	x
Emberizidae	Cabanis's bunting	*Emberiza cabanisi*	s	K		x
Mammals						
Sciuridae	Red-legged sun squirrel	*Heliosciurus rufobrachium*	s	SE	x	x
Cercopithecidae	White-crowned mangabey	*Cercocebus a. lunulatus*	o	W		x
	Lowe's monkey	*Cercopithecus c. lowei*	o	W		x
	Lesser spot-nosed monkey	*C. petaurista*	o	W		x
	Olive baboon	*Papio anubis*	o	W	x	x

Chapter 7 (continued)

7. 2 Fruit Removal and Seed Predation in two African Trees (*Lannea acida* and *Lannea welwitschii*, Anacardiaceae)

with K. E. Linsenmair

(Submitted)

Abstract Fruit removal is an important component of plant fitness. We investigated the role of different frugivores in removal efficiency of two small-fruited trees, *Lannea acida* and *L. welwitschii* (Anacardiaceae), at Comoé National Park, north-eastern Ivory Coast.

At least twelve bird species, the red-legged sun squirrel (*Heliosciurus rufobrachium*) and four primate species consumed the fruits of the *L. acida* focal tree. Crop removal efficiency varied between 21% and 30% in two consecutive years. Up to 100% of the harvest and fruit fall were unripe fruits. Removal efficiency in *L. welwitschii* was higher (48.5%) despite lower visitation rates and only two species observed feeding. Most *L. welwitschii* fruits were removed during and after maturation but pre-dispersal seed predation by *H. rufobrachium* left only 19.9% of the total crop to potential seed dispersal. In contrast, *H. rufobrachium* rarely fed on *L. acida* seeds.

Sun squirrels consumed about twice (*L. acida*) to ten times as much (*L. welwitschii*) fruits (seeds) per visit than birds. Primates removed 20 to 30 times more *L. acida* fruits and about 30 times more *L. welwitschii* fruit per visit than birds, but birds are able to compensate for lower food intake per visit by visiting a feeding tree more frequently. Birds and primates may thus both be important seed dispersers of *Lannea* seeds in terms of quantity.

As a consequence of the large amount of unripe fruit fall and high pre-dispersal seed predation by vertebrates the reproductive output of the focal trees during the study period in terms of dispersed seeds was low. Regeneration in *L. acida* and *L. welwitschii* might thus be source limited as well as dissemination limited, at least in certain years. Because interannual and intraspecific variation in fruit removal can be substantial, further research is required to determine long-term reproductive output in the two species.

7.2.1 INTRODUCTION

Fruit removal by frugivores is a prerequisite of seed dispersal in animal-dispersed plants and thus an important component of plant fitness (Jordano 2000; Izhaki 2002). Removal efficiency, i.e. the proportion of the total fruit crop removed from an individual plant, provides a first estimate of seed-dispersal success relative to the number of fruits produced by the plant (reviewed in Izhaki 2002). Fruit removal, however, does not necessarily equate effective dispersal (*sensu* Schupp 1993). For example, fruits may be removed before maturation of seeds or seeds may be destroyed during consumption. Frugivores can largely differ in the overall amount of fruits they remove from a plant and in the number of seeds they disperse according to variation in the number of visits made to the plant and the number of fruits removed per visit (reviewed in Schupp 1993; Jordano & Schupp 2000). Yet, quantitative data, particularly on African tree species and their fruit consumers, are rare.

We investigated removal efficiency in the two dioecious trees, *Lannea acida* A. Rich. and *L. welwitschii* (Hiern) Engl. (Anacardiaceae). *L. acida* is widespread throughout West-African savannas and may also occur along forest edges (Hovestadt 1997; Arbonnier 2000). *L. welwitschii*, the only West African forest species in the genus, occurs from Ivory Coast to Angola, Uganda and Gabon (Hutchinson *et al.* 1954-1968; Steentoft 1988). Fruiting starts at the end of the dry season/beginning of the rainy season when trees are leafless, and lasts one to two months in both species. The small, single-seeded drupes (average size *L. acida* 9.6 x 8.5 mm, *L. welwitschii* 8.6 x 6.8 mm, Kunz, unpubl. data) are edible and are clustered in infructescences. Drupes appear dark-purple (*L. acida*) to purple-black (*L. welwitschii*) to the human eye when mature.

In the Comoé National Park (CNP), north-eastern Ivory Coast, at least 23 bird and five mammal species (the sun squirrel *Heliosciurus rufobrachium* and four primate species) feed on fruits or seeds of *L. acida* and/or *L. welwitschii* (Hovestadt 1997; Kunz & Linsenmair, in press). There were no indications of nocturnal fruit consumers (Hovestadt 1997; Kunz & Linsenmair, in press). In the present paper we provide data on the quantitative contribution of the consumers to fruit removal and seed dispersal in both trees.

7.2.2 METHODS

The study site was situated in the Southwest of the CNP (08°30-09°36' N, 003°07'-004°25' W), north-eastern Ivory Coast. The vegetation comprises a mosaic of savanna, forest islands and gallery forest and is described in more detail elsewhere (Poilecot 1991; Porembski 1991, 2001; Hovestadt *et al.* 1999). The climate is characterized by a dry season from November to March. Mean annual precipitation from January 1994 to December 1999 was 1,053 mm year^{-1}. The CNP harbours a rich flora and fauna. So far, 498 bird species (Salewski 2000; Salewski & Göken 2001; Rheindt *et al.* 2002) and 152 mammal species have been recorded (Poilecot 1991; Mess & Krell 1999; Fischer *et al.* 2000; Fischer *et al.* 2002).

We monitored fruit removal by frugivores in one *L. acida* tree (Laac1) in 1999 and 2000 and in one *L. welwitschii* tree (Lawe) in 2000. Trees were 13 and 12 m high; dbh (at 1.20 m) was 66.0 and 45.5 cm, respectively. Both trees were situated at the forest edge within 50 m from each other and were chosen with regards to fruiting and good visibility of the crown.

To determine removal efficiency of each tree, we estimated each tree's fruit crop at the onset and end of the study as well as fruit fall per tree prior to study onset and during the study. The first crop size estimation took place when crops were unripe (Laac, at 21 March 1999 and 2000) or at the very start of maturation (Lawe, at 14 April 2000). We multiplied the average fruit number from a minimum of five infructescences by the mean number of infructescences from four branches of similar size and the number of equal branches of the tree. Infructescences and branches were selected haphazardly.

We considered fruit fall prior to study onset by counting the number of fallen fruits in two quadrants (30 x 30 cm) randomly placed within each 45° angle beneath the crown and extrapolated the mean fruit number over all quadrants to the crown area projected to the ground (CAG). A tree's CAG was calculated from the area spanned by lines connecting the peripheral points of the tree crown measured at 45° angles from the trunk.
As we did not note any remarkable activity of fruit consumers in the trees prior to study onset, we equated the number of fruits on each tree plus the fruit fall up to that time with total fruit production.

Six 1m^2-fruit traps placed randomly under each tree at one meter height documented fruit fall throughout the study. We emptied the traps every other day and categorized fallen fruits as either unripe (green to greenish-purple) or mature (purple to purple-black). Fruits with seeds emptied by squirrels were counted separately, whatever state of maturity. We extrapolated the mean number of fruits and predated seeds, respectively, to the CAG. Fruit trapping terminated when the crop was reduced to $< 5\%$ of its total fruit production or when fruits remaining on the tree desiccated and were no longer attractive to frugivores (Laac1: 21 April 1999 and 5 April 2000, *L. welwitschii*: 12 June 2000).

To obtain data on visitation rates and food intake by frugivores, we observed the trees between 6:00 a.m. and 7:00 p.m. for three to five hours daily. Observation hours were about evenly distributed across daytime hours. We observed Laac1 during the same period in which fruit trapping took place (63 hours in 1999, 53 hours in 2000). To increase the number of feeding observations we likewise monitored a neighbouring *L. acida* tree (Laac2) in 1999 for another 45 hours. Observations of Lawe started with fruit trapping and ended on 3 May 2000 after constantly low visitation rates (< 2 / hour) had not increased significantly during three weeks of observation (totalling 44 observation hours).

Observation distance to all focal trees was about 20 m, where we were partly screened from view by other trees. Diurnal nonhuman primates inhabiting the site were used to the presence of researchers. We scanned a tree's crown every five minutes for one minute, using binoculars. Identification of foraging species was verified using Mackworth-Praed & Grant (1970-1973), Serle & Morel (1977), Brown *et al.* (1982-1992), Kingdon (1997), and Borrow & Demey (2001).

Further data collection and analyses focused on species that removed entire fruits (in birds: swallowers, which swallow fruits entirely). We assessed each foraging individual seen in a given scan as one record, and calculated the mean hourly number of records per tree and year.

In between scans, we noted the individuals' length of stay as well as the number of fruits (seeds) consumed per minute. We assessed removal effectiveness of animal species based on the average number of fruits/seeds consumed per minute, the mean length of stay, and the mean number of feeding visits over all observation hours per tree species (Schupp 1993; Cordeiro *et al.* 2004).

Many primate species occupy large home ranges and infrequently return to the same feeding tree. To increase sample size on food intake and length of feeding stays of primates, we included data from two habituated olive baboon groups in CNP as well as occasional observations of other primate species, in *L. acida* and *L. welwitschii* trees other than the focal ones (Kunz & Linsenmair 2008; Kunz & Linsenmair, in press).

7.2.3 RESULTS

Crop sizes, fruit fall and the total amount of fruit removal from the focal trees Laac1 and Lawe are displayed in (Table 1). Most fruit fell beneath the crown. Between 82% (Lawe) and to 100% (Laac1) of the fruit fall was of unripe fruit. We observed twelve bird species, the red-legged sun squirrel (*Heliosciurus rufobrachium*) and two primate species feeding on *L. acida* fruits in 1999 (Appendix 1). Removal efficiency of Laac1 in this year was 30%. In 2000, we recorded five bird species, the red-legged sun squirrel and three primate species. Removal efficiency (21%) was lower than in the previous year.

In both years, birds visited *L. acida* trees more regularly, and more often per hour than sun squirrels and primates, who in turn visited the trees for longer feeding sessions (Table 2). However, birds other than village weavers (*Ploceus cucullatus*), starlings (*Cinnyricinclus leucogaste*r, *Lamprotornis sp.)*, common bulbuls (*Pycnonotus barbatus*), and African thrushes (*Turdus pelios*) were rarely observed.

We recorded only *P. barbatus* and *H. rufobrachium* feeding in *L. welwitschii*, but broken branches and torn-off infructescences beneath the crown indicated feeding visits by primates outside observation hours. Despite the overall low visitation rate, removal efficiency (48.5%) was higher than in Laac1, and most fruits were removed during and after maturation. Yet, seed eating by *H. rufobrachium* accounted for more than half of the total fruit removal from Lawe, corresponding to pre-dispersal seed predation of over one-quarter of the total fruit crop. In contrast, *H. rufobrachium* was rarely observed in *L. acida* (Table 2) and predated seeds did fail to turn up in seed traps in either year.

Sun squirrels consumed about twice (*L. acida*) to ten times as much (*L. welwitschii*) fruits (seeds) per visit than birds. Primates removed 20 to 30 times more *L. acida* fruits and about 30 times more *L. welwitschii* fruits per visit than birds (Table 2).

Table 1 Fruit production, fruit fall and fruit removal from *L. acida* (Laac1) in 1999 and 2000 and *L. welwitschii* (Lawe) in 2000

Study periods: Laac1 21 March to 21 April 1999 and 21 March to 5 April 2000; Lawe 14 April to 12 June 2000. Number of fruits estimated to the nearest hundred. CAG: crown area projected to the ground.

	Laac1 (1999)	**Laac1 (2000)**	**Lawe (2000)**
CAG [m^2]	140.1	134.3	123.5
Fruit fall prior to study onset	60,200	38,100	11,000
Crop size at study onset	187,600	157,500	154,400
Total fruit production	**247,800**	**195,600**	**165,400**
Fruit fall during study	104,600	113,800	74,200
Total fruit fall*(%)	**164,800 (66.5)**	**151,900 (77.7)**	**85,200 (51.5)**
Unripe fruit fall (%)*	65.1	77.7	42
Fruit crop size at end of study	8,200	2,000	10
Removal efficiency [%] (n)	**30.2 (74,800)**	**21.3$^{\#}$ (41,700)**	**48.5^{x} (80,190)**

*: referring to total fruit production including fruit fall prior to study onset; $^{\#}$: all fruits removed were unripe; ^{x}: 59% of the removed fruits (28.6% of total crop) were predated by *H. rufobrachium*

Table 2 Estimated fruit consumption of bird and mammal species in *L. acida* and *L. welwitschii* trees

* observations in Laac1 and Laac2 are pooled. When data on fruit consumption included trees other than the focal ones superscript numbers in brackets $^{()}$ indicate the number of observations in the focal tree

	Birds					**Mammals**				
	P. barbatus	*T. pelios*	*Lamprotornis sp.*	*C. leucogaster*	*P. cucullatus*	*H. rufobrachium*	*C. t. lunulatus*	*C. m. lowei*	*C. petaurista*	*P. anubis*
L. acida										
Mean n^{o}. of fruits / min* ± *sd*	4.5 ± 1.7	4.5 ± 2.8	1.7 ± 0.5	2.7 ± 2.1	3.1 ± 2.0	3.2 ± 0.8	22.0 ± 7.0	-	19.7 ± 3.5	19.4 ± 7.8
N^{o} of observations	47	10	6	32	21	10	22	-	3	$42^{(11)}$
Mean length of stay [min] ± *sd*	3.6 ± 2.6	2.3 ± 1.8	-	3.3 ± 2.7	3.1 ± 1.2	11.5 ± 5.9	9.5 ± 5.4	-	12.0 ± 1.4	19.3 ± 14.5
N^{o} of observations	53	18	-	15	13	6	6	-	2	$30^{(6)}$
Mean n^{o}. of fruits / stay	16.4	10.4	-	8.8	9.8	36.8	209.5	-	236.0	346.1
Laac1										
Mean n^{o}. of records / h (1999 & 2000)	2.30	0.79	-	0.81	1.27	0.09	0.44	0.05	0.02	0.35
Mean n^{o}. fruits / observation h	37.6	8.2		7.2	12.4	3.3	92.1	-	4.7	121.1
Laac2										
Mean n^{o}. of records / h (1999 & 2000)	0.28	0.15	-	0.03	0.88	0.13	0.01	-	-	-
Mean n^{o}. fruits / observation h	4.6	1.5	-	0.3	8.6	4.8	2.3	-	-	-
L. welwitschii (*Lawe*)										
Mean n^{o}. of fruits / min ± *sd*	3.8 ± 1.3	-	-	-	-	5.9 ± 1.8	-	-	-	28.7 ± 11.9
N^{o} of observations	6	-	-	-	-	20	-	-	-	$62^{(0)}$
Mean length of stay [min] ± *sd*	4.4 ± 2.1	-	-	-	-	30.3 ± 14.1	-	-	-	16.0 ± 8.1
N^{o} of observations	11	-	-	-	-	15	-	-	-	$7^{(0)}$
Mean n^{o}. of fruits / stay	16.7	-	-	-	-	177.5	-	-	-	459.8
Mean n^{o}. of records / h	0.54	-	-	-	-	0.41	-	-	-	-
Mean n^{o}. fruits / observation h	9.0	-	-	-	-	72.8	-	-	-	-

7.2.4 DISCUSSION

Fruit removal efficiency in both trees yielded less than 50% of the total crop. Though higher removal rates from woody plants are not uncommon (e.g. Jordano 1989; Korine *et al.* 2000; Ortiz-Pulido *et al.* 2007), in many animal dispersed tree species most fruits fall below the parent's canopy (Clark *et al.* 2005). Fruit fallen to the ground may be dispersed secondarily by ground foraging animals (Feer 1995; Brewer & Rejmanek 1999). In both focal trees, however, almost all fruit fall was of unripe fruit. As seeds from unripe *L. acida* and *L. welwitschii* fruits failed to germinate (Kunz & Linsenmair, in press, Kunz, unpubl. data) unripe fruit fall in the focal trees presumably has to be considered seed loss.

Twenty-two bird and five mammal species (four primates and the sun squirrel *H. rufobrachium*) were recorded feeding in *L. acida* in previous studies in CNP, compared to 13 bird and the same five mammal species in *L. welwitschii* (Hovestadt 1997; Kunz & Linsenmair, in press, Kunz, unpubl. data). Shinozaki curves showing the number of frugivorous bird species as a function of an increasing number of observed trees indicate that, like in the present study, generally more species are expected to feed on *L. acida* than on *L. welwitschii* fruits (Hovestadt 1997).

Nevertheless, the total fruit removal from Lawe (48.5%) was higher than from Laac1 (30.2% in 1999 and 21.3% in 2000), suggesting consumer visits to Lawe peaked outside observation hours. Torn-off infructescences and broken branches in fruit traps indicated that this is due partially to infrequent and irregular feeding visits by primates.
Primates generally removed more fruits per feeding visit than birds, but birds are able to compensate for lower food intake per visit by visiting a feeding tree more frequently. Birds and primates may thus both be important seed dispersers in terms of quantity. During the study period, however, up to 100% of the fruit removal from Laac1 by birds and primates was unripe fruit and thus likely accounts for seed predation (Kunz & Linsenmair, in press). In Lawe most fruits were removed during and after maturation. Seed predation by *H. rufobrachium*, however, accounted for 28.6% of total crop size, leaving only 19.9% to potential seed dispersal.

As a consequence of a large amount of unripe fruit fall and the high pre-dispersal seed predation by vertebrates the reproductive output during the study period in terms of dispersed seeds was low, and in Laac1 in 2000 presumably zero. We had difficulties to find *Lannea* trees bearing ripe fruit in 2000 (particularly *L. acida*) for fruit size measurements (Kunz, unpubl. data) indicating that trees other than the focal ones were also depleted early in the fruiting period while crops were unripe. Keeping in mind the small sample size of this study, our data suggest that regeneration in individual *L. acida* and *L. welwitschii* trees may be source limited as well as dissemination limited (*sensu* Schupp, *et al.* 2002), at least in certain years. However, interannual and intraspecific variation in fruit removal can be substantial (reviewed in Izhaki 2002) and further research is required to determine long term reproductive output in the two species.

7.2.5 ACKNOWLEDGEMENTS

We thank S. Berger and S. Luedemann for field assistance. S. Berghoff made helpful comments on the manuscript. The "Ministère de l'Agriculture et des Ressources Animales" and the "Ministère de l'Enseignement Supérieure et de la Recherche Scientifique", Abidjan, kindly granted research permissions for CNP. The study was funded by PhD scholarships from the German Academic Exchange Service (DAAD) and the University of Wuerzburg (HSP III). The research camp in CNP was constructed with generous funds from the Volkswagen-Foundation.

7.2.6 REFERENCES

Arbonnier, M. 2000. *Arbres, arbustres et lianes des zones sèches d'Afrique de l'Ouest.* Muséum National d'Histoire Naturelle, Paris.

Borrow, N. & Demey, R. 2001. *The guide to the birds of Western Africa.* Princeton University Press, Princeton.

Brewer, S. W. & Rejmanek, M. 1999. Small rodents as significant dispersers of tree seeds in a Neotropical forest. *Journal of Vegetation Science* 10: 165-174.

Brown, L. H., Urban, E. K., Newman K., Fry, C. H. & Keith, S. 1982-1992. *The birds of Africa.* Vols. I-IV. Academic Press, London.

Clark, C. J., Poulsen, J. R., Bolker, B. M., Connor, E. F. & Parkerc, V. T. 2005. Comparative seed shadow of bird-, monkey-, and wind dispersed trees. *Ecology*: 86: 2684–2694.

Cordeiro, N. J, Patrick, D. A. G., Munsini, B. & Gupta, V. 2004. Role of dispersal in the invasion of an exotic tree in East African submontane forest. *Journal of Tropical Ecology* 20: 449-457.

Feer, F. 1995. Seed dispersal in African forest ruminants. *Journal of Tropical Ecology* 11: 683-689.

Fischer, F., Groß, M. & Kunz, B. 2000. Primates of the Comoé National Park, Ivory Coast. *African Primates* 4: 10-15.

Fischer, F., Groß, M. & Linsenmair, K. E. 2002. Updated list of the larger mammals of the Comoé National Park, Ivory Coast. *Mammalia* 66: 83-92.

Hovestadt, T. 1997. Fruchtmerkmale, endozoochore Samenausbreitung und ihre Bedeutung für die Zusammensetzung der Pflanzengemeinschaft. Untersuchungen im Wald-Savannenmosaik des Comoé Nationalparks, Elfenbeinküste. PhD thesis. University of Würzburg, Germany.

Hovestadt, T., Yao, P. & Linsenmair, K. E. 1999. Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoé National Park, Ivory Coast. *Plant Ecology* 144 :1-25.

Hutchinson, J., Dalziel, J. M. & Keay, R. W. J. 1954-1968. *Flora of West Tropical Africa.* Vols. I-III. Crown Agents for Oversea Governments and Administrations, London.

Izhaki, I. 2002. The role of fruit traits in determining fruit removal in an East Mediterranean ecosystem. Pp. 161-176 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation*. CABI, Wallingford.

Jordano, P. 1989. Pre-dispersal biology of *Pistacia lentiscus* Anacardiaceae: cumulative effects on seed removal by birds. *Oikos* 55: 375-386.

Jordano, P. 2000. Fruits and frugivory. Pp. 125-165 In Fenner, M. (ed.). *Seeds. The ecology of regeneration in plant communities.* CABI, Wallingford.

Jordano, P. & Schupp, E. 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* 70: 591-615.

Kingdon, J. 1997. *The Kingdon field guide to African mammals*. Academic Press, San Diego.

