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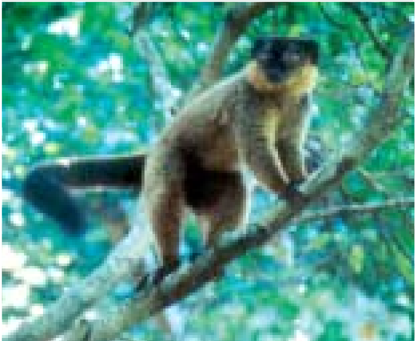
Fruit-frugivore interactions in a Malagasy littoral forest: a community-wide approach of seed dispersal
An BOLLEN





UNIVERSITEIT ANTWERPEN
Faculteit Wetenschappen
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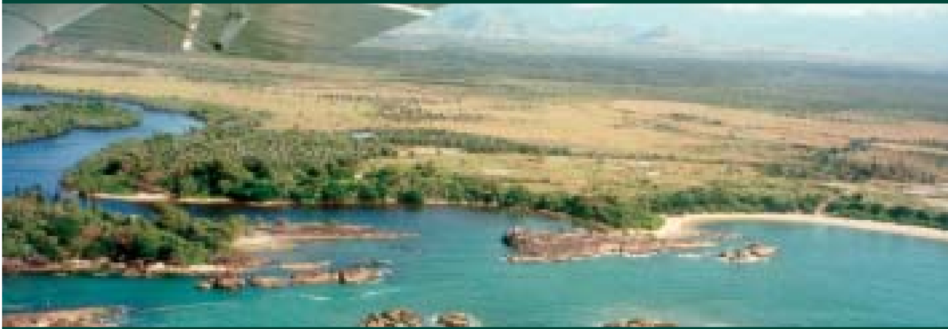

Proefschrift voorgelegd tot het behalen van
de graad van doctor in de Wetenschappen
aan de Universiteit Antwerpen te verdedigen door

An BOLLEN

ANTWERPEN 2003

Promotoren: Prof. dr. L. Van Elsacker
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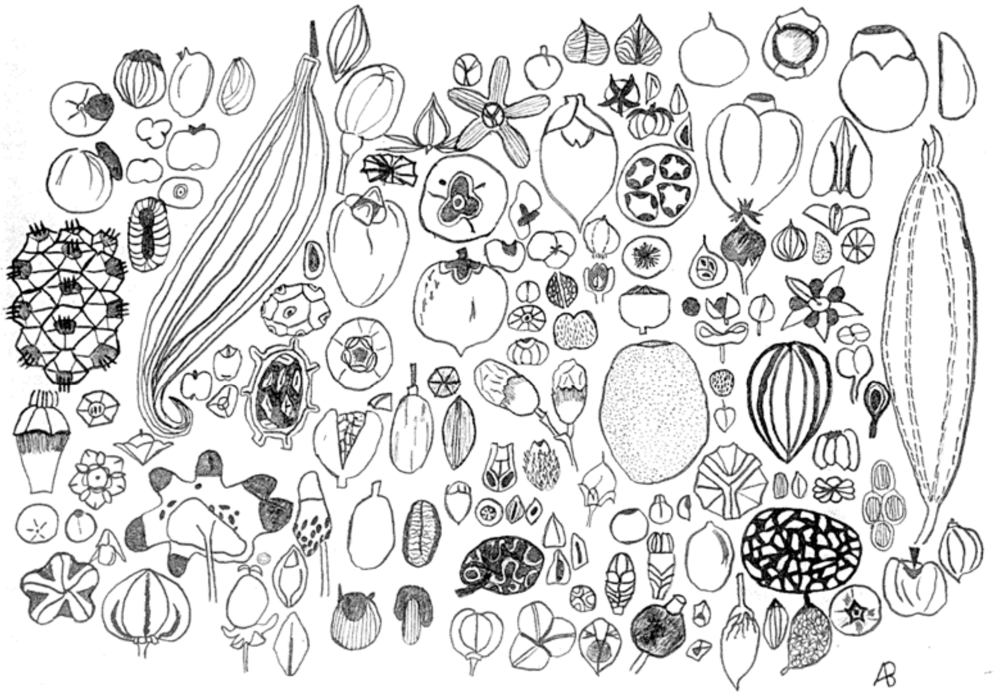

Interacties tussen vruchten en frugivoren in een Madagaskisch littoraal regenwoud: een benadering van zaadverspreiding op niveau van het ecosysteem

Proefschrift voorgelegd tot het behalen van de graad van doctor in de Wetenschappen
aan de Universiteit Antwerpen te verdedigen door

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Cover photographs:

Front:

-‘ambora’ *Tambourissa purpurea* (Monimiaceae) © An Bollen
-‘bodono’ *Cheirogaleus medius* (Cheirogaleidae) © Han Remaut
-‘hazombato’ *Campylospermum obtusifolium* (Ochnaceae) © An Bollen
-‘horovana’ *Hypsipetes madagascariensis* (Pycnonotidae) © Han Remaut
-‘tsilantria’ *Vaccinium emirnense* (Ericaceae) © An Bollen
-‘varika’ a male *Eulemur fulvus collaris* (Lemuridae) © An Bollen
-aerial photograph of the Sainte Luce area (middle) © An Bollen

Back:

-‘sanirambavy’ fruits of *Tina thouarsiana* (Sapindaceae) with bill traces of *Coracopsis nigra* (Psittacidae) © An Bollen
-‘fanihy’ *Pteropus rufus* (Pteropodidae) © An Bollen
-‘rotry mena’ *Syzygium* sp.2’ (Myrtaceae) © An Bollen
-seeds of ‘voapaky vavy’ *Uapaca littoralis* (Euphorbiaceae) with gnawing marks of ‘voalava’ rodents © An Bollen
-*Eulemur fulvus collaris* feeding in a fruiting tree © An Bollen
-‘sjihely’ sardine-like fishes in Dec ‘00 in the village of Ambandriky © An Bollen
-the people of the Ambandriky at the landing strip of Martin Pêcheur in front of the hill of S17 © An Bollen

Throughout this PhD taxonomic names of the plant species follow the Flora of Madagascar (Humbert 1936-1984), the data base of Missouri Botanical Garden (http://mobot.mobot.org/W3T)

ISBN 90-5728-042-6

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ACKNOWLEDGEMENTS

Many people have provided me with assistance, guidance and support during the time it has taken me to complete this PhD for which I am very grateful:

First of all I want to thank my supervisor, Linda Van Elsacker, who has supported me from the beginning of this PhD, never losing faith. Thanks for letting me introduce not only lemurs but also bats, birds and rats within this primatological group and for always being ready to read my manuscripts over and over again, to exchange ideas and to motivate me to present research to the larger public. Sincere thanks as well to Rudi Verheyen who was ready to act as my co-promoter and who has encouraged me throughout the PhD.

It was Jörg Ganzhorn who got me to Madagascar in the first place. He helped me greatly during field research, in the analyses and written part of this PhD. Many of the interpretations presented here were developed in discussion with him. His impressive list of publications and unique expertise in tropical ecology have been an ideal guide for me during these four years. Jörg, thank you very much for the appreciated help and all the time you put into this work while not really having any spare time.

I would also like to express my gratitude to all my CRC colleagues on whom I could count for correcting ‘rough’ drafts and providing useful suggestions. In particular I would like to thank Catherine Roden, Jeroen Stevens, Adinda Sannen, Rebekka Deleu, Isra Deblauwe, Hilde Vervaecke and Kristin Leus. My special thanks to Adinda who helped me greatly in the final phase, guiding me through all the official procedures and lay-out options. Many thanks as well to Vera Cuypers and Paule Stevens who made all the administrative paperwork a lot easier.

Language-wise I was very lucky to get help from Eric Arnhem who was ready to correct the French summary of this PhD. As for English, it was wonderful to work together with Don and Val Sibley who closely scanned my drafts for awkward phrases, grammatical errors and other mistakes. Previous versions of the chapters benefited greatly from the comments of Steve Goodman and Paul Adrian Racey, for which many thanks.

I am very grateful to Irene Tomaschewski from the Department of Conservation and Ecology (University of Hamburg) for carrying out biochemical analyses on the fruits.

Thanks to the statistical advice of Dries Bonte and Stefaan Van Dongen SAS became a little less incomprehensible to me. They put me back on the right track when I was lost in the complex world of statistical tests and models. My sincere thanks for your help!

I would further like to thank the members of the jury who have taken time to read through this PhD, I am looking forward to your comments. In this respect I am very grateful for the useful suggestions and constructive criticism of Prof Luc Lens on the first version of this PhD.

Obviously this PhD would never have been possible in the first place without the funding of the FWO (Funds for Scientific Research, Flanders), for which many thanks. I further thank the Centre for Research and Conservation (Antwerp Zoo) and the Department of Biology (University of Antwerp) as well as DOCOP (University of Antwerp) for additional funding.

A special word of thanks to the whole team of QMM in Fort-Dauphin for welcoming me at their study site and for helping me out with transport, radio-contact and food. Thanks to Rufen for the 'architectural' innovations at the campsite, which greatly improved our living standards. Laurent Randrihasipara and Jean-Baptiste Ramanamanjato, thanks for putting up with *'la belge exigeante'* and Manon Vincelette, thank you for always taking time to answer my numerous questions.

Having a degree in Zoology, it was great to be surrounded by excellent botanists familiar with the Malagasy flora. Petra De Block was the first to introduce me to the existing literature on taxonomy of Malagasy plants. Johny Rabenantoandro and Faly Mbolatiana from the Missouri Botanical Garden managed to replace most 'vernacular' names into scientific ones, which is not at all simple! Thanks for your patience in trying to guide me through the herbaria at Tana.

Prof. Berthe Rakotosamimanana (*Dept. Anthropologie*) and Prof Daniel Rakotondravony (*Dept Biologie Animale*) of the University of Antananarivo helped me to obtain research permits and saved me from weeks of administrative hassle, for which my sincere thanks. I further acknowledge ANGAP, the *Ministère des Eaux et Forêts* and the *Commission Tripartite* of the Malagasy government for their collaboration and permission to work in Madagascar.

The great help of my field assistants was essential in my field research. Thanks to them I managed to recognize many different tree species and find my way in the forest. In particular I would like to acknowledge Sambo Givet and 'Ramanga' (Honoré Aly) with whom I spend many hours in the forest. It was an enriching experience and unforgettable cooperation in *'équipe fruit'*. I am very grateful as well to Josette, our cook, for spoiling us daily with fresh *sisika*[1] and *rano apango*[2] and to Kadoffe for his work in phenology and his companionship. Ramisi Edmond, our local plant specialist, helped me tremendously in identifying and recognizing plant species. Many other *Antanosy* helped me in the field (Julson, Bruno, Claude, Rivo, …). *Misaotra*![3] I would further like to express my appreciation for the assistance and goodwill of the people of Ambandrika, Ampanosatomboky et Manafiafy. They always welcomed me and I have great respect for the *Présidents des villages* (Olaf Abel Isaia, Leonnaise, Sambo Pierre, Milson) who were always ready to discuss about conservation issues.

During my field research numerous Malagasy and foreign students joined me at the campsite for shorter or longer periods. They contributed a lot to a great and stimulating working environment. Thanks for sharing all those wonderful moments Jack, Tolona, Andreas, Nicoletta, Valentina, Rick, Petra, Kaï, Odon and Jose.

Closer to home I would like to acknowledge my friends and family who supported me throughout this PhD in different ways, for which my sincere thanks. The risk of forgetting someone is too big, which is why I have not tried to list everyone here but I am sure they know I deeply appreciate their support!

My parents have been a great support to me for as long as I can remember. They always have been very open-minded and accepted my wish to get out into the world and explore far away places. Thanks for being there for me unconditionally and for encouraging me to follow my 'idealistic' dreams. My brother always supports me too and I am happy to see how close we still are even though both of us spend a lot of time at different places on the globe.

Finally there is someone special to whom I am most grateful. Giuseppe Donati has been of crucial importance to me during this PhD. How could I ever forget the year we spent together in the forest, my neighbour from the tent next-door; the long nights talking about our exciting findings in the forest; endless discussions trying hard to find solutions to the conservation issues; *Sanzinia*[4] at breakfast; Italian salami for Belgian chocolates. We shared both great and tough moments. Too much to describe here but I am sure he knows what I am talking about! *Misaotra betsaka zoky be an ala*!!! [3]

Then of course there is the forest with all its mysteries and wonders that I was able to explore a little more each day. It is a precious place and I feel very fortunate to have been able to work out there. I hope this unique littoral forest of Sainte Luce will survive for many more generations to come…

Misaotra betsaka! [3] Antwerp, 25 October '03

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[1] shrimps, [2] rice water, [3] Thanks!, [4] *Sanzinia madagascariensis* : boa

PREFACE

This work brings together the main data collected during a 14-month field research in the littoral forest of Sainte Luce, south-east Madagascar. Nearly all chapters have been written to be suitable for publication and can as such be read independently from each other. Overlap in the introduction, materials and methods sections of the different papers was therefore unavoidable. In the different chapters distinct sub-samples from the fruit database and phenological data were used depending on the research question under consideration.

The work can be subdivided into three major sections: the introduction, the main section containing five chapters and the conclusion. The introduction situates the main topic of this work, describes the study site and the goal of this study. It further gives the outline of the thesis. At the time of compiling this thesis one chapter has been published (Chapter 3a), one is in course of publication (Chapter 4) and four are being reviewed (Chapter 1, 2, 3, 3b). Chapter 5 gives an overview of the conservation issues in the littoral forest and outlines possible applications, which will be used for conservation suggestions in a later publication. Finally the conclusion links all chapters together, summarizing the most relevant findings of this study.

Unfortunately the four year period was too limited to integrate all collected data into this work. It will therefore not finish with this doctoral study. Other parts of my work such as the more experimental preliminary work on seed predation and germination have been presented during conferences in the form of oral and poster contributions: the British Ecological Society (BES) meeting in Reading in 2001 (Bollen and Van Elsacker 2001), the Association for Tropical Biology and Conservation (ATBC) meeting in Panama 2002 (Bollen et al. 2002; Bollen and Van Elsacker 2002b), the ATBC meeting in Aberdeen 2003 (Bollen and Van Elsacker 2003) and the Benelux Congress of Zoology in Antwerp (Bollen and Van Elsacker 2002c). A lecture given at the University of professional education Larenstein in the Netherlands as part of a course on Tropical Ecology completes this list. As I work with the Centre for Research and Conservation, which is based at the Antwerp Zoo, there were several occasions on which written and oral media on this seed dispersal project were presented to a larger audience (Zoo Magazine, Course Primatology, Op de Koffie, Save the Bonobos, Africamatters).

GENERAL INTRODUCTION

ZOOCHORY AND FRUGIVORY

Scientists and evolutionary biologists as early as Darwin (1859), Wallace (1879) and Kerner (1898) acknowledged the importance of seed dispersal. The number of studies on dispersal ecology has only increased substantially during the last three decades. There was a great interest in understanding the role played by frugivory and seed dispersal in the dynamics of forests, particularly those in tropical forests. Van der Pijl (1969) was the first to give an elaborate survey of the modes of seed dispersal. This was based on the classification of Ridley (1930), who defined the agent of transport as the criterion for the main dispersal classes. Seeds are not mobile themselves, so their movement must be effected by dispersal vectors, whether abiotic or biotic. The main classes of seed dispersal are autochory, anemochory, hydrochory and zoochory, which respectively means seed dispersal by the plant itself, by wind, water or animals (Van der Pijl 1969). Each of these categories can be further subdivided into several subclasses, but I will only elaborate on zoochory, since this is the focus of my research. The unit of dispersal is a diaspore, which in zoochorous plants is nearly always the seed. Three different types of zoochory can be distinguished; endo-, syn- and epi- (or exo-) zoochory. Endozoochory occurs when diaspores are transported within the animal, either intentionally or accidentally. Synzoochory takes place when diaspores are intentionally carried in the mouth and epizoochory when diaspores are accidentally carried on the outside of the animal (Van der Pijl 1969). In tropical rainforest zoochory, in particular endo- and synzoochory, is the most common way of seed dispersal (Charles-Dominique 2001). About 75% or more of all plant species depend on vertebrates for the dispersal of their seeds (Howe & Smallwood 1982). In Mediterranean scrubland and tropical dry woodland only 50-70% of the plants are zoochorous and in temperate forests the percentages are even lower (30-40%). Zoochorous plant species are even virtually absent in alpine and desert vegetation (Jordano 2000).

The general principle of zoochory is fairly simple. Frugivores rely on fruits as their essential food source for survival, while at the same time, as seed dispersers, they represent the dynamic link between the fruiting plant and the seedlings. Fruits facilitate the dispersal of seeds by providing benefits to seed dispersers (Van der Pijl 1969; Witmer and Van Soest 1998; Jordano 2000). The seed is associated with soft and fleshy edible fruit pulp with attractive signals (colours, smell) on which the frugivores orient themselves to locate ripe fruit. The rewards offered by the plants include nutritious fruit pulp, while through directed dispersal by frugivores plants can colonize new vacant areas and avoid disproportionate mortality near the parent plant (Janzen 1970; Connell 1971; Chapman and Chapman 1996; Wenny 2000). Of course other animals also exploit this mutualism. For example, some invertebrate and vertebrate frugivores capitalize on fleshy fruits without dispersing the seeds or, even worse, by destroying them. In this respect, frugivore species can be subdivided based on their role in the ecosystem (Gautier-Hion et al. 1985; Debussche and Isenmann 1992; Jordano 2000). First of all legitimate seed dispersers swallow fruits entirely, digest the pulp and defecate or regurgitate intact seeds. Secondly, fruit pulp specialists or seed droppers tear off the pulp and drop the seeds.

Finally, seed predators discard the pulp, extract and digest or crack the seed. The latter can be considered as granivores.

Fruit-frugivore interactions represent an important aspect in tropical forest dynamics. Fruit resources are thought to be crucial in sustaining certain vertebrate populations in some tropical areas (Terborgh 1986a; Gautier-Hion and Michaloud 1989; Julliot 1997). While zoochorous fruits are very abundant in the tropics, frugivores make up the bulk of vertebrate biomass in tropical forests (Fleming et al. 1987; Gautier-Hion et al. 1985). In general, birds and mammals (mainly primates and bats) are the most important vertebrate frugivores, which swallow and defecate, regurgitate or spit seeds away from the parent plant. However some records of frugivory by reptiles, fish and invertebrates exist as well (Van der Pijl 1969; Corlett 1998). Obligate and occasional frugivory are the extremes along a gradient of fruit-eating. Most frugivores supplement their fruit diet to a greater or lesser extent with animal prey, flowers, leaves, nectar, and seeds (Fleming et al. 1987; Corlett 1998). According to Terborgh's definition (1986a) are frugivores only those animal species whose diet is composed of at least 50% fleshy fruits. Worldwide, 17 bird families can be considered strictly frugivorous (Snow 1981). Among mammals, obligate frugivores are rare with the exception of Pteropodids (Old World bats, Marshall 1983). As for primates, fruit is found in the diet of 91% of the species studied to date (Jordano 2000).

Seed dispersal is a complex multi-step process that links the end of the reproductive cycle of adult plants with the establishment of their offspring (Wang and Smith 2002). The pre-dispersal, dispersal and post-dispersal phases make up the intermediate processes between seed production and recruitment of adult trees (Fig. 1). The pre-dispersal phase is actually the fleshy fruit-frugivore interface, which includes the probability of the fruit to be selected, eaten and dispersed by a certain frugivore. The major focus in this phase is the fruit as food source with its morphological display and nutritional reward, including its spatial and temporal availability both seasonally and annually. Fruit production, fruiting period and fruit crop size are other traits influencing this phase (Garber and Lambert 1998). The actual dispersal phase indicates mainly the stage at which the consumers forage and feed on the fruits. Here, fruit and seed handling and processing determine the roles different frugivores may fulfil in this ecosystem. Finally in the post-dispersal phase the seed fate is concentrated on, which includes seed shadow, germination and growth of seedlings. This phase further includes secondary seed dispersal and seed predation. Since seed dispersal takes place at the final stage of a plant's reproductive life cycle, it has the potential to wipe out previous effects of pollination and fruit growth phases (Jordano 2000) and thus also to alter vegetation recruitment (Wang & Smith 2002).

SEED DISPERSAL HYPOTHESES

The study of frugivory and zoochory has led to early conceptual contributions. Several hypotheses were developed trying to explain the evolution within zoochorous fruits. First of all during the 1980s the field of frugivory and seed dispersal focused on a central paradigm: **co-evolution** (Janzen 1980; Levey and Benkman 1999). In this process organisms interact closely, influencing each other's evolution, which leads to reciprocal adaptations. With respect to seed dispersal, certain plant species may evolve specific fruit and seed traits to facilitate dispersal while the behaviour and diet of the frugivore responds to these changes. Tight co-evolutionary fruit-frugivore interactions have been proposed by several authors (Howe 1977; Tutin et al. 1991; Chapman et al. 1992b).

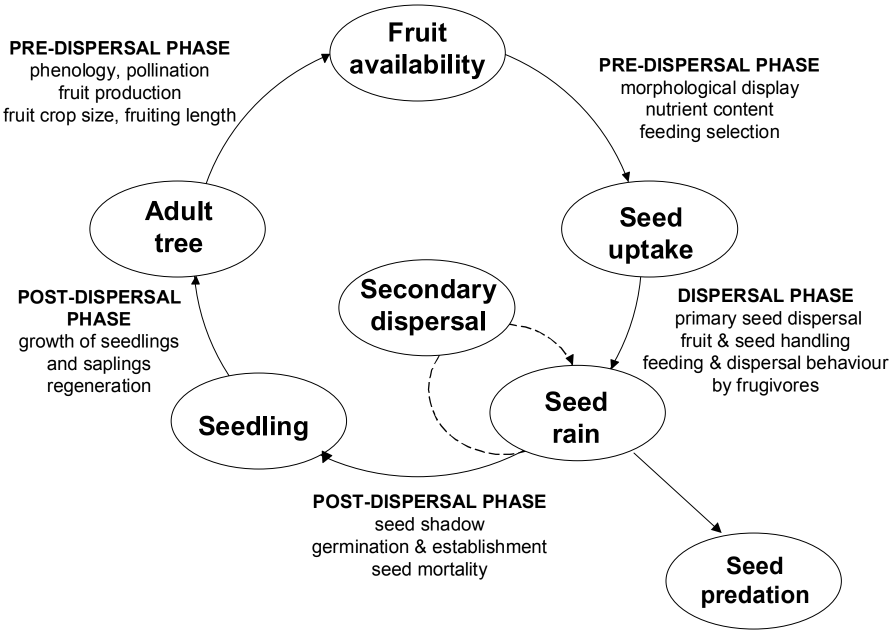


Fig 1. The seed dispersal cycle (based on Wang and Smith 2002)

Secondly based on the idea of co-evolution, a dichotomy of **low and high investment** plants has been put forward (Snow 1971; McKey 1975; Howe 1977; Howe and Estabrook 1977; Howe 1993). Low investment plants or generalists were described to invest little in the nutritional value of their fruits, having watery and sugary pulp. They produce large fruit crops during short periods, attracting as many opportunist frugivores as possible. On the contrary, high investment plants or specialists produce highly nutritious fruits, during elongated periods of time. They have a smaller fruit crop and often large one-seeded fruits attracting few specialist frugivores. This dichotomy has further contributed to the more differentiated concept of **dispersal syndromes**. Syndromes represent diffuse co-evolution among taxa and include mainly broad morphological co-adaptations of fruit and seed traits that attract certain taxonomic groups of seed dispersers. Each disperser type corresponds to a more or less diversified group of frugivorous animals whose size, anatomy and behaviour are compatible with the fruit features. This concept has been widely used in literature (Van der Pijl 1969; Howe and Smallwood 1982; Janson 1983; Knight and Siegfried 1983; Gautier-Hion et al.; 1985; Willson et al. 1989; Julliot 1996; see also Fischer and Chapman 1993; Jordano 1995; Voigt 2001). These three hypotheses highlight the importance, mechanisms and consequences of seed dispersal.

STUDY SITE: LITTORAL FOREST OF SAINTE LUCE (SE-MADAGASCAR)

The littoral forest of Madagascar represents a particular study site to carry out seed dispersal research. First of all, Madagascar is a hotspot of biodiversity and endemism (Mittermeier et al. 1998) with high priority for conservation. The majority of all plant species is endemic to Madagascar (Dumetz 1999; Schatz 2001), with percentages as high as 98% for the littoral forest (Rabevohitra et al. 1996; Razafimizanilala 1996). So studying fruit-frugivore interactions contributes to a better understanding of the dynamics within this ecosystem, that differs greatly in flora as well as fauna from those previously studied. Secondly most studies in Madagascar regarding seed dispersal focused only on the role of the larger lemur species (Hemingway 1996; Dew and Wright 1998; Overdorff and Strait 1998; Birkinshaw 1999, 2001; Ganzhorn et al. 1999a). Frugivory and zoochory by bats, birds and the smaller lemurs have only poorly been studied in Madagascar and not at all in the littoral forest. There is thus a great need for a community-wide approach of zoochory in Malagasy ecosystems, which is carried out for the littoral forest in this study. Thirdly, the Malagasy frugivore guild can be considered atypical in its composition. There are very few frugivorous bird and bat species here compared to other tropical sites, while at the same time large mammals are missing. Furthermore, since humans arrived on the island one third of its lemur species has disappeared (Godfrey et al. 1997). This relatively species-poor frugivore guild allows us to sample data on all involved species. Besides, this particular composition stresses the importance of the remaining frugivores in seed dispersal, which will provide crucial data that can be implemented in conservation management plans. At present the highly degraded and fragmented littoral forest is under severe threat and in urgent need of conservation. Finally, Sainte Luce lies at the southernmost position of a rainforest, being south of Capricorn, which may have led to a differential impact of abiotic factors here. The high degree of endemism and biodiversity, together with the awkward frugivore composition, the southernmost position and the urgent need for data on plant-animal interactions in this threatened forest type have all contributed to the choice of the littoral forest to focus on community-wide seed dispersal.

THESIS OUTLINE

In this PhD the results of a 14-month field research (November ’99 - February ‘01) are presented. Throughout the research, a close collaboration was established with the University of Hamburg (Germany), the University of Antananarivo, the Ministry of Water and Forestry, Qit Madagascar Minerals and Missouri Botanical Garden in Antananarivo (Madagascar).

This study aims at understanding community-wide seed dispersal in the Malagasy littoral forest. Research on both pre-dispersal and dispersal phase was carried out. The central focus of the doctoral study is to unravel how phenological, morphological and biochemical fruit traits determine and interact in fruit-frugivore dynamics. Seed dispersal is approached both ways, from the perspective of trees and frugivores. In the first part, fruits are studied with respect to the trees’ investment in morphological display and nutritional reward along with their temporal availability. To get insight into the overall fruit availability in the littoral forest together with its intra- and inter-annual fluctuation, phenological transects and fruit trails were carried out (Chapter 1). Dispersal strategies are tested based on existing hypotheses such as co-evolution, low-high investment model and dispersal syndromes (Chapter 2). In the next part, the influence of the morphological and biochemical traits on the frugivores’ fruit choice, feeding selection and fruit and seed processing is investigated. The role of the complete frugivore guild in this ecosystem as seed dispersers or predators is determined (Chapter 3). The feeding ecology and disperser role of *Pteropus rufus* (Chapter 3a) and predator role of *Coracopsis nigra* (Chapter 3b) are elaborated on. Subsequently, an inter-site comparison between fruit traits and feeding ecology of *Eulemur fulvus* and *Cheirogaleus medius* is made to test the validity of my results at other forest types. Both sites have similar frugivore guilds, but involve completely different forest types: the dry deciduous forest of Kirindy (west Madagascar) and the humid littoral forest of Sainte Luce (south-east Madagascar)(Chapter 4). Finally, the present degradation and fragmentation of the littoral forest as well as the disruption of fruit-frugivore mutualisms in Sainte Luce is discussed. Based on my understandings of seed dispersal dynamics, certain findings can be integrated within existing conservation measures (Chapter 5).

’Hazo tokana tsy mba ala’

One tree does not make a forest

Malagasy proverb
Drawing of flower and fruit of *Ravenala madagascariensis* (Strelitziaceae) © An Bollen

1

Phenology of the littoral forest of Sainte Luce, south-east Madagascar

AN BOLLEN, GIUSEPPE DONATI

BIOTROPICA (SUBMITTED)

ABSTRACT

From January 2000 through December 2002 phenological transects were carried out to assess monthly leaf, flower and (ripe) fruit presence for 423 individual plants (95 plant species, 43 families) within the littoral forest of Sainte Luce. Fruit-on-trail-counts were conducted additionally in the year 2000 to allow comparison between both methods. Despite low climatic seasonality and absence of a dry season in the littoral forest, inter-annual phenological patterns were seasonal at our site. Within-year variability was present with clear periods of abundance and scarcity. All phenophases were highly inter-correlated and peak from November through February. This was found in other humid Malagasy forests as well, while in dry Malagasy forests phenophases seemed to be more spaced in time due to the more seasonal climate. Day length seems to have the strongest impact on all phenophases, while rainfall is associated with flushing only and temperature with fruiting and 'ripe fruiting'. Differences in presence of ripe fruits when comparing between both sampling methods can be explained by the differential contribution of several life forms in both methods, which influence overall fruiting patterns.

INTRODUCTION

Phenological studies address the timing of reproductive events in plants such as bud formation, flowering and fruiting along with vegetative processes like leaf flushing and shedding. Tropical trees display an enormous variety in temporal patterns of flowering and fruiting. Both flowers and fruits are patchily distributed in time and space and are relatively scarce food items compared to leaves and insects (Howe 1984). Therefore it is critical to study food availability and distribution in order to understand the behavioural ecology of tropical wildlife. In the tropics, many animal species are frugivorous to a lesser or greater degree and in terms of biomass, frugivores are the dominant trophic group in most tropical forest mammalian communities (Terborgh 1983). This is further reflected by the dominance (60-90%) of zoochorous plant species producing fleshy fruits (Howe and Smallwood 1982).

Quantifying fruit availability has been a primary objective in many studies, which focus on the ecology of tropical fruiting trees and their consumers (Chapman et al. 1992a; Janson and Chapman 1999). During the alternation of seasons and years in rain forests, the availability of vegetative and reproductive plant parts is irregular and induces periods of abundance and scarcity of food for consumers (Brugiere et al. 2002). These temporal changes in resource availability are both affected by abiotic or climatic variables as well as by biotic factors through herbivory, pollination and seed dispersal.

Up to present, several short-term phenological studies have been published for Madagascar, where 96% of the tree species are endemic (Schatz 2001). Phenological studies have been carried out in dry deciduous and semi-deciduous forests in the West (Meyers and Wright 1993; Sorg and Rohner 1996; Curtis and Zaramody 1998; Rasmussen 1999; Yamashita 2002) as well as in lowland and mid-altitude rainforest in the East (Andrianisa 1989; Overdorff 1993a, 1993b; Rigamonti 1993; Freed 1996; Hemingway 1996, 1998; Andrews and Birkinshaw 1998). Most of these studies represent data from one year and often include only a limited number of species. At present, no data are available for the littoral forest. This paper presents the first findings from a detailed phenology of plant guilds in the littoral forest of Sainte Luce (south-east Madagascar) in the interest of revealing broad community-wide patterns of leafing, flowering, fruiting in the course of three years. This study generates indices to the food supply available to animal consumers, but also addresses the impact of abiotic factors. Furthermore, we compare phenological patterns of different Malagasy forest types.

In this study several aspects will be looked at closely. First, we describe the temporal fluctuations of flushing, flowering and fruiting inter- and intra-annually based on data from phenological transects and fruit-on-trail-counts, which are considered to be the most common phenological methodologies (Chapman et al. 1992a; Chapman and Wrangham 1994). Secondly, we look for correlations between these phenological patterns and different abiotic factors such as rainfall, temperature and day length, that may trigger phenological events. Finally, we compare our data with the results of other Malagasy study sites.

METHODS

Study site

The littoral forest of Sainte Luce (24º45'S 47º11'E) is located in south-eastern Madagascar, 50km up north of Fort-Dauphin. Research was carried out in a 377-ha large forest fragment, called S9 (Fig. 1). Littoral forest is characterised by a relatively open or non-continuous canopy, which is 6 to 12m in height with emergents up to 20m. The diameter at breast height (DBH) of trees rarely exceeds 30-40cm. Littoral forest grows on sandy soils and occurs within 2-3km of the coast at an altitude of 0-20m (Lewis Environmental Consultants 1992a).

Abiotic factors

Daily rainfall was measured with a plastic rain gauge (TruCheck) during the research period. Rainfall data from February till September 2001 were not available for Sainte Luce. A thermo-hygrograph (Box Pro) was placed in primary forest at one meter height to record the daily march of temperature and relative humidity. Variation in day length was calculated using Stephen Moshier’s Ephemeris Program v5.1 (Moshier 1991) for the Sainte Luce latitude. Mean monthly values were calculated for all abiotic factors.

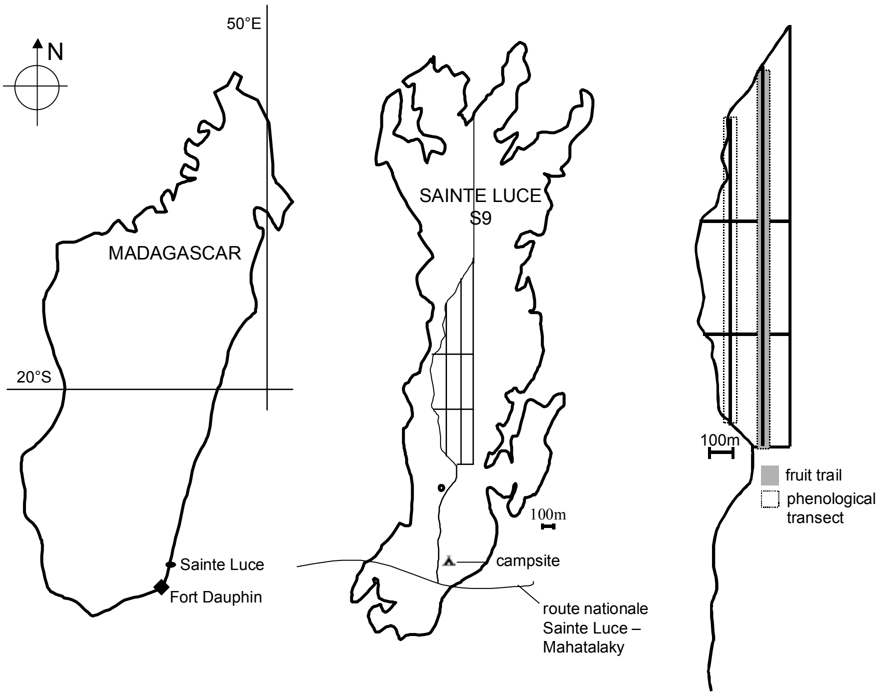


Fig. 1. Map of Madagascar with indication of the study site together with an enlargement of the forest fragment 'S9' where the study was carried out. A detail of the grid with corresponding phenology transects and fruit trails is shown as well.

Phenological transect

A systematic floristic and phenology inventory was conducted as part of two doctoral research projects in the littoral forest: one on the behavioural ecology of *Eulemur fulvus collaris* (Donati 2002) and the other on seed dispersal and predation by the frugivorous guild (Bollen and Van Elsacker 2002, Chapter 3a; Bollen et al. in press, Chapter 4). All plant species with DBH greater than 5cm (conform to other Malagasy studies, see Meyers and Wright 1993; Overdorff 1993a; Hemingway 1996) within 5m of each side of the transects were tagged with fluorescent flags provided by an individual code. Ideally, five individuals per species were marked. Additional tree species were added to this list. These involved important known frugivore resources that did not occur on the transect or only at very low densities. The complete phenological transect consisted of 423 individuals of 95 species (74 genera; 43 families) sampled over two botanical transects covering 2320x10m² (Fig. 1). Eighteen trees died naturally or were cut during the sampling period, resulting in a complete data set of 405 individuals. The different vegetation types, such as primary, secondary and swamp forest as well as abandoned *tavy* (slash and burn areas) were represented in the phenological transect.

Phenological data were recorded once a month as of January 2000 up to present. Here we present data from January 2000 through December 2002. The different categories considered are the following:

Leafing: no leaves, presence of young leaves, full of leaves, leaf fall;
Flowering: no flowers, flower buds, open flowers, fallen flowers;
Fruiting: no fruits, fruit buds, unripe, ripe or fallen fruits, dry fruits of last season.

For analyses we narrowed these categories down to complete leaf fall, presence or absence of young leaves, flowers, ripe and other fruits. Observations on leafing, flowering and fruiting were always made by the same team of two field assistants, who scanned the canopy with binoculars and checked the litter below for fallen flowers and/or fruits. A species was scored flushing, flowering or fruiting if at least one individual of this species was in this phenophases. To differentiate between unripe and ripe fruits, we focused on differences in colour, size and consistency.

No attempt was made to estimate overall fruit production. Neither did we use quantitative scores nor relative abundance of leaves, flowers and fruits as we lacked previous knowledge on crop sizes. Furthermore the high variability of crop sizes intra- and inter-specifically in time, related to tree size, makes it difficult to objectively quantify these reproductive events. Moreover, various measures are used in different studies which makes comparison problematic and according to Chapman et al. (1992a) inter-observer variability is high.

We further subdivided our species sample by life form into large trees (>6m), small trees (<6m), shrubs, vines and epiphytes. For analyses these categories were lumped to large trees and others. For data on synchronicity and regularity in flowering and fruiting, we used the following definitions. If all individuals of a certain plant species were flowering and/or fruiting at the same time they were considered synchronous, otherwise asynchronous. Synchronicity was only determined when four or more individuals of a certain species were present in our dataset (N=70). Species were considered annual if the interval between flowering and fruiting patterns was one year. Irregular fruiting or flowering occurred when no regular interval could be found between the reproductive phases. Continuous flowering and fruiting of a species occurred when throughout the whole year flowers and fruits were present. When reproductive phases lasted for more than six months we considered this as extended flowering or fruiting.