Korine, C., Kalko, E. K. V. & Herre, E. A. 2000. Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. *Oecologia* 123: 560-568.

Kunz, B. K. & Linsenmair, K. E. 2008. The disregarded West: diet and behavioural ecology of olive baboons in the Ivory Coast. *Folia Primatologica* 79: 31-51.

Kunz, B. K. & Linsenmair, K. E. In press. Variation of dispersal agents? Frugivore assemblages and fruit handling in a typical 'bird-dispersed' tree (*Lannea acida*, Anacardiaceae). *Ecotropica*.

Mackworth-Praed, C. W. & Grant, C. H. B. 1970-1973. *Birds of West Central and Western Africa.* Vols. I-II. Longman, London.

Mess, A. & Krell, F. T. 1999. Preliminary list of rodents and shrews living in the Comoé National Park, Ivory Coast (Mammalia: Rodentia, Insectivora: Soricidae). *Stuttgarter Beiträge zur Naturkunde Serie A*: 1-11.

Ortiz-Pulido, R., Albores-Barajas, Y. V. & Anaid-Diaz, S. 2007. Fruit removal efficiency and success: influence of crop size in a Neotropical treelet. *Plant Ecology* 189: 147-154.

Poilecot, P. 1991. *Un écosystème de savane soudanienne: le Parc National de la Comoé (Côte d'Ivoire).* UNESCO, Paris.

Porembski, S. 1991. Beiträge zur Pflanzenwelt des Comoé-Nationalparks (Elfenbeinküste). *Natur und Museum* 121: 61-82.

Porembski, S. 2001. Phytodiversity and structure of the Comoé river gallery forest (NE Ivory Coast). Pp 1-10 In Gottsberger, G. & Liede, S. (eds.). *Life forms and dynamics in tropical forests*. Dissertationes Botanicae. Borntraeger, Berlin.

Rheindt, F. E., Grafe, T. U. & Linsenmair, K. E. 2002. New bird records in Comoé National Park, Ivory Coast. *Malimbus* 24: 38-40.

Salewski, V. 2000. The birds of Comoé National Park, Ivory Coast. *Malimbus* 22: 55-76.

Salewski, V. & Göken, F. 2001. Black-and white mannakin *Lonchura bicolor*, new for Comoé National Park, Ivory Coast. *Malimbus* 23: 56.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108: 15-29.

Schupp, E. W., Milleron, T. & Russo, S. E. 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forests. Pp. 19-33 In Levey, D. J., Silva, W. R. & Galetti, M. (eds.). *Seed dispersal and frugivory: ecology, evolution and conservation.* CABI, Wallingford.

Serle, W. & Morel, G. 1977. *Birds of West Africa.* Collins, London.

Steentoft, M. 1988. *Flowering plants in West Africa*. Cambridge University Press, Cambridge.

Appendix 1 Species observed feeding on fruits or seeds of *L. acida* and *L. welwitschii* focal trees at Comoé National Park, Ivory Coast

			L. acida		***L. welwitschii***
	Common name	*Scientific name*	1999	2000	2000
Birds					
Musophagidae	Green Turaco	*Tauraco persa*	x		
	Western grey plantain-eater	*Crinifer piscator*	x		
Capitonidae	Yellow-rumped tinkerbird	*Pogoniulus bilineatus*	x		
	Yellow-fronted tinkerbird	*Pogoniulus chrysoconus*	x		
Pycnonotidae	Common bulbul	*Pycnonotus barbatus*	x	x	x
Turdidae	African thrush	*Turdus pelios*	x	x	
Platysteiridae	Senegal batis	*Batis senegalensis*	x		
Sturnidae	Bronze-tailed glossy starling	*Lamprotornis cf. chalcurus*	x		
	Violet-backed starling	*Cinnyricinclus leucogaster*	x	x	
Ploceidae	Village weaver	*Ploceus cucullatus*	x	x	
Fringillidae	Yellow-fronted canary	*Serinus mozambicus*	x	x	
Emberizidae	Cabanis's bunting	*Emberiza cabanisi*	x		
Mammals					
Sciuridae	Red-legged sun squirrel	*Heliosciurus rufobrachium*	x	x	x
Cercopithecidae	White-crowned mangabey	*Cercocebus t. lunulatus*	x	x	
	Lowe's monkey	*Cercopithecus m. lowei*		x	
	Lesser spot-nosed monkey	*Cercopithecus petaurista*		x	
	Olive baboon	*Papio anubis*	x		

Chapter 8

Habitat Differences in Dung Beetle Guilds (Coleoptera, Scarabaeidae) in the Savanna-Forest Mosaic of West Africa and Implications for Secondary Seed Dispersal from Baboon Faeces

with F. T. Krell and K. E. Linsenmair
(in prep.)

Abstract Dung beetles (Coleoptera, Scarabaeidae) of the roller and tunneler guild are important secondary dispersers of seeds from primate dung in tropical ecosystems; their activity can affect seed distribution locally and can increase the number of seeds that end up in safe sites. The probability and pattern of secondary seed dispersal by dung beetles depend on the structure and composition of the dung beetle community at the site of primary deposition, which, in turn, seems to be strongly determined by vegetation type. One would thus expect pronounced differences in secondary seed dispersal by dung beetles between forests and open habitats with potential implications for plant regeneration, but direct comparisons are rare. We provide for the first time comparative data on secondary seed dispersal by dung beetles in both forest and adjacent savanna in West Africa, using dung from the olive baboon (*Papio anubis* Lesson 1827, Cercopithecidae).

We found high dung beetle activity at baboon faeces from a total of 99 species, representing 26 genera. The number of dung beetle species in the gallery forest (N = 47) was about as high as species numbers attracted to primate dung in most studies in Neotropical forests, but in contrast to the Neotropics, species number (N = 85) and abundance in the study area were much higher in the open habitat. Most species showed a clear preference for one habitat. Within each habitat, the proportion of roller to tunneler species was 1 : 4, but the variation in the distribution of roller and tunneler individuals was highly significant between habitats. In the savanna, rollers and tunnelers each accounted for about 50%, whereas in the gallery forest tunnelers made up 96% of all individuals in the two guilds. A standardized RDA analysis showed that habitat clearly is the dominating factor explaining 15% of the variation in dung beetle assemblages at a highly significant level.

Both roller and tunneler species were larger in the savanna than in the forest, and nocturnal species were larger than diurnal ones. The higher abundance of rollers in the savanna and the larger beetle size resulted in faster removal of standardized dung portions.

Rollers dispersed a wide array of seed sizes (up to 18 mm) naturally present in baboon dung. Secondary dispersal distances were larger in the savanna. In contrast to other studies, small rollers were most active in dispersal of large seeds, which were seemingly mistaken for dung balls.

Our results indicate that in comparison with seeds dispersed by baboons into the forest, seeds that end up in the savanna generally (a) have a higher overall probability of being removed by dung beetles, (b) have a higher probability of being horizontally scattered by rollers, (c) are more likely of being rapidly removed from the place of primary deposition and (d) of being secondarily dispersed over larger distances. Size comparison between roller dung balls and seeds from baboon faeces suggests that dung beetles at the study site are capable of removing seeds from any plant species naturally dispersed in baboon dung.

8. 1 INTRODUCTION

Most tropical tree species produce seeds embedded in fleshy fruit for endozoochorous dispersal by frugivorous animals (Howe & Smallwood 1982). After primary dispersal by a frugivore, seeds may be exposed to a variety of potential post-dispersal hazards which can affect both seed and seedling survival. As a result, the probability for any seed to establish is very low (Wenny 2001, and references therein). Post-dispersal seed fate thus is a crucial aspect in understanding plant-frugivore interactions (Andresen 2003; Vander-Wall *et al.* 2005). Potential mortality risks of dispersed seeds include unfavourable conditions for germination and plant establishment, fungi and pathogen attack, and predation of seeds (Fenner & Thompson 2005). Faeces from frugivore mammals attract seed eating animals like rodents and ants. Post-dispersal predation of seeds can be severe (Andresen 1999; Feer 1999) and may reach 100% in some species (Chapman & Chapman 1996).

Many large frugivores deposit seeds in clumps leading to density-dependent mortality of seeds and seedlings (Howe 1989). Secondary seed dispersal can positively affect plant recruitment by reducing these risk factors (Chambers & MacMahon 1994; Andresen & Levey 2004).

Whereas rodents and ants may act as both, secondary dispersers and post-dispersal seed predators (reviewed in Vander-Wall *et al.* 2005), dung beetles (Coleoptera, Scarabaeidae) attracted to vertebrate dung use the faecal material as source of food for themselves and their larvae and do not feed on seeds. Dung beetles are globally distributed and are abundant both in tropical and warm temperate ecosystems (Hanski & Cambefort 1991b).

According to their dung relocation behaviour, dung beetles can be assigned to one of four functional groups (guilds). *'Rollers'* remove small portions of dung as balls and roll them on the soil surface some distance away from the dung pile. Dung balls may or may not be buried, and those that are left on the surface are often hidden under tussocks or leaf litter. *'Tunnelers'* pull portions of dung into self-burrowed tunnels and brood-chambers in the soil under or near the dung pat. *'Dwellers'* feed and reproduce inside the dung pat without removing dung from the site of deposition, and the small *'kleptoparasites'* use the dung portions relocated by rollers and tunnelers (Cambefort & Hanski 1991).

During relocation of dung both rollers and tunnelers may accidentally remove some of the seeds present in the frugivore dung (Andresen 1999). Horizontal distribution of seeds by rollers can reduce density-dependent mortality of seeds and competition of seedlings at the site of primary deposition (Estrada & Coates-Estrada 1991; Shepherd & Chapman 1998; Andresen & Levey 2004). Seeds burrowed by either rollers or tunnelers have a higher probability of escaping detection by rodents compared to seeds remaining on the soil surface, and seed detection probability decreases with increasing burial depth (reviewed in Andresen & Feer 2005). Moreover, dung beetles bury many of the seeds at depths that are favourable for seedling emergence (Estrada & Coates-Estrada 1991; Shepherd & Chapman 1998) and bioturbation by the beetles may increase soil aeration and water porosity (reviewed in Nichols *et al.* 2008). The faecal material around the seeds serves as organic fertilizer for seedling development (Vander Wall & Longland 2004). Rollers and tunnelers are thus important secondary seed dispersers which affect seed distribution and potentially increase the number of seeds that end up in safe sites (reviewed in Andresen & Feer 2005).

The efficiency with which dung beetles remove seeds varies with dung beetle species (size and guild affiliation) and seed size (reviewed in Andresen & Feer 2005). For dung beetles, seeds in the frugivore dung represent unusable contaminants and large seeds are less frequently dispersed and burrowed than small seeds. Seeds > 30 mm are seldom buried (reviewed in Andresen & Feer 2005). The probability and pattern of secondary seed dispersal and burial by dung beetles for a given seed thus depend on the structure and composition of the dung beetle community at the site of primary deposition (Vulinec 2002; Andresen & Feer 2005).

Dung beetle community organization seems to be strongly determined by the vegetation type (Hanski & Cambefort 1991b; Krell *et al.* 2003). Many dung beetle species are highly habitat specific (e.g. Barbero *et al.* 1999; Spector & Ayzama 2003; Vernes *et al.* 2005). Comparisons of dung beetle communities between forests and more open vegetation formations such as savannas, pastures and clear-cuts mostly revealed nearly complete dung beetle species turn-over with generally lower species richness and diversity in more open habitats (e.g. Spector & Ayzama 2003; Scheffler 2005; Nielsen 2007; but see Krell *et al.* 2003). Communities in open habitats are often characterized by a hyper-abundance of few small-bodied species (Krell *et al.* 2003; Nichols *et al.* 2007; but see Vulinec 2002). One would thus expect pronounced differences in secondary seed dispersal by dung beetles between forests and open habitats with potential implications for plant regeneration, but to date only one study made direct comparisons between these habitat types (Vulinec 2002). Studies on secondary seed dispersal by dung beetles in the tropics focused on forests ecosystems, with a strong emphasis on the Neotropics (see Andresen & Feer 2005, and references therein). Few studies took place in Africa (Shepherd & Chapman 1998; Chapman *et al.* 2003) and open habitats have been all but neglected, despite the fact that African savannas cover about 65% of the African continent (Tischler 1993) and support the richest dung beetle fauna world wide (about 1500 species from 75 genera, Cambefort 1991).

According to Cambefort (1991), African savannas provide two main types of mammalian dung for dung beetles: dung from large herbivores, and dung from omnivores as well as smaller herbivores. Most dung beetles prefer or are even specialized on one of these two dung types (Cambefort 1991). Omnivores and small herbivores present their dung in smaller droppings than large herbivores. However, the dung of true omnivores generally is richer in protein (Hanski & Cambefort 1991c).

In the Guinea savanna-forest mosaic of West Africa 70% of the woody plant species produce fleshy fruit the seeds of which are dispersed by animals (Hovestadt *et al.* 1999), and large frugivorous mammal species can be abundant (Fischer *et al.* 2000; Fischer *et al.* 2002). An important frugivore and primary seed disperser in West Africa that uses both savanna and forest habitats is the olive baboon (*Papio anubis* Lesson, Cercopithecidae) (Lieberman *et al.* 1979; Kunz & Linsenmair 2008a, b). In an area of 145 km^2 in the Comoé National Park, north-eastern Ivory Coast, ten olive baboon groups disperse seeds from at least 65 plant species ranging in seed size from 1 to 27 mm. The baboon population in the area disperses an estimated 1,483 intact seeds d^{-1} km^{-2} (Kunz & Linsenmair 2008b). Dung beetle communities at herbivore dung in CNP revealed strong differences in guild structure between savanna and forest: rollers are dominant in the savanna during the day and tunnelers at night, and tunnelers and dwellers dominate in the gallery forest both during day and at night (Krell *et al.* 2003).

In the present study, we ask whether these differences are also present in dung beetle communities at frugivore dung and if and how these differences affect dung removal, secondary dispersal probabilities and seed distribution patterns in both habitats. We provide for the first time comparative data on secondary seed dispersal by dung beetles in both forest and adjacent savanna in West Africa. We focused on habitat differences in the composition, abundance, body size and biomass of roller and tunneler species - the two dung beetles guilds relevant for secondary seed dispersal. Specifically we were interested in the implications for dispersal of seeds of various sizes that were naturally present in the faeces of olive baboons, including secondary dispersal distances and whether or not dung balls are buried. In a more general approach we analysed the secondary dispersal potential of rollers in both habitats (measured by their dung ball sizes and weights) and compared it to the size of seeds dispersed by the dung beetles as well as to the size of species commonly dispersed by olive baboons in the study area during peaks of dung beetle abundance. We discuss the data emphasising differences to seed dispersal by dung beetles in the Neotropics.

8. 2 METHODS

8.2.1 STUDY AREA

The Comoé National Park (CNP), north-eastern Ivory Coast (08°30-09°36' N, 003°07'-004°25' W), covers approximately 11,500 km^2 at an average altitude of 250-300 m asl (Poilecot 1991). Our study took place in the southern part, which belongs to the 'Guinea-Congolia / Sudania regional transition zone' (*sensu* White 1983).

The climate is characterized by a rainy season from March/April to October. After the onset of the first rains precipitation often fluctuates during the following months, resulting in two to three smaller peaks of precipitation prior to the main period of rain from August to October. Mean annual temperature was 26.3°C from 1997 to 2000 and mean annual precipitation was 1,053 mm.

The vegetation in the study area consists of a mosaic of different savanna formations (~91 %), forest islands of different extent (7 %), and continuous gallery forest (2 %) along the main rivers (FGU-Kronberg 1979). The gallery forest may be up to 600 m broad and comprises of plant species usually only found further South (Porembski 2001). Large areas of open grassland are lacking at the study site (FGU-Kronberg 1979; Pomeroy & Service 1986). The origin of the savanna-forest mosaic is not completely clear, but a mosaic landscape pattern of the savanna-forest border in northern Ivory Coast was already established in pre-colonial times (Wohlfarth-Bottermann 1994), and is maintained by annual fires (reviewed in Cambefort 1991; see also Goetze *et al.* 2006; Hennenberg *et al.* 2006).

The CNP is rich in animal-dispersed plant species, both in the savanna and forests (Hovestadt *et al.* 1999). The vegetation is described in more detail in Poilecot (1991), Porembski (1991) and Hovestadt *et al.* (1999).
Soils are impoverished sandy to loamy Ferralsols on Precambrian granites (Goetze *et al.* 2006).

The olive baboon is the most abundant among the nine nonhuman primate species recently recorded in the study area (Fischer *et al.* 2000). It uses both, savanna and forest habitats intensively (Kunz & Linsenmair 2008a). The dung beetle fauna in the CNP is also rich. To date, about 160 sympatric dung beetles species have been identified (Bordat 1983; Hanski & Cambefort 1991b; Krell, unpubl. data).

8.2.2 DUNG BEETLES AND SECONDARY SEED DISPERSAL

We collected dung beetles (Scarabaeidae: Scarabaeinae and Aphodiinae) from all four guilds but confined our analyses to rollers and tunnelers, as only these are relevant for secondary seed dispersal. In each experiment, we exposed one pile of 30 g of olive baboon dung in the savanna ($N = 32$) and in the gallery forest ($N = 31$) at randomly selected places within 1 km distance from the Lola field station of the University of Würzburg (08° 45' 095" N, 003° 48' 990" W). The mass of 30 g is about the fresh weight of a single defecation of a juvenile baboon in CNP (Kunz, unpubl. data). Using this quantity allowed us to split larger faeces for simultaneous experiments (see below).
We used fresh faeces collected *ad libitum* from the ten baboon groups in the study area and stored the samples in sealed plastic bags and containers in the shade (Kunz & Linsenmair 2008b). Samples were exposed within three days of collection.

Experiments took place after the onset of the first rains and at the onset and towards the end of the main rainy season when dung beetles are especially abundant (Cambefort 1984): in 1999 at the end of March/beginning of April ($n = 7$ experiments), in July ($n = 10$), September ($n = 5$), October ($n = 14$) and in 2000 from April to June ($n = 27$). During seasonal peaks of dung beetle abundance the first individuals arrive at the faeces within minutes after defecation and it is impossible to find fresh dung that has not already been colonized. Prior to the experiment, we carefully extracted dung beetles already present at the collected faeces. We cannot guarantee that we never overlooked single individuals, particularly tiny Sisyphini, but these single specimens are unlikely to have significant effects on the results.

Baboon faeces can contain hundreds to thousands of seeds (Kunz & Linsenmair 2008b). With regard to the long handling times necessary to extract and count every single seed per faecal sample we recorded only presence-absence data of seed species present in faecal samples and used the dung with the seeds in the experiments. We identified the seed species using a reference collection established in previous years by T. Hovestadt and P. Poilecot, supplemented by seeds taken from fresh fruits of identified plants during the study. We identified plants using Hutchinson *et al.* (1954-1968), von Maydell (1990), Arbonnier (2000), and Kasparek (2000). Plant nomenclature follows the International Plant Names Index (Royal Botanic Gardens Kew, the Harvard University Herbaria, and the Australian National Herbarium), http://www.ipni.org/.

Olive baboons in the CNP use both savanna and forest during the day but always spend the night in the forest (Kunz & Linsenmair 2008a). Following baboons' ranging behaviour, experiments in the savanna started between 9:00 and 18:30h, and in the gallery forest between 6:00 h and 20:00 h. Most diurnal dung beetles in West Africa become active not before 10:00 h (Cambefort 1991; Krell-Westerwalbesloh *et al.* 2004). "Nocturnal" dung beetles in West Africa are actually "dawn and dusk" species, starting their activity around 18:00 (Cambefort 1991; Krell-Westerwalbesloh *et al.* 2004). Our focus was thus on hours between 10:00 and 18:00 h, across which daytime experiments were about evenly distributed (29 in the savanna, 29 in the gallery forest). Seven additional experiments covered hours after dusk (three in the savanna, maximum until 21:00 h), four in the gallery forest, maximum until 23:00 h).

When facilitated by field assistance and the amount of dung available, we started experiments simultaneously in the savanna and gallery forest (n = 12 x 2 experiments, 20 minutes maximum time elapse between the onset of two experiments). Otherwise, we alternated between habitats in consecutive experiments (n = 39). For statistical analyses, each two simultaneous experiments were treated as a pair of experiments. Consecutive experiments were also matched to pairs according to chronological sequence and time of day at which the experiment took place. The median number of days between experiments of a pair was $x_{\mathrm{md}} = 0$ ($q1 = 0$, $q3 = 1$).

We always used dung from the same faecal sample in pairs of simultaneous experiments to control for potential variation in dung attractiveness to dung beetles. Consequently, one part of the faecal sample was exposed in the habitat that was not the habitat of origin. Single specimen that we may have overlooked prior to exposure of the dung did not, however, confound species list of the two habitats. All dung beetle species that were collected in the savanna from a pile that originated from the gallery forest were also found at faecal samples that originated from the savanna, and vice versa.

To minimize edge effects we placed dung piles in the gallery forest about 50 to 100 m away from the forest border.

Every 30 minutes, we estimated the cumulative proportion of faeces that dung beetles had removed from the dung pile (0, ≤ 10%, > 10 ≤ 25%, > 25 ≤ 50%, > 50 ≤ 75%, > 75%) (following Feer 1999). Observation per sample in the savanna lasted for a maximum of four hours or until ≥ 75% of the pile had been removed, whichever first. However, when dung beetle activity had been constantly low (< 10 % of dung removed after two hours of observation) we terminated the experiment. The mean duration of savanna experiments was $x \pm sd = 141 \pm 46$ min.

Whereas colonization of dung piles in the savanna generally was very rapid, arrival of the first dung beetles in the gallery forest took much longer and removal of dung generally was very slow. We therefore exposed dung for a maximum of five hours or until dung beetles had removed ≥ 50% of the dung, and a minimum of 3 hours. The average duration of experiments in the gallery forest was $x \pm sd = 181 \pm 73$ min.

To obtain data on dung beetle guild structure in either habitat, we carefully scanned the dung pat at 30-minute intervals and collected dung beetles from the pile using tweezers. When roller beetles were about to leave with dung balls, we collected beetles and dung balls together and stored them separately. Across all experiments, four Sisyphini and about 15 Gymnopleurini escaped. Because we collected dung beetles from the pile, the amount of dung removed during any fixed time interval except the first probably is an underestimate. As, however, the time interval of collection was similar in both habitats, comparisons of the rate of dung removal and the number of individuals across habitats are nonetheless informative. On the other hand, recolonization of the dung pats may overestimate the number of individuals, particularly when dung beetle abundance is high. Because we still allowed for removal of dung, although decelerated, the overestimation of dung beetle individuals is likely to be less pronounced than in commonly used pitfall traps.

In between the 30-minute intervals we either collected additional roller beetles with their dung balls, as they were about to leave the pile, or followed individuals until they abandoned the dung ball at the surface or burrowed it. Choice of rollers and procedure followed a list of random numbers (1-6) (e.g. in the first 30 minute interval collect the fourth beetle leaving the dung pile with a dung ball, subsequently collect the next roller removing a dung ball, afterwards follow the second roller leaving the dung pile with a dung ball). When we followed individual rollers, we marked the location from where we collected the dung ball and measured the distance to the dung pile with a tape.

At the end of each experiment, we collected the remaining dung pat and excavated the surrounding soil (about 30 cm diameter, 20 cm depth). We floated the dung and soil in buckets of water to extract dung beetles (particularly tunnelers) (Krell *et al.* 2003). We stirred the mass thoroughly for about five seconds and collected the dung beetles with small sieves from the water. The process was repeated until five consecutive stirrings of five seconds each revealed no more beetles.

We stored the dung beetles in Scheerpeltz solution (Krell 2007) until identified to the species level by F.T. Krell. Names of dung beetle species generally follow Cambefort (1991) with a few updates. The specimens are deposited in The Natural History Museum London and the Denver Museum of Nature & Science. We recorded the number of individuals per species and experiment, measured the beetles' body length and classified each species into one guild following Cambefort (1984), Hanski & Cambefort (1991b), Krell *et al.* (2003). Data on fresh mass of the identified dung beetle species come from Cambefort (1984), who collected dung beetles in the southern part of the CNP, near the village Kakpin. To estimate dung beetle biomass at experimental dung piles in the savanna and gallery forest we multiplied the mean fresh weight of each species by its abundance in the experiment.
Classification into diurnal and nocturnal species and habitat occurring of species are following (Cambefort 1984). We assigned a habitat preference for species occurring in both habitats with a total minimum of 10 individuals collected, if distribution of individuals to habitats differed at least by 2 : 1.

To obtain data on the dispersal potential of dung beetles in terms of maximum seed sizes and mass we measured the maximum diameter of the dung balls on the day of collection using a sliding calliper (accuracy 0.1 mm) and the fresh weight with an electronic balance (accuracy 0.002 g). When dung balls were damaged during collection or transport, we measured fresh weight only. The dung balls were stored at a dry place at air temperature until further analysed in the laboratory at the University of Würzburg, Germany, where they were placed in a drying cabinet at 35°C until they could be crumbled carefully by hand. We checked the crumbled material for seeds using a binocular (magnification 6.4-40x) and measured the maximum diameter of the seeds with a sliding calliper (as above). Because seeds < 2 mm were difficult to measure accurately we use a value of 2 mm in all analyses.

To identify which seeds are likely to be dispersed secondarily by dung beetles from baboon faeces, we compared the median dung ball sizes per habitat to the median sizes of seed species that olive baboons disperse in their faeces in CNP between March and October (Kunz & Linsenmair 2008b; Kunz, unpubl. data). Details on the sampling method of baboon faeces and faecal analyses are given in Kunz & Linsenmair (2008b). We focused on seed species that occurred in $\geq 2\%$ of the total 396 faecal samples collected and of which we found at least one intact seed in the samples (Kunz & Linsenmair 2008b). We measured those seeds as above.

To analyse whether rainfall prior to experiments affects the abundance of rollers and tunnelers we measured precipitation with a simple rain gauge at the field station.

8.2.3 DATA ANALYSIS

We performed statistics in SPSS version 15.0 and 16.0, SsS version 1.0 (Rubisoft Software) and Canoco for Windows 4.51 (Biometris, Wageningen Lepš & Šmilauer 2003). When data were not normally distributed (Kolmogorov-Smirnov test) we calculated the median (x_{md}) and 25% ($q1$) and 75% ($q3$) percentiles instead of the mean. All tests were two-tailed and the level of significance was set at 95%. We used exact tests for small sample sizes (SPSS Exact Extension).

A standardized redundancy analysis (RDA) (Canoco) using log transformed guild data shows the relationship between environmental parameters and abundances. The significance of environmental variables is tested by a Monte Carlo Permutation Test (Canoco; 999 permutations).

We applied Wilcoxon's matched-pairs signed ranks test to analyse variation in species and individual number, and biomass across the two habitats. We compared the distribution of species and individuals, respectively, to guilds across habitats using $\chi 2$ test of n x n contingency tables.

We used Mann-Whitney *U*-test to compare mean sizes of nocturnal and diurnal roller and tunneler species, respectively. We also applied the *U*-test to analyse differences in dung ball sizes removed by one and ≥ 2 individuals as well as variation in dung ball size and weight, respectively, between habitats. In the same way we tested for variation in secondary dispersal distances between habitats, and variation in dispersal distances between dung balls and single seeds mistaken for dung balls.

We applied Spearman's rank correlation to identify correlations between (1) mean dung ball size and mean dung ball weight, respectively, per species and mean size of roller species, (2) mean body mass of dung beetle species and mean dispersal distance of dung balls, and (3) between mean seed sizes and secondary dispersal distances.

8. 3 RESULTS

8.3.1 DUNG BEETLE GUILDS AND DISTRIBUTION OF ROLLERS AND TUNNELERS ACROSS HABITATS

All experiments together yielded 4,149 dung beetles from 99 species, representing 26 genera. Eighty-five species occurred in the savanna and 47 in the gallery forest.
Eighteen percent of the total species were rollers, 58.6% tunnelers, 11.1% dwellers, and 12.1% kleptoparasites. Tunnelers accounted for more than half of the individuals (57.0%), rollers for 27.5%, whereas dwellers and kleptoparasites were less abundant (7.3 % and 8.3% respectively). The most abundant species were the small roller *Sisyphus goryi* Harold and the small tunneler *Onthophagus bandamai* Cambefort (Appendix 1), representing together 41.6 % of all individuals collected.

Although experiments on average lasted 40 min less in the savanna than in the gallery forest, dung piles in the savanna attracted 1.7 times as much roller and tunneler species (Table 1). Eighty-nine percent of the total 18 roller species occurred in the savanna, compared to 44.4% in the gallery forest. Eighty-three percent of the 58 tunneler species were present in the savanna and 50% in the gallery forest. Fifty-six percent of the roller species and 48.3% of the tunneler species occurred only in the savanna, whereas 11% of the roller species and 20.7% of the tunneler species were restricted to the gallery forest. Of the 25 roller and tunneler species shared between habitats, 17 showed a clear habitat preference for the savanna and two for the gallery forest.

During simultaneous experiments in both habitats dung piles in the savanna attracted significantly more roller species than dung piles in the forest ($x \pm sd$ savanna = 3 ± 2.5, gallery forest = 1 ± 0.8; Wilcoxon's paired signed ranks test $Z = -2.328$, $p_{\text{exact}} < 0.05$). The number of tunneler species did not vary significantly ($x \pm sd$ savanna = 4.9 ± 3.4, gallery forest = 5.5 ± 3.0; $Z = -0.855$, $p_{\text{exact}} > 0.05$).

In both habitats the species number of tunnelers was four times that of rollers (Table 1), without significant differences between habitats ($\chi 2$ test for 2 x 2 contingency tables = 0.059, $df = 1$, $p > 0.05$.
Regarding individuals, dung beetles were about twice as abundant in the savanna than in the gallery forest (Table 1). During simultaneous experiments significantly more roller individuals occurred at dung piles in the savanna than in the forest (savanna $x_{\text{md}} = 11.0$, $q1 = 1.25$, $q3 = 57.5$, gallery forest $x_{\text{md}} = 2.0$, $q1 = 0.25$, $q3 = 2.75$; Wilcoxon's paired signed ranks test: $Z = -2.312$), but tunneler individuals were more abundant during experiments in the gallery forest (savanna $x_{\text{md}} = 6.0$, $q1 = 2.25$, $q3 = 37.5$, gallery forest $x_{\text{md}} = 36.0$, $q1 = 18.25$, $q3 = 56.0$; $Z = -2.397$) ($p_{\text{exact}} < 0.05$, $n = 10$).

Table 1 Guild distribution of dung beetle species and individuals collected during experiments with fresh baboon dung in the savanna and gallery forest at Comoé National Park, Ivory Coast (Rollers and tunnelers only)

Guild	Total		Savanna		Forest	
	Species (N=76)	Individuals (N=3502)	Species (n=64)	Individuals (n=2367)	Species (n=37)	Individuals (n=1135)
%Rollers (n)	23.7 (18)	32.5 (1139)	25.0 (16)	46.2 (1093)	21.6 (8)	4.1 (46)
%Tunnelers (n)	76.3 (58)	67.5 (2363)	75.0 (48)	53.8 (1274)	78.4 (29)	95.9 (1089)

Between habitats, variation in the distribution of individuals to the two guilds was highly significant ($\chi^2 = 618.35$, $df = 1$, $p < 0.0001$). Rollers and tunnelers were about equally abundant in the savanna, whereas in the gallery forest rollers accounted for only 4% of the individuals collected in this habitat (Table 1).

Relationships between environmental parameters and guild abundances are shown by a RDA (Figure 1). The habitat explains 15 % of the variation at a highly significant level.

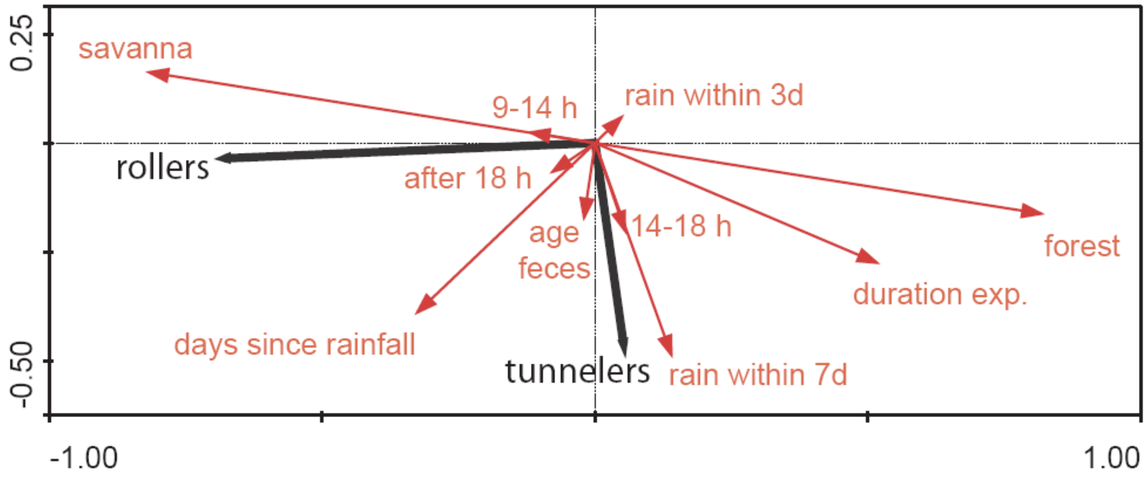


Figure 1 RDA ordination biplot of the roller and tunneler dung beetle guilds and environmental variables, based on log-transformed guild abundance data.
Eigenvalues: axis 1: 0.230, axis 2: 0.068. Baboon faeces were exposed in two different habitats savanna, forest) and during three different time periods: between 9:00 and 14:00 (9-14 h), between 14:00 and 18:00 (14-18 h), and after 18:00 (after 18 h). 'Duration of experiment': time [min] experiments lasted; 'age faeces': number of days from the day of collection of a faecal sample to exposition in experiment; 'days since rainfall': number of days since last rainfall (> 5 mm); 'rain within 3 days': cumulative amount of rainfall [mm] during three days prior to the experiment; 'rain within 7 days': cumulative amount of rainfall [mm] during seven days prior to the experiment.

The only other significant variable is 'days since rainfall' which explains additional 5 % of the variation (Table 2). All other variables (quantity of rainfall, time period of the experiment, duration of the experiment, storage time of faeces) are not significant at guild level although the abundance of tunnelers is correlated with the amount of precipitation in the preceding seven days, and the abundance of rollers with the savanna habitat.

Table 2 Eigenvalues and significance level of the environmental variables in the RDA at guild level

Marginal Effects		Conditional Effects		
Variable	λ1	Variable	λA	*p*
Savanna	0.15	Savanna	0.15	0.001
Forest	0.15	Days since last rain	0.05	0.045
Duration of experiment	0.06	Precipitation within 7 d	0.02	0.231
Days since last rain	0.03	Duration of experiment	0.02	0.41
Precipitation within 7 d	0.01	Precipitation within 3 d	0	0.468
9:00-14:00 h	0	14:00-18:00 h	0.02	0.261
14:00-18:00 h	0	after 18:00 h	0.01	0.676
After 1:00 h	0	9:00-14:00 h	0.03	0.116
Storage time	0	Storage time	0	0.815
Precipitation within 3 d	0			

The size of tunnelers was between 2.4 and 28.0 mm, rollers were between 3.8 mm and 30.0 mm long. The largest species were the nocturnal rollers (*Anachalcos* spp., *Scarabaeus goryi*) (Appendix 1). The median size among roller and tunneler species, respectively, was larger in the savanna than in the gallery forest (Figure 2). Differences between habitats were more pronounced in the roller guild.

Nocturnal rollers and tunnelers, respectively, were larger than diurnal ones (rollers diurnal: x_{md} = 9 mm, $q1$ = 5.9 mm, $q3$ = 11.8 mm, nocturnal x_{md} = 20.0 mm, $q1$ = 20.0 mm, $q3$ = 24.5 mm, Mann-Whitney U = 1.00, $p_{\mathrm{exact}} < 0.01$; tunnelers diurnal: x_{md} = 5.3 mm, $q1$ = 4.4 mm, $q3$ = 7.2 mm, nocturnal x_{md} = 7.5 mm, $q1$ = 5.6 mm, $q3$ = 15.0 mm, U = 186.5; $p_{\mathrm{exact}} < 0.01$).

In savanna experiments, the higher number of individuals and the larger median size of the species resulted in a significantly higher dung beetle biomass compared to forests. The median biomass of rollers and tunnelers per experiment in the savanna was 731.5 mg ($q1$ = 160.5 mg, $q3$ = 3935.6 mg, range 0-32,750.0 mg), and 509.0 mg in the gallery forest ($q1$ =

264.0 mg, *q3* = 1,333.5 mg, range 0-7,502.0 mg) (Wilcoxon's paired signed ranks test $Z = 2.691$, $p < 0.01$).

According to the greater biomass of dung beetles in the savanna, dung removal was generally more rapid in the savanna than in the gallery forest. After two hours, > 50% of the dung was removed in 75% of the savanna experiments, compared to only 26% of the experiments in the gallery forest.

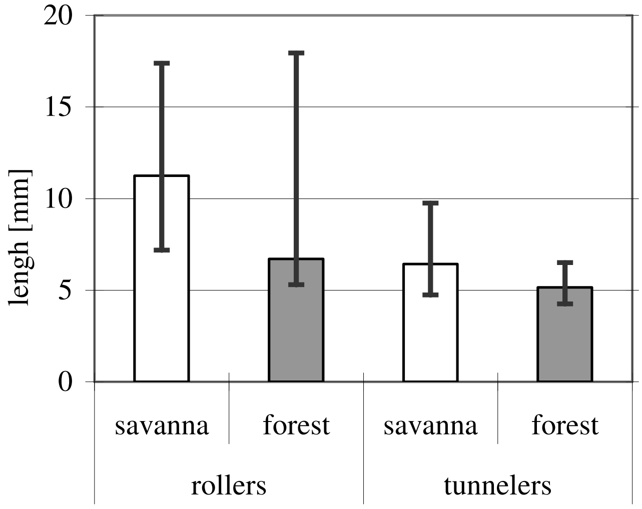


Figure 2 Median size of roller and tunneler species found at piles of olive baboon dung exposed in the savanna and gallery forest at Comoé National Park, Ivory Coast Columns: median values across species, bars: first and third percentile. $N = 16$ roller species in the savanna, 8 in the gallery forest, and 48 tunneler species in the savanna and 29 in the gallery forest.

8.3.2 REMOVAL AND FATE OF DUNG BALLS

We recorded 210 dung balls being removed by rollers in the savanna, and, due to the low abundance of rollers in the gallery forest only 15 dung balls in this habitat. In the savanna, single rollers removed 79.5 % of the dung balls, 18.0 % were rolled away by a pair, and 2.4 % by three rollers together. In the gallery forest, all dung balls but one were rolled away by single telecoprids. In the most abundant roller species, *S. goryi*, we tested whether dung balls removed by two or three rollers were larger than those removed by one individual, but size of dung balls did not vary significantly (Mann-Whitney $U = 50.5$, $p > 0.05$, $n = 28$).

Across species, dung beetles rolled away dung portions that were 6.5 times (median) heavier than the species' mean body weight ($q1$ = 2.7, $q3$ = 8.9, maximum 20, n = 12 roller). Overall, dung beetles in the savanna formed dung balls that tended to be smaller than in the gallery forest (Mann-Whitney U = 151, p = 0.075, n = 80) (Table 3). Differences in dung ball weight were more pronounced and, despite the small sample size in the gallery forest, statistically significant (Mann-Whitney $U = 311.5$, $p < 0.05$, $n = 121$).
There was a strong positive relationship between mean size of roller species and both, mean size and weight of species' dung balls (size dung balls $r_s = 0.875$, weight dung balls $r_s = 0.879$, $p < 0.001$, $N = 10$ species).

Table 3 Diameter and fresh weight of dung balls from rollers collected in the savanna and in the gallery forest at Comoé National Park

	Diameter [mm]		Weight [mg]	
	Savanna (N=73)	Gallery forest (N=7)	Savanna (N=111)	Gallery forest (N=10)
Median value	7.1	26.5	178	1,476
1. percentile	5.8	6.9	91	157
3. percentile	10.4	30.0	405	8,077
Minimum	2.2	4.8	8	116.9
Maximum	22.6	34.2	5,666	18,000

Formation of dung balls on average took seven times longer in the gallery forest ($x \pm sd$ = 68.4 ± 48.7 min, n = 7) than in the savanna ($x \pm sd$ = 9.7 ± 3.7 min, n = 11). Once dung balls were formed, the rollers in the savanna removed them quickly and relatively straight on away from the dung pile, sometimes sidetracked by tussocks or stones. In contrast, roller movements in the gallery forest were hampered by the leaf litter on the ground, resulting in dung beetles circling around for hours without gaining much distance from the dung pile. Consequently, the distances telecoprids rolled dung balls away from the dung pat were significantly larger in the savanna (x_{md} = 1.35 m, $q1$ = 0.85 m, $q3$ = 2.10 m, max 20.3 m, n = 125) than in the gallery forest (x_{md} = 0.35 m, $q1$ = 0.24 m, $q3$ = 0.650 m, max 3.0 m, n = 9) (Mann-Whitney U = 258, p < 0.01). Mean distance per roller species in the savanna was not correlated with mean body mass across five beetle species tested (r_s = -0.0873, $p > 0.5$. Mean beetle size across species tested ranged from 3.75 to 15.5.mm).
Dung beetles in the savanna buried 67.2 % of the observed dung balls (N = 125). Eighteen percent were left abandoned at the surface, of which three dung balls were subsequently removed by other rollers. Seven percent were seemingly lost (e.g. fell in a crack of soil and

dung beetles obviously were unable to relocate them albeit intensive searching), and in 8% of the cases the fate was unclear, *e.g.* when dung beetles fell into a small crack together with the dung ball).

All dung beetles observed in the gallery forest buried their dung balls.

8.3.3 SEEDS DISPERSED BY DUNG BEETLES

Faeces used in experiments contained seeds of a total of 27 different plant species. Identified plant species are given in Table 4. Five seed species remain to be identified, of which all but one had seeds < 4 mm.

At least 13 seed species were incorporated into and secondarily dispersed with roller dung balls. Altogether, 62.4% of the dung balls collected contained seeds (n = 120 in the savanna, n = 13 in the gallery forest). The median number of seeds per dung ball was 1 ($q1$ = 0, $q3$ = 6), though up to 297 were incorporated in a single ball. Very large numbers of seeds in dung balls were due to tiny seeds like *Ficus* spp. Dung balls with seeds contained on average 1.3 ± *sd* 0.7 (max = 4) seed species (n = 83).

Eighty-four percent of the dung balls with seeds contained the small seeds (< 2 mm) of either *Ficus* spp., or *Sarcocephalus* sp., or both genera. Twenty-two percent contained seeds ≥ 2 mm length.

Rollers in the gallery forest incorporated seeds up to 16.6 mm (a seed of *Saba senegalensis*) into their large dung balls. Seeds in roller dung balls in the savanna had a maximum size of only 3.5 mm (unidentified seed species).