Fruit-on-trail-counts or fruit trails

As the previous method excluded small trees, shrubs, vines, herbs and epiphytes with DBH smaller than 5cm, fruit trails were carried out once a month to complete the phenology data. Fruit-on-trail-counts or fruit trails determine the number of individuals and species fruiting along a transect (1350m) scoring fruits in the canopy and fallen fruits and seeds on the ground at respectively 5m and 1m on both sides of the transect (Fig. 1). These fruit trails were carried out by the first author and a field assistant from February 2000 through January 2001. This method was modified based on Gautier-Hion et al. (1981) with the difference that canopy data were included as well. As with the phenological transect, the different forest types were included (with the exception of *tavy*) and the complete fruit trail covered 1350x10m² on canopy level and 1350x2m² on ground level.

Herbarium

Tree identifications were made provisionally in the field using vernacular names obtained from the local field assistants and herbarium specimens of all taxa were collected whenever possible. Scientific names were obtained after determination at the national herbaria with the help of the botanists Johny Rabenantoandro and Faly Randriatafika of the Missouri Botanical Garden in Antananarivo, Madagascar. We checked for correct taxonomic information for floral species in TROPICOS database on the Missouri Botanical Garden website.

Statistical analyses

Because phenological data are not independent in time and not normally distributed, we used non-parametric statistics for repeated measures. To test for inter-annual variability in phenophases we used Kendall's Coefficient of Concordance, while the Friedman test (ANOVA) showed whether significant differences exist in the number of species flushing, flowering or fruiting among years. Spearman Rank Correlation Analyses were used to examine overall relationships in phenophases, climatic and feeding data. Chi-square analyses were conducted to compare between flowering and fruiting on the basis of different classes of synchronicity and regularity, as well as to compare between life forms used in fruit trail and phenology. Mann Whitney U tests compared the number of species with ripe and other fruits between two phenological methods. All statistical tests were carried out according to Siegel (1956) with the statistical software SAS and STATISTICA for Windows.

RESULTS

Abiotic factors

There was considerable year to year variation in the seasonal distribution of rainfall and temperature. No significant correlations could be found for both variables between years (Table 1, Fig. 2). Mean annual rainfall during 2000-2002 was 2690mm (±228 SD). Figure 2 gives monthly distribution in rainfall and monthly average temperature, indicating an obvious wet season from November through February. No clear dry season could be detected. Driest months were September and October (average 79mm ±37 SD). During July 2000 rainfall was unusually high for this time of the year. Temperatures were highest from December through March after which they declined to a minimum in July and August. Mean monthly temperature was 23°C (±2.3 SD, N=30) ranging from 18.5 to 25.6°C. As expected for a site below the Tropic of Capricorn, we found a considerable difference in day length in Sainte Luce (Fig. 2) with a minimum in summer solstice (June: 10.6h) and a maximum in winter solstice (December: 12.6h).

Phenology

Overall, we monitored the fruiting phenology of 423 individuals of 95 plant species belonging to 74 genera and 43 families (Appendix I). The median number of individuals per species was five, ranging from one to nine. Most represented plant families were Clusiaceae, Flacourtiaceae, and Myrtaceae, with six plant species each and Rubiaceae and Euphorbiaceae with five species. The majority of the remaining families were represented by only one or two species. Most studied plants were large trees (71%) followed by small trees and shrubs (23%). Vines and epiphytes only made up 5% and 1% respectively of the complete sample.

The flowering peak occurred always at the beginning of the rainy season, mainly in November, when on average 38 species (±7 SD, range 33-47) were blooming. Of all flowering events (N=2054) during three years, 15% (N=309) occurred in November. Flowering patterns over years were significantly correlated (W=0.46, df=2, N=12, P<0.01) (Table 1, Fig 3). There were significantly more species blooming in 2000 as in the other years (F=10.96, df=2, N=12, P=0.004). The monthly average of species blooming in 2000 was 26 (±9 SD) while in 2001 and 2002 this number was considerably lower; 19 (±8 SD) and 20 (±9 SD) respectively.

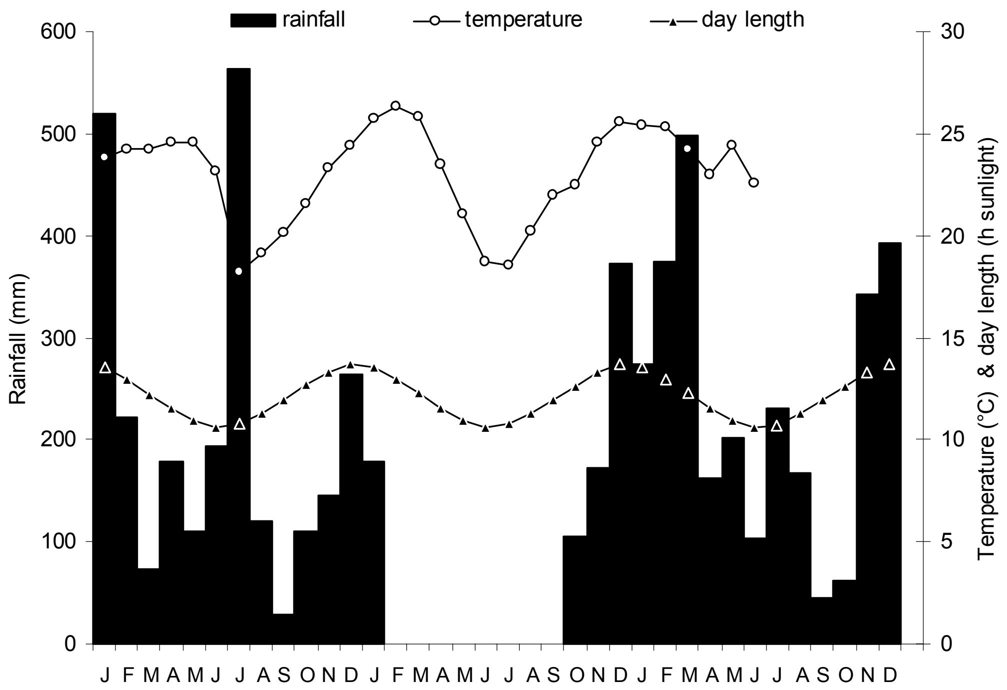


Fig. 2. Seasonal variation in the climate of the littoral forest of Sainte Luce is given together with monthly rainfall, mean temperature and day length recorded over a three year period (2000-2002).

Table 1. Spearman rank correlations for interannual patterns within temperature, rainfall, flushing, flowering and fruiting. r_s-values are given. * $P<0.05$, ** $P<0.01$.

	Temperature				
Temperature	2000	N	2001	N	2002
2000	1				
2001	0.54	12	1		
2002	0.14	6	0.6	6	1

	Rainfall				
Rainfall	2000	N	2001	N	2002
2000	1				
2001	0.80	4	1		
2002	0.32	12	0.80	4	1

	Young leaves				
Young leaves	2000	N	2001	N	2002
2000	1				
2001	0.39	8	1		
2002	0.20	8	0.33	12	1

	Flowers				
Flowers	2000	N	2001	N	2002
2000	1				
2001	0.54	12	1		
2002	0.63*	12	0.56	12	1

	Fruits				
Fruits	2000	N	2001	N	2002
2000	1				
2001	0.18	12	1		
2002	0.72**	12	0.47	12	1

	Ripe fruits				
Ripe fruits	2000	N	2001	N	2002
2000	1				
2001	0.39	12	1		
2002	0.38	12	0.34	12	1

The highest number of fruiting species were recorded from November through February of each year, the fruiting peak coinciding with high rainfall. In general, fruiting lagged behind flowering by one or two months. Among 2832 effective fruiting events during 36 months, 36% was concentrated between November and February of each year. Kendall's Concordance showed that fruiting patterns among years were significantly associated (W=0.53, df=2, N=12, P<0.01). Spearman Rank showed high correlation in fruiting in particular between 2000 and 2002 (r_s=0.72, N=12, P=0.008) (Table 1, Fig. 3). The inter-annual variability in the number of fruiting species was highly significant (F=12.67, df=2, N=12, P=0.002). The year 2000 seemed to be particularly rich in fruits (monthly average 41±6 SD species), especially from May to August compared to the other years. Of the 95 species monitored each month, 41 (±6 SD) were fruiting on average in 2000. On the contrary, 2001 and 2002 can be considered difficult years for frugivores with a monthly average of only 28 (±13 SD) and 29 (±8 SD) species respectively.

Since ripe fruits better represent what is actual available for frugivores, we narrowed down the data to ripe fruits only. Annual profiles were still correlated (W=0.41, df=2, N=12, P<0.01) (Fig. 3). Peaks of ripe fruit availability occurred mainly in January. There was a significant quantitative difference in number of species carrying ripe fruits among years (F=9.91, N=12, df=2, P=0.007). Periods of fruit scarcity differed strongly inter-annually. In 2000, there was a lower 'ripe fruit' availability in March and July-August (average 10 sp ±2 SD). Lean periods in the following years occurred mainly from August till October 2001 (4 sp ±1 SD) as well as in May and June 2002 (3 sp ±1 SD).

Impact of abiotic factors

The phenophases are highly inter-correlated when looking at overall flushing, flowering and fruiting patterns (Table 2) with the exception of flowering and ripe fruiting. With regard to climatic factors, leaf emergence is the only phase that was positively correlated with rainfall. Temperature on the other hand is correlated with fruiting and highly associated with ripe fruiting (Table 2). All three phenophases are highly correlated with the duration of light hours (Table 2).

Synchronicity and regularity in flowering and fruiting

Of all species recorded in phenology 49% flowered and 43% fruited each year. There was a similar amount of species showing synchronicity as well as asynchronicity both in flowering and fruiting (Table 3). Species were more irregular in fruiting (53%) as in flowering (40%), where more species had annual flowering patterns (39%) than annual fruiting patterns (31%). Continuous flowering occurred in 11% of all species studied, while this was 13% for continuous fruiting. A considerable proportion of all plant species monitored had extended flowering (17%) or fruiting (37%). Even though these overall differences existed between flowering and fruiting, statistically they were not significant, with the exception of extended fruiting that was more common than extended flowering at our study site (Table 3).

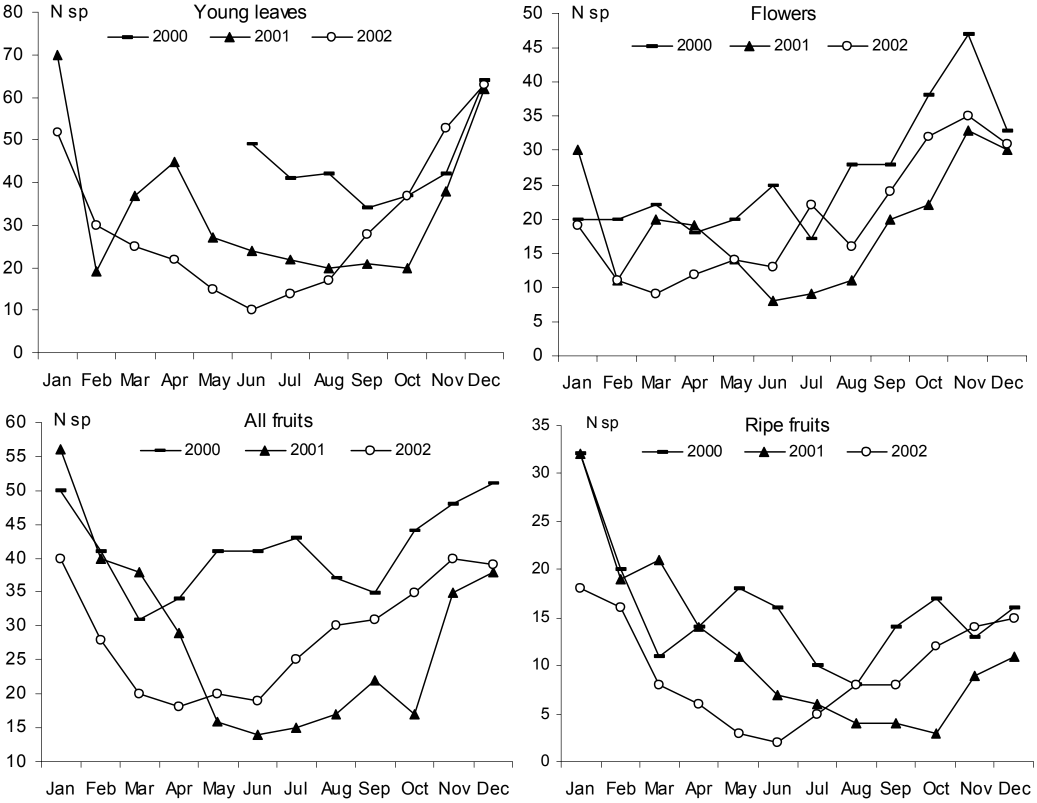


Fig. 3. Phenological flushing, flowering, and fruiting (all fruits and ripe fruits) are given for the three years with indication of the monthly average of number of species present.

Comparison between phenological transect and fruit trail data

Over a 12-month period a total of 113 species were monitored fruiting on the fruit trail. These species belonged to 75 genera and 48 families. Fourteen plant species could not be identified. The fruit trail and phenological transect have 60 species in common. Large trees made up 43% of the fruit trail species, while for smaller trees, shrubs, vines, herbs and epiphytes this was 57% (App. I). The distribution of growth types within phenological transect and fruit trail were significantly different ($X^2=16.33$, df=1, $P<0.001$)(Fig. 4).

Data from the fruit trail showed that there were two periods when ripe fruits were abundant in the year 2000. The first moderate peak was from May through August, when on average 17.0 (±1.8 SD) species carried ripe fruits. The majority of these species (72%) involved small trees, shrubs, vines and epiphytes. A much higher peak occurred in January when ripe fruits of 22 species were available. Here, the large trees were mainly responsible (59%) for this. Periods with lower fruit availability occurred as well, specifically in April and November when only seven and six species carried ripe fruits. The lean period in April in particular was due to the low number of large trees with ripe fruits while in November fruiting in both large trees and other life forms was equally low (Fig. 4).

Table 2. Spearman rank correlations of three year data between number of species with young leaves (YL), flowers (FL), fruits (FR), ripe fruits (RIPE), temperature (TEMP), rainfall (RAIN) as well as day length (DL). r_s-values are given. * P<0.05, ** P<0.01, *** P<0.001.

	YL	N	FL	N	FR	N	RIPE	N	TEMP	N	RAIN	N	DL
YL	1												
FL	0.61***	32	1										
FR	0.63***	32	0.63***	36	1								
RIPE	0.57***	32	0.32	36	0.78***		1						
TEMP	0.21	26	0.17	30	0.41*	30	0.57***	30	1				
RAIN	0.41*	24	-0.21	28	0.26	28	0.27	28	0.33	22	1		
DL	0.61***	32	0.52**	36	0.55***	36	0.53***	36	0.59***	30	0.33	28	1

Table 3. Chi-square results for comparison between flowering and fruiting based on different categories of synchronicity, regularity and duration. ** P<0.01. Number of species are given for each category.

		Flowering	Fruiting	X^2	df
Synchronicity	Synchronous	27	27	0.02	1
	Asynchronous	38	40		
	No data	30	28		
Regularity	Annual unimodal	37	29	2.59	2
	Irregular	38	50		
	Continuous	10	12		
	No data	10	4		
Duration	Extended (>6 months)	16	35	8.22**	1
	<6 months	70	57		
	No data	9	3		

When comparing results of phenological transect and fruit trail, the abundance of ripe fruits in January corresponded but there was a discrepancy mainly during the months July and August when the phenological transect showed that few tree species (July N=10, August N=8) had ripe fruits, while this was not the case for the fruit trail (July N=18, August N=15). Clearly this was a result of the lower representation of small trees and shrubs in the phenology, which had their period of ripe fruit abundance in austral winter. Both periods of low fruit abundance corresponded in both methods, even though they were less pronounced in the phenological transect and one or two months earlier. Overall patterns of ripe fruit availability of fruit trail and phenology were not correlated (r_s =0.32, N=12, P=0.31), but quantitative comparison shows that the number of species with ripe fruits did not differ when comparing between methods (Z=-0.78, P=0.43). If we consider all fruits in both methodologies differences in fruiting patterns were smaller and even correlated (r_s=0.64, N= 12, P=0.03), but quantitatively there was a significant difference in number of species fruiting (Z=-3.24, P=0.0012).

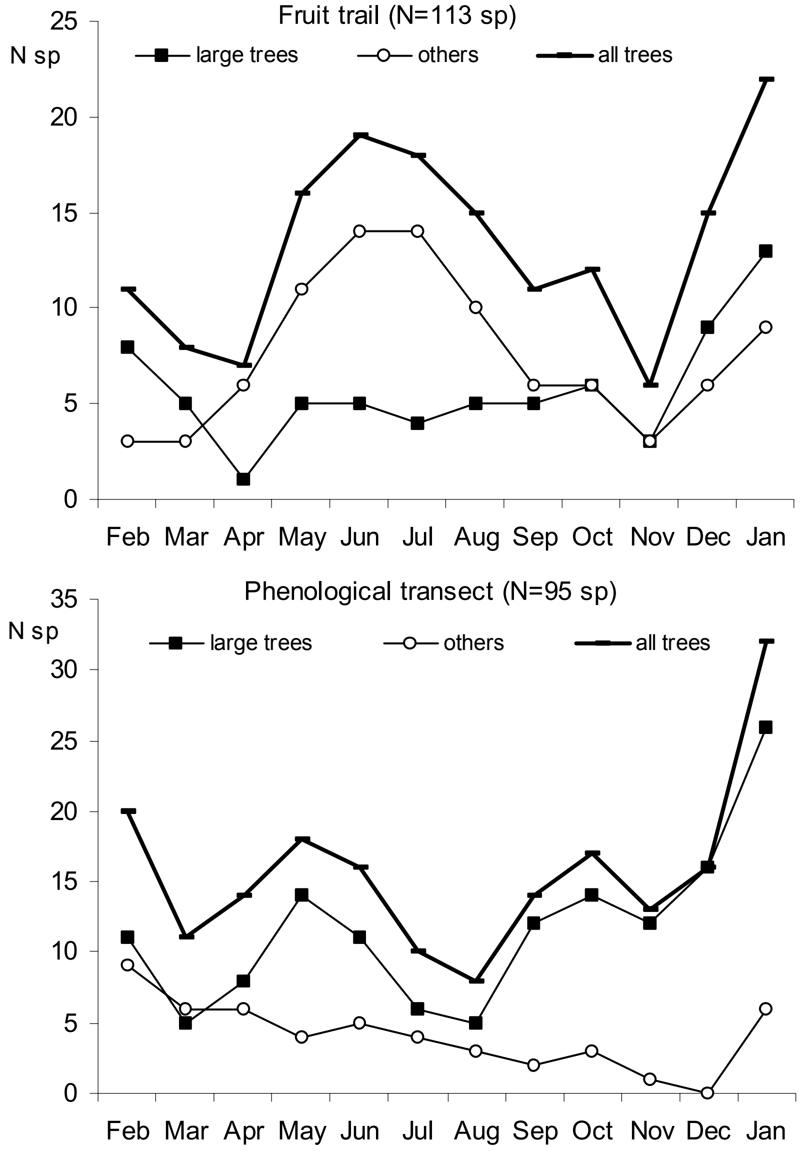


Fig 4. Comparison of data from the phenological transect and fruit trail is shown with indication of the number of species with overall ripe fruits present as well as the distinction between life forms.