In an additional 26 cases, however, we observed that rollers in the savanna (but not in the gallery forest) seemingly mistook single seeds from eight different plant species as dung balls and rolled them away (Table 4). The median dispersal distance of these single seeds was 1.63 m ($q1$ = 0.72 m, $q3$ = 3.33 m, n = 22). Thirteen seeds were buried, five were abandoned at the surface, and the fate of four seeds is unknown as we lost track of the beetles. Secondary dispersal distances of the single seeds mistaken as dung balls did not vary significantly from removal distances of "true" dung balls (Mann-Whitney U = 1227.5, p > 0.05), and was not correlated to seed size ($r_S = -0.364$, 0 > 0.05).

We observed five roller species that dispersed seeds instead of dung balls (one to six times per beetle species): *Allogymnopleurus umbrinus* (n = 1), *Gymnopleurus coerulescens* (n = 1), *G. puncticollis* (n = 6), *Sisyphus biarmatus* (n = 4) as well as the most abundant roller species *S. goryi* (n = 6). Figures 3a and 3b show that the latter three roller species moved away single seeds from a comparatively wide range of sizes, including seeds that fall in size above the standard deviation of the beetles own dung ball sizes. Outside regular observations, we recorded one Sisyphini individual (not collected) rolling away *S.*

senegalensis seeds (seed length $x \pm sd = 17.9 \pm 2.4$ mm, $n = 195$). The maximum diameter across all collected dung balls from Sisyphini was 11.5 mm ($N = 48$).

Table 4 Identified seed species in faecal samples exposed in experiments
'b': seed species was incorporated into dung balls by rollers, 'S': single seeds of the species were removed by rollers instead of dung balls.

Plant species	Secondary dispersal by rollers
Anacardiaceae	
Lannea acida	b , S
L. barteri	b , S
L. welwitschii	b , S
Annonaceae	
Uvaria chamae	
Apocynaceae	
Saba senegalensis	b , S
Dichapetalaceae	
Tapura fischeri	
Euphorbiaceae	
Drypetes floribunda	S
Phyllanthus sp.	
Fabaceae	
Dialium guineense	b , S
Erythrophleum suaveolens (syn. guineense)	
Parkia biglobosa	
Moraceae	
Ficus sp.	b
Rubiaceae	
Canthium sp.	
Oxyanthus racemosum	
Sarcocephalus cf. xanthoxylon	b
Sapotaceae	
Manilkara obovata (syn. mutinervis)	b , S
Mimusops kummel	b , S
Solanaceae	
Solanum incanum	b
Vitaceae	
Cissus populnea	
Verbenaceae	
Vitex doniana	
Graminaceae (2 species)	b

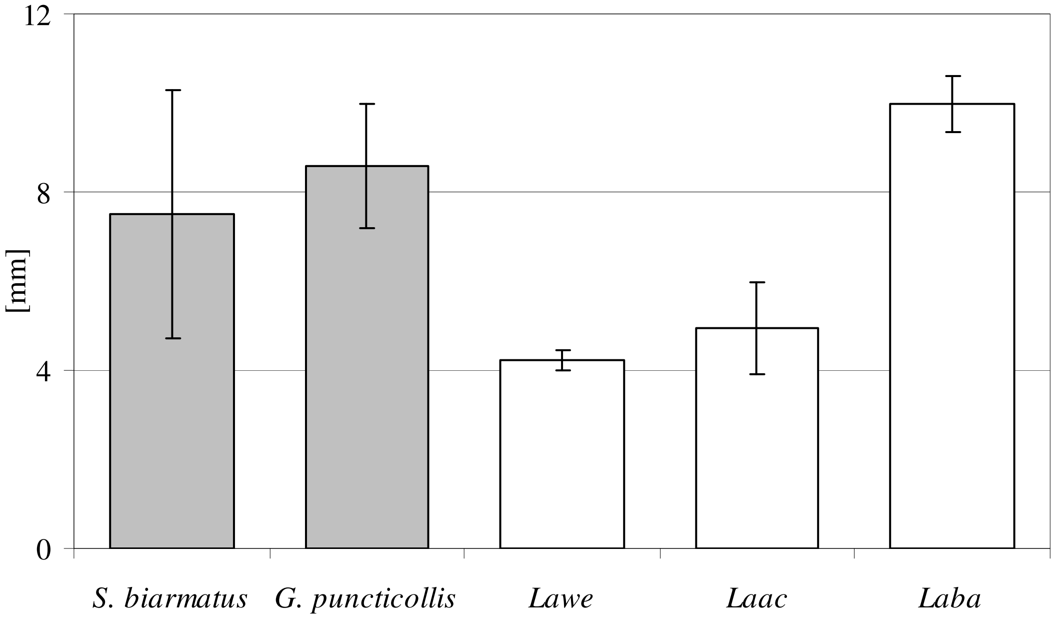


Figure 3a Mean diameter of dung balls of the roller species *Sisyphus biarmatus* (*n* = 5) and *Gymnopleurus puncticollis* (*n* = 7) in the savanna compared to mean length of seeds the species mistook as dung balls

Lawe: *Lannea welwitschii*, Laac: *L. acida*, and Laba: *L. barteri*. Bars: standard deviation.

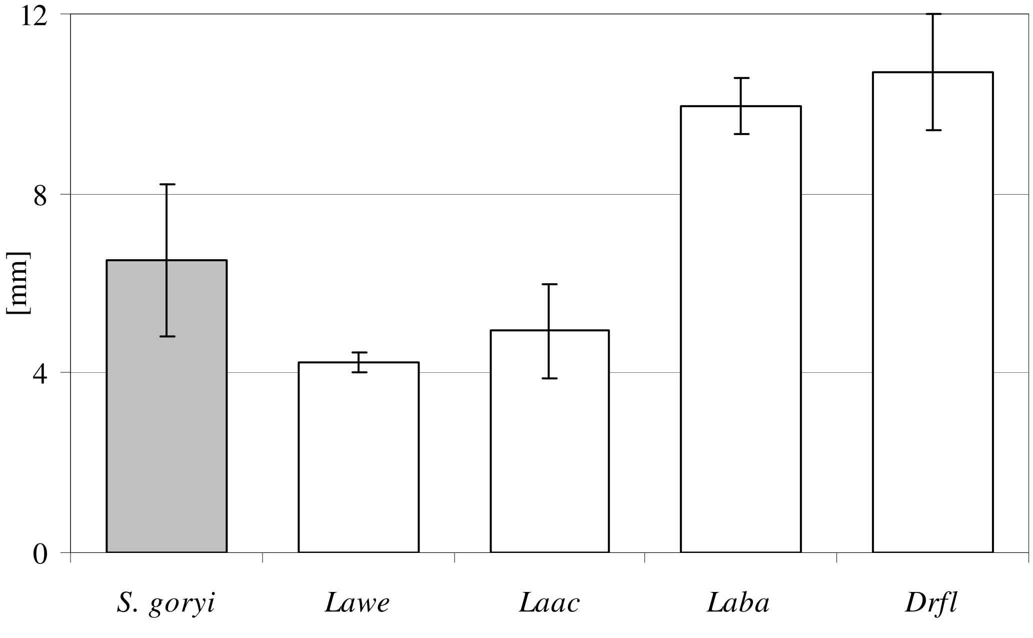


Figure 3b Mean diameter of dung balls of the roller species *Sisyphus goryi* (n = 23) in the savanna compared to mean length of seeds the species rolled away singly instead of dung balls

Lawe: *Lannea welwitschii*, Laac: *L. acida*, and Laba: *L. barteri*, Drfl: *Drypetes floribunda*. Bars: standard deviation.

Seventy-three percent of the seed species that olive baboons in CNP disperse intact and that we commonly found in baboon faeces have a median seed size smaller than the third percentile of roller dung ball sizes in the savanna. All those plant species have seed sizes that are smaller than the median dung ball size of rollers in the gallery forest (Figure 4).
All seed species have seeds smaller than the maximum size of dung balls in the savanna (22.6 mm) and gallery forest (34.2 mm), and may thus be dispersed secondarily by dung beetles in both habitats.

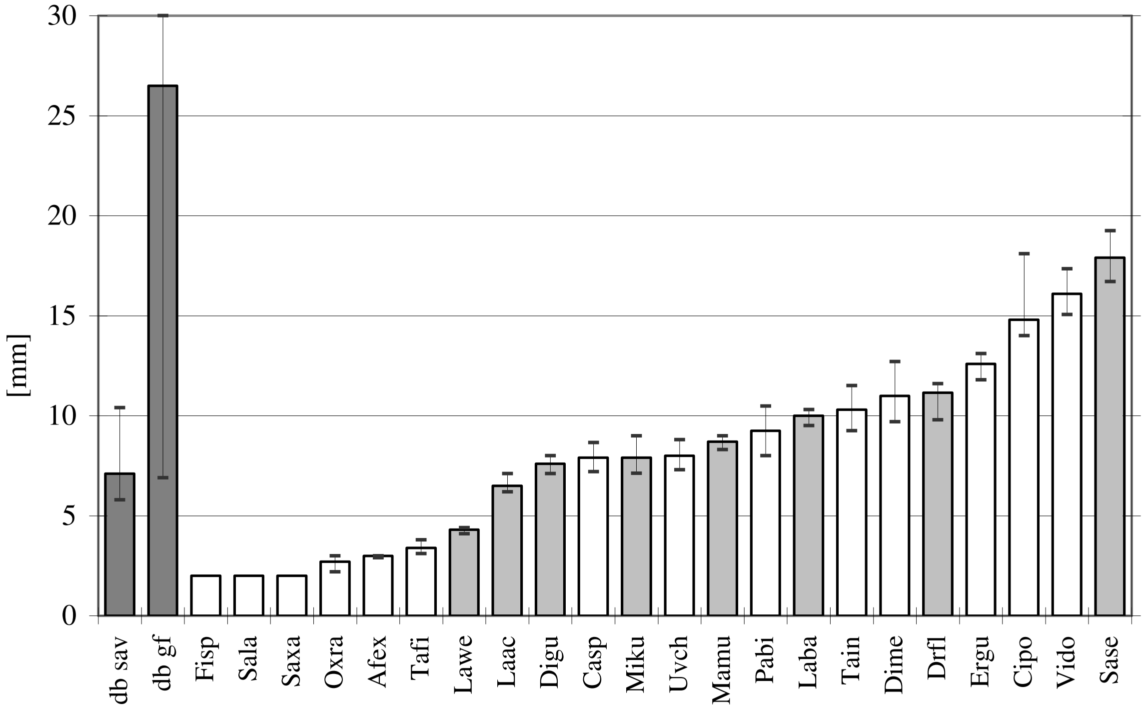


Figure 4 Comparison of dung ball sizes of rollers in the Comoé National Park, and sizes of seeds extracted from faeces of olive baboons inhabiting the same area

Columns: median sizes, bars: first and third percentile. Columns in light grey indicate seed species single seeds of which were removed by rollers in the savanna instead of dung balls. Seed species are shown that were found in ≥2% of a total of 396 samples of baboon faeces and had at least one undamaged seed dispersed by baboons, or were dispersed secondarily by dung beetles instead of dung balls. Usually, the median seed length is shown, except for *Canthium* sp. and *Drypetes floribunda* whose seeds are wider than long. db sav: dung balls collected in the savanna (*n* = 90), db gf: dung balls collected in the gallery forest (*n* = 7), Afex: *Aframomum excarpum* (*N* = 186), Casp: *Canthium* sp. (*N* = 151), Cipo: *Cissus populnea* (*N* = 37), Digu: *Dialium guineense* (*N* = 509), Dime: *Diospyros mespiliformis* (*N* = 298), Drfl: *Drypetes floribunda* (*N* = 294), Ergu: *Erythrophleum guineense* (*N* = 169), Fisp: *Ficus* spp. (55), Laac: *L. acida* (*N* = 241), Laba: *L. barteri* (*N* = 60), Lawe: *L. welwitschii* (*N* = 31), Mamu: *Manilkara multinervis* (*N* = 55), Miku: *Mimusops kummel* (*N* = 10), Oxra: *Oxyanthus racemosus* (*N* = 111), Pabi: *Parkia biglobosa*, Sala: *Sarcocephalus latifolius* (*N* = 10), Sase: *Saba senegalensis* (*N* = 195), Saxa: *Sarcocephalus* cf. *xanthoxylon* (*N* = 10), Tafi: *Tapura fischeri* (*N* = 55), Tain: *Tamarindus indica* (*N* = 191), Uvch: *Uvaria chamae* (*N* = 238), Vido: *Vitex doniana* (*N* = 52).

8. 4 DISCUSSION

The study revealed high dung beetle activity at baboon faeces and clear differences in the distribution of rollers and tunnelers between the savanna and forest in CNP. Where dung beetle communities have been compared at the same site in forests and open habitats in the tropics elsewhere, total species numbers per site ranged from 19 to 78 in the Neotropics (Estrada *et al.* 1998; Halffter & Arellano 2002; Vulinec 2002; Spector & Ayzama 2003; Scheffler 2005) and 40 to 83 species in East and South Africa (Jankielsohn *et al.* 2001; Davis & Philips 2005). Keeping in mind that direct comparisons are hampered by the fact that different studies used different types and amounts of dung over varying time periods, a comparatively high number of dung beetle species ($N = 99$) was attracted to baboon dung in CNP. In contrast to general findings in the Neotropics (whether in natural habitat mosaics or in habitats recently modified by humans, e.g. Spector & Ayzama 2003; Scheffler 2005), species number and abundance in CNP were higher in the open habitat than the forest. Cambefort & Walter (1991) also found a much higher dung beetle species richness and abundance at human dung and elephant dung in the savanna South of the CNP compared to the rainforest of the Tai National Park (southern Ivory Coast). The number of dung beetle species and individuals at a given site is positively related to the number of non-flying mammal species (Hanski & Cambefort 1991d; Estrada *et al.* 1998), and African savannas support the most diverse mammal fauna on Earth (Cambefort 1991).

The lower number of 47 dung beetle species in the gallery forest in CNP compared to the savanna ($N = 85$) is about as high or higher than species numbers attracted to nonhuman primate dung in most studies in Neotropical forests (Estrada & Coates-Estrada 1991; Andresen 1999, 2002, 2005; Feer 1999; but see Castellanos *et al.* 1999). Most nonhuman primate species in CNP are more or less tight to the forest (Fischer *et al.* 2000), and other fruit eating mammals are also present in this habitat (Fischer *et al.* 2002; Kunz pers. observ.). We suppose that the high number of dung beetle species on baboon dung in the savanna results from a high number of true generalists and/or species that generally prefer herbivore dung but also feed on omnivore dung when available (see also Hanski & Cambefort 1991c). For example *Sisyphus goryi* prefers cattle over human dung (Cambefort 1991) but was by far the most abundant species we found on baboon dung in the savanna. However, the higher number of dung beetle individuals attracted to dung piles in the savanna in CNP might also be explained, as least partly, by a larger radius of attraction in the open vegetation compared to the forest (Cambefort & Walter 1991).

Similar to other studies (e.g. Cambefort 1991; Hill 1996; Spector & Ayzama 2003; Scheffler 2005), dung beetle species in forest and open habitat were quite distinct and most roller and tunneler species showed a clear preference for one of the two habitats. However, the relative distribution of species to the roller and tunneler guild was very similar in both habitats (1 roller species : 4 tunneler species). In the Neotropics, the number of roller species generally also seems much lower than the number of tunneler species (1 : 3 Andresen 1999, 2002; 1 : 1.4 Estrada & Coates-Estrada 1991; 1 : 4 Feer 1999).

The striking difference between dung beetle assemblages in savanna and forest in CNP lies in the different proportions of roller and tunneler individuals: whereas the number of individuals in the savanna is about equally distributed between rollers and tunnelers, extremely few rollers are active in the gallery forest where tunnelers clearly dominate numerically. Habitat is clearly the dominating factor explaining the variation in dung beetle assemblages, followed by the time since the last rain, as shown by the redundancy analysis. A previous study in the same area on beetle assemblages at buffalo dung showed that habitat explains over 30% of the variation in those assemblages (Krell *et al.* 2003), and the importance of rainfall events for the activity of necrophagous scarab beetles was stated by Krell-Westerwalbesloh *et al.* (2004).

In Africa, the absolute number of roller species and individuals generally is higher in open habitats (Cambefort 1991) where high temperatures enable rollers to quickly perform their energetically demanding dung relocation behaviour (Heinrich & Bartholomew 1979; Krell *et al.* 2003). Accordingly, roller abundance in the savanna peaks around midday when air temperature is highest (Krell-Westerwalbesloh *et al.* 2004). By exploiting the dung resource rapidly, rollers become the competitive superior guild that decreases the change for reproduction of tunnelers and dwellers (Doube 1990; Hanski 1991; Krell *et al.* 2003).

In contrast, rollers in the Neotropics are more abundant in forest than in open habitats of various degrees of habitat disturbance (Estrada & Coates-Estrada 2002; Vulinec 2002).

Corroborating findings by Cambefort (1991), most roller species in the savanna of the CNP belonged to the tribes Sisyphini and Gymnopleurini and were small and diurnal, whereas nocturnal rollers included the largest species found and belonged to the tribes Scarabaeini and Canthonini. Andresen (2002, 2005) found that the mean body size of nocturnal dung beetles in Neotropical forests was larger than of diurnal ones, indicating either more large species or a higher abundance of large individuals at night. In contrast to the study by Cambefort (1991) and studies in the Neotropics (Vulinec 2002; Spector & Ayzama 2003; Escobar 2004; Scheffler 2005; Nichols *et al.* 2007) however, both roller and tunneler species in CNP were larger in the open habitat than in the forest. Basically, the rollers and tunnelers in the gallery forest represented a subset of the species in the savanna.

Several general implications for secondary seed dispersal by dung beetles in the savanna-forest mosaic of CNP result from the differences in dung beetle abundance, size and biomass, and distribution of rollers and tunnelers. Seeds dispersed primarily by baboons into the savanna should have a higher probability of removal by dung beetles than in the forest, and seeds deposited in the savanna should also have a much higher probability of being horizontally dispersed some distance away from the dung pile by rollers compared to seeds in the forest.

Because larger rollers and tunnelers remove larger amounts of dung than small ones (following Doube 1990; Horgan 2001) they are potentially able to remove not only more seeds, but also larger seeds with these dung portions. Several studies found that dung beetle size is positively correlated with the size of a seed removed by a beetle (Doube 1990; Feer 1999; Andresen 2001; see also Vulinec 2002). One would thus presume that in general the larger dung beetles in the savanna remove more large seeds than in the gallery forest, and that the largest seeds would be dispersed by the large nocturnal roller species in both habitats.

We found, however, that rollers in the gallery forest produced larger and heavier dung balls than in the savanna. This may an artefact of the very small sample size of roller dung balls collected in the forest, which, despite random sampling, comprised a disproportionate high proportion of large dung balls from nocturnal rollers compared to the abundance of these species. Movements of these large species were slow and making of the large dung balls took comparatively long. Seeds deposited by baboons in the savanna are thus also more likely to be removed more rapidly than in the gallery forest. Where post-dispersal predation risk is high, rapid removal to safe sites can be an important advantage (Estrada & Coates-Estrada 1991; Andresen 1999).

Time taken for dung ball formation may also depend on competition at the dung pat. Heinrich & Bartholomew (1979) noted that dung ball making in the large roller *Scarabaeus laevistriatus* took longer when other competitors were excluded from the dung source. When competition is low, dung beetles might separate a relatively larger dung portion from the pile of which the dung ball subsequently is formed, than at times of high competition. Larger portions potentially can contain larger seeds. Dung beetles might, however, also remove dung contaminants, like seeds attached to the dung portion, more thoroughly when competition is low.

Dung pats are patchy, relatively small and highly ephemeral resources at which severe competition can occur (Hanski & Cambefort 1991a; Krell-Westerwalbesloh *et al.* 2004). We observed fights at the dung pat only once in the gallery forest, but fights were common in the savanna. Particularly when dung beetle abundance was high rollers often tried to steal balls made by other individuals (Kunz, pers. observ.; see also Heinrich & Bartholomew 1979). We suppose that as a consequence of high competition rollers in the savanna quickly remove whatever resembles a dung ball, leading to dispersal of large single seeds. Heinrich & Bartholomew (1979) showed that dung beetles also removed artificial clay balls covered with fluid of elephant dung.

It is important to recognize that small rollers of the tribe Sisyphini and Gymnopleurini (≤ 10.8 mm body size) were most active in dispersal of large single seeds (up to 18 mm seed length). The data contrast with findings from other studies in which mostly larger dung beetles dispersed large seeds (Andresen 1999, 2002; Feer 1999; Vulinec 2002), or in which small rollers of < 11.5 mm body length had little effect on seed removal (Slade *et al.* 2007). For example, (Andresen 2002) found that in the Amazonian rainforest seeds between 11 and 27 mm were only buried by beetles > 10 mm.

For the three abundant and relatively small roller species (< 11 mm) that we studied in more detail, seeds dispersed singly were within the 75%-range size of dung ball sizes produced by each roller species, but seed species that deviated in seed size up to about 4 mm were also taken. Seeds regularly dispersed by olive baboons seem too small to be mistaken singly for adequate dung balls by the large nocturnal roller species in CNP (*Anachalcos* spp., *Scarabaeus goryi*), but the largest seeds of up to 27 mm size infrequently dispersed by baboons (Kunz & Linsenmair 2008b) might profit from single dispersal by these large rollers as their size corresponds to the median size of the dung balls measured in the gallery forest. Regarding sizes and weights of single seeds that small rollers are able to move it needs to be tested if some of the medium sized rollers are also able to remove these large seeds. Caution should be taken when classifying dung beetles into more or less effective seed dispersers of large seeds by beetle or dung ball size alone.

All seed species but one that were mistaken for dung balls were also incorporated into dung balls. Dispersal of comparatively small numbers of seeds and seed species per roller dung ball reduced the primary clumping of seeds in baboon faeces considerably, particularly in the savanna. Faeces of olive baboons in CNP contain on average intact seeds from 2.0 ± 1.5 species (max = 10) and a median seed number of 20.5 seeds per sample (max = 13,258) (Kunz & Linsenmair 2008b). Because removal distance of dung balls seems not correlated to the body size of roller species in CNP, and because large dung balls of large rollers will generally include more seeds than small ones (Feer 1999; Andresen 2001), small roller beetles will scatter seeds locally more than large ones (see also Vulinec 2002). Corresponding to the few studies which report secondary dispersal distances (Andresen 1999, 2002; Andresen & Levey 2004; Wehncke & Dalling 2005; Ponce-Santizo *et al.* 2006), most of the dung balls and single seeds removed by rollers in CNP did not go beyond the first few meters around the dung pat. In several studies, however, a few seeds were moved over larger distances (10 to 15 m, reviewed in Nichols *et al.* 2008). The largest distance a dung ball was moved in the present study was > 20 m, when a single *Gymnopleurus* sp. rolled the ball in the savanna and over large parts on a dirt road, before being raided by a pair of other dung beetles. Our data suggest that the substrate is an important factor influencing secondary dispersal distances and that these are larger where leaf litter on the ground does not obstruct movements of dung beetles.

In several studies secondary dispersal distances and probability of burial by dung beetles decreased with seed size (Shepherd & Chapman 1998; Andresen 1999, 2002; Feer 1999). We did not find a significant difference between the distance single large seeds and dung balls (potentially including also smaller seeds) were removed, nor did dispersal distances correlate with seed size in seeds mistaken as dung balls. Most dung balls and single seeds removed by rollers of which we observed seed fate were burrowed in either habitat. If burrowing depth is similar in both habitats, than seeds removed by rollers might generally benefit from reduced seed predation in the forest as well as in the savanna (following Estrada & Coates-Estrada 1991; Shepherd & Chapman 1998; Andresen 1999; Feer 1999).

Where animal-dispersed plant species are abundant in open habitats such as in the Guinea-savanna of West Africa, dung beetles can become important dispersers of seeds from frugivore dung, both quantitatively and qualitatively, dispersing a wide array of different seed sizes. Savannas cover about 65% of the African continent (Tischler 1993) and harbour the highest diversity of dung beetle species world wide (Cambefort 1991), but are under severe pressure from land degradation with considerable impacts on biodiversity (UNEP 2007). Abundant variations to Neotropical forests, from which to date most of the available data on secondary seed dispersal by rollers and tunnelers come from, call for further research to extend our knowledge on post-dispersal seed fate and the effects on plant regeneration in these ecosystems.

8. 5 REFERENCES

Andresen, E. 1999. Seed dispersal by monkeys and the fate of dispersed seeds in a Peruvian rain forest. *Biotropica* 31: 145-158.

Andresen, E. 2001. Effects of dung presence, dung amount and secondary dispersal by dung beetles on the fate of *Micropholis guyanensis* (Sapotaceae) seeds in Central Amazonia. *Journal of Tropical Ecology* 17: 61-78.

Andresen, E. 2002. Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. *Ecological Entomology* 27: 257-270.

Andresen, E. 2003. Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. *Ecography* 26: 87-97.

Andresen, E. 2005. Effects of season and vegetation type on community organization of dung beetles in a tropical dry forest. *Biotropica* 37: 291-300.

Andresen, E. & Feer, F. 2005. The role of dung beetles as secondary dispersers and their effect on plant regeneration in tropical rain forests. Pp. 331-349 In Forget, P. M., Lambert, J. E., Hulme, P. E. & van der Wall, S. B. (eds.). *Seed fate: predation, dispersal and seedling establishment.* CABI, Wallingford.

Andresen, E. & Levey, D. 2004. Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. *Oecologia* 139: 45-54.

Arbonnier, M. 2000. *Arbres, arbustres et lianes des zones sèches d'Afrique de l'Ouest*. Muséum National d'Histoire Naturelle, Paris.

Barbero, E., Palestrini, C. & Rolando, A. 1999. Dung beetle conservation: effects of habitat and resource selection (Coleoptera: Scarabaeoidea). *Journal of Insect Conservation* 3: 75-84.

Bordat, P. 1983. Contribution à la connaissance des Aphodiidae de la Côte d'Ivoire (Coleoptera, Scarabaeoidea). *Revue Française d'Entomologie (n.s.)* 5: 64-70.

Cambefort, Y. 1984, Etude écologique des coléoptères Scarabaeidae de Côte d'Ivoire. PhD thesis. Muséum National d'Histoire Naturelle, Paris & University of Abidjan, Ivory Coast.

Cambefort, Y. 1991. Dung beetles in tropical savannas. Pp. 156-178 In Hanski, I. & Cambefort, Y. (eds.). *Dung beetle ecology*. Princeton University Press, Princeton.

Cambefort, Y. & Hanski, I. 1991. Dung beetle population biology. Pp. 36-50 In Hanski, I. & Cambefort, Y. (eds.). *Dung beetle ecology*. Princeton University Press, Princeton.

Cambefort, Y. & Walter, P. 1991. Dung beetles in tropical forests in Africa. Pp. 199-210 In Hanski, I. & Cambefort, Y. (eds.). *Dung beetle ecology*. Princeton University Press, Princeton.

Castellanos, M. C., Escobar, F. S. & Stevenson, P. R. 1999. Dung beetles (Scarabaeidae: Scarabaeinae) attracted to woolly monkey (*Lagothrix lagothricha* Humboldt) dung at Tinigua National Park, Colombia. *The Coleopterists Bulletin* 53: 155-159.

Chambers, J. C. & MacMahon, J. A. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural managed systems. *Annual Review of Ecology and Systematics* 25: 263-292.

Chapman, C. A. & Chapman, L. J. 1996. Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. *Journal of Tropical Ecology* 12: 491-504.

Chapman, C. A., Chapman, L. J., Vulinec, K., Zanne, A. & Lawes, M. J. 2003. Fragmentation and alteration of seed dispersal processes: an initial evaluation of dung beetles, seed fate, and seedling diversity. *Biotropica* 35: 382-393.

Davis, A. L. V. & Philips, T. K. 2005. Effect of deforestation on a Southwest Ghana dung beetle assemblage (Coleoptera: Scarabaeidae) at the periphery of Ankasa Conservation Area. *Environmental Entomology* 34: 1081-1088.

Doube, B. M. 1990. A functional classification for analysis of the structure of dung beetle assemblages. *Ecological Entomology* 15: 371-383.

Escobar, F. 2004. Diversity and composition of dung beetle (Scarabaeinae) assemblages in a heterogeneous Andean landscape. *Tropical Zoology* 17: 123-136.

Estrada, A. & Coates-Estrada, R. 1991. Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: ecological interactions of Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 7: 459-474.

Estrada, A. & Coates-Estrada, R. 2002. Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas, Mexico. *Biodiversity and Conservation* 11: 1903-1918.

Estrada, A., Coates-Estrada, R., Anzures Dadda, A. & Cammarano, P. 1998. Dung and carrion beetles in tropical forest fragments and agricultural habitats at Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 14: 577-593.

Feer, F. 1999. Effects of dung beetles (Scarabaeidae) on seeds dispersed by howler monkeys (*Alouatta seniculus*) in the French Guianan rain forest. *Journal of Tropical Ecology* 15: 129-142.

Fenner, M. & Thompson, K. 2005. *The ecology of seeds*. Cambridge University Press, Cambridge.

FGU-Kronberg. 1979. Gegenwärtiger Status der Comoé- und Tai-Nationalparks sowie des Azagny-Reservats und Vorschläge zu deren Erhaltung und Entwicklung zur Förderung des Tourismus. Technical Report. Deutsche Gesellschaft für Technische Zusammenarbeit GmbH, Eschborn.

Fischer, F., Groß, M. & Kunz, B. 2000. Primates of the Comoé National Park, Ivory Coast. *African Primates* 4: 10-15.

Fischer, F., Groß, M. & Linsenmair, K. E. 2002. Updated list of the larger mammals of the Comoé National Park, Ivory Coast. *Mammalia* 66: 83-92.

Goetze, D., Hoersch, B. & Porembski, S. 2006. Dynamics of forest-savanna mosaics in north-eastern Ivory Coast from 1954 to 2002. *Journal of Biogeography* 33: 653-664.

Halffter, G. & Arellano, L. 2002. Response of dung beetle diversity to human-induced changes in a tropical landscape. *Biotropica* 34: 144–154.

Hanski, I. 1991. The dung insect community. Pp. 5-21 In Hanski, I. & Cambefort, Y. (eds.). *Dung beetle ecology*. Princeton University Press, Princeton.

Hanski, I. & Cambefort, Y. 1991a. Competition in dung beetles. Pp. 305-329 In Hanski, I. & Cambefort, Y. (eds.). *Dung beetle ecology*. Princeton University Press, Princeton.

Hanski, I. & Cambefort, Y. (eds.). 1991b. *Dung beetle ecology*. Princeton University Press, Princeton.

Hanski, I. & Cambefort, Y. 1991c. Resource partitioning. Pp. 330-349 In Hanski, I. & Cambefort, Y. (eds.). *Dung beetle ecology*. Princeton University Press, Princeton.

Hanski, I. & Cambefort, Y. 1991d. Species richness. Pp. 350-365 In Hanski, I. & Cambefort, Y. (eds.). *Dung beetle ecology*. Princeton University Press, Princeton.

Heinrich, B. & Bartholomew, G. A. 1979. The ecology of the African dung beetle. *Scientific American* 241: 118-126.

Hennenberg, K. J., Fischer, F., Kouadio, K., Goetze, D., Orthmann, B., Linsenmair, K. E., Jeltsch, F. & Porembski, S. 2006. Phytomass and fire occurrence along forest–savanna transects in the Comoé National Park, Ivory Coast. *Journal of Tropical Ecology* 22: 303-311.

Hill, C. J. 1996. Habitat specificity and food preference of an assemblage of tropical Australian dung beetles. *Journal of Tropical Ecology* 12: 449-460.

Horgan, F. G. 2001. Burial of bovine dung by coprophagous beetles (Coleoptera: Scarabaeidae) from horse and cow grazing sites in El Salvador. *European Journal of Soil Biology* 37: 103-111.

Hovestadt, T., Yao, P. & Linsenmair, K. E. 1999. Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoé National Park, Ivory Coast). *Plant Ecology* 144: 1-25.

Howe, H. F. 1989. Scatter and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* 79: 417-426.

Howe, H. F. & Smallwood, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201-228.

Hutchinson, J., Dalziel, J. M. & Keay, R. W. J. 1954-1968. *Flora of West Tropical Africa.* Vols. I-III. Crown Agents for Oversea Governments and Administrations, London.

Jankielsohn, A., Scholtz, C. H. & Louw, S. V. 2001. Effect of habitat transformation on dung beetle assemblages - a comparison between a South African nature reserve and neighboring farms. *Environmental Entomology* 30: 474-483.

Kasparek, M. 2000. *Flore du Parc National de Tai (Côte d'Ivoire).* Kasparek, Heidelberg.

Krell, F. T. 2007. Dung beetle sampling protocols. *Denver Museum of Nature and Science Technical Report* 6: 1-11.

Krell, F. T., Krell-Westerwalbesloh, S., Weiss, I., Eggleton, P. & Linsenmair, K. E. 2003. Spatial separation of Afrotropical dung beetle guilds: a trade-off between competitive superiority and energetic constraints (Coleptera: Scarabaeidae). *Ecography* 26: 210-222.

Krell-Westerwalbesloh, S., Krell, F. T. & Linsenmair, K. E. 2004. Diel separation of Afrotropical dung beetle guilds - avoiding competition and neglecting resources (Coleptera: Scarabaeidae). *Journal of Natural History* 38: 2225-2249.

Kunz, B. K. & Linsenmair, K. E. 2008a. The disregarded West: diet and behavioural ecology of olive baboons in the Ivory Coast. *Folia Primatologica* 79: 31-51.

Kunz, B. K. & Linsenmair, K. E. 2008b. The role of the olive baboon (*Papio anubis*, Cercopithecidae) as seed disperser in a savanna-forest mosaic of West Africa. *Journal of Tropical Ecology* 24: 235-246.

Lepš, J. & Šmilauer, P. 2003. *Multivariate analysis if ecological data using CANOCO*. Cambridge University Press, Cambridge.

Lieberman, D., Hall, J. B., Swaine, M. D. & Lieberman, M. 1979. Seed dispersal by baboons in the Shai Hills, Ghana. *Ecology* 60: 65-75.

Nichols, E., Larsen, T., Spector, S., Davis, A. L., Escobar, F., Favila, M., Vulinec, K. & Network, S. R. 2007. Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. *Biological Conservation* 137: 1-19.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M. E. & Network, T. S. R. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation* 141: 1461-1474.

Nielsen, S. T. 2007. Deforestation and biodiversity: effects of bushland cultivation on dung beetles in semi-arid Tanzania. *Biodiversity and Conservation* 16: 2753-2769.

Poilecot, P. 1991. *Un écosystème de savane soudanienne: le Parc National de la Comoé (Côte d'Ivoire).* UNESCO, Paris.

Pomeroy, D. E. & Service, M. W. 1986. *Tropical ecology*. Longman, Harlow.

Ponce-Santizo, G., Andresen, E., Cano, E. & Cuaron, A. D. 2006. Primary dispersal of seeds by primates and secondary dispersal by dung beetles in Tikal, Guatemala. *Biotropica* 38: 390-397.

Porembski, S. 1991. Beiträge zur Pflanzenwelt des Comoé-Nationalparks (Elfenbeinküste). *Natur und Museum* 121: 61-82.

Porembski, S. 2001. Phytodiversity and structure of the Comoé river gallery forest (NE Ivory Coast). Pp. 1-10 In Gottsberger, G. & Liede, S. (eds.). *Life forms and dynamics in tropical forests*. Borntraeger, Berlin.

Scheffler, P. Y. 2005. Dung beetle (Coleoptera: Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia. *Journal of Tropical Ecology* 21: 9-19.

Shepherd, V. E. & Chapman, C. A. 1998. Dung beetles as secondary seed dispersers: impact on seed predation and germination. *Journal of Tropical Ecology* 14: 199-215.

Slade, E. M., Mann, D. J., Villanueva, J. F. & Lewis, O. T. 2007. Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *Journal of Animal Ecology* 76: 1094-1104.

Spector, S. & Ayzama, S. 2003. Rapid turnover and edge effects in dung beetle assemblages (Scarabaeidae) at a Bolivian Neotropical forest-savanna ecotone. *Biotropica* 35: 394–404.

Tischler, W. 1993. *Einführung in die Ökologie*. Fischer, Stuttgart.

UNEP. 2007. Global environment outlook (GEO-4). Technical Report. http://www.unep.org/geo/geo4/media/

Vander Wall, S. B. & Longland, W. S. 2004. Diplochory: are two seed dispersers better than one? *Trends in Ecology & Evolution* 19: 155-161.

Vander-Wall, S. B., Kuhn, K. M. & Beck, M. J. 2005. Seed removal, seed predation, and secondary dispersal. *Ecology* 86: 801-806.

Vernes, K., Pope, L. C., Hill, C. J. & Bärlocher, F. 2005. Seasonality, dung specificity and competition in dung beetle assemblages in the Australian Wet Tropics, north-eastern Australia. *Journal of Tropical Ecology* 21: 1-8.

von Maydell, H. J. 1990. *Trees and shrubs of the Sahel. Their characteristics and uses.* Josef Margraf, Weikersheim.

Vulinec, K. 2002. Dung beetle communities and seed dispersal in primary forest and disturbed land in Amazonia. *Biotropica* 34: 297-309.

Wehncke, E. V. & Dalling, J. W. 2005. Post-dispersal seed removal and germination selected tree species dispersed by *Cebus capucinus* on Barro Colorado Island, Panama. *Biotropica* 37: 73-80.

Wenny, D. G. 2001. Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research* 3: 51-74.

White, F. 1983. *The vegetation of Africa*. UNESCO, Paris.

Wohlfarth-Bottermann, M. 1994. Anthropogenen Veränderungen der Vegetationsbedeckung in Côte d'Ivoire seit der Kolonialisierung. *Erdwissenschaftliche Forschung* 30: 301-480.

Appendix 1 List of roller and tunneler dung beetle species (Scarabaeidae: Scarabaeinae and Aphodiinae) attracted to piles of fresh dung from olive baboons exposed in the Comoé National Park, Ivory Coast

Habitat, diel activity (Diel) and fresh weight are following Cambefort (1984) with a few exceptions. d = diurnal, n = nocturnal, c = day and night, *= diel classification according to our own data (species not listed in study by Cambefort (1984); S = savanna, F = forest. F^{1} indicates that the species was previously only recorded in the savanna, and S^{2} indicate that a species was only found in the gallery forest by Cambefort (1984).

Species per guild	Diel	Habitat	Weight [mg]	Length [mm]	N^{o}. of indiv.	
					in S	in F
Telecoprids (rollers)						
Allogymnopleurus umbrinus (Gerstaecker)	d	S	140.0	12.0	15	
Allogymnopleurus youngai Endrődi	d	S	175.0	11.8	1	
Anachalcos aurescens Bates	n	S	1738.0	24.5	5	
Anachalcos convexus Boheman	n	S,F^{1}	1165.0	20.0	15	1
Anachalcos cupreus (Fabricius)	n	S,F	1600.0	20.0	1	5
Anachalcos suturalis Janssens	n	S	517.0	16.5	31	
Garreta azureus (Fabricius)	d	S,F	344.0	17.3		1
Garreta nitens (Olivier)	d	S	310.0	15.5	12	
Gymnopleurus coerulescens (Olivier)	d	S	62.0	9.0	17	
Gymnopleurus puncticollis Gillet	d	S	130.0	10.5	141	
*Neosisyphus armatus (*Gory)	d	S,F^{1}	49.0	7.5	16	1
Neosisyphus gladiator (Arrow)	d	S	155.0	10.8	3	
Scarabaeus goryi (Castelnau)	n	S	1675.0	30.0	2	
Sisyphus biarmatus Felsche	d	S	46.0	6.3	47	
Sisyphus eburneus Cambefort	d	F	10.7	4.7		18
Sisyphus gazanus Arrow	d	S,F	25.0	5.5	13	6
Sisyphus goryi Harold	d	S,F	17.0	5.9	683	7
Sisyphus seminulum Gerstaecker	d	S,F	8.2	3.8	91	7
Paracoprids (tunnelers)						
Caccobius anthracites d'Orbigny	n	S	119.0	9.8	3	
Caccobius auberti d'Orbigny	d	S,F	5.0	3.0	34	3
Caccobius ivorensis Cambefort	d	S,F	7.0	4.3	30	2
Caccobius mirabilepunctatus Cambefort	d	S,F^{1}	12.0	5.1	24	1
Caccobius punctatissimus Harold	n	S		4.5	1	
Catharsius eteocles (Castelnau)	n	S	1267.0	28.0	2	
Catharsius ninus Gillet	n	F,S^{2}	255.0	15.0	1	
Catharsius pseudolycaon Ferreira	n	S,F	1107.0	23.0	1	1
Catharsius sesostris Waterhouse	n	S,F	566.0	20.0	1	
Copris carmelita Fabricius	n	S,F	464.0	17.0		2
Diastellopalpus tridens (Fabricius)	c'	F	380.0	14.5		11
Digitonthophagus gazella (Fabricius)	n	S	129.0	10.3	1	
Drepanocerus laticollis Fåhraeus	d	S,F^{1}	8.0	5.3	1	7
Euoniticellus parvus (Kraatz)	d	S,F^{1}	5.0	3.5	1	1
Euonthophagus carbonarius (Klug)	n	S	45.0	8.0	4	
Hyalonthophagus pseucoalcyon (d'Orbigny)	d	S	62.0	8.5	1	

Appendix 1 (continued)

Paracoprids (tunnelers)	Diel	Habitat	Weight [mg]	Length [mm]	N°. of indiv.	
					in S	in F
Metacatharsius inermis (Castelnau)	n	S	130.0	12.5	2	
Milichus apicalis Fåhraeus	n	S,F	31.0	6.5	2	
Milichus serratus d'Orbigny	n	S,F	32.0	6.4	5	
Onitis cupreus Castelnau	n	S,F	463.0	15.0	21	2
Onitis multidentatus Gillet	n	S	490.0	19.5	2	
Onthophagus altidorsis d'Orbigny	c'	S,F	24.0	5.2		3
Onthophagus atridorsis d'Orbigny	c	S,F	3.0	3.4	24	9
Onthophagus bandamai Cambefort	d	F,S[2]	15.0	5.0	4	775
Onthophagus bidens Olivier	d	S,F	35.0	7.0	2	
Onthophagus borassi Cambefort	d	S,F	7.0	3.7	6	5
Onthophagus cribellum d'Orbigny	d	S	18.0	5.3	5	
Onthophagus cupreus Harold	d	S	105.0	8.3	6	
Onthophagus cyanochlorus d'Orbigny	d	S,F	12.0	4.8	26	66
Onthophagus decorsei d'Orbigny	d*	S,F		6.0	2	
Onthophagus denudatus d'Orbigny	n	F	23.0	5.3		1
Onthophagus feai d'Orbigny	d	F,S	28.0	6.5		24
Onthophagus fimetarius Roth	n	S,F[1]	27.0	6.0	62	1
Onthophagus flaviclava d'Orbigny	d	S,F	14.0	3.8	64	2
Onthophagus flexicornis d'Orbigny	n	S	31.0	7.5	28	
Onthophagus hilaris d'Orbigny	d	F	13.0	4.8		10
Onthophagus kindianus Frey	c'	F	67.0	7.5		21
Onthophagus lobi Cambefort	n	S	33.0	7.3	1	
Onthophagus longipilis d'Orbigny	d	S,F	35.0	5.8	1	5
Onthophagus lutaticollis d'Orbigny	d	S	17.0	4.8	8	
Onthophagus micros d'Orbigny	d	S	3.0	2.4	1	
Onthophagus miles d'Orbigny	d	F	18.0	5.1		35
Onthophagus mucronatus Thomson	d	S,F	11.0	4.3	158	44
Onthophagus mucronifer d'Orbigny	n	S	10.0	4.8	114	
Onthophagus pullus Roth	d	S,F	3.0	2.7	40	9
Onthophagus raffrayi d'Orbigny	d	F	16.0	5.3		24
Onthophagus reticulatus d'Orbigny	n	S	44.0	6.8	1	
Onthophagus rufonotatus d'Orbigny	d	S,F	48.0	7.5	199	1
Onthophagus sellatulus d'Orbigny	n	S,F	14.0	4.7	3	
Onthophagus sipilouensis Cambefort	c'	F	9.0	4.1		15
Onthophagus stehliki Balthasar	d	S,F	45.0	7.2	87	4
Onthophagus tripartitus d'Orbigny	n	S	17.0	5.0	12	
Onthophagus ulula Balthasar	n	S,F	15.0	4.7	150	
Phalops iphis (Olivier)	d	S	124.0	9.8	1	
Phalops vanellus Lansberge	d	S	68.0	10.0	1	
Proagoderus auratus (Fabricius)	d	S	213.0	12.5	4	
Proagoderus yvescambeforti Moretto	d*	S		12.0	3	
Tiniocellus spinipes (Roth)	d	S,F	18.0	6.5	124	5

Summary and Outlook

Frugivory and seed dispersal are crucial for maintaining the structural and dynamic properties of diverse tropical ecosystems. Frugivorous nonhuman primates[1] are among the major groups of frugivores in the tropics. They can harvest considerable amounts of fruit crops from a wide variety of plant species. When destroying large numbers of seeds during consumption, or dispersing intact seeds over relatively wide areas, they can influence the spatial and genetic structure of plant populations and may contribute to plant community dynamics.