DISCUSSION

Abiotic factors

A pronounced island-wide environmental seasonality is said to characterise Madagascar (Morland 1993). This is true in particular for the ambient temperature that appears to vary in consistent, seasonal cycles throughout Madagascar, which corresponds with data from our study site. On the contrary, rainfall does vary widely among regions in Madagascar

(Table 4). While the North and West are characterised by prolonged annual dry seasons and the South by sparse and irregular rainfall, the East has no clear dry season (Morland 1993; Kappeler and Ganzhorn 1994; Hemingway 1998; Britt 2000; Vasey 2000). When comparing our rainfall data with those from eastern low alititude forests Nosy Mangabe, Masoala and Betampona (Morland 1993; Britt 2000; Vasey 2000) and the inland mid altitude rainforest Ranomafana (Overdorff 1993a; Hemingway 1998), all sites have their driest months in September and October, with a prolongation into November for the Masoala peninsula. The mid altitude forest of Ranomafana approaches a more seasonal climate as it has relatively fewer rain from April through September. Low altitude coastal forests are clearly more aseasonal when considering rainfall which is conform to our study site. Thus, no seasons were considered in the littoral forest of Sainte Luce. It seems to follow the definition of an aseasonal tropical wet climate (Morellato et al. 2000), as it is characterised by mean monthly temperatures of at least 18°C, annual rainfall above 2000mm and either no dry season or a short drier period of less than four consecutive months with rainfall below 100mm per month. The situation in Sainte Luce corresponds with that in other tropical wet forests worldwide. In summary, rainfall seems more important in determining local seasonality rather than temperature which has less fluctuation (Sakai et al. 1999) and, overall seasonality is said to be lower in humid than in dry forests (Koptur et al. 1988).

Phenological transect

The phenology of the community as a whole followed a flowering, fruiting and ripe fruiting pattern which was repeated from year to year in a regular seasonal cycle, while for leafing patterns inter-annual variability is high. However, the number of species flowering and fruiting differed substantially from year to year. Over three years flushing, flowering, fruiting and ripe fruiting were all inter-correlated and the peak of all phenophases occurred in the same period (November and February). This corresponds with the fact that in many evergreen species flushing and flowering occur close in time as they are both triggered by solar irradiance and young leaves and flowers develop from the same new shoots (Van Schaik et al. 1993).

We found an important quantitative difference between availability of ripe versus all fruits, which is probably related to the fact that unripe fruits were often aborted. Unripe fruit abortion is considered common in the tropics (Smyte 1970; Medway 1972). This can occur due to several reasons such as climate (Janson and Chapman 1999), insect predation (Koptur et al. 1988) or other factors. Abnormal high rain in July 2000 resulted in fruit abortion in many species as the number of ripe fruits was considerably lower in July and August 2000 compared to other years.

In our data, the large differences between number of species flowering compared to the ones fruiting is not biologically meaningful and is an artefact of the methodology. This is probably because the category of all fruits includes fruit buds, unripe, ripe and even rotten fruits as well as old dry fruits from the previous season, which leads to higher numbers of species fruiting during an ‘artificially’ prolonged time. As for flowers, monthly scoring is probably not sufficient (De Block pers. comm.) as flowers in general have a short existence only and thus may be missed. As a matter of fact, in five species no flowers were observed even though these species fruited.

Table 4. Data on phenology in different sites throughout Madagascar (ND: no data available, RNF: Ranomafana).

Study site Location	Forest type Altitude (m) Rainfall (mm)	Climate	Phenology sample Duration
Ambatonakolahy NE Madagascar	mid altitude rainforest 450-650 4200	max rain: Feb-Mar min rain: Sep	511 ind 72 sp Dec '90-Nov '91 5 mo
Vatoharanana RNF 21°02-25'S 47°18-37'E	mid altitude rainforest 1125 2300	max: Dec-Mar min: Sep-Oct	104 ind 26 sp Jul '88-Aug '89 1 yr
Vatoharanana RNF 21°02-25'S 47°18-37'E	mid altitude rainforest 1100 2300	max: Dec-Mar min: Sep-Oct	1354 ind 127 sp Jan '91-Jul '92 1.5 yr
Daraina 13°14'S 49°39'E	dry forest 400-1100 1445	max rain: Dec-Mar min rain: Sep	499 ind 150 sp Jul '90-Jun '91 1 yr
Kirindy 20°04'S 44°40'E	dry deciduous forest 18-40 800	rainy season: Dec-Feb dry season: Apr-Oct	80 ind 56 sp 78-'87 9 yr
Anjamena 16°03'S 45°55'E[1]	dry semideciduous forest ND 1189	rainy season: Dec-Apr dry season: May-Nov	19 sp Oct '94-Sep '95 1 yr
Ampijoroa 16°19'S 46°49'E[1]	dry semideciduous forest 75-390 1771	rainy season: Dec-Mar dry season: May-Oct	317 ind Jun '96-Jun '97 1 yr
BezaMahafaly SW-Madagascar	dry deciduous forest ND 866	rainy season:Nov-Mar dry season: Apr-Oct	10 plots (2x50m) Feb '99-Feb '00 9 mo
Lokobe 13°23'S 48°18'E	primary lowland rainforest 0-430 2356	aseasonal max rain: Nov-May	278 ind Nov '92-Dec '93 1 yr
Montagne d'Ambre NW Madagascar	mid altitude rainforest 850-1474 3585	aseasonal max rain: Dec-Mar	ND
Nosy Mangabe NE Madagascar	primary lowland rainforest 0-331 3806	aseasonal max rain: Jan-May	ND
Sainte Luce 24°45'S 47°11'E	littoral forest 0-20 2690	aseasonal max rain: Dec-Mar	423 ind 95 sp Jan '00- Dec '03 3 yr

[1] general geografic data are from the authors or from Preston (1991).

Table 4 Continued

Flushing	Flowering	Fruiting	Literature cited
constant	peak: Aug	high: Oct-Nov low: July	Rigamonti (1993)
high: Jan, May low: Jun-Oct	peak: Aug, Nov-Dec	peak: Aug-Oct, Feb low: Apr-Aug	Overdorff (1992,1993a, 1993b) Meyers and Wright (1993)
corr with rainfall	corr with rainfall	peak: Oct-Dec low: Apr-Jul	Hemingway (1996,1998)
peak: wet seasor	peak: Oct-Nov	peak: Dec-Mar	Meyers and Wright (1993)
peak: Nov-Dec	peak: Oct-Dec	all year available	Sorg and Rohner (1996)
peak: Dec-Mar low: Jun-Oct	peak: Oct	peak: Oct low: Jun	Curtis (1997)
peak: Dec-Feb	peak: Jan, Sep, Feb	peak: Jun-Jul, Sep, May	Rasmussen (1999)
peak: Nov-Jan	peak: Nov	peak: Apr-Jun	Yamashita (2002)
ND	ND	low: Mar-Jun	Andrews and Birkinshaw (1998)
ND	similar to RNF	similar to RNF	Freed (1996) in Vasey (2000)
ND	peak: Dec-Jan	peak: Nov-Feb	Andrianisa (1989) in Vasey (2000)
peak: Nov-Jan	peak: Nov	peak: Nov-Jan low: Aug-Oct	Bollen and Donati (this study)

Relation with abiotic factors

Climatic parameters such as temperature, rainfall, day length, cloud cover and irradiance are the proximate factors that affect the timing of phenophases (Smythe 1970; Van Schaik et al. 1993) and among them rainfall has often been identified as the principal external factor, directly or indirectly controlling the period rhythms of tropical forests (Medway 1972; Lieberman 1982; Sorg and Rohner 1996; Morellato et al. 2000). However, transect-wide flowering and fruiting patterns were not related to rainfall in Sainte Luce as opposed to many other sites (Hemingway 1996; Sorg and Rohner 1996). On the contrary, leaf emergence did correspond positively with rainfall as in most other tropical forests (Lieberman 1982; Hemingway 1996, 1998; Rasmussen 1999). Flowering was not correlated with temperature nor with rainfall, while fruiting was positively associated with temperature and for “ripe fruits” this correlation was even stronger. Smythe (1970) mentioned that organic composition is slow throughout the dry season but as rains begin, the combination of high temperature and high relative humidity allows decomposition of the accumulated materials to proceed very quickly. The dropping of seeds at a time when there is a sudden rather brief abundance of nutrients may increase the probability of survival of seedlings, which may explain this correlation. Day length, our rough estimation of solar irradiance, was highly correlated with all three phenophases. This result is in agreement with the findings of Van Schaik et al. (1993). They highlighted the importance of irradiance in enhancing photosynthetic processes during flushing and flowering. Given the latitude of Sainte Luce, at the southernmost range for a rain forest, this abiotic factor could be particularly important in triggering phenological cycles here. Caution has to be taken while interpreting these results as both temperature and rainfall data are incomplete and impact of edaphic factors was not studied. Besides external factors, plant species obviously also have endogenous rhythms and their expressions are affected by changes in internal tree functions that are not necessarily linked with environmental patterns (Marco and Paez 2002).

Synchronicity

Our results showed that there is a complete gradient from species with strong seasonality, either annually or continuously flowering and fruiting to those with weak seasonality without obvious periodicity or an extended flower and fruit production throughout most of the year. This high variability in synchronicity and flower-fruit periodicity has also been found in other tropical sites (Gautier-Hion et al. 1981; Van Schaik 1986; Van Schaik et al. 1993). However, we can extract some general trends at our site. Almost half of all species monitored had flowers and fruits each year, which indicates that there is some stable level of food availability for nectarivores and frugivores. While flowering is annual in about 39% of the species, for fruiting this percentage is reduced to 31%. This difference together with the higher number of species that has irregular fruiting, indicates that many species failed to set fruits even though flowers were present. Janson and Chapman (1999) mentioned that in species that attempt to reproduce every year, fruiting failure is common in many years due to between year climatic variation. Absence of pollination, climatic and other environmental as well as physiological factors may be responsible for this (Medway 1972, Koptur et al. 1988). The category of irregular species may include species with bi-annual and tri-annual rhythms, but long-term data are needed to reveal these longer flower-fruit intervals. Extended flowering and fruiting occur in most tropical forest at higher or lower percentages depending on the site (Frankie 1975; Koptur et al. 1988; Van Schaik et al. 1993; Sakai et al. 1999; Morellato 2000). It makes biologically sense that this occurs more for fruiting than flowering as unripe fruits often take a longer time to mature than flowers.

Comparison between phenological transect and fruit trail

By selecting trees above a specific size as in the phenological transect, one makes the assumption that trees with a DBH smaller than 5cm are unable of producing fruit. In this way all smaller trees, shrubs, herbs, epiphytes and vines are excluded, although they may influence overall fruiting patterns. Our data revealed that fruiting patterns in general were indeed correlated between both methods. This trend was found as well in a study by Wallace and Painter (2002) when comparing between both methods. However, when considering ripe fruits only it was evident that in Sainte Luce during austral winter smaller vegetation forms carried more ripe fruits than the phenological transect showed. Thus, fruit trail data compensate for the underestimation of smaller trees and shrubs in phenological transects. As both methods are complementary it is useful to include both to get the global picture and reveal different phenological trends for large trees and other life forms. Furthermore fruit trails have the advantage of adding a density effect to the data as this is a more quantitative phenological approach where all trees in fruit encountered on the transect are scored each month. On the contrary, during phenological transects, only phenophases of a fixed number of tree species are scored, which represent only a sub-sample of all tree present in an ecosystem selected on their DBH. Moreover, phenology transects are especially appropriate for scoring resource availability for arboreal frugivores, while fruit trails are more appropriate for terrestrial frugivores (Wallace and Painter 2002). In this respect we can explain the lag in time in periods of fruit scarcity between both methods as in phenology only fruits in the canopy are scored, which are earlier available than the subsequently fallen fruits, that are included in fruit-on-trail-counts (cf. Wallace and Painter 2002). To conclude, combining both methods is ideal to get insight into the complete food availability for the frugivorous guild as a whole. Furthermore, our results show the importance of differentiating between unripe and ripe fruits in both methods, which often lacks in other studies, to indicate the ‘true’ severity of bottlenecks in fruit availability that frugivores face in tropical forests.

Comparison with other Malagasy sites

Since methodologies and representation of data differ between sites, we restricted our comparison to general phenological patterns. In eastern humid forests (Ranomafana and Sainte Luce, Table 4) flushing coincides with the wettest period of the year. In the dry semi-deciduous and deciduous forests the emergence of young leaves starts at the end of the dry season and attains a peak at the onset of the rainy season (Table 4). Given the much stronger seasonal climate of dry forests, where flushing is restricted in time, young leaves anticipate the first rains and create the possibility for plants to maximally benefit of the favourable rainy season. In all sites flowering seems to occur in October and November. As mentioned before, flushing and flowering occur close in time and are both triggered by high irradiance (Van Schaik et al. 1993), which is elevated in these months when rainfall is ubiquitously low and the sky rarely covered. Fruiting patterns are much more diverse between sites and peaks differ from site to site. In Ranomafana, Nosy Mangabe, Montagne d’Ambre and Sainte Luce fruiting occurred at the same time as flowering and flushing (Table 4). The dry forests may have fruiting peaks in austral summer (Meyers and Wright 1993), winter (Curtis and Zaramody 1998; Rasmussen 1999; Yamashita 2002) or throughout the year (Sorg and Rohner 1996). In summary, the

Malagasy rainforests display an associated pattern for all phenophases, while in the dry forests phenophases are more spaced in time (Kappeler and Ganzhorn 1994; Curtis 1997; Rasmussen 1999). Therefore, the lean fruit period in the littoral forest and mid altitude rainforest does not appear to be compensated by flower and/or young leaf bursts. This pattern together with significant inter-annual variation in food availability may explain the lower frugivore biomass in humid forests as opposed to dry forests (Ganzhorn et al. 1999b; Donati 2002).

CONCLUSION

While the littoral forest can be considered aseasonal regarding climate, there are however consistent year to year patterns in flowering and fruiting. Intra-annual differences occur in phenophases leading to periods of abundance and scarcity. Typically for the littoral forest and other Malagasy humid forests in general but very different from dry Malagasy forests, is the inter-correlation of all phenophases that peak almost simultaneously in the wettest period (November-February). Irradiance seems to be the most important abiotic factor in triggering phenophases, due to its importance in photosynthetic processes especially at this extreme southern latitude for a tropical wet forest. Fruit trails and phenological transects have shown to be complementary methods by unravelling fruiting patterns of different life forms and different sub-samples of all present plant species, including both fruit data on canopy and ground level.

ACKNOWLEDGEMENTS

This study was carried out under the Accord de Collaboration between Department of Animal Biology and Department of Anthropology of the University of Antananarivo, the Institute of Zoology of Hamburg University and QIT Madagascar Minerals (QMM). Our thanks go out to QMM for providing logistics and infrastructure at the campsite. In particular we acknowledge Manon Vincelette, Jean-Baptiste Ramanamanjato, Laurent Randrihasipara of the QMM Environmental and Conservation Team for following up phenology and climatic data (QMM unpubl. data) at the site after we left and sharing these data with us. Many thanks as well to Give Sambo and Dauphin Mbola, the two local field assistants who helped with the collection of phenology and fruit trail data. The first author is supported by a grant of the Belgian Fund for Scientific Research, Flanders (FWO). We further thank the Flemish Government for structural support to the Centre for Research and Conservation (CRC) of the Royal Zoological Society of Antwerp (RSZA). The second author was supported by a doctoral grant of the Italian Ministry for Scientific Research (MURST) and the University of Pisa. Many thanks as well to Jörg Ganzhorn, Linda Van Elsacker and Silvana Borgognini Tarli for their support during our research.

Appendix I. Overview of plant species included in both phenological transect (PH) and fruit trail (FT) with indication of life form (LT: large tree, ST: small tree or shrub, V: vine, E: epiphyte). Family, species and vernacular name are given. For species without vernacular names, codes (x1 or FT1) were given.

Family Name	Species name	Vernacular name	PH	FT	Life form
Anacardiaceae	*Poupartia chapelieri*	sisikandrongo	x	x	LT
	Campnosperma micranteia	roandria	x		LT
	Rhus thouarsii	kangy	x		LT
Annonaceae	*Monanthotaxis* cf. *malacophylla*	vahihazo	x	x	V
	Polyalthia capuronii	menapeka	x		V
	Polyalthia madagascariensis	fotsivavo	x		LT
	Polyalthia sp.1	fotsivavo géante	x	x	LT
Apocynaceae	*Cabucala madagascariensis*	tandrokosy	x		ST
Araliaceae	*Cuphocarpus aculeatus*	voatsilana marécage	x	x	LT
	Schefflera rainaliana	voatsilana	x	x	LT
Arecaceae	*Dypsis fibrosa*	boakandambo	x	x	ST
	Dypsis prestoniana	boakabe	x	x	LT
	Dypsis scottiana	raosy		x	ST
Asteraceae	*Senecio* sp.	witte pluisjes		x	ST
Bignoniaceae	*Phyllarthron ilicifolium*	zahambe		x	LT
	Ophiocolea delphinensis	akondronala	x		ST
Burseraceae	*Canarium boivinii*	ramy	x	x	LT
Canellaceae	*Cinnamosma madagascariensis*	vahabatra 3eM		x	LT
Capparaceae	*Crataeva obovata*	belataka	x	x	ST
	Physena madagascariensis	FT 85		x	ST
Celastraceae	*Mystroxylon aethiopicum*	voavoantatsimo	x	x	ST
	Elaeodendron sp.	aramboazo	x		LT
	Polycardia phyllanthoides	fandrianakanga		x	LT
Clusiaceae	*Garcinia chapelieri*	haziny tomate	x		LT
	Garcinia cf/aff. *madagascariensis*	disaky kely	x	x	ST
	Mammea bongo	disaky be	x		LT
	Symphonia fasciculata	haziny voany be	x		LT
	Symphonia sp.	haziny fleur rouge	x	x	LT
	Calophyllum sp.	vitano	x		LT
Combretaceae	*Terminalia fatraea*	katrafa	x	x	LT
Connaraceae	*Agelaea pentagyna*	rehiba vahimainty	x	x	V
Dichapetalaceae	*Dichapetalum* sp.	vahikatepoka		x	V
Dilleniaceae	*Dillenia triquetra*	varikanda	x		LT
Ebenaceae	*Diospyros myriophylla*	forofoka	x		LT
	Diospyros sp.1	hazomainty blanc		x	ST
	Diospyros sp.2	hazomainty	x	x	ST
	Diospyros sp.3	hazomainty kely	x		ST
	Diospyros sp.4	FT 82		x	ST
Elaeocarpaceae	*Elaeocarpus alnifolius*	sanga		x	LT
Ericaceae	*Vaccinium eminense*	tsilantria	x		ST
Erythroxylaceae	*Erythroxylum buxifolium*	fangora sp.1		x	ST
	Erythroxylum nitidilum	fangora sp.2		x	LT
Euphorbiaceae	*Anthostema madagascariensis*	bamby	x		LT
	Blotia leandriana	x225		x	ST
	Blotia mimosoides	fantsikaitra		x	LT