Many primates frequently disperse high numbers of seeds in single dung pats. Because post-dispersal seed loss at such clumped seed patches often is severe, secondary dispersal of seeds by dung beetles (Coleoptera, Scarabaeidae) can be crucial for plant establishment from primate faeces. Telecoprid[2] and paracoprid[3] dung beetles can alter the pattern of primary dispersed seeds locally and potentially increase the numbers of seeds that end up in safe sites suitable for germination and seedling establishment, by accidentally incorporating small numbers of seeds in the dung portions, which they remove and often burrow.

The interplay between fruiting plants, primates and dung beetles has been studied mostly in (Neo)tropical forests whereas savanna systems remain largely unexplored. Savannas cover about 65% of the African continent. They are home to several primate species and harbour the richest dung beetle community worldwide. The Guinea savanna-forest mosaic of West Africa is particularly rich in animal-dispersed plants. The role of primates and dung beetles in natural plant regeneration and biodiversity maintenance in this ecosystem, however, is still poorly understood.

This study investigated the role of the olive baboon (*Papio anubis* Lesson 1827) as primary seed disperser and pre-dispersal seed predator as well as the effects of dung beetles on secondary dispersal of seeds from baboon dung. Research took place in the Comoé National Park (CNP) (08°30'-09°36' N, 003°07'-004°25' W), north-eastern Ivory Coast, during 24 months from November 1997 to July 2000. The study area (~ 145 km^2) was situated in the southern part of the national park within the species rich Guineo-Congolia / Sudania transition zone. The vegetation is a mosaic of Guinea savanna, forest islands, and gallery forest.

The olive baboon is the largest and most widely distributed monkey in Africa. It is the only baboon species in CNP, and the primate with the highest biomass in the study area.

---

[1] For better readability I henceforth refer to nonhuman primates as 'primates'

[2] Telecoprids (Rollers) remove small portions of dung from the place of primary deposition by forming dung balls and rolling them some distance away. Dung balls are often buried.

[3] Paracoprids (Tunnelers) burrow tunnels and brood chambers into the soil under or near the dung pat into which they pull small portions of dung.

Olive baboons live in groups comprising one to several adult males, several adult females and their offspring. What we know today about the socioecology and behavioural ecology of olive baboons, however, almost exclusively derived from populations in East Africa.

A prerequisite to describe the baboons' role in seed dispersal and pre-dispersal seed predation in the ecosystem of the CNP were basic data on the number of baboons present in the study area, their ranging behaviour, habitat use, diet and time budget. I monitored baboon abundance and group sizes at least fortnightly along transects. For detailed observations on baboon diet and behaviour I habituated and followed two groups of different size (GP-group 9-13 individuals, 1S-groups 36-44 individuals).

Against expectations for the kind of habitat, the individual density of olive baboons was low, yielding only 1.2 baboons / km^2. Ten groups occupied the study area. In comparison with other olive baboon populations, group sizes were small, averaging 15 individuals (max. 44 individuals), and the proportion of one-male groups (50-63 %) was remarkably high.

The two habituated groups had large home ranges compared to groups studied at other partially forested sites elsewhere. Both groups in CNP used forests more often than expected by random. Several studies showed that group size can affect primate time budget. In CNP, the time budget of the two groups differed only with regards to resting, yet against expectations the larger group spent more time resting than the small group. I argue that regular subgrouping of the larger focal group and different habitat quality countervailed size-dependent differences in the time budget between groups. Differences to other study sites, however, are not completely explained by current models on baboon (socio)ecology.

The baboons in CNP were highly frugivorous, spending about 50% of their feeding time on fruits and seeds. Using direct feeding observations and analyses of faecal samples I recorded a total of 79 woody fruit plant species in their diet (fruits/seeds consumed from trees, shrubs, lianas). One pivotal question in primate-plant interactions is about the traits that influence primate fruit choice among the plant species available at a given site. Specifically I was interested in the suites of traits that best predict fruit choice and seed handling by baboons.

Seventy-four woody plant species in baboon diet in CNP were identified to at least the genus level, representing 25% of the woody plant species in the study area. Relative to the availability in the regional pool of woody plant species, baboons preferred trees to shrubs and lianas as fruit sources. Otherwise, baboons seemed to consume whatever fruit type, colour, and size of fruit and seeds available, though they especially included larger fruit into their diet. Against expectations from the African 'bird-monkey fruit syndrome' of brightly coloured drupes and berries (but in concordance with the mammal-fruit syndrome

postulated for other regions), baboons ate mostly species having large, dull-coloured fruit. In a logistic regression model, fruit type and colour best described whether baboons included a species into their diet, whereas fruit type and seed size best predicted whether baboons predated upon the seeds of a food plant species.

To proof seed dispersal by olive baboons I analyzed 396 faecal samples from the 10 groups in the study area in terms of quantitative and qualitative aspects of seed handling and dispersal (excluding grasses and sedges). Eighty-nine percent of the faecal samples contained at least one intact seed. Seventy-three per cent of the seeds in the faecal samples were undamaged. Intact seeds were from 65 species. On average, baboon defecations contained intact seeds from 2.0 species (range = 0-10). I estimated that the baboon population in the study area disperses 1,483 intact seeds d^{-1} km^{-2}.

Eighteen out of 19 species tested in germination experiments were viable after ingestion by baboons, but effects of gut passage upon germination varied widely.

The size of seeds dispersed by olive baboons varied between 1 and 27 mm, and 77% of the species had medium-sized to large seeds (> 5 mm). No linear correlation between mean seed size and seed damage was found.

Seed size is an important plant fitness trait that can influence several steps between fruiting and the establishment of a plant's offspring. Seed size varies not only between plant species but often also considerably within and among individuals of the same species. The relevance of the trait for intraspecific fruit choice by primates and its implications for tree regeneration has, however, received little attention. Primates may select for certain seed sizes within a species for a number of reasons, e.g. to decrease indigestible seed load or to increase pulp intake per fruit.

I studied baboon feeding behaviour and fruit choice in a typical 'mammal fruit', the African locust bean (*Parkia biglobosa*, Mimosaceae), which I presumed was almost exclusively harvested by baboons at the study site. To define selectivity in baboons I used direct observations of the two habituated groups as well as indirect evidence from faecal analysis and from leftovers of the large pods after feeding events.

Olive baboons acted as both seed predators and dispersers for *Parkia biglobosa*. They fed on and destroyed unripe seeds, and swallowed and dispersed intact ripe seeds when consuming mature fruit pulp.

The baboons harvested > 96% of fruit crops from each of the seven focal trees. Predation rates of the trees were high; baboons dispersed only 10% of the seed crops (median value). Predation and dispersal of seeds was linked to seed number and size. Olive baboons increased food gain per fruit by selecting unripe pods containing a significantly higher seed number and larger and heavier seeds. Consequently, only pods with fewer and smaller seeds remained on the trees for maturation. Thereafter, baboons fed on mature pods containing the smallest seeds, and exploited pods with more seeds to a greater extent than those with fewer seeds. Consequently, pods with small seeds *and* an intermediate seed number contributed the most to dispersal by baboons.

To analyse whether baboon fruit selection criteria are similar in other plant species, I compared seed sizes from randomly collected fresh fruits to the sizes of seeds extracted from baboon dung within each of ten additional plant species in baboon diet. Species differed in fruit type and seed number per fruit. Baboons commonly fed on the fruit pulp of nine of the species and on the seeds of one species. Across plant species, the baboons dispersed both seeds that were significantly smaller and larger in size than seeds extracted manually from fresh fruits. In two species, sizes of ingested seeds and seeds from fresh fruits did not differ significantly. Baboons frequently spat out seeds of *Drypetes floribunda* (Euphorbiaceae) but not of other plant species having seeds of equal size. Oral processing of *D. floribunda* seeds depended on seed size: seeds that were spat out were significantly larger, and swallowed seeds smaller, than seeds from randomly collected fresh fruits. I argue that seed size selection by olive baboons is influenced, among other traits, by the amount of pulp rewarded per fruit relative to seed load, which varies with fruit and seed shape.

Whereas in *P. biglobosa* I investigated the role of olive baboons in seed dispersal of a typical 'mammal-fruit', I assessed their role in relation to other frugivores by monitoring quantitative and qualitative aspects of seed dispersal in typical 'bird-dispersed' tree species, *Lannea acida* and *L. welwitschii* (Anacardiaceae). Given the type and size of the fruits (small, juicy drupes) *Lannea* should be attractive to a wider range of arboreal frugivores. I recorded frugivore assemblages, feeding activity during crop maturation, fruit removal, and fruit handling by different frugivores at focal trees.

Removal efficiency from *L. acida* was up to 30% in two consecutive years, but most of the harvest as well as fruit fall was unripe (up to 100%). Birds were the most common frugivores in the canopy of *L. acida* but predominantly consumed unripe, green fruit, the seeds of which failed to germinate in germination trials. Baboons and the three other primate species observed feeding on *L. acida* fruits tended to visit trees after the onset of fruit maturation. Nearly all seeds found in faeces of olive baboons were undamaged and had a significantly higher germination success compared to undispersed seeds from fresh ripe fruits.

Removal efficiency was higher in *L. welwitschii* (48.5%) and most fruits were removed during and after maturation, yet pre-dispersal seed predation by the sun squirrel *Heliosciurus rufobrachium* accounted for 28.6% loss of total crop. Consequently, only 19.9% of the seed crop was left to potential seed dispersal by primates and birds. In contrast, *H. rufobrachium* rarely fed on *L. acida* seeds.

Birds were able to compensate for lower food intake per visit by visiting a feeding tree more frequently. Birds and primates may thus both be important seed dispersers of *Lannea* seeds in terms of quantity. However, non-granivorous birds that otherwise may be legitimate seed dispersers can become quantitatively important seed predators when consuming unripe fruits, for example during times of fruit scarcity. Regeneration in *L. acida* and *L. welwitschii* seems to be 'source limited' as well as 'dissemination limited', at least in certain years and tree individuals. Because interannual and intraspecific variation in fruit removal can be substantial, further research is required to determine long-term reproductive output in the two species.

The last chapter focused on the fate of seeds dispersed by olive baboons in CNP: I investigated how secondary seed dispersal by dung beetles alters primary dispersal patterns locally. The probability and pattern of secondary seed dispersal by dung beetles depend on the structure and composition of the dung beetle community, which, in turn, seems to be strongly determined by vegetation type. I thus expected pronounced differences in secondary seed dispersal by dung beetles between seeds deposited by baboons in the savanna and in the forest. For the first time, comparative data on secondary seed dispersal by dung beetles in both habitats in West Africa are provided.

Dung beetle activity at baboon faeces deposited in the two habitats was high, totalling 99 species from 26 genera. The number of dung beetle species in the gallery forest ($N = 47$) was about as high as species numbers attracted to primate dung in most studies in Neotropical forests, but in contrast to the Neotropics, species number ($N = 85$) and abundance in the study area were much higher in the open habitat (in CNP: savanna). The variation in the distribution of telecoprid and paracoprid individuals across the two guilds was highly significant between habitats. In the savanna, telecoprids and paracoprids each accounted for about 50% of the individuals, whereas in the gallery forest, paracoprids made up 96% of the individuals. A standardized RDA analysis showed that habitat clearly is the dominating factor explaining 15% of the variation in dung beetle assemblages at a highly significant level.

The higher abundance of telecoprids in the savanna and the larger beetle size resulted in faster removal of standardized dung portions. Telecoprids dispersed a wide array of seed sizes (up to 18 mm) naturally present in baboon dung. Secondary dispersal distances were larger in the savanna. Contrasting other studies, small telecoprids were most active in dispersal of large seeds, which were seemingly mistaken for dung balls.

The results indicate that compared to seeds dispersed by baboons into the forest, seeds that end up in the savanna generally have a higher probability of (a) being removed by dung beetles, (b) being horizontally scattered by telecoprids, (c) being rapidly removed from the place of primary deposition and (d) being secondarily dispersed over larger distances. Size comparisons between telecoprid dung balls and seeds dispersed by baboons suggest that dung beetles at the study site are capable of removing even the largest intact seeds deposited naturally in baboon faeces during seasonal peaks of dung beetle activity.

The study showed that 'western' olive baboons differ in several ways from their conspecifics in East Africa. Their social organization is more flexible than assumed from studies on eastern populations. Baboons (including other *Papio* species) are often regarded as being predominantly seed predators for woody fruit plant species. I demonstrated that olive baboons are important frugivores and quantitative as well as qualitative important seed dispersers in the savanna-forest mosaic of West Africa. In CNP, they harvest high amounts of fruits from a wide variety of plant species, fruit types, and fruit sizes, and disperse considerable numbers of intact seeds from at least 22% of the regional pool of woody plant species. Being a habitat generalist (with a preference for forest habitats) and able to move comparatively long distances, the olive baboon might be especially important for the biodiversity maintenance of distant forest islands. Because most woody plant species at the study site had medium-sized to large fruits and seeds, olive baboons may be crucial for seed dispersal and plant recruitment in this ecosystem, particularly as other large frugivores have become rare. Their importance for seed dispersal of plants with small fruits should not, however, be underrated. The study showed that classification of seed dispersers on the basis of fruit syndromes alone can be misleading.

Baboons disperse seeds in their faeces in a clumped manner, which generally is regarded disadvantageous for plants. Yet, seeds from *all* plant species being naturally present in baboon dung during seasonal peaks of dung beetle activity apparently can be scattered locally by telecoprid and paracoprid dung beetles. In general, savanna plants and plant habitat generalists the seeds of which baboons disperse into the savanna should profit most from secondary seed dispersal by dung beetles.

Africa's savannas are highly vulnerable to land degradation with considerable impact on land cover and biodiversity. Baboons are widely distributed across sub-Saharan Africa and are still relatively abundant in many areas. Considering the large extent of African savannas, the importance of baboons and dung beetles on plant population dynamics in these ecosystems merits further study, particularly with regard to seed size selectivity and its effects on seed shadows, post-dispersal seed fate, and seedling establishment.

Zusammenfassung und Ausblick

In den Tropen, in denen Frugivorie und Samenausbreitung von besonderer Bedeutung für den Erhalt und die Funktion der diversen Ökosysteme sind, kommt den fruchtfressenden Arten unter den nicht-menschlichen Primaten[1] oft eine herausragende Rolle als Samenausbreiter, aber auch als Samenprädatoren zu. Verglichen mit anderen Frugivoren konsumieren viele Primatenarten große Mengen verschiedenster Früchte von einer Vielzahl Pflanzenarten. Indem sie die Samen dieser Früchte dabei zerstören oder intakt über relativ weite Gebiete ausbreiten, können sie die räumliche und genetische Struktur von Pflanzenpopulationen und die Dynamik innerhalb von Pflanzengemeinschaften beeinflussen.
Vor allem größere Primatenarten breiten in der Regel mehrere Samen pro Fäzes aus, was oftmals zu erhöhter Samen- und Keimlingsmortalität am Ort der primären Ausbreitung führt. Sekundäre Samenausbreitung durch Dungkäfer (Coleoptera, Scarabaeidae) kann das Überleben dieser Samen entscheidend beeinflussen. Telekopride[2] und parakopride[3] Dungkäfer sichern sich kleine Dungmengen, indem sie diese vom Ort der primären Deposition entfernen und oftmals vergraben. Enthalten diese Dungkugeln Samen, kann das primäre Ausbreitungsmuster lokal verändert und die Anzahl der Samen erhöht werden, die an für die Keimung der Samen und Etablierung der Keimlinge geeignete Orte (sogenannte 'safe sites') gelangen.
Die Interaktionen zwischen Fruchtpflanzen, Primaten und Dungkäfern wurden fast ausschließlich in (neo)tropischen Wäldern untersucht, wohingegen Savannensysteme in dieser Hinsicht kaum erforscht sind. Savannen bedecken etwa 65% des Afrikanischen Kontinents. Sie beherbergen eine Vielzahl Primatenarten sowie die artenreichste Dungkäfergemeinschaft der Erde. Das Guinea Savanne-Wald-Mosaik Westafrikas weist einen hohen Artenreichtum an Pflanzenarten auf, deren Samen durch Frugivore ausgebreitet werden. Über die Bedeutung von Primaten und Dungkäfern für die Regeneration dieser Pflanzen und den Erhalt der Biodiversität ist in diesem Ökosystem jedoch bislang kaum etwas bekannt.

Diese Arbeit beschäftigt sich mit der Rolle des Anubis Pavians (*Papio anubis* Lesson 1827) als primärer Samenausbreiter und Samenprädator und der Bedeutung von Dungkäfern für die sekundäre Ausbreitung von Samen aus Pavianfäzes im Comoé Nationalpark (CNP) im Nordosten der Elfenbeinküste (08°30-09°36' N, 003°07'-004°25' W).

---

[1] im Folgenden der Einfachheit halber als „Primaten“ bezeichnet

[2] Telekopride Dungkäfer (Roller, „Pillendreher“) sichern sich Dungportionen indem sie diese zu Kugeln formen und sie von den Fäzes wegrollen. Die Kugeln werden an anderer Stelle abgelegt, oft auch vergraben.

[3] Parakopride (Tunneler) graben Gänge und Brutkammern in den Boden unterhalb oder in unmittelbarer Nähe des Dunghaufens und statten diese Kammern mit Dungportionen aus.

Das Untersuchungsgebiet erstreckte sich über eine Fläche von etwa 145 km^2 im südlichen Teil des Nationalparks, inmitten des artenreichen Übergangsbereichs von Guinea- und Subsudanzone. Die Vegetation im Untersuchungsgebiet setzt sich aus Guinea-Savanne mit darin eingestreuten Inselwäldern sowie Galeriewald zusammen. Die Untersuchungen führte ich während 24 Monaten zwischen November 1997 und Juli 2000 durch.

Der Anubis Pavian ist die, mit Ausnahme der großen Menschenaffen, größte und am weitesten verbreitete Primatenart Afrikas. Im CNP ist er die einzige Pavianart und die Primatenart mit der größten Biomasse. Anubis Paviane leben in Gruppen mit einem oder mehreren adulten Männchen, mehreren adulten Weibchen und deren Nachwuchs. Kenntnisse über die Ökologie und Ethologie der Tiere beruhen fast ausschließlich auf Untersuchungen ostafrikanischer Populationen.

Um die Bedeutung des Anubis Pavians für die Samenausbreitung im Untersuchungsgebiet abschätzen zu können, war es erforderlich, Grundlagendaten über die Individuendichte der Paviane, ihr Streifverhalten, ihre Habitatnutzung, ihre Nahrung und ihr Zeitbudget zu erheben. Hierfür erfasste ich die Anzahl und Größe der Gruppen im Untersuchungsgebiet regelmäßig entlang von Transekten. Die Beobachtung zweier von mir habituierter Gruppen unterschiedlicher Größe (Gruppe GP mit 9-13 Individuen, Gruppe 1S mit 36-44 Individuen) lieferte ausführliche Daten über die Nahrungszusammensetzung und das Verhalten der Paviane.

Entgegen den Erwartungen für die Art des Habitats, fiel die Individuendichte mit 1,2 Pavianen / km^2 sehr gering aus. Zehn Gruppen verteilten sich über das Untersuchungsgebiet. Im Vergleich zu anderen untersuchten Populationen des Anubis Pavians waren sowohl die durchschnittliche (15 Individuen) als auch die maximale Gruppengröße (44 Individuen) gering. Der Anteil an Ein-Männchen-Gruppen war mit 50-63% im Laufe der Untersuchungsperiode außergewöhnlich hoch.

Die Streifgebiete der beiden habituierten Gruppen waren relativ groß verglichen mit anderen Gruppen in Gebieten ähnlicher Vegetation. Bezogen auf den Flächenanteil nutzten beide Gruppen die bewaldeten Bereiche ihres Streifgebietes überproportional häufig.

In mehren Studien anderer Autoren hat sich gezeigt, dass die Gruppengröße einen Einfluss auf das Zeitbudget von Primaten haben kann. Im CNP wirkte sich die Gruppengröße lediglich auf die Zeit aus, die die Tiere mit Ruhen verbrachten; entgegen den Erwartungen war dieser Zeitanteil in der großen Gruppe höher. Maßgeblich hierfür waren wahrscheinlich die unterschiedliche Habitatqualität der Streifgebiete und wiederholte, temporäre Aufspaltungen der großen Gruppe in kleinere Teilgruppen. Unterschiede zu Pavianpopulationen in anderen Untersuchungsgebieten können durch die gängigen Modelle der Sozioökologie der Paviane nicht vollständig erklärt werden.

Die Paviane im CNP ernährten sich zu einem Großteil frugivor, etwa 50% der Zeit, die sie mit Fressen zubrachten, entfiel auf Früchte und Samen. Insgesamt konnte ich 79 Gehölzpflanzenarten (Bäume, Sträucher, Lianen), von deren Früchten und/oder Samen sich die Paviane ernährten, anhand von Nahrungsbeobachtungen und Fäzesanalysen ermitteln. Hinsichtlich des Nahrungsspektrums der Paviane stellt sich die Frage, nach welchen Kriterien die Tiere ihre Nahrungspflanzen aus dem regionalen Artenpool auswählen. Um zu untersuchen, ob die Paviane Gehölzpflanzen mit bestimmten morphologischen Merkmalen bevorzugen, habe ich den Anteil verschiedener Fruchtmerkmale sowie die Wuchsform der Nahrungspflanzenarten mit dem Anteil dieser Merkmale in der Gesamtheit der Gehölzpflanzenarten im Untersuchungsgebiet verglichen.
Vierundsiebzig der von Pavianen genutzten Gehölzpflanzenarten im CNP wurden taxonomisch identifiziert, das entspricht 25% des Artenbestandes der Gehölzpflanzen im Untersuchungsgebiet. Der Anteil der Baumarten im Nahrungsspektrum der Paviane war signifikant höher als es aufgrund des Anteils an Baumarten im regionalen Artenpool der Gehölzpflanzen zu erwarten war. Hinsichtlich der untersuchten Fruchtmerkmale (Fruchttyp, Fruchtfarbe, Größe der Früchte und Samen) gab es keine signifikanten Unterschiede verglichen mit dem Anteil dieser Merkmale im Artenpool, jedoch waren Fruchtarten, die von Pavianen gefressen wurden, signifikant größer als diejenigen, die nicht gefressen wurden.
Im Widerspruch zum für *afrikanische* Gehölzpflanzen postulierten „Vogel-Affen-Fruchtsyndrom“ farblich auffallender Steinfrüchte und Beeren, beinhaltete die Liste der Nahrungspflanzenarten der Paviane im CNP überwiegend Früchte, die groß und unauffällig pigmentiert sind. Dies stimmt mit dem für andere Regionen definierten „Säuger-Fruchtsyndrom“ überein.
Mit Hilfe logistischer Regressionen konnte ich zeigen, dass sich Fruchttyp und Farbe von den untersuchten Merkmalen am besten eignen um vorherzusagen, ob die Früchte einer Art Nahrungsbestandteil der Paviane im CNP sind. Fruchttyp und Samengröße wiederum eignen sich am besten, um auf die Art der Nutzung (potentielle Samenausbreitung bzw. Samenprädation) zu schließen.

Um nachzuweisen, welche Nahrungspflanzenarten (ohne Gräser und Seggen) durch Paviane tatsächlich ausgebreitet werden, analysierte ich insgesamt 396 Fäzesproben von Individuen aller im Untersuchungsgebiet vorkommenden 10 Paviangruppen hinsichtlich quantitativer und qualitativer Aspekte der Samenbehandlung und Samenausbreitung. Neunundachtzig Prozent der Fäzesproben enthielten mindestens einen intakten Samen, 73% aller Samen in den Proben waren unbeschädigt. Insgesamt fand ich intakte Samen von 65 Pflanzenarten, im Mittel enthielten Fäzes intakte Samen von zwei Arten (max. 10). Anhand der ermittelten Populationsdichte und der mittleren Samenzahl der Fäzesproben schätzte ich die täglich durch die Paviane ausgebreitete Samenmenge auf 1483 Samen / km^2.

In Keimversuchen erwiesen sich achtzehn von 19 getesteten Samenarten aus Pavianfäzes als keimfähig, aber die Unterschiede in der Keimfähigkeit zu Samen aus frischen, reifen Früchten variierten stark zwischen den Arten.
Die Paviane breiteten Samen sehr unterschiedlicher Größe aus (1-27 mm). Über Dreiviertel der ausgebreiteten Samenarten hatten mittelgroße bis große Samen (> 5 mm). Es bestand kein linearer Zusammenhang zwischen Samengröße und Beschädigungsgrad der Samen.

Die Samengröße einer Pflanze ist ein wichtiges Fitnessmerkmal, das verschiedene Abschnitte von der Fruchtentwicklung bis zur Etablierung des Keimlings beeinflussen kann. Sie variiert nicht nur zwischen den Arten, es treten bei vielen Pflanzenarten auch erhebliche intraspezifische Schwankungen auf. Erstaunlicherweise wurde die Relevanz dieses Fruchtmerkmals für die Auswahl von Früchten durch Primaten *innerhalb* einer Pflanzenart und die sich daraus ergebenden Auswirkungen auf die Pflanzenregeneration bislang kaum, und ausschließlich in der Neotropis, untersucht. Primaten könnten aus unterschiedlichen Gründen Früchte mit bestimmter Samengröße auswählen, zum Beispiel um unverdaulichen Ballast zu reduzieren oder weil Früchte mit einer bestimmten Samengröße eine überproportional große Menge Fruchtfleisch enthalten.
Um zu untersuchen, ob Paviane innerhalb einer Pflanzenart bestimmte Frucht- und Samengrößen bevorzugen, wählte ich die Baumart *Parkia biglobosa* (Mimosaceae), deren lange, braune Hülsen charakteristisch für eine „Säugerfrucht“ sind, und die im Untersuchungsgebiet wahrscheinlich fast ausschließlich von Pavianen gefressen werden. Ich analysierte die Fruchtauswahl der Paviane mittels direkter Beobachtungen und Fäzesanalysen sowie mit Hilfe unterschiedlich stark ausgebeuteter Hülsen unter den Nahrungsbäumen.
Die Paviane agierten sowohl als Samenprädatoren als auch als Samenausbreiter für *P. biglobosa*. Einerseits fraßen sie - und zerstörten dabei - die noch weichen Samen unreifer Früchte (das Perikarp blieb ungenutzt), andererseits verschluckten sie intakte Samen beim Fressen des Perikarps reifer Früchte und schieden den Großteil dieser Samen unbeschädigt wieder aus.
Die Paviane ernteten > 96% der ursprünglichen Fruchtproduktion der von mir untersuchten Nahrungsbäume (N = 7). Die Prädationsraten der Bäume waren hoch; im Median wurden nur 10% der Samen pro Baum durch die Paviane ausgebreitet. Die Paviane wählten unreife und reife Früchte so, dass sie die jeweils größtmögliche Nahrungsmenge pro Frucht erzielten. Sie beuteten bevorzugt unreife Hülsen mit signifikant größeren Samen und einer höheren Samenzahl aus. Demzufolge gelangten nur Früchte mit weniger und kleineren Samen zur Fruchtreife. Von diesen bevorzugten die Paviane das Fruchtfleisch aus Hülsen mit nunmehr vergleichsweise kleinen Samen und beuteten reife Früchte mit mehr Samen signifikant stärker aus als solche mit geringerer Samenzahl. Folglich wurden aus dem insgesamt produzierten Samenpool überwiegend kleine Samen aus Hülsen mit mittlerer Samenzahl durch die Paviane ausgebreitet.

Um zu prüfen, ob sich diese Auswahlkriterien auch auf andere Pflanzenarten und Fruchttypen übertragen lassen, verglich ich die Größen der durch Paviane ausgebreiteten Samen, mit den Größen von Samen aus frischen Früchten innerhalb jeder von neun weiteren Arten, deren Fruchtfleisch die Paviane fressen. Zusätzlich untersuchte ich eine weitere Art, deren Samen den Pavianen als Nahrung dienen. Die Arten unterschieden sich in Fruchttyp und Samenzahl pro Frucht.

Je nach Art breiteten die Paviane signifikant kleinere oder größere Samen aus; bei zwei Arten wiesen ausgebreitete Samen und Samen aus frischen Früchten keine signifikanten Größenunterschiede auf. Die Samen von *Drypetes floribunda* (Euphorbiaceae) wurden von den Pavianen sowohl ausgespuckt als auch in Fäzes ausgebreitet. Der Ausbreitungsmodus hing signifikant mit der Samengröße zusammen: größere Samen wurden ausgespuckt, kleinere wurden verschluckt. Für die intraspezifische Fruchtauswahl der Paviane scheint unter anderem das je nach Frucht- und Samenform unterschiedlich variierende Verhältnis von Fruchtfleisch zu Samen eine Rolle zu spielen.

Während ich in meinen Untersuchungen der Pflanzenart *P. biglobosa* die Rolle der Paviane für die Ausbreitung einer typischen „Säugerfrucht“ analysierte, verglich ich quantitative und qualitative Aspekte der Samenausbreitung durch Paviane mit anderen Frugivoren an zwei Baumarten mit typischen „Vogelfrüchten“ (*L. acida* und *L. welwitschii*, Anacardiaceae). Aufgrund der Fruchtgröße und des Fruchttyps (kleine, saftige Steinfrüchte) erwartete ich, dass die Früchte für ein weites Spektrum frugivorer Arten attraktiv sind. Ich erfasste das Artenspektrum der Nahrungsgäste an ausgewählten Beobachtungsbäumen, die Besuchsrate im Laufe der Fruchtreife, die Fruchthandhabung und Aufenthaltsdauer einzelner Frugivorer sowie deren Fruchtkonsum pro Zeiteinheit.

In zwei Folgejahren lag die Ernterate ('removal efficiency') von *L. acida* bei max. 30% der gesamten Fruchtproduktion, jedoch war der größte Teil der geernteten Früchte sowie des Fruchtfalls unreif (bis zu 100%). Vögel stellten die häufigste Gruppe der Nahrungsgäste, konsumierten jedoch fast ausschließlich grüne, unreife Früchte, deren Samen sich im Keimversuchen als nicht keimfähig erwiesen. Paviane sowie drei weitere beobachtete Primatenarten wurden dagegen häufiger während der Fruchtreife angetroffen. Fast alle von Pavianen ausgebreiteten *L. acida* Samen waren intakt; diese wiesen eine signifikant höhere Keimungsrate auf, als Samen aus frischen reifen Früchten.

Die Ernterate von *L. welwitschii* war mit 48,5% wesentlich höher, und die meisten Früchte wurden im reifenden und reifen Zustand gefressen. Dies schloss jedoch einen Prädationsanteil von 28,6% der Fruchtproduktion durch das Sonnenhörnchen *Heliosciurus rufobrachium* ein. Abzüglich Prädation und Fruchtfall verblieben lediglich 19,9% der Fruchtproduktion zur potentiellen Samenausbreitung durch Vögel und Primaten. Als Prädator von *L. acida* Samen spielte *H. rufobrachium* dagegen kaum eine Rolle.

Vögel kompensierten die, im Vergleich zu Primaten, geringere Anzahl pro Aufenthalt gefressener Früchte, durch eine insgesamt höhere Besuchsrate. Die Untersuchungen zeigten jedoch, dass frugivore Vögel, die aufgrund der Fruchtmerkmale von *Lannea* sp. als eigentliche Hauptgruppe der Samenausbreiter anzusehen wären, zu quantitativ wichtigen Samenprädatoren werden können, wenn sie, zum Beispiel in Zeiten der Nahrungsknappheit, überwiegend unreife Früchte fressen.

Die natürliche Regeneration beider Baumarten scheint, zumindest für einzelne Individuen und in bestimmten Jahren, sowohl begrenzt durch die Anzahl verfügbarer reifer Samen ('source limited') als auch ausbreitungslimitiert ('dissemination limited') zu sein. Da Ernterate und Ausbreitungserfolg stark zwischen verschiedenen Fruchtperioden und Pflanzenindividuen derselben Art variieren können, sind weitergehende Untersuchungen notwendig, um den langfristigen Reproduktionserfolg innerhalb der Arten abzuschätzen.

Im letzten Kapitel beschäftigte ich mich mit dem Schicksal der von Pavianen ausgebreiteten Samen: Ich untersuchte, inwieweit Dungkäfer das primäre Ausbreitungsmuster lokal verändern. Sowohl die Wahrscheinlichkeit sekundärer Samenausbreitung durch Dungkäfer als auch das sekundäre räumliche Ausbreitungsmuster hängen von der Struktur und Zusammensetzung der Dungkäfergemeinschaft am Ort der primären Ausbreitung ab. Die Dungkäfergemeinschaft wiederum scheint stark von der Vegetation beeinflusst zu sein. Im Savannen-Wald-Mosaik Westafrikas erwartete ich daher deutliche Unterschiede in der sekundären Ausbreitung zwischen Samen, die von Pavianen in die Savanne bzw. im Wald primär ausgebreitet werden. Diese Arbeit liefert die ersten vergleichenden Daten über sekundäre Samenausbreitung durch Dungkäfer in Wald und Savanne Westafrikas.

Die Dungkäfer-Aktivität im Untersuchungsgebiet an experimentell ausgelegten Pavianfäzes war hoch, insgesamt konnte ich 99 Arten aus 26 Gattungen nachweisen. Die Artenzahl im Galeriewald ($N = 47$) ist vergleichbar mit Ergebnissen aus Neotropischen Wäldern. Im Gegensatz zur Neotropis waren jedoch Artenzahl und Abundanz der Käfer im offenen Habitat (hier: Savanne, $N = 85$ Arten) wesentlich höher. Die Verteilung der Individuen auf die für die Samenausbreitung wichtigen Gilden der Telekopriden und Parakopriden unterschied sich signifikant zwischen Wald und Savanne. In der Savanne stellten Telekopriden und Parakopriden jeweils etwa die Hälfte der Individuen, während Parakopriden im Galeriewald dominierten und 96% der Individuen ausmachten. Eine standardisierte Redundanz Analyse (RDA) ergab „Habitat“ (Savanne, Wald) als dominanten Faktor, der alleine bereits 15% der Variation in der Gildenstruktur auf einem hochsignifikanten Niveau erklärt.

Aufgrund der höheren Abundanz der Telekopriden und der größeren Arten in der Savanne, wurden standardisierte Mengen Pavianfäzes in der Savanne schneller abgebaut, als im Galeriewald. Telekopride breiteten Samen von bis zu 18 mm Länge aus, die natürlicherweise in Pavianfäzes vorkamen. Die sekundären Ausbreitungsdistanzen der Samen waren größer in der Savanna als im Galeriewald. Im Gegensatz zu anderen Studien, die sich mit sekundärer Samenausbreitung durch Dungkäfer beschäftigten, waren es überwiegend kleine Telekopride, die große Samen ausbreiteten; einzelne große Samen wurden von ihnen offenbar für Dungkugeln gehalten und anstelle einer solchen weggerollt.

Die Ergebnisse zeigen, dass Samen, die von Pavianen in die Savanne ausgebreitet werden, im Gegensatz zu Samen in Pavianfäzes im Galeriewald, eine höhere Wahrscheinlichkeit haben (a) überhaupt sekundär durch Dungkäfer ausgebreitet zu werden, (b) horizontal von Telekopriden vom Ort der primären Deposition wegbewegt zu werden, (c) relativ schnell aus den Fäzes entfernt zu werden und (d) über relativ größere Distanzen ausgebreitet zu werden. Ein Größenvergleich zwischen Dungkugeln der Telekopriden und Samen, die während der saisonalen Aktivitätsphase der Dungkäfer natürlicherweise in Pavianfäzes zu finden sind, deutet darauf hin, dass die im CNP vorkommenden Telekopriden die Samen aller dieser von Pavianen ausgebreiteten Pflanzenarten potentiell sekundär ausbreiten können.

Meine Untersuchungen haben gezeigt, dass sich westafrikanische Populationen des Anubis Pavians in verschiedener Hinsicht von Populationen in Ost Afrika unterscheiden. Ihre soziale Organisation ist offenbar flexibler als bislang aufgrund von Studien an ostafrikanischen Anubis Pavianen angenommen. Paviane (einschließlich anderer Arten der Gattung *Papio*) werden zumeist vornehmlich als Prädatoren der Samen ihrer Nahrungspflanzen angesehen. Ich konnte jedoch belegen, dass dies für das Savannen-Wald-Mosaik Westafrikas nicht gilt: Hier ernähren sich die Paviane überwiegend frugivor und sind quantitativ und qualitativ bedeutende Samenausbreiter einer Vielzahl von Gehölzpflanzenarten mit unterschiedlichen Fruchttypen und -größen. Sie breiten beträchtliche Mengen intakter Samen von mindestens 22% der Gehölzpflanzenarten des regionalen Artenpools aus. Als Habitatgeneralisten (mit einer Präferenz für Waldhabitate), die relativ große Gebiete durchstreifen, scheinen sie besonders wichtig für den genetischen Austausch der Pflanzen zwischen entfernten Waldinseln. Da die meisten Gehölzpflanzenarten im Savannen-Wald-Mosaik des CNP mittelgroße bis große Früchte und Samen haben, kommt den Pavianen eine herausragende Rolle bei der Samenausbreitung und natürlichen Regeneration dieses Ökosystems zu, insbesondere da andere große Frugivore vergleichsweise selten geworden sind. Die Bedeutung der Paviane für die Samenausbreitung von Pflanzenarten mit kleinen Früchten sollte jedoch nicht unterschätzt werden. Meine Daten weisen darauf hin, dass eine qualitative und quantitative Beurteilung verschiedener Frugivorengruppen allein aufgrund der Fruchtsyndrome nicht immer zuverlässig ist.

Anubis Paviane breiten in der Regel mehrere Pflanzensamen in einzelnen Fäzes aus. Üblicherweise wird solch eine geklumpte Ausbreitung als ungünstig für die Pflanze angesehen. Ich konnte jedoch zeigen, dass die Samen aller Pflanzenarten, die in Pavianfäzes während Zeiten saisonal hoher Dungkäferaktivität zu finden sind, potentiell von Dungkäfern ausgebreitet werden können. Generell sollten Savannenpflanzen und Habitatgeneralisten unter den Pflanzenarten, deren Samen von Pavianen in die Savanne ausgebreitet werden, am ehesten von sekundärer Ausbreitung durch Dungkäfer profitieren.

Afrikas Savannen sind zunehmend durch Landdegradation gefährdet, die erhebliche Auswirkungen auf die Vegetationsbedeckung und Biodiversität dieser Gebiete hat. Paviane sind über weite Bereiche des Subsaharischen Afrikas verbreitet und, im Vergleich zu vielen anderen großen Frugivoren, noch relativ häufig. Auch in Anbetracht der Fläche, die Savannen auf dem afrikanischen Kontinent einnehmen, sind weitere Studien wünschenswert, die zum Verständnis der Interaktionen zwischen Pavianen, ihren Nahrungspflanzen und Dungkäfern und deren Einfluss auf die Dynamik der Pflanzenpopulationen in diesen Ökosystemen beitragen. Besondere Berücksichtigung sollten dabei die Mechanismen der Samenselektion durch Paviane sowie die daraus resultierenden Konsequenzen für das räumliche Ausbreitungsmuster und das Schicksal der Samen und Keimlinge finden.

Danksagung

Zum Abschluss dieser Dissertationsschrift ist es mir ein herzliches Anliegen, den Menschen zu danken, die auf die eine oder andere Weise zur Entstehung meiner Arbeit beigetragen haben.

Prof. Dr. K.E. Linsenmair hat mit seinem Engagement in der Elfenbeinküste den Rahmen geschaffen, der diese Arbeit überhaupt erst ermöglicht hat. Ich danke ihm, dass er mir als Doktorvater sowohl bei der Planung als auch Durchführung und Fertigstellung der Arbeit viel Freiraum gelassen hat und immer gesprächsbereit und offen für meine Ideen war.

Sehr gefreut hat mich, dass sich Herr PD Dr. Eckhard Heymann, Deutsches Primatenzentrum Göttingen, auf meine Anfrage hin sofort bereit erklärte, als Zweitgutachter zu fungieren. Seinen eigenen Forschungen zur Samenausbreitung durch Tamarine in Peru habe ich viele wertvolle Anregungen zu verdanken.

Ich hatte das Glück, dass Dr. Frank-Thorsten Krell, jetzt Denver Museum of Nature & Science, USA, zu Beginn meiner Untersuchungen ebenfalls zur Feldarbeit im Comoé Nationalpark war. Seiner Fachkenntnis der Afrikanischen Dungkäfer-Fauna ist es zu verdanken, dass das letzte Kapitel dieser Dissertationsschrift mit einer Artenliste der Scarabaeiden an Pavianfäzes aufwarten kann – er bestimmte fast 6000 Dungkäfer, die ich gesammelt hatte. Darüber hinaus stand er mir sowohl bei der Planung der Experimente zur sekundären Samenausbreitung als auch bei der Auswertung der Daten beratend zur Seite. Ich möchte ihm an dieser Stelle herzlich für die freundschaftliche und unkomplizierte Zusammenarbeit danken. Keinen geringen Anteil an der Bearbeitung der Käfer hatte auch Sylvia Krell-Westerwalbesloh, der dafür ebenfalls ganz herzlich gedankt sei.