Appendix I Continued

Family Name	Species name	Vernacular name	PH	FT	Life form
Euphorbiaceae	*Euphorbia tetraptera*	famanta		x	ST
	Macaranga perrieri	mocarana	x		LT
	Uapaca ferruginea	voapaky lahy	x	x	LT
	Uapaca littoralis	voapaky vavy	x	x	LT
	Uapaca thouarsii	voapaky vavy ZJ	x		LT
	genus indet.	randramboay		x	ST
Fabaceae	*Cynometra* cf. *cloiselii*	mampay	x	x	LT
	Intsia bijuga	harandrato	x	x	LT
	Phylloxylon xylophylloides	sotro	x	x	LT
Flacourtiaceae	*Bembicia uniflora*	bemalemy	x	x	LT
	Homalium albiflorum	tapinandro[1]		x	LT
	Homalium albiflorum	lapivatra[1]	x		LT
	Homalium louvelianum	ramirisa	x		LT
	Homalium planiflorum	hazofotsy	x	x	ST
	Homalium sp.	marakoditra	x	x	LT
	Scolopia orientalis	zoramena	x	x	LT
Grossulariaceae	*Brexia* sp.	kambatrikambatri	x	x	ST
Hamamelidaceae	*Dicoryphe stipulaceae*	zorala		x	LT
Hippocrataceae	*Salacia madagascariensis*	voatsimatra	x	x	V
Icacinaceae	*Apodytes* sp. nov.	hazomamy an ala	x		LT
Lauraceae	genus indet.	varongy sp2	x		LT
	Beilschmiedia madagascariensis	resonzo	x		LT
	Cryptocarya sp.	tavolohazo	x	x	LT
	Ocotea sp.	varongy be	x		LT
Liliaceae	*Dracaena reflexa* var. *nervosa*	falinandrobe[1]	x	x	ST
	Dracaena reflexa var. *nervosa*	falinandrokely[1]		x	ST
	Dracaena reflexa var. *nervosa*	tavolobotroka[1]		x	ST
Loranthaceae	*Bakerella ambongoensis*	velomihanto sp1	x	x	E
	Bakerella sp.	velomihanto sp2		x	E
Loganiaceae	*Anthocleista longifolia*	lendemilahy	x	x	ST
Menispermaceae	*Burasaia madagascariensis*	faritsaty	x	x	ST
Monimiaceae	*Tambourissa purpurea*	ambora[1]	x	x	ST
	Tambourissa purpurea	amboralahy[1]		x	ST
Moraceae	*Trilepisium madagascariense*	beronono	x	x	LT
Myristicaceae	*Brochoneura madagascariensis*	mafotra	x	x	LT
Myrsinaceae	*Monoporus spathulatus*	FT 88		x	V
Myrtaceae	*Eugenia cloiselii*	ropasy sp.1	x	x	LT
	Eugenia sp.1	ropasy sp.2	x		LT
	Eugenia sp.2	ropoaky	x	x	LT
	Syzygium emirnense	rotry sosimaro	x		ST
	Syzygium sp.1	rotry ala	x		LT
	Syzygium sp.2	rotry mena	x	x	LT
Ochnaceae	*Campylospermum obtusifolium*	hazombato	x		ST
	Diporidium ciliatum	sakambolava	x	x	ST
Oleaceae	*Jasminum kitchingii*	vahifotsy kely		x	V
	Noronhia cf. *lanceolata*	hazondraotry		x	ST
	Noronhia ovalifolia	zorafotsy	x	x	LT

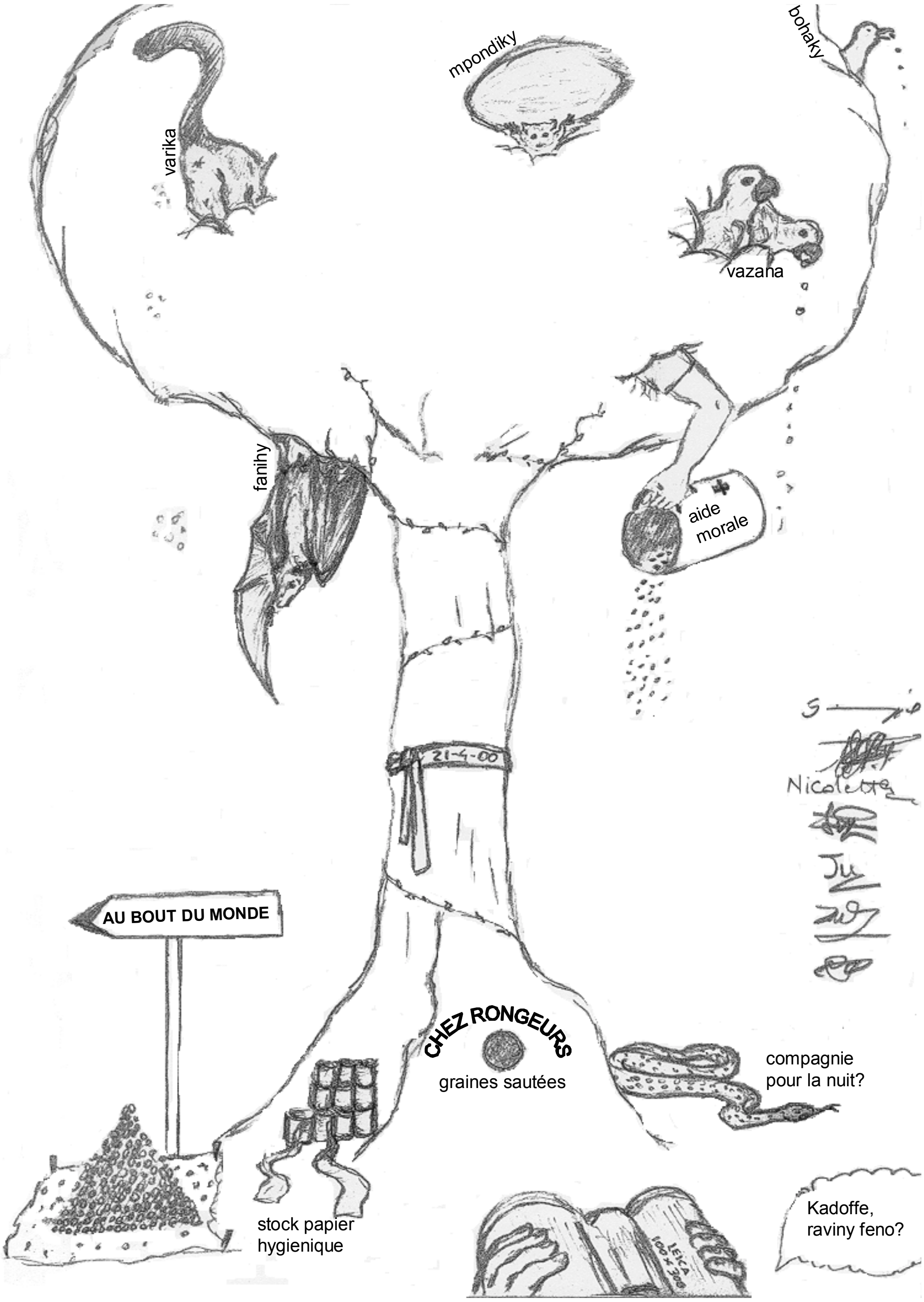
Appendix I Continued

Family Name	Species name	Vernacular name	PH	FT	Life form
Oleaceae	*Noronhia* sp.1	belavenoka	x	x	LT
	Olea sp.	vahabatra	x	x	LT
Pandanaceae	*Pandanus* aff. *longistylus*	fandranabo	x		LT
	Pandanus dauphinensis	vakoanala	x		ST
	Pandanus rollotii	fandranabotonboky	x	x	LT
Pittosporaceae	*Pittosporum polyspermum*	x202		x	ST
Rhopalocarpaceae	*Rhopalocarpus coriaceus*	tsilavimbinanto	x	x	LT
Rubiaceae	*Canthium variistipula*	fantsikaitramainty	x	x	ST
	Cremocarpon lantzii	x220		x	ST
	Ixora sp.	x203		x	ST
	Morinda cf. *umbellata*	vahilengo		x	V
	Peponidium sp.	fantsikaidroka		x	LT
	Mapouria aegialodes	x210a		x	ST
	Psychotria sp.	tanatananala	x		ST
	Mapouria sp.	x210		x	ST
	Pyrostria sp.	fantsikaitrafotsy	x		LT
	Rothmannia mandenensis	taholagna	x	x	LT
	Saldinia littoralis	mangavoa		x	ST
	Tarenna thouarsiana	FT 62		x	ST
	Tricalysia cf. *cryptocalyx*	hazongalala	x	x	ST
	Tricalysia sp.	kotofotsy		x	ST
Rutaceae	*Vepris eliottii*	ampoly[1]	x	x	LT
	Vepris eliottii	ampolylahy[1]	x	x	LT
Sapindaceae	*Macphersonia radlkoferi*	sanirambaza		x	LT
	Filicium decipiens	lahinvoatsilana	x		LT
	Plagioscyphus jumellei	ambirimbarika pionair	x		ST
	Tina thouarsiana	sagnirambavy	x	x	LT
	Tinopsis conjugata	sagnira sp.3	x		LT
Sapotaceae	*Donella delphinensis*	hazomteraka	x		LT
	Fauchera hexandra	natohetiki	x	x	LT
	Sideroxylon beguei var. *sabouraui*	ambirimbarika	x	x	LT
Sarcolaenaceae	*Leptolaena* sp.	fotonbavy	x	x	LT
	Sarcolaena multiflora	meramaintso	x	x	LT
	Schizolaena elongata	fotondahy	x	x	LT
Smilaceae	*Smilax anceps*	fandrikatani		x	V
Sphaerosepalaceae	*Podocarpus madagascariensis*	harambilo	x		LT
Taccaceae	*Tacca leontopetaloides*	tavolo		x	H
Theaceae	*Asteropeia micraster*	fanolamena	x	x	LT
	Asteropeia multiflora	fanolafotsy	x	x	LT
Ulmaceae	*Trema orientalis*	andrarezona	x		LT
Verbenaceae	*Clerodendrum* sp.	nofotrako marecage	x	x	LT
Violaceae	*Rinorea pauciflora*	memboloa		x	ST
?	?	FT 100		x	ST
?	?	liane fleur jaune		x	V
?	?	FT 112		x	ST
?	?	FT 20		x	ST
?	?	FT 49		x	ST

Appendix I Continued

Family Name	Species name	Vernacular name	PH	FT	Life form
?	?	FT 51		x	ST
?	?	FT 8		x	ST
?	?	FT 80		x	ST
?	?	FT 91		x	ST
?	?	FT 93		x	LT
?	?	FT 95		x	ST
?	?	FT 96		x	ST
?	?	menahi		x	ST
?	?	vahifotsy be	x	x	V

[1] as indicated by their vernacular name certain plant species correspond to the same scientific name. They could represent different ecotypes of the same species or different species that have no taxonomic names yet. As this is difficult to affirm at the moment we preferred including all plant species as separate units throughout this paper.


mpondiky
bohaky
varika
vazana
fanihy
aide morale
21-4-00
Nicoletta
Ju
AU BOUT DU MONDE
CHEZ RONGEURS
graines sautées
compagnie pour la nuit?
stock papier hygienique
LEICA 100 x 300
Kadoffe, raviny feno?

‘Ataovy toy ny voankazo an ala,
ka ny mamy no atelemo, ny mangidy aloavy’

Do as with the fruits of the forest,
the sweet ones you swallow, the bitter ones you spit out

Malagasy proverb
Drawing © Giuseppe Donati 2000

2

Tree dispersal strategies in the littoral forest of Sainte Luce (south-east Madagascar)

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OECOLOGIA (SUBMITTED)

ABSTRACT

Zoochory is the most common mode of seed dispersal for the majority of plant species in the tropics. Based on the assumption of tight plant-animal interactions several hypotheses have been developed to investigate the origin of life history traits of plant diaspores and their dispersers, such as species-specific co-evolution, the low-high investment model (low investment in single fruits but massive fruiting to attract many different frugivores versus high investment in single fruits and fruit production for extended periods to provide food for a few specialised frugivores), and the evolution of dispersal syndromes which represent plant adaptations to larger taxonomic groups of dispersers. To test these hypotheses the frugi-granivorous vertebrate consumers and dispersal strategies of 34 tree species were determined in the littoral forest of Sainte Luce (SE-Madagascar) with the help of fruit traps and tree watches. The impact of fruit consumers on the seeds was determined based on detailed behavioural observations. Phenological, morphological and biochemical fruit traits from tree species were measured to look for co-variation with different types of dispersal. There was no evidence for species-specific co-evolution nor any support for the low/high investment model. However diaspores dispersed by birds, mammals or both groups (mixed dispersed tree species) differ in the size of their fruits and seeds, fruit shape, and seed number, but not in biochemical traits. Five large-seeded tree species seem to depend critically on the largest lemur, *Eulemur fulvus collaris*, for seed dispersal and recruitment. However, this does not represent a case of tight species-specific co-evolution. It rather seems to be a consequence of the extinction of larger frugivorous birds and lemurs which also might have fed on these large fruits. It seems that the species-poor guild of frugivores in Madagascar and in the littoral forest in particular did not allow the evolution of specialised dispersal strategies. In particular, the low species diversity of avian frugivores resulted in significantly few bird fruits compared to other sites.

Introduction

In tropical forests, active transport of seeds by animals (zoochory) is the most common means of seed dispersal, involving more than 75% of all plant species (McKey 1975; Charles-Dominique et al. 1981; Howe and Smallwood 1982; Janson 1983; Gautier-Hion et al. 1985; Jordano 1992). Seed dispersal away from the parent tree seems essential for the successful establishment of seedlings (e.g. Janzen 1970; Connell 1971; Howe and Smallwood 1982; Terborgh et al. 2001). Therefore attracting frugivores is crucial for a plant in order to ensure reproduction.

Several hypotheses have been proposed to explain the evolution of zoochory. First, under the assumption that the evolution of life history traits of plants, their diaspores and their consumers are mutually dependent, the most restrictive hypothesis assumes very tight co-evolutionary relationships between one single fruit and frugivore species. So far no evidence has been found in support of this hypothesis (Howe and Smallwood 1982; Herrera 1984; Howe 1984; Gautier-Hion et al. 1985; Fisher and Chapman 1993; Chapman 1995; Erikkson and Ehrlen 1998; Lambert and Garber 1998). Secondly, from the plants' point of view McKey (1975) postulated different patterns of resource investment in plants that rely on multiple versus specialised seed dispersers. According to this model low investment plants (generalists) invest little in single fruits but display large fruit crops during a short fruiting period to attract a large variety of opportunistic frugivores. In contrast, the high investment plants (specialists) have fruit pulp with higher nutrient content, a more limited fruit production and extended fruiting seasons that attract few specialists (Howe 1979). Again not much support could be found for this idea so far (Dowsett-Lemaire 1988; Wenny 2000; Wütherlich et al. 2001; but see Wheelwright 1986). Thirdly the hypothesis of dispersal syndromes postulates broad morphological adaptations of fruit traits associated with different consumer taxa, mostly distinguishing diaspores dispersed by birds, mammals or both groups (mixed fruits). This model emphasizes the taxonomy and phylogenetic heritage of dispersers with their associated sensory capacities (Van der Pijl 1969; Janson 1983; Knight and Siegfried 1983; Gautier-Hion et al. 1985; Martinez del Rio 1994; Corlett 1996; Kalko et al. 1996; Korine et al. 2000; Pizo 2002; Voigt 2001).

The forests of Madagascar provide good opportunities to test the above hypotheses. There is a high level of floral and faunal endemism in Madagascar with 96% endemics among the tree species (Schatz 2001), more than 50% of its birds (Langrand 1990) and 90% of its mammals (Goodman et al. in press). This results in communities with an evolutionary history, which is largely independent from the communities for which the hypotheses have been developed and tested and therefore allows independent tests for these hypotheses. For this, we selected 34 different tree species of the evergreen littoral forest of south-eastern Madagascar in order to answer the following questions;

1. Which frugivores feed on the different fruiting tree species and what is their impact on the seeds?
2. Is there evidence for tight species-specific co-evolution?
3. Can tree species be categorized as low or high investment species according the McKey's hypothesis?
4. Are there trees which rely on certain taxonomic groups for dispersal and if so: do fruits with different dispersal strategies vary significantly in their morphological and biochemical attributes?

METHODS

Study site and the frugivorous guild

The littoral forest of Sainte Luce (24º45'S 47º11'E) is located in south-eastern Madagascar, 50km north of Fort-Dauphin. The first author collected data between November 1999 and February 2001 in a 377-ha forest fragment, called 'S9'. Average annual rainfall is 2,690mm. Mean monthly temperature is about 23°C and ranges from 12°C to 33°C. For a more detailed description of the study site we refer to Bollen et al. (in press, Chapter 4). At Sainte Luce, the trophical guild of frugivores consists of 13 strictly or partially frugivorous vertebrate species (Table 1).

Focal tree species

For this study 34 tree species, which are thought to be important food sources for certain animal species were chosen (App. I). Fruit traps were installed under 29 tree species and tree watches were carried out for 27 tree species. Herbarium specimens of all taxa were collected. Vernacular '*antanosy'* names were provided by local research assistants. Scientific names were obtained after determination of voucher specimens at the national herbaria of Antananarivo with the help of botanists from Missouri Botanical Garden (App. I). Voucher specimens were deposited at the Missouri Botanical Garden of Antananarivo (Madagascar).

Fruit traps

In order to estimate relative fruit production and consumption, fruit traps were placed on the ground under the tree in the zone of fruit fall (following Goodman et al. 1997a). In total 29 tree species were studied, fruit traps being placed under one individual per tree species. Each fruit trap was 1m² in size and was made out of black plastic sheeting. Fruit traps were blocked at the sides with upturned edges to avoid loss of the content due to rain washing. The number of fruit traps per individual tree depended on the crown size, on average being one trap per 3.2m² (±1.6 SD) of the crown area. Total fruit crop size was obtained by extrapolating the data from the area sampled by the traps to the total crown area. Fruit traps were inspected and emptied every other morning between 06h00-10h00 throughout the fruiting period. Ideally, fruit traps were installed before fruit ripening had started and were removed at the end of the fruit production. For five tree species, fruit traps were installed shortly after the onset of fruiting, due to a delay in noticing that a species was fruiting (Table 2).

Analyses of the contents of each fruit trap involved counting and checking the condition of fruits and seeds, which were coded using the following categories;

Neutral effect:	intact fruits (unripe, ripe or rotten)
	pulp partially eaten, intact seeds
	pulp completely consumed, intact seeds
Dispersal:	empty fruit husks, pulp eaten and seeds swallowed
Predation:	partially eaten seeds or empty seed husks with gnaw marks

Percentages of all categories were calculated per tree species. Additionally, defecated seeds from the focal tree or other tree species present in the fruit traps were scored as well. Several animals leave distinctive feeding marks on the discarded fruit and seed remains. Therefore it was often possible to determine the consumer species or at least the larger taxonomic group.

Tree watches

Observations on feeding assemblages of frugivores were carried out during the peak fruiting period of 27 tree species. These so-called 'tree watches' (Chapman and Chapman 1996; Scharfe and Schlund 1996; Goodman et al. 1997a; Böhning-Gaese et al. 1999) consisted of intermittent 36h observations (two cycles 06h00-00h00) of one

Table 1. The frugivore guild at Sainte Luce with indication of their diet (F: frugivorous, G: granivorous, O: omnivorous), their activity budget (D: diurnal, N: nocturnal, C: cathemeral), feeding height (A: arboreal, T: terrestrial), body mass (in g) and length (in cm) and their potential role as seed dispersers (D) or seed predators (P) in this ecosystem.

Family	Scientific name	English name	Diet	Active	Feeding height	Body[1] mass	Body[1,2] Length	Role[3]
AVES								
Columbidae	*Treron australis*	Malagasy Green Pigeon	F	D	A	215	32	D
	Alectroenas madagascariensis	Malagasy Blue Pigeon	F	D	A	ND	28	D
	Streptopelia picturata	Madagascar Turtle Dove	G	D	T	190	28	P
Pycnonotidae	*Hypsipetes madagascariensis*	Madagascar Bulbul	F	D	A	45	24	D
Psittacidae	*Coracopsis nigra*	Lesser Vasa Parrot	G	D	A	218	35	P
	Coracopsis vasa	Greater Vasa Parrot	G	D	A	ND	50	P
MAMMALIA								
RODENTIA								
Muridae	*Rattus rattus*	Black Rat	O	N	AT	100	15-23	P
Nesomyinae	*Eliurus webbi*	Webb's Tuft-Tailed Rat	O	N	AT	88	10-16	P
CHIROPTERA								
Megachiroptera								
Pteropodidae	*Pteropus rufus*	Madagascar Flying Fox	F	N	A	500-750	23-27	D
PRIMATES								
Lemuridae	*Eulemur fulvus collaris*	Collared Brown Lemur	F	C	A	2000-2300	40-47	D
Cheirogaleidae	*Microcebus rufus*	Brown Mouse Lemur	O	N	A	42	12.5	D
	Cheirogaleus major	Greater Dwarf Lemur	O	N	A	443	25	D
	Cheirogaleus medius	Fat-tailed Dwarf Lemur	O	N	A	119-282	20	D

[1] Data from Langrand (1990), Fietz and Ganzhorn (1999), Garbutt (1999), Ganzhorn et al. (1999a), Donati (2002).

[2] Body length (BL) is total length for birds and bats but head/body length for lemurs and rodents.

[3] Data from Goodman et al. (1997b); Ganzhorn et al. (1999a); Bollen and Van Elsacker (2002a); Donati (2002); Bollen (unpubl. data).

individual tree per species. Six species were observed for less than 36 hours due to a very short fruiting period or heavy rains during the fruiting peak (Table 3). Observations were made within 10m of the focal tree, which allowed an unobstructed view of approximately 70-100% of the canopy. During the day binoculars (Leica 10x42) were used while at night a headlight (Petzl), which reflects the *tapetum lucidum* of the eyes of lemurs, flying foxes and rats, aided observations. Additionally, if moonlight conditions were favourable, night goggles (Litton Electron Devices) were used as well. Tree watches provided data on the animal species feeding in the tree and their handling and feeding behaviour. This allowed us to classify them as seed-dispersers, seed droppers or fruit pulp consumers and seed predators. This behaviour could be easily observed during the day but not always at night when one needed to rely on evidence such as falling fruit husks, fruits or seeds. Species visiting the tree without eating were not considered in the analyses.

According to the model of dispersal syndromes, tree and fruit characteristics evolved in response to the community of frugivores and their taxonomic affinities. Both literature and detailed observations during tree watches allowed us to classify the different consumer species as seed dispersers, fruit-pulp consumers and/or seed predators (Goodman et al. 1997a; Ganzhorn et al. 1999a; Bollen and Van Elsacker 2002a, Chapter 3, 3a; Donati 2002). Based on this knowledge, the following dispersal groups were distinguished;

-mixed fruits: eaten by both birds and mammals
-bird-fruits: eaten by fruit pigeons and/or bulbul
-mammal-fruits: eaten by lemurs and flying foxes
-fruits eaten only by *Eulemur fulvus collaris*

Morphological and biochemical characterisation

The number of seeds per fruit were counted, fruits and seeds were weighed fresh using spring or electronic balances and measured using callipers with 0.01g and 0.01mm precision, respectively. In addition the ratio between length and width (L/W) was used as an index of fruit shape (Pizo 2002). Most fruits are typically zoochorous, including soft and juicy drupes or berries.

Ripe fruits were dried in the sun or in a drying oven, ground to pass through a 2mm sieve, and dried again overnight at 50-60°C prior to analyses. Lipids were determined by the Soxleth method. Total nitrogen (N) was determined using the Kjeldahl procedure. Multiplying N by 6.25 converted total nitrogen to crude protein. However it should be noted that a conversion factor of 6.25 overestimates the protein actually available for frugivores in some fruits (Levey et al. 2000). Soluble carbohydrates and procyanidin (condensed) tannins were extracted with 50% methanol. Concentrations of soluble sugar were determined as the equivalent of galactose after acid hydrolization of the 50% methanol extract. This measurement correlates well with concentrations obtained with enzymatic analyses of glucose, fructose and galactose (Ganzhorn and Tomaschewski unpubl. data). Concentrations of procyanidin tannin were measured as equivalents of quebracho tannin (Oates et al. 1977; Porter and Hemingway 1990). Samples were analysed for acid detergent fibre (ADF) (Goering and Van Soest 1970; Van Soest 1994) modified according to the instructions for use in an ANKOM FIBER ANALYZER. Biochemical analyses were carried out at the Institute of Zoology, Department of Ecology and Conservation (University Hamburg).

Statistical analyses

To visualise dispersal types and to test for fruit trait co-variation consistent with these dispersal types, two principal component analyses (PCA) were conducted using morphological and biochemical fruit trait data of 29 tree species. As data were not normally distributed, morphological and biochemical traits were log-transformed prior to analyses. Factor loadings were used to determine the strength of association of each fruit trait with each principal component. Mann Whitney U tests, Spearman rank correlations and Kruskal Wallis were carried out according to Siegel (1956) with the statistical software SAS for Windows.

RESULTS

Fruit traps

Considering fruit trap analyses, there was substantial variation in the three main categories (neutral, dispersal, predation) among different tree species (Table 2, Fig. 1). Based on all fruit trap data, a substantial proportion (median: 70%, quartiles 39-98%) of seeds remained under the parent plant; including unripe, ripe and rotten fruits (47%) that had not been eaten as well as partially eaten fruits that still contained their seed (13%) or intact seeds (9%) that were dropped after the fruit pulp had been swallowed (Table 2). In all these cases the animals had a neutral effect on the seeds, since they were neither dispersed nor predated. For 18 species the number of fruits or seeds dropped under the parent plant was higher than 50% (Fig. 1). Evidence of seed dispersal involved empty fruit husks (median 9%, quartiles 0-61%) that were discarded after consumers swallowed the fruit pulp and seeds. This proportion was relatively large (>50%) for only eight tree species. The proportion of predated seeds was low (median 2%, quartiles 0-5%) and exceeded 5% for only six tree species (Table 2, Fig. 1).

Faecal droppings, collected in fruit traps, provided complementary but non-quantitative information on seed dispersal. Ninety percent of all faecal samples collected under focal trees were found to contain seeds from other tree species, thus indicating seed dispersal. Of the 29 tree species sampled, seeds of 13 species were found in droppings of *Eulemur fulvus collaris* and one species in droppings of *Alectroenas madagascariensis*. For the majority of these species (9 out of 14) hardly any empty fruit husks were found in the fruit traps as proof of seed dispersal (0-3%) (Table 2) because dispersed seeds involve completely swallowed fruits, which are not accounted for in this method. For the other remaining 5 species, more empty fruit husks (42-89%) were retrieved in the fruit traps, indicating that, here, consumers most often scooped out and swallowed fruit pulp and seeds and discarded the remaining fraction.

Fourteen plant species had the majority of their fruits eaten. Non-eaten fruits were most abundant in eight species and equal percentages of eaten and non-eaten fruits occur for 7 species (Table 2). Identification of the consumers was based on faecal droppings or feeding marks. On the species level, faecal droppings of *E. f. collaris* and *A. madagascariensis* are obviously distinguishable and recognizable by size and consistency. The bill mark is typical for both *Coracopsis* spp. Stripped off pulp parts are typical marks of *Pteropus rufus*' sharp teeth. Lemur tooth marks can be species-specific based on their size, but were most often assigned to larger taxonomic group of nocturnal lemurs (involving *Cheirogaleus* spp. and *Microcebus rufus*) or lemurs (involving all four lemur species) (App. II). Rodents leave typical gnawing marks, but these do not always allow identification to species-level. The other frugivorous bird species most often swallow the fruit entirely and thus leave no identifiable marks.

Table 2. Percentages of the different categories used in fruit trap analyses, involving neutral or dropped, dispersed and predated seeds, eaten and non-eaten fruits are given. For these different categories highest percentages are given in bold. An asterisk indicates non-quantitative dispersal evidence by faecal dropping, which leads to underestimation of this category.
(P and S part. Eaten: pulp and seeds partially eaten, FS: faecal seeds,
Am: *Alectroenas madagascariensis,* Efc: *Eulemur fulvus collaris).*

Impact on seed:	Neutral effect				Dispersal		Predation		
Category:	Intact fruits	P part eaten[1]	Intact seeds[2]	Sum	Empty husks	FS	S part eaten	Eaten	Not eaten
Apodytes dimidiata [3]	21	66	13	**100**	0		0	**79**	21
Brexia sp.	19	2	4	25	**69**		**7**	**81**	19
Brochoneura acumineata	14		1	15	**76**		**10**	**86**	14
Burasaia madagascariensis	8	24	24	**56**	9		**36**	**93**	8
Canarium boivinii	54	16	20	**90**	8		2	46	54
Canthium variistipula [3]	23	5	72	**100**	0*	Efc	0	**77**	24
Cinnamosma madagascariensis	5	3	31	39	**61**		0	**95**	5
Diospyros sp.[3]	11	10	32	**53**	42*	Efc	5	**89**	11
Dypsis prestoniana	53	15	30	**98**	0*	Am	2	47	54
Elaeocarpus alnifolius	54	36	9	**99**	0*	Efc	1	46	55
Eugenia cloiselii	67	24	9	**100**	0*	Efc	0	33	**67**
Eugenia sp.	82	6	12	**100**	0*	Efc	0	18	**82**
Garcinia cf. *madagascariensis*	63		7	**70**	28		3	37	**63**
Leptolaena multiflora	95	2		**97**	3*	Efc	0	5	**95**
Olea sp.	79	18	1	**98**	0*	Efc	3	21	**79**
Poupartia chapelieri	4	1	24	29	**69***	Efc	2	**96**	4
Rothmannia mandenensis			31	31	**69**		0	**100**	0
Sarcolaena multiflora	11			11	**89***	Efc	1	**89**	11
Schizolaena elongata	78	14	1	**93**	3*	Efc	4	22	**79**
Scolopia orientalis	35	12	2	49	45		**7**	**65**	35
Syzygium sp.1	54	21	2	**77**	23		1	47	54
Syzygium sp.2 [3]	58	20	21	**99**	0*	Efc	1	42	**58**
Terminalia fatraea	49	34	8	**91**	9		1	51	49
Tina thouarsiana	40	3	2	45	1		**54**	**60**	40
Uapaca ferruginea	49			49	50*	Efc	2	52	49
Uapaca littoralis	45	1	6	**52**	48*	Efc	1	55	46
Uapaca thouarsii	64		18	**82**	2		**16**	36	**64**
Vepris eliotii	21	7		28	**67**		5	**79**	21
Vepris fitoravina	10		5	15	**85**		0	**90**	10
median	47	13	9	70	9		2	55	46
quartiles	18-59	3-21	9-24	39-98	0-61		0-5	42-86	14-58

[1] This category refers to fruits of which the pulp is partially eaten, but intact seeds remain.

[2] This category refers to fruits of which all pulp and husk are eaten, but intact seeds were dropped.

[3] For these five tree species fruit traps were installed shortly after the onset of fruiting, due to a delay in noticing that this species was fruiting.

Overall fruit trap data documented 77 plant-animal interactions of which the majority (n=63) could be identified on feeding marks alone. Additional interactions (n=14) were revealed through analyses of faecal samples. For seven interactions, faecal samples confirmed data from feeding marks. Of all interactions, 65% (n=50) could be assigned to a single consumer species, while 35% could only be assigned to a larger taxonomic group, such as lemurs in general (n=9), nocturnal lemurs (n=10) or rodents (n=8).

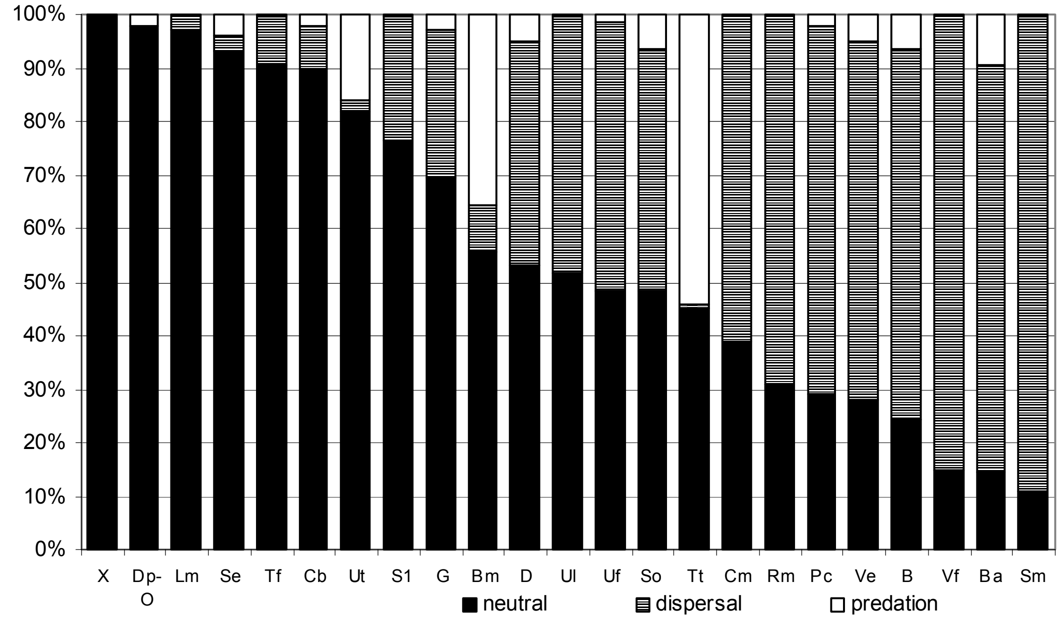


Fig 1. Indication of percentages of different categories of seed dispersal, predation, and neutral seed dropping per plant species. X includes six plant species being Cv, Ad, Ec, E, Ea, S2. For abbreviations of tree species, see Appendix I.

Tree watches

Tree watches were carried out for 27 species, for a total of 928 observation hours (median of 36h/species) during 107 observation days (median 6 days/sp., range 3-10 days/sp.) at the peak of the fruiting periods (Fig. 2). Observational data on the feeding behaviour revealed whether species had a neutral, positive or negative impact on the seeds. For *Coracopsis nigra, Eliurus webbi* and *Rattus rattus* the destruction of seeds is very clear. *Streptopelia picturata* feeds on seeds on the ground and is likely a seed predator but detailed feeding observations of this very shy dove were not possible. The lemur and flying fox species can act as seed dispersers but often also drop seeds under the parent plant during fruit handling or after swallowing fruit pulp and hence have a neutral effect on seeds. *Hypsipetes madagascariensis, Treron australis* and *Alectroenas madagascariensis* act as seed dispersers swallowing all fruits entirely (Bollen et al., Chapter 3).

If we consider all combinations of consumer-plant species interactions (n=100) of the plant species that were included in both fruit trap analyses and tree watches, most of these (n=62) were confirmed by both tree watches and fruit trap analyses, even if some of the fruit trap data only referred to the larger taxonomic group (App II). In general, tree watches further refined the fruit trap data to species level but also added 24 new consumer-plant interactions to the list. Fruit trap data detected 14 interactions that were not confirmed by tree watches and these involved mainly shy consumer species that were difficult to observe. In Appendix II, twelve tree species were not considered, as data on these species had not been sampled by both fruit traps and tree watches.

Data on general phenology of ripe fruits (Bollen and Donati, Chapter 1) are presented in Figure 2 to indicate when the fruiting peak of the different focal tree species occurred and how this related to the overall fruit availability of canopy tree species in the littoral forest. The number of fruit tree species selected each month more or less corresponds with the monthly fruiting diversity throughout the year 2000.

Dispersal strategies

It is difficult to actually 'test' co-evolution but this paradigm is based on tight interactions between one single fruit and disperser species. In this respect there are five plant species that are exclusively dispersed by *Eulemur fulvus collaris*, namely *Canarium boivinii* (ramy)*, Diospyros* sp. (hazomainty), *Eugenium* sp. (ropasy sp. 2), *Rothmannia mandenensis* (taholagna)*, Cinnamosma madagascariensis* var. *namoronensis* (vahabatra 3eM). These fruits were significantly heavier (fruit weight: Z=3.26, P=0.0011) and longer (fruit length: Z=3.38; P=0.0007) than the other fruits. No significant difference could be found for any of the other morphological and biochemical traits.

According to McKey's (1975) model, high investment trees have small crop size, long fruiting period and few seed dispersers, whereas the opposite is valid for low investment trees. However no significant correlations could be found among these traits (fruiting period-crop size: r_s=0.18, P=0.41; fruiting period-number seed dispersers: r_s=-0.08, P=0.70; crop size-number of seed dispersers r_s=0.13, P=0.53). Investment was considered to be represented by the concentrations of nutrients such as sugars, lipids and protein. The only significant correlation found was among protein and lipid content (r_s=0.51, P=0.005) and among sugar content and fruiting period (r_s=-0.43, P=0.04). Sugar, lipid and protein content were not correlated with the number of seed dispersers as the model predicts. Any division in low and high investment trees thus seems to be arbitrary here and does not represent a valid classification to test the McKey model.

Based on data from fruit traps and tree watches, 29 tree species were divided into species in which fruits were eaten and dispersed only by *Eulemur fulvus collaris*, by birds, by mammals or by both groups. This classification into disperser 'syndromes' is based on the taxonomic composition of the consumers (Table 3). Mammal fruits account for 55% (n=16) of all species, while both mixed (n=5) and specialist (n=5) tree species accounted for 17% each and bird dispersed species (n=3) for 11%. First we tested for correlations among all fruit traits, both morphological (n=6) and biochemical (n=5). Using sequential Bonferroni adjustment only four Spearman rank correlations remained significant: fruit weight and fruit length (r_s=0.76, P<0.0001), fruit length and seed mass (r_s=0.59, P=0.0008), fruit length and seed length (r_s=0.72, P<0.001), seed weight and seed length (r_s=0.80, P<0.0001). No significant correlations between morphological and biochemical traits could be found. Therefore two separate principal component analyses (PCA) were conducted to look for fruit trait co-variation in relation to the dispersal syndromes mentioned above. The first two principal components accounted for 81% of the total variation associated with morphological traits (Table 4). The first PCA axis, accounting for 52% of the total variance (eigenvalue=3.11) separates small and light fruits and seeds from larger and heavier fruits and seeds. The second axis (29% of the total variance; eigenvalue=1.75) further differentiates few-seeded and elongated fruits from multi-seeded

Table 3. Morphological and biochemical traits used for PCA analyses. Weights are given in g, length in mm. Fruit shape is fruit length divided by fruit width. Biochemical components are given in percentages dry weight. The disperser type we assigned the plant species is given in the last column. ND: no data available, Efc refers to fruits that are dispersed by *Eulemur fulvus collaris* only.