Viele Anregungen habe ich auch aus den Arbeiten von und persönlichen Gesprächen mit Herrn PD Dr. Thomas Hovestadt, Ökologische Station Fabrikschleichach, Zoologie III, Universität Würzburg, erhalten. Neben seiner Kenntnis der Thematik war auch seine statistische Fachkenntnis immer eine große Hilfe! Bei statistischen Problemen konnte ich dankenswerterweise auch auf die Erfahrung von Prof. Dr. Elisabeth Obermaier, Zoologie III, Universität Würzburg und zu Beginn auch von Prof. Dr. Erhard Strohm, jetzt Evolutionary Ecology Research Group, Universität Regensburg, zurückgreifen.

Dr. Norbert Reintjes ist sicherlich derjenige, mit dem ich Ideen für meine verschiedenen Untersuchungen am häufigsten durchgesprochen habe. Unsere ausgiebigen Diskussionen in Würzburg und in der Elfenbeinküste und seine Unterstützung haben viel dazu beigetragen, den “Weg im Feld und im Datendickicht” zu finden bzw. nicht wieder zu verlieren.

Bei der Feldarbeit haben mir außerdem mit Rat und Tat zur Seite gestanden: Koffi Yao Maizan (Lakado), der mir mit unendlicher Geduld und Freundlichkeit bei der Erhebung von Pflanzendaten zur Hand ging. Silke Berger und Siiri Lüdeman, die im Rahmen ihres F2-Praktikums in der Zoologie III an der Universität Würzburg meine Datenaufnahme zu Kapitel 7 ergänzten. Koffi Kouadio und Prof. Dr. Stefan Porembski, die mir halfen, mich in die westafrikanische Flora einzuarbeiten. Koffi Kouadio, Dr. Norbert Reintjes, und Dr. Karsten Mody, die dankenswerterweise die Keimversuche während meiner Abwesenheit überwachten. Außerdem eine Vielzahl unerschrockener Menschen, die während ihrer eigenen Feldarbeit Pavianfäzes für mich gesammelt und so die Stichpro-

benzahl vergrößert haben! Dank an alle!

In der Zoologie III (einschließlich "Ehemaliger") gilt mein besonderer Dank Dr. Stefanie Berghoff-Merker, Mirjana Bevanda (Mimo), Constanze Grohmann, Melanie Hauber, Matthias Jäger, Dorkas Kaiser, Dr. Timo Moritz, Dr. Elisabeth Obermaier, Prof. Dr. Mark-Oliver Rödel (MO) und Marcus Stüben sowie den Mitarbeiterinnen und Mitarbeitern des Lehrstuhls, die für eine herzliche Atmosphäre gesorgt haben. Dank an MO und Mimo auch für die Gesellschaft an den Wochenenden und den Kaffee! Ausdrücklich danken möchte ich noch Norbert Schneider, der nach wagen Beschreibungen wahre Meisterstücke in der Werkstatt herstellte, die auch schwierigsten Anforderungen der Feldarbeit standhielten! Thomas Igerst und Gerhard Vonend haben mich mehr als einmal vor dem Computer-Gau bewahrt. Ohne die Hilfe von Dr. Klaus Hennenberg, Universität Rostock, Dr. Konstantin König, Universität Frankfurt, sowie Johannes Penner und Martin Wegmann, (ehemals) Universität Würzburg, würde ich vermutlich heute noch verzweifelt versuchen, die im Feld erhobenen GPS Daten in ArcView einzulesen und darstellbar zu machen.

Für kritisch-konstruktive Anmerkungen zu verschiedenen Entstehungsstadien der Manuskripte danke ich Dr. Stefanie Berghoff-Merker, Prof. Dr. Eckhard Heymann, PD Dr. Thomas Hovestadt, Dr. Frank-Torsten Krell, Dr. Norbert Reintjes, Dr. Simone Teelen, Finoula Walravens, und Dr. Ymke Warren. Ihr hattet meistens Recht!

Herr PD. Dr. Michael Abs hat sich freundlicherweise die Zeit genommen, Schnabelgrößen verschiedener westafrikanischer Singvögel an Bälgen des Naturkundemuseums Berlin für mich zu messen. Dr. Elmar Robbrecht, Jardin Botanique National de Belgique, war so freundlich einige für mich unbestimmbare Rubiaceen zu identifizieren. Der Direktor des Zoologischen Gartens in Abidjan, Dr. Frédéric Diéko Aoussou, hat es mir netterweise ermöglicht, dort Fütterungsversuche an Pavianen zur Ermittlung der Passagedauer von Samen durchzuführen.

Das Ministère de l’Agriculture et des Ressources Animales und das Ministère de l‘Enseignement Supérieure et de la Recherche Scientifique, Abidjan, waren so freundlich, die notwendigen Forschungsgenehmigungen zu erstellen. Ich möchte an dieser Stelle auch den damaligen Mitarbeitern der Deutschen Botschaft in der Elfenbeinküste danken, die sich um unser Wohlergehen gekümmert haben, als die politische Situation in der Elfenbeinküste schwierig wurde.

Der Deutsche Akademische Austauschdienst (DAAD) ermöglichte mir 24 Monate Feldarbeit durch ein Promotionsstudium. Eine Anschlussfinanzierung im Rahmen des III. Hochschulsonderprogramms der Universität Würzburg sicherte die Dateneingabe nach meiner Rückkehr aus Afrika. Die Forschungsstation (Lola Camp) im Comoé Nationalpark wurde mit Geldern der Volkswagen-Stiftung ermöglicht.

"With a little help from my friends..." 'Last but not least' möchte ich meinen Freundinnen und Freunden und meiner Familie danken, die nicht aufgehört haben, an mich zu glauben – allen voran Anette Rödelbronn und Dr. Helmut Weinläder! Danke!

General Appendix I Variation in plant names and plant classifications following different sources used in this study

Hutchinson *et al.* (1954-1968) and the IPNI[1]	**The African Flowering Plants Database**[2]
Ampelidaceae	Vitaceae
Cissus populnea	
Cissus sp.	
Apocynaceae	
Landolphia amoena [a,b]	*Ancylobotrys amoena*
Buxaceae	
Notobuxus acuminata	*Buxus acutata*
Caesalpiniaceae	Fabaceae
Afzelia africana	
Cassia sieberiana [a]	
Cynometra megalophylla	
Daniellia oliveri	
Detarium microcarpum	
Detarium senegalense	
Dialium guineense	
Erythrophleum guineense	*Erythrophleum suaveolens*
Isoberlinia doka	
Piliostigma thonningii	
Tamarindus indica	
Chailletiaceae	Dichapetalaceae
Tapura fischeri	
Mimosaceae	Fabaceae
Albizia sp.	
Dichrostachys glomerata	*Dichrostachys cinerea*
Leucaena glauca	*Leucaena leucocephala*
Parkia biglobosa	
Tetrapleura tetraptera	
Moraceae	
Antiaris africana	*Antiaris toxicaria*
Chlorophora excelsa	*Milicia excelsa*
Papilionaceae	Fabaceae
Craibia atlantica	
Rubiaceae	
Canthium venosum	*Keetia venosum*
Canthium sp.	*Keetia*sp.
Sapotaceae	
Malacantha alnifolia	*Pouteria alnifolia*
Manilkara multinervis	*Manilkara obovata*

---

[1] IPNI International Plant Names Index www.ipni.org/

[2] African Flowering Plants Database http://www.ville-ge.ch/musinfo/bd/cjb/africa/index.php?langue=an

General Appendix II Number of baboons faecal samples (fs) per month collected from November 1997 to July 2000 for seed dispersal analyses in the Comoé National Park, and occurrence of identified seed species in samples

For each species the number of dispersal events per month is given in parentheses. fs_n: total number of faecal samples containing a given species, DE_n: total number of dispersal events for a given species. A dispersal events is defined as the occurrence of at least one ripe intact seed of a given species.

	November 1997 - July 2000													
	Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**		
n°. of fs / month	27	19	45	39	39	54	45	6	42	32	22	26	**fs_n**	**DE_n**
plant species														
Aframomum exscapum						8 (8)	6 (6)						14	14
Afzelia africana						1 (0)							1	0
Annona senegalensis	1 (1)						1 (1)						2	2
Anogeissus leiocarpa												1 (1)	1	1
Antiaris africana												1 (1)	1	1
Bridelia ferruginea										3 (3)			3	3
Canthium sp. (2?)		1 (0)				4 (3)		1 (1)		8 (8)	1 (1)		15	13
Canthium venosum	3 (2)		1 (1)						1 (1)				5	4
Celtis sp.							1 (1)						1	1
Chlorophora excelsa							1 (1)			4 (4)		1 (1)	6	6
Christiana africa										1 (1)			1	1
Cissus populnea							4 (4)		3 (3)	1 (1)			8	8
Cissus sp.				1 (1)									1	1
Cola cordifolia									1 (1)				1	1
Combretum sp.	1 (0)												1	0
Cremaspora triflora			1 (1)									1 (1)	2	2
Crossopteryx febrifuga						1 (1)							1	1
Cynometra megalophylla						2 (2)							2	2
Dialium guineense	1 (0)		11 (11)	9 (9)	7 (6)	15 (15)	25 (25)	1 (1)	1 (1)			2 (2)	72	70
Dichrostachys cinerea	1 (1)											1 (1)	2	2
Diospyros abyssinica									1 (1)				1	1

General Appendix II (continued)

	November 1997 - July 2000													
	Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**		
n^o. of fs / month	27	19	45	39	39	54	45	6	42	32	22	26	**fs$_n$**	**DE$_n$**
plant species														
Diospyros mespiliformis	12 (11)	7 (6)	4 (4)	3 (1)	3 (2)	3 (2)	2 (0)				1 (0)	11 (11)	46	37
Drypetes floribunda					1 (1)	23 (23)	12 (12)		2 (2)				38	38
Drypetes gilgiana					1 (1)								1	1
Erythrophleum guineense					6 (3)	7 (7)			1 (1)				14	11
Ficus spp. (3)	10 (10)	2 (2)	2 (2)	8 (7)	6 (6)	12 (11)	5 (5)	3 (3)	10 (10)	21 (20)	7 (4)	5 (5)	91	85
Gardenia aqualla									1 (1)			1 (1)	2	2
Grewia cf. bicolor				2 (2)									2	1
Kigelia africana				1 (1)									1	1
Lannea acida			1 (1)	3 (3)									4	4
Lannea barteri					1 (1)								1	1
Lannea welwitschii			1 (0)	6 (6)	1 (1)								8	7
Leucaena glauca												1 (1)	1	1
Malacantha alnifolia				2 (2)	1 (1)								3	3
Mallotus oppositifolius									1 (1)	2 (2)	1 (1)		4	4
Manilkara multinervis					2 (2)	3 (3)							5	5
Mimusops kummel										1 (1)			1	1
Notobuxus acuminata										1 (0)			1	0
Oxyanthus racemosus	1 (1)								10 (9)	6 (6)			17	16
Parinari curatellifolia	1 (1)					1 (1)	1 (0)	1 (0)					4	2
Parkia biglobosa			12 (9)	7 (4)	2 (2)								21	15
Phyllanthus sp.									2 (2)	1 (1)			3	3
Piliostigma thonningii	3 (3)	1 (1)											4	4
Psychotria vogeliana									2 (1)	3 (3)			5	4
Ricinodendron heudelotii				1 (1)									1	1

General Appendix II (continued)

	November 1997 - July 2000													
	Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**		
n^o. of fs / month	27	19	45	39	39	54	45	6	42	32	22	26	**fs$_n$**	**DE$_n$**
Saba senegalensis			1 (1)	5 (5)	16 (15)	10	3 (3)						35	34
Sarcocephalus latifolius	4 (3)	5 (5)	3 (2)	2 (2)	1 (1)						13 (11)	7 (6)	35	30
Sarcocephalus cf. xanthoxylon						5 (5)	9 (9)	5 (5)	33 (33)	27 (27)			79	79
Solanum incanum						1 (1)			1 (0)	1 (1)		2 (2)	5	4
Strychnos "großfrucht"			3 (3)	3 (3)									6	6
Tamarindus indica	13 (12)	9 (7)	9 (8)	12 (12)	1 (1)							13 (12)	57	52
Tapura fischeri							6 (5)	1 (1)	1 (0)				8	6
Tetrapleura tetraptera	7 (0)	3 (0)	1 (0)	1 (0)								1 (0)	13	0
Tricalysia sp.						1 (1)				1 (1)			2	2
Uapaca togoensis				1 (0)	1 (1)						1 (1)		3	2
Uvaria chamae							11 (11)	4 (4)	3 (3)				18	18
Vitex doniana								1 (1)	9 (8)	2 (2)			12	11
Ximenia americana			2 (1)	2 (2)			1 (0)						5	3

Publications

PUBLISHED

Kunz B. K. & Linsenmair K. E. 2008. Seed size selection by olive baboons. *Primates* 49, 239-245.

Kunz B. K. & K. E. Linsenmair 2008. The role of the olive baboon (*Papio anubis*, Cercopithecidae) as seed disperser in a West African savanna-forest mosaic. *Journal of Tropical Ecology* 24, 1-12.

Kunz B. K. & Linsenmair K. E. 2008. The disregarded West: diet and behavioural ecology of olive baboons in the Ivory Coast. *Folia Primatologica* 79, 31-51.

Kunz B. K. & Linsenmair K. E. 2007. Changes in baboon feeding behavior: maturity-dependent fruit and seed size selection within a food plant species. *International Journal of Primatology* 28, 819-835.

Beck, J. & Kunz B. K. 2007. Cooperative self-defence: matabele ants *(Pachycondyla analis)* against African driver ants *(Dorylus* sp.; Hymenoptera: Formicidae). *Myrmecological News* 10: 27-28.

Fischer F., Groß M. & Kunz B. 1999-2000. Primates of the Comoé National Park. *African Primates* 4, 10-15.

IN PRESS

Kunz B. K., Hovestadt T. & Linsenmair K. E. In press. Variation of dispersal agents? Frugivore assemblages and fruit handling in a typical 'bird-dispersed' tree (*Lannea acida*, Anacardiaceae). *Ecotropica.*
(First part of Chapter 7 of this work)

SUBMITTED

Kunz B. K. & Linsenmair K. E. Fruit traits in baboon diet: a comparison with plant characteristics in West-Africa. Submitted to *Biotropica.*
(Chapter 3 of this work)

Kunz B. K. & Linsenmair K. E. Fruit removal and seed predation in two African trees (*Lannea acida* and *Lannea welwitschii*, Anacardiaceae). Submitted to *West African Journal of Applied Ecology*.
(Second part of Chapter 7 of this work)

IN PREP.

Kunz B. K., Krell F. T. & Linsenmair K. E. Habitat differences in dung beetle guilds (Coleoptera, Scarabaeidae) in a savanna-forest mosaic of West Africa and implications for secondary seed dispersal from baboon faeces.
(Chapter 8 of this work)

Conferences Attended

08/08	Differential seed size selection by olive baboons (*Papio anubis*) and implications for plant regeneration. Oral presentation. *XXII Congress* of the *International Primatological Society,* Edinburgh, UK
11/06	Seed dispersal by baboons and dung beetles in West Africa. Oral presentation. *Second Gashaka Field Day,* Roehampton University, UK
08/05	Selectivity in baboon diet and implications for tree regeneration: considering fruit and seed size within a single plant species. Oral presentation. *First Congress of the European Federation for Primatology,* Göttingen
10/03	Behavioural ecology of olive baboons (*Papio anubis*) in a forest-savannah mosaic of West-Africa. Oral presentation. *Annual Meeting of the Deutsche Gesellschaft für Primatologie*, Leipzig
09/03	The role of olive baboons in seed dispersal and seed predation of a West African savannah tree (*Parkia biglobosa*, Mimosaceae). Oral presentation. *International Conference on Tropical Savannas & Seasonally Dry Forests,* Edinburgh, UK
07/03	Predicting secondary seed dispersal from baboon faeces by dung beetles: a matter of seed size, time, and habitat. Oral presentation. *British Ecological Society Special Symposium and Annual Meeting of the Association for Tropical Biology and Conservation*, Aberdeen, UK
07/03	Olive baboons as seed dispersers and seed predators in the Comoé National Park, Ivory Coast. *Poster. British Ecological Society Special Symposium and Annual Meeting of the Association for Tropical Biology and Conservation,* Aberdeen, UK
02/03	The role of olive baboons in seed dispersal and seed predation of a West African savannah tree (*Parkia biglobosa*, Mimosaceae). Oral presentation. *Annual Meeting of the Gesellschaft für Tropenökologie*, Rostock
08/00	Observations of frugivorous birds and mammals in the tree *Lannea barteri* (Anacardiaceae). *Poster. Third International Symposium-Workshop on Frugivores and Seed Dispersal,* Sao Pedro, Brazil
08/00	Secondary seed dispersal from baboon feces by dung beetles: differences between savanna and gallery forest. *Poster. Third International Symposium-Workshop on Frugivores and Seed Dispersal,* Sao Pedro, Brazil
08/00	Seed dispersal and seed predation by olive baboons in the Comoé National Park, Ivory Coast. Poster. *Third International Symposium-Workshop on Frugivores and Seed Dispersal,* Sao Pedro, Brazil
03/00	Beobachtungen frugivorer Vögel und Säuger in *Lannea barteri* (Anacardiaceae). *Poster. Annual Meeting of the Gesellschaft für Tropenökologie,* Würzburg
03/00	Sekundäre Samenausbreitung aus Pavianfäzes durch koprophage Käfer: Savanne versus Galeriewald. *Poster. Annual Meeting of the Gesellschaft für Tropenökologie,* Würzburg

Curriculum vitae

seit 04.2008	Wissenschaftliche Mitarbeiterin am Lehrstuhl für Tierökologie und Tropenbiologie, Universität Würzburg
03.03 - 03.08	Hauptberuflich als selbstständige Biologin tätig, u.a. tierökologische Untersuchungen im Rahmen von Fachgutachten, Umweltverträglichkeitsprüfungen, Spezielle Artenschutzprüfungen; Lehraufträge
09.01 - 02.03	Verschiedene Tätigkeiten zur Finanzierung der Doktorarbeit und des Lebensunterhalts, u.a. mehrere Kurzzeit-Verträge als Wissenschaftliche Hilfskraft am Lehrstuhl für Tierökologie und Tropenbiologie, Universität Würzburg
09.00 - 08.01	Stipendiatin im Rahmen des Hochschulsonderprogramms HSP III
11.97 - 08.00	Stipendiatin des Deutschen Akademischen Austauschdienstes
11.97	Beginn der Doktorarbeit am Lehrstuhl für Tierökologie und Tropenbiologie, Universität Würzburg
01.97 - 11.97	Vorbereitungen und Organisation der Doktorarbeit: vorbereitender Feldaufenthalt, Drittmittelanträge
05.96 - 10.96	Mitarbeit im NRO-Projekt Songhai, Benin, West-Afrika, Bereich Fischzucht
04.96 - 11.96	Realisierung eines Kleinprojektes mit der NRO-Cecidec und der Deutschen Botschaft in Benin.
09.95 - 11.95	Ornithologische Freilandforschungen in Benin und Burkina Faso
10.88 - 06.95	Studium der Biologie (Diplom) und Geografie (Nebenfach), Ruhr-Universität, Bochum. Diplomarbeit zur Autökologie, Brutbiologie und Bestandsentwicklung der Ecuadoramazone (*Amazona autumnalis lilacina*) in West Ecuador
03.94 - 05.94	Mitarbeit im NRO-Projekt Eduardo Aspiazu, Ecuador, Aufzucht und Wiederauswilderung konfiszierter Papageien
1990 - 1993	Studentische Vertreterin im Fakultätsrat der Biologie, Ruhr-Universität Bochum
1989 - 1993	Verschiedene Tätigkeiten zur Finanzierung des Studiums, u.a. ökologische Kartierungsarbeiten, Studentische Hilfskraft am Lehrstuhl für Allgemeine Botanik und Lehrstuhl für Spezielle Botanik, Ruhr-Universität Bochum
1989 - 1993	Mitarbeit im Fachschaftsrat Biologie, Ruhr-Universität Bochum
11.87 - 07.88	Sprachstudium an der Escuela Officale de Idiomas in Barcelona
08.87 - 10.87	Praktikum am Polka Children's Theatre, Wimbledon, England
10.85 - 07.87	Ausbildung am Figurentheater Kolleg, Bochum
11.84 - 07.85	Au-Pair-Aufenthalt und Sprachstudium am Institute Catholique, Paris
1971 - 1984	Schulausbildung in Frankfurt am Main, Allgemeine Hochschulreife

Auszeichnungen

08.2005	Auszeichnung Zweitbester Vortrag (Doktoranden & Postdoktoranden), First Congress of the European Federation for Primatology, Göttingen
10.2003	Auszeichnung bester Vortrag (Doktoranden & Postdoktoranden), Jahrestagung der Deutschen Gesellschaft für Primatologie, Leipzig

Würzburg, im Dezember 2008

(Britta Kunz)

Erklärung

gemäß § 4 Abs. 3 Ziff. 3, 5 und 8
der Promotionsordnung für die Fakultät für Biologie
der Bayerischen Julius-Maximilians-Universität Würzburg vom 15. März 1999

Hiermit erkläre ich ehrenwörtlich, die vorliegende Arbeit in allen Teilen selbstständig und nur mit den angegebenen Quellen und Hilfsmitteln angefertigt zu haben.

Diese Dissertation hat weder in gleicher noch in ähnlicher Form in einem anderen Prüfungsverfahren vorgelegen.

Von der Ruhr-Universität Bochum wurde mir das Recht zugestanden, mich als Diplombiologin zu bezeichnen. Darüber hinaus habe ich keine akademische Grade erworben und auch nicht versucht zu erwerben.

Würzburg, den 17.12.2008

(Britta Kunz)