	Morphological					
Plant species	Number seeds	Fruit weight	Fruit length	Seed weight	Seed length	Fruit shape
Apodytes dimidiata	1	0.45	12.34	0.23	10.61	1.55
Brexia sp.	1	1.57	20.19	0.21	15.12	1.64
Canarium boivinii	1	9.69	31.14	4.17	27.01	1.29
Canthium variistipula	2	0.31	7.80	0.06	6.0	0.85
Cinnamosma madagascariensis	10	6.22	21.99	0.14	8.42	0.98
Dyospiros sp.	5	16.48	30.71	1.89	19.74	0.93
Dypsis prestoniana	1	0.59	14.85	0.34	12.92	1.85
Eugenia cloiselii	1	1.59	13.20	1.26	11.64	0.90
Eugenia sp.	1	4.20	23.81	1.64	15.33	1.33
Leptolaena multiflora	2	0.06	5.60	0.01	2.90	1.19
Ludia antanosarum	6	1.04	12.47	2.98	3.22	1.07
Macaranga perrieri	1	0.04	4.55	0.03	3.06	1.00
Olea sp.	1	0.90	16.98	0.80	15.85	1.56
Polyalthia madagascariensis	1	0.30	12.22	0.12	7.80	1.73
Polyscias sp.	1	0.04	5.03	0.01	3.64	1.31
Poupartia chapelieri	1	0.54	15.43	0.36	15.24	1.52
Rothmannia mandenensis	100	35.33	40.36	0.03	4.35	1.04
Sarcolaena multiflora	5	0.67	14.11	0.01	2.73	1.32
Schizolaena elongata	2	0.77	8.89	0.01	3.05	0.63
Scolopia orientalis	3	0.52	10.52	0.02	3.75	1.11
Syzygium sp.1	1	0.64	10.23	0.64	9.32	0.90
Syzygium sp.2	1	0.54	9.55	0.31	6.56	0.98
Terminalia fatraea	1	0.37	13.19	0.13	8.12	1.91
Trema orientalis	1	0.02	3.24	0.01	2.17	1.00
Uapaca ferruginea	3	1.42	13.59	0.19	10.66	1.03
Uapaca littoralis	3	4.86	23.63	0.52	15.03	1.19
Uapaca thouarsii	3	1.67	12.53	0.22	9.64	0.88
Vepris eliotii	3	0.57	9.86	0.04	6.84	1.05
Vepris fitoravina	2	8.15	8.47	0.16	6.76	1.15

Table 3 Continued

	Biochemical					
Plant species	Fat	Crude protein	Sugar	Tannin	ADF	Disperser type
Apodytes dimidiata	2.85	6.86	64.06	0.00	ND	mixed
Brexia sp.	2.82	2.69	18.23	0.00	18.64	mammal
Canarium boivinii	12.98	9.19	2.17	0.00	38.59	Efc
Canthium variistipula	4.91	5.63	18.18	0.18	20.1	mammal
Cinnamosma madagascariensis	4.96	5.31	26.01	1.74	12.44	Efc
Dyospiros sp.	0.55	3.13	6.53	0.55	27.69	Efc
Dypsis prestoniana	3.04	7.19	15.37	0.16	16.62	mixed
Eugenia cloiselii	2.11	7.31	31.24	0.20	19.59	mammal
Eugenia sp.	1.17	3.94	18.48	0.00	24.8	Efc
Leptolaena multiflora	2.24	5.63	2.95	0.16	35.61	mammal
Ludia antanosarum	1.24	2.88	23.38	0.39	21.71	mammal
Macaranga perrieri	4.51	5.38	2.87	0.00	42.32	bird
Olea sp.	1.69	3.75	38.53	0.14	22.39	mammal
Polyalthia madagascariensis	1.23	5.44	49.44	0.48	22.46	mixed
Polyscias sp.	2.12	4.19	17.8	0.00	46.4	bird
Poupartia chapelieri	0.65	5.69	12.63	0.00	14.97	mammal
Rothmannia mandenensis	0.32	4.63	8.12	0.13	35.68	Efc
Sarcolaena multiflora	3.93	4.25	14.98	0.15	34.47	mammal
Schizolaena elongata	2.22	6.24	26.57	0.00	13.72	mammal
Scolopia orientalis	0.75	3.06	33.38	0.35	12.78	mammal
Syzygium sp.1	7.13	4.38	31.94	0.19	17.88	mammal
Syzygium sp.2	3.36	4.94	43.36	1.07	19.07	mixed
Terminalia fatraea	3.11	7.81	16.40	0.38	35.68	mixed
Trema orientalis	44.67	13.97	3.38	0.15	16.69	bird
Uapaca ferruginea	5.73	5.88	2.26	0.00	51.01	mammal
Uapaca littoralis	2.05	4.44	7.49	0.4	29.93	mammal
Uapaca thouarsii	ND	ND	ND	ND	ND	mammal
Vepris eliotii	14.74	7.89	6.42	0.00	17.21	mammal
Vepris fitoravina	7.37	5.38	19.82	1.23	15.39	mammal

depressed seeds (Fig. 3a). The distribution of the species along the first axis shows slightly more variation than on the second axis where the majority of fruits have few seeds and a spherical or elongated fruit shape. The first axis clearly separates the bird-species from all other species. They have smaller and lighter fruits and seeds. Furthermore the mixed fruits have average or intermediate sizes while the specialist fruits are clearly larger and more variable in shape and seed number. The mammal fruits are intermediate in size, all rather spherical in shape and few-seeded. So the different disperser types can be more or less separated into groups by both axes.

The first two factors of the PCA conducted with the biochemical traits accounted for 73% of the total variance (Table 4). The first axis of the PCA included parameters associated with sugar and crude protein content and explained 43% of the variance (eigenvalue=2.17). The second axis was determined by concentrations of fat and acid detergent fibre and explained 30% of the variance (eigenvalue=1.52; Table 4). When considering the different disperser types no clear patterns arise according to these axes (Fig. 3b). Thus, chemical traits failed to group species according to disperser type.

To support the conclusions of this descriptive analyses, a Kruskal-Wallis test was carried out for the disperser syndromes with the first two principal components of each PCA. For the morphological parameters, the four disperser syndromes showed a significant difference for PCA1 (P=0.001), meaning traits related to fruit size but not for PCA2 (seed number, fruit shape; P=0.31). For the biochemical parameters no significant difference could be found among the disperser syndromes based on PCA1 (P=0.14), involving sugar and crude proteins, nor for PCA2 (P=0.31) involving fat and ADF (Table 4).

Table 4. Principal component analyses for morphological and biochemical traits of 29 tree species. Each factor represents an ordination axis. Kruskal Wallis test results of the disperser type with the principal components given as well (**P<0.01, NS not significant).

Morphological traits	Factors		Biochemical traits	Factors	
	PCA1	PCA2		PCA1	PCA2
Fruit length	**0.53**	0.15	Fat	0.41	**0.54**
Fruit weight	**0.49**	0.32	Crude protein	**0.47**	0.47
Seed length	**0.48**	-0.32	Sugar	**-0.58**	0.16
Seed weight	**0.46**	-0.24	ADF	0.37	**-0.53**
Number of seeds	0.13	**0.68**	Tannin	-0.36	0.40
Fruit shape	0.12	**-0.50**			
Eigenvalue	3.11	1.75	Eigenvalue	2.17	1.52
% variance explained	52%	29%	% variance explained	43%	30%
Cumulative variance	52%	81%	Cumulative variance	43%	73%
Kruskal Wallis (P=)	0.001**	0.05 NS		0.14 NS	0.31 NS

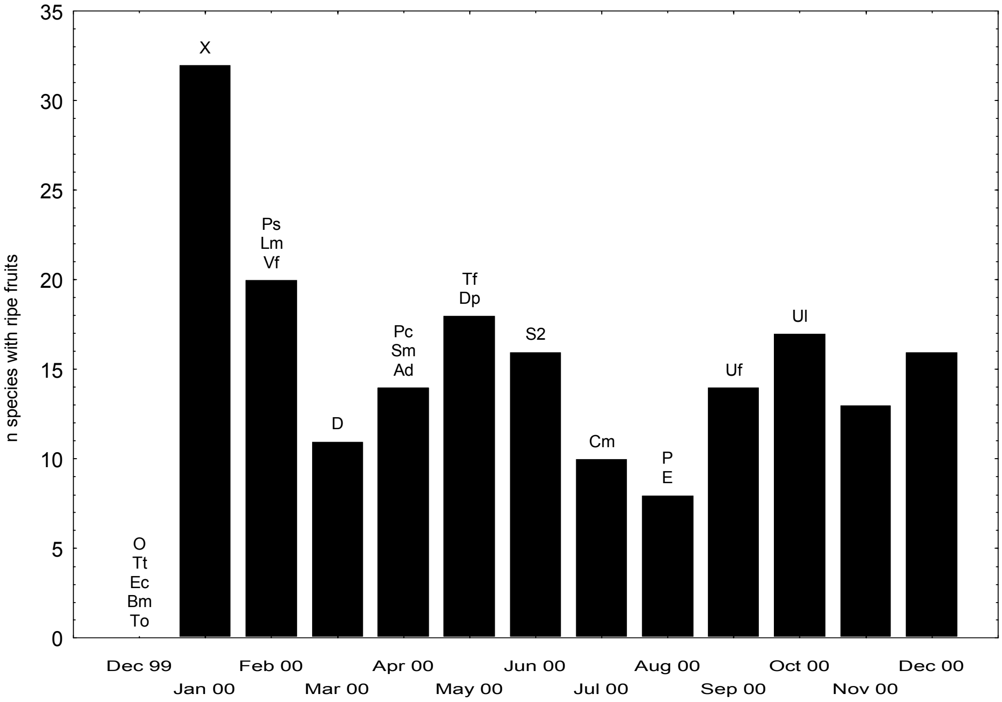


Fig. 2. Number of tree species bearing ripe fruits in 2000. The height of the fruiting peak of the tree species involved in tree watches is indicated as well. X includes the following seven species: So, La, S1, Cb, Mp, Ve, Se according the abbreviations in Appendix I.

DISCUSSION

In the present study we investigated three hypotheses for evidence of co-evolution between life history traits of plants, their diaspores and animal consumers. These were tight, species-specific interactions, different investment patterns of plants in their fruits in relation to the specialization of dispersers and dispersal syndromes as adaptations to taxonomically diverse groups of dispersers with different sensory capabilities (colour vision in birds, olfaction in mammals).

There was no evidence for tight co-evolution between specific tree and consumer species. This is consistent with findings of most studies (Howe and Smallwood 1982; Howe 1984; Gautier-Hion et al. 1985; Herrera 1986; Fisher and Chapman 1993; Chapman 1995; Erikkson and Ehrlen 1998; Lambert and Garber 1998). Most plant species do not depend on one single disperser species. The only possible indication of co-evolution in our study are the five tree species for which *Eulemur fulvus collaris* is the only seed disperser. However, this lemur species is a very opportunistic feeder. A comparative study between the dry deciduous forest of Kirindy and the littoral forest of Sainte Luce (Bollen et al. in press, Chapter 4) confirms the absence of co-evolutionary plant-animal interactions here and shows that this lemur species has a rather high dietary flexibility. However, even though the dietary breath of *E. f. collaris* is quite large, this species is a sequential specialist and as such selects two or three dominant fruit species each month (Donati 2002). *Canarium boivinii* and *Eugenia* sp. make up important

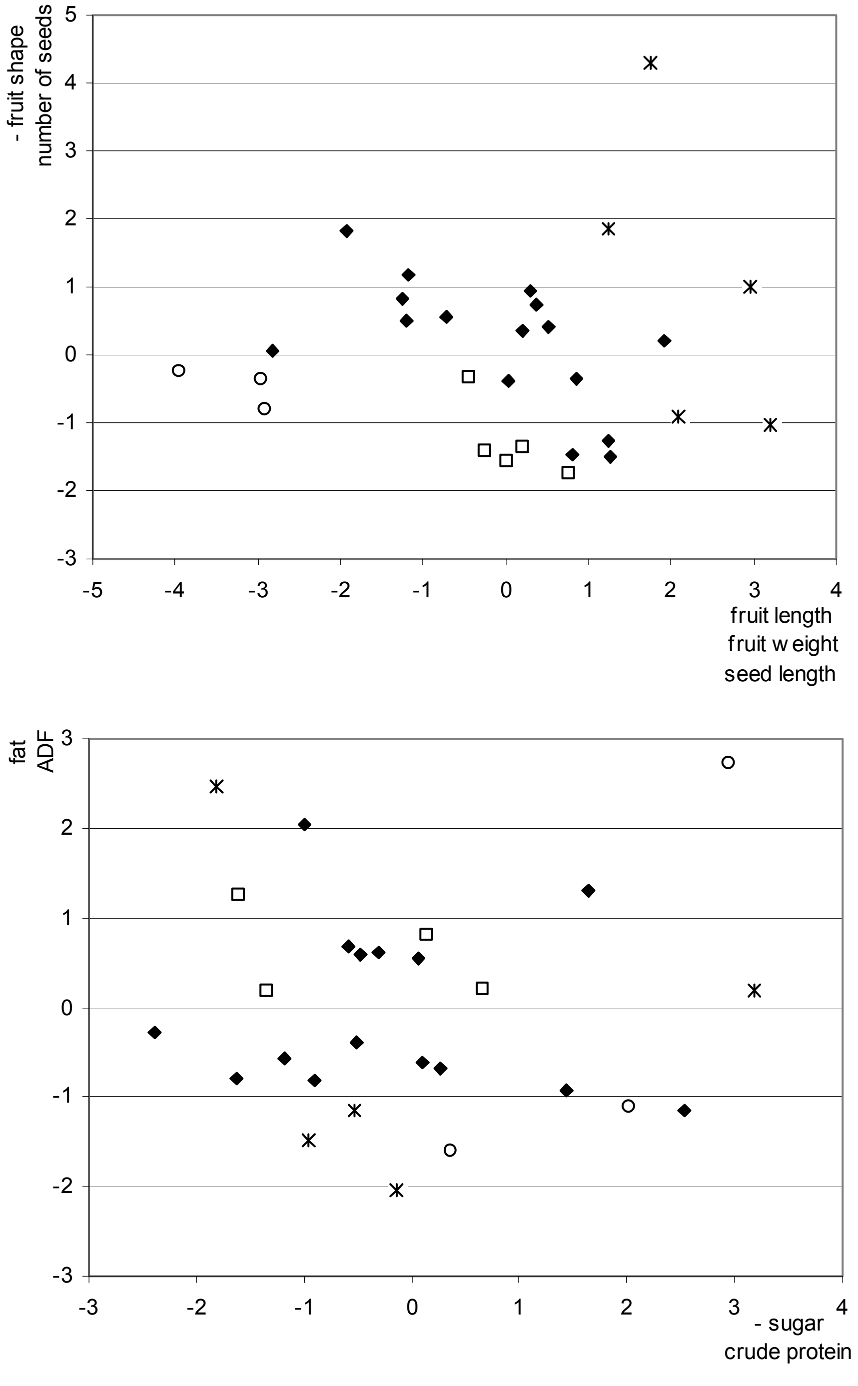


Fig. 3. Ordination plot of the 29 tree species on the first two axes of a prinicipal component analyses of (a) morphological traits and (b) biochemical traits. The asterisks stand for dispersal by E. f. collaris only, the diamonds for mammal species, the open circles for bird species and the open squares for mixed species.

portions of the monthly diet in Sainte Luce, being 23% of the total diet in January 2001 and 12% in July and August 2000 respectively (Donati 2002). The remaining three species are rather marginal dietary items. Nevertheless, co-evolution in the strict sense does not seem to occur here as it is mainly the large fruit size and weight that physically excludes the other frugivores with smaller gape size. *E. f. collaris* is simply the last of the remaining large-bodied lemur species in this littoral forest that can ingest these large-sized seeds, thus matching the situation of brown lemurs in some of Madagascar's dry deciduous forests (Ganzhorn et al. 1999a). Many large-bodied frugivores have disappeared in Madagascar recently and the extinction of at least 16 large lemur species in the Holocene could have included some specialised seed dispersers (Godfrey et al. 1997). All these ‘specialist’ tree species depend critically on *Eulemur fulvus collaris* for seed dispersal and recruitment. Even though these lemurs often drop the large seeds (up to 30mm seed length) under the parent plant, occasionally seeds are swallowed and defecated or dropped some distance away from the parent plant. Thus in terms of conservation these relationships are of crucial importance to conserve the integrity of the littoral forest.

Our attempt to test McKey's model was problematic for a variety of reasons. First, the predictions are qualitative rather than quantitative in nature. ‘Investments’ are difficult to specify and may not be the same at nutrient-poor as at nutrient-rich sites or at sites of differing seasonality. Also, it is problematic to decide whether short but massive fruiting might actually be less expensive for a tree than extended fruiting over longer periods of time. Furthermore, the model was developed for bird-dispersed trees in the Neotropics and its validity largely depends on the composition of the frugivore guild. With as few as eight vertebrate seed dispersers in the littoral forest any ranking or subdivision into specialists and generalists is likely to show too much variation to be detected statistically in descriptive field studies. For the littoral forest of Madagascar, it might be risky for any tree species to depend on only one of these few frugivores and therefore most tree species seem to be characterised by a mixture of general traits from both the low and high investment model. Even though in general there is little evidence for the McKey model (but see Wheelwright 1986), the depauperate frugivore guild of Madagascar might not be suitable to test this concept.

Of the three hypotheses to be tested, the distinction into dispersal syndromes was the only one that could be supported by the present data. Fruits consumed and dispersed by birds and mammals differ distinctly in fruit and seed size and weight, fruit shape and seed number. Moreover, in a similar PCA analysis, Pizo (2002) found the same importance of fruit size, fruit width, seed length (PCA1), fruit shape and seed number (PCA2) which distinguished primate fruits from the bird and mixed fruits. Bird fruits tend to be smaller and more elongated than primate fruits. Our results thus agree with studies on fruit syndromes in other assemblages of plants and animals in different regions (Janson 1983; Knight and Siegfried 1983; Gautier-Hion et al 1985; Pizo 2002; Voigt et al. 2001). The rather uniform results suggest that these syndromes are biologically meaningful. However for biochemical traits no significant differences could found, which corresponds to the findings of Pizo (2002) and Corlett (1996). Even though it has been shown that mammals favour fruits rich in sugars while birds prefer fruits with high lipid and protein content (Snow 1981; Fleming et al. 1987; Debussche and Isenmann 1989; Galetti 2000), the present study only showed a slightly lower sugar and higher protein content in fruits eaten by birds.

On a community level the low number of frugivores seems to have a profound impact on the composition and relative contribution of functional groups to regional ecosystems. Neotropical sites have very speciose frugivorous guilds with more than 50 bird species (Wheelwright 1986; Galetti and Pizo 1996). In contrast Madagascar has very few frugivores and specifically very few frugivorous bird species (Fleming et al. 1987), which seems to be reflected in the striking low number of 'actual' bird fruits. These circumstances obviously narrow down the options for tree species to specialise on certain bird species in Sainte Luce. In a comparison of fruits in deciduous forests of Madagascar and South Africa, Bleher and Böhning-Gaese (2001) and Voigt et al. (2001) showed that the latter has much more bird-dispersed fruits, whereas in Madagascar more mammal fruits exist. This is consistent with our findings from the humid evergreen littoral forest. The lack of bird fruits is opposed to the findings in India (Ganesh and Davidar 2000), Hong Kong (Corlett 1996), La Selva in Costa Rica (Levey et al. 1993) and Malawi (Dowsett-Lemaire 1988). At all these sites the majority of fruits are dispersed by birds or by both birds and mammals. In our dataset, there are only slightly more mixed fruits and the majority are mammal fruits, again indicating low dependence for most tree species on birds but high dependence on lemurs and flying foxes for seed dispersal.

Even though dispersal strategies may include some specifically selected morphological traits known as syndromes, general traits make up the bulk of the floral diversity in the littoral forest. In particular the nutritional reward for the animals does not seem to be taxa related in Sainte Luce, as is also the case in Corlett (1996) and Pizo (2002). Many tree species attract their seed dispersers by more or less generalist fruit traits. However we have to be cautious as Zamora (2000) stressed that in community-wide studies 'the noise often overwhelms the pattern' and thus the diffuse co-adaptations we found may be the result of the complexity of interactions, few strong ones but many weak ones. Thus we cannot exclude the possibility that certain strong interactions were overlooked in this study, even though the impact of the species poor frugivore guild seems to be determining in this ecosystem.

In summary, it seems that in the littoral forest of Madagascar the combination of life history traits of tree species have not been shaped under the constraints imposed by vertebrate seed dispersers upon the trees as co-evolution and the low-high investment model of McKey (1975) state. A classification based on taxonomic affiliation of seed dispersers does provide a more clear pattern supporting the idea that animals eat what is available and what they can swallow and digest, mainly based on size characteristics. The observed links between traits of fruits and seeds and their consumers may be more a consequence of the morphological and physiological heritage and constraints of the consumers but not the result of co-evolution. The lack of tight co-evolutionary interactions makes sense in Madagascar, as the community of vertebrate frugivores is so species poor that there might have been few options for co-evolution. It could have been too dangerous for a tree species to rely on a single animal species for seed dispersal. Or simply, the species poor community of frugivores in Madagascar might not have had a large enough impact to produce specific tree traits. Nevertheless, some large seeds can only be dispersed by *E. f. collaris*. These tree species are likely to suffer from the extinction of the larger frugivorous lemur species.

ACKNOWLEDGEMENTS

We are QMM very grateful for providing logistics and infrastructure at the campsite. In particular we thank Manon Vincelette, Jean-Baptiste Ramanamanjato, Laurent Randrihasipara of the QMM Environmental and Conservation Team. Plant determinations were carried out with the help of the botanists Faly Randriatafika and Johny Rabenantoandro of the Missouri Botanical Garden (MBG, Antananarivo). Voucher specimens are currently at MBG in Antananarivo. This manuscript benefited greatly from numerous suggestions of two anonymous reviewers. This study was carried out under the "Accord de Collaboration" between the Departments of Animal Biology and Anthropology of the University of Antananarivo and the Institute of Zoology of Hamburg University and QMM. I also thank Dries Bonte and Willem Talloen for providing help with statistics. The first author is supported by a grant from the Belgian Fund for Scientific Research, Flanders (FWO). We thank the Flemish Government for structural support to the CRC of the RZSA.

Appendix I. List of abbreviations used in Figures 1 and 2 with family, scientific and vernacular name.

Abbreviation	Family name	Scientific name	Vernacular name
Pc	Anacardiaceae	*Poupartia chapelieri*	sisikandrongo
Pm	Annonaceae	*Polyalthia madagascariensis*	fotsivavo
P	Araliaceae	*Polyscias* sp.	voatsilana
Dp	Arecaceae	*Dypsis prestoniana*	boakabe
Cb	Burseraceae	*Canarium boivinii*	ramy
Cm	Canellaceae	*Cinnamosma madagascariensis*	vahabatra 3eM
G	Clusiaceae	*Garcinia* cf/aff. *Madagascariensis*	disaky kely
Tf	Combretaceae	*Terminalia fatraea*	katrafa
D	Ebenaceae	*Diospyros* sp.2	hazomainty
Ea	Elaeocarpaceae	*Elaeocarpus alnifolius*	sanga
Mp	Euphorbiaceae	*Macaranga perrieri*	mocarana
Uf		*Uapaca ferruginea*	voapaky lahy
Ul		*Uapaca littoralis*	voapaky vavy
Ut		*Uapaca thouarsii*	voapaky lahy ZJ
La	Flacourtiaceae	*Ludia antanosarum*	zorafotsy
So		*Scolopia orientalis*	zoramena
B	Grossulariaceae	*Brexia* sp.	kambatrikambatri
Ad	Icacinaceae	*Apodytes dimidiata*	hazomamy
Bm	Menispermaceae	*Burasaia madagascariensis*	faritsaty
Ba	Myristicaceae	*Brochoneura acumineata*	mafotra
Ec	Myrtaceae	*Eugenia cloiselii*	ropasy sp.1
E		*Eugenia* sp.	ropasy sp.2
S1		*Syzygium* sp.1	rotry ala
S2		*Syzygium* sp.2	rotry mena
O	Oleaceae	*Olea* sp.	vahabatra
Cv	Rubiaceae	*Canthium variistipula*	fantsikaitramainty
Rm		*Rothmannia mandenensis*	taholagna
Ve	Rutaceae	*Vepris eliotii*	lahinampoly
Vf		*Vepris fitoravina*	fitoravina
Tt	Sapindaceae	*Tina thouarsiana*	sanirambavy
Lm	Sarcolaenaceae	*Leptolaena multiflora*	fotonbavy
Sm		*Sarcolaena multiflora*	meramaintso
Se		*Schizolaena elongata*	fotondahy
To	Ulmaceae	*Trema orientalis*	andrarezona

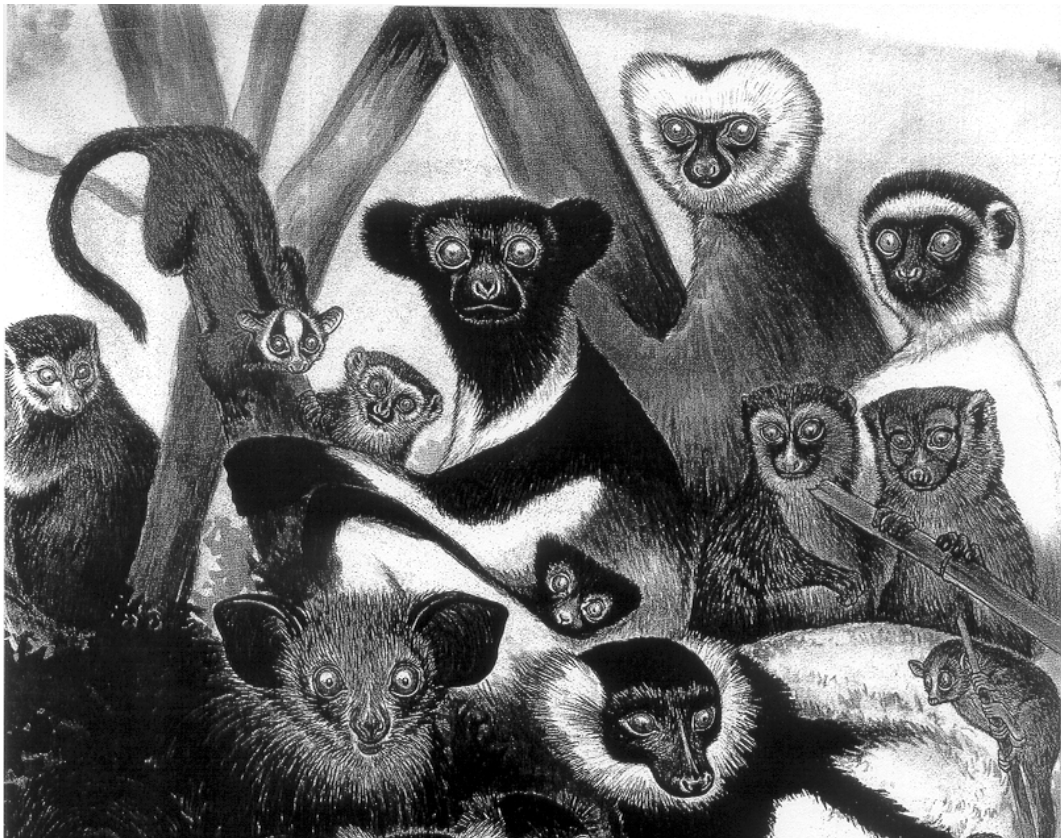
Appendix II. Plant-animal interactions based on fruit traps (T), droppings (F), tree watches (W). The number of fruit traps, observation hours, crop size and fruiting period are given as well as the number of consumer, disperser and predator species. The abbreviations are Am for *Alectroenas madagascariensis*, Hm for *Hypsipetes madagascariensis*, Ta for *Treron australis,* Efc for *Eulemur fulvus collaris*, L for lemurs, NL for nocturnal lemurs, Cm for *Cheirogaleus medius*, CM for *Cheirogaleus major, Mr* for *Microcebus rufus,* Pr for *Pteropus rufus,* C for *Coracopsis spp.,* Sp for *Streptopelia picturata,* Em for *Eliurus myoxinus* and Rr for *Rattus rattus.*

Impact on seed: Category:	Fruit traps (N)	Tree watches (h)	Crop size (N fruits)	Fruiting period (N days)	Number consumer species	Number disperser species
Apodytes dimidiata	2	36	309	19	7	6
Brexia sp.	1	-	461	143	4	3
Brochoneura acumineata	3	-	1324	41	1	0
Burasaia madagascariensis	2	36	114	49	4	2
Canarium boivinii	4	36	772	412	2	1
Canthium variistipula	1	-	1280	59	4	3
Cinnamosma madagascariensis	2	26.5[1]	1445	59	1	1
Diospyros sp.	3	25[1]	676	73	1	1
Dypsis prestoniana	1	36	1006	51	8	6
Elaeocarpus alnifolius	2	-	749	53	3	1
Eugenia cloiselii	2	27.5[1]	395	17	2	2
Eugenia sp.	2	36	1712	107	1	1
Garcinia sp.	1	-	46	26	2	1
Leptolaena multiflora	4	36	959	71	5	4
Ludia antanosarum	-	31[1]	-	-	5	4
Macaranga perrieri	-	36	-	-	2	1
Olea sp.	5	36	4816	67	5	3
Polyalthia madagascariensis	-	36	-	-	5	5
Polyscias sp.	-	36	-	-	5	3
Poupartia chapelieri	3	36	800	45	6	4
Rothmannia mandenensis	2	-	21	37	2	1
Sarcolaena multiflora	3	36	3010	53	6	4
Schizolaena elongata	5	36	1654	36	3	2
Scolopia orientalis	2	30.5[1]	5476	54	5	3
Syzygium sp.1	3	36	1769	62	5	3
Syzygium sp.2	4	36	2416	59	7	6
Terminalia fatraea	2	36	2018	145	7	5
Tina thouarsiana	4	36	4395	62	5	2
Trema orientalis	-	36	-	-	3	3
Uapaca ferruginea	3	36	381	143	6	4
Uapaca littoralis	4	36	6800	328	5	3
Uapaca thouarsii	3	-	1586	295	4	3
Vepris eliotii	2	31[1]	1612	55	3	3
Vepris fitoravina	3	36	7086	44	4	3

[1] No complete set of 36 hours could be obtained due to a very short fruiting period or difficult climatic conditions.

Appendix II Continued

			Seed dispersers							Number	Seed predators			
	Birds					Lemurs			Bats	predator	Birds		Rodents	
Am	Hm	Ta	Efc	L	NL	Cm	CM	Mr	Pr	species	C	Sp	Em	Rr
W	W		W	T		TW	TW	TW		1	TW			
			T		T	T		T		1			T	
										1			T	
			W	T			W			2			T	T
			TW							2			T	T
			F	T		TW		W		1	T			
			TW							0				
			FW							0				
FW	W		W	T		W	W		W	2	TW	W		
			FT							2			T	T
			FW	T		W				0				
			TFW							0				
			T							1			T	
			FW		T	W	W	W		1		W		
			W			W		W	T	1	W			
	W									1	W			
			TFW		T		W	W		3	W		T	T
W	W		W			W		W		0				
W	W	W								2	W	W		
			FW	T		W	W	W		2	W		T	
			T							1			T	
			TFW		T	W	W	W		2	W	W		
			TFW			W				1		W		
			TW		T	TW		W		2		W	T	
			TW		T	W		W		2			T	T
W	W		TFW	T		W		W	W	1	W			
W			W			W		W	TW	2	W		T	
			W	T				TW		3	TW		TW	TW
W	W	W								0				
			FW		T	W	W		W	2			T	T
			TFW		T		TW	W		2	T		T	
			T			T		T		1				T
			TW		T	TW		W		0				
			W	T	T	W		W		1	TW			



‘Ataovy dian-tana: jerena ny aloha,
todihana ny afara’

Behave like the chameleon:
look forward and observe behind

Malagasy proverb

3

Relations between fruits and disperser assemblages in the littoral forest of south-east Madagascar: a community level approach

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JOURNAL OF TROPICAL ECOLOGY (SUBMITTED)

ABSTRACT

Interactions among fleshy fruits and frugivore assemblages are presented from a one-year study in the littoral forest of Sainte Luce, south-eastern Madagascar. This community level approach allows us to evaluate the relative contribution of different frugivores to seed dispersal and predation. For this, interactions between 136 consumed fruit species and 13 frugivorous species were studied. Fruit and seed size are the most important physical factors determining food selection of all consumer species. While birds favour lipid-rich fruits, mammals seem to avoid them. The lemur species that go into hibernation clearly prefer sugar rich fruit pulp. In general, there is substantial dietary overlap among consumer species and animals seem to be quite flexible to eat whatever is available. This might be related to unpredictable fruit availability, which in turn, might be one of the reasons for the evolution of the depauperate frugivore guild here. Nevertheless all frugivores have different impacts on seed dispersal. *Eulemur fulvus collaris* is particularly important for the dispersal of large-seeded species. Birds and flying foxes ensure genetic exchange and plant regeneration between and outside forest fragments. In terms of conservation, heterogeneous seed transport is particularly important for this severely degraded littoral forest.

INTRODUCTION

Interactions between fleshy-fruited plant species and the community of vertebrate frugivores have been studied in the tropics worldwide (Leighton 1982; Gautier-Hion et al. 1985; Dowsett-Lemaire 1988; Corlett 1996; Kitamura et al. 2002; Ingle 2003), where zoochorous plant species make up the majority of the flora (Howe and Smallwood 1982; Fleming et al. 1987). The fleshy pulp of endozoochorous fruits attracts its consumers by a wide array of morphological traits and offers a nutritional reward for potential seed dispersers. In general, fruits are eaten and dispersed by a variety of animals even though some fruit traits are more likely to attract one taxonomic group of potential dispersers than another (Howe 1984; Gautier-Hion et al. 1985; Herrera 1987; Dowsett-Lemaire 1988; Terborgh 1990; Jordano 1992, 1995; Fisher and Chapman 1993; Erikkson and Ehrlen 1998). In this respect diffuse and broad co-adaptations are revealed when analysing feeding selection resulting in ‘fruit character syndromes’ (Van der Pijl 1969; Gautier-Hion et al. 1985). However, the definition of syndromes is problematic as traits are defined differently in each study. Therefore it is necessary to evaluate diets of different consumer species, unbiased, by looking for morphological and biochemical traits that may or may not indicate certain feeding preferences instead of trying to fit preconceived syndromes.

Frugivorous animals have been shown to be important for seed dispersal and forest regeneration in Madagascar. Most field studies in Malagasy forests have focused on the feeding ecology and dispersal role of frugivore species such as lemurs (Ralisoamalala 1996; Scharfe and Schlund 1996; Dew and Wright 1998; Overdorff and Strait 1998; Birkinshaw 1999, 2001; Ganzhorn et al. 1999a) or flying foxes (Bollen and Van Elsacker 2002a, Chapter 3a), while others have studied the association between focal tree species and their frugivore consumers (Scharfe and Schlund 1996; Goodman and Ganzhorn 1997; Goodman et al. 1997a; Böhning-Gaese et al. 1999). However, apart from some combinations of literature and field studies (Phillipson 1996; Bleher and Böhning-Gaese 2001; Voigt 2001) no community wide dispersal study has been carried out in Madagascar up to now. This current study focuses on interactions between the community of vertebrate frugivores present in the littoral forest and the plant species they consume, with emphasis on fruit morphology and nutrient content of each plant species and with respect to the individual roles of consumers as seed dispersers or predators.

The study on fruit-frugivore interactions is particularly relevant for Madagascar as this island has a high percentage of botanical and faunal endemism (Lowry et al. 1997; Schatz 2001) and at the same time a rather depauperate frugivore community (Langrand 1990; Mittermeier 1994; Goodman et al. 1997a). An attempt was made to unravel aspects of animal-plant interactions that determine the dynamics of the littoral forest, which presently suffers from severe fragmentation and degradation. Given these aspects, it is important to understand these interactions to urgently integrate them in conservation management plans for this area.

The following research questions are addressed:

1. Which plant species are included in the diet of the frugivores present in the littoral forest?
2. On the basis of which morphological and biochemical fruit and seed characteristics do frugivores select their food resources and are certain feeding preferences prevalent?
3. To what extent does dietary overlap occur between these frugivores?
4. What is the impact of these frugivores on the fruits they eat? Can they be considered as efficient seed dispersers, rather neutral seed droppers or more destructive seed predators?

STUDY SITE

This research was conducted by the first author from November 1999 through January 2001 in a 377-ha forest fragment (S9) of the littoral forest of Sainte Luce (24°45'S 47°11'E, south-east Madagascar). At the moment, the south-eastern littoral forest is represented by 2500 ha only, which is located in the surrounding area of Fort-Dauphin (Petriky, Mandena, Sainte Luce) (Ganzhorn et al. 2001; Vincelette pers. comm.). The most intact littoral forest can be found at Sainte Luce, which includes forest fragments ranging in size from 3 up to 377ha (Fig. 1). Littoral forest grows on sandy soils and occurs within 3km of the coast (Dumetz 1999). A relatively open or non-continuous canopy characterises this forest, which is 6 to 8m in height with emergents up to 18m (Dumetz 1999). The diameter at breast height (DBH) of trees rarely exceeds 30 to 40cm

(Rabevohitra et al. 1996; Dumetz 1999). Average annual rainfall at this site is about 2690mm, with a marked rainy season from November through February while no clear dry season could be detected (Bollen and Donati, Chapter 1). Mean monthly temperature is 23°C (QMM unpubl. data). Fruit production is seasonal, with a peak in abundance of ripe fruits in December and January and with periods of fruit scarcity that differ strongly inter-annually (Bollen and Donati, Chapter 1).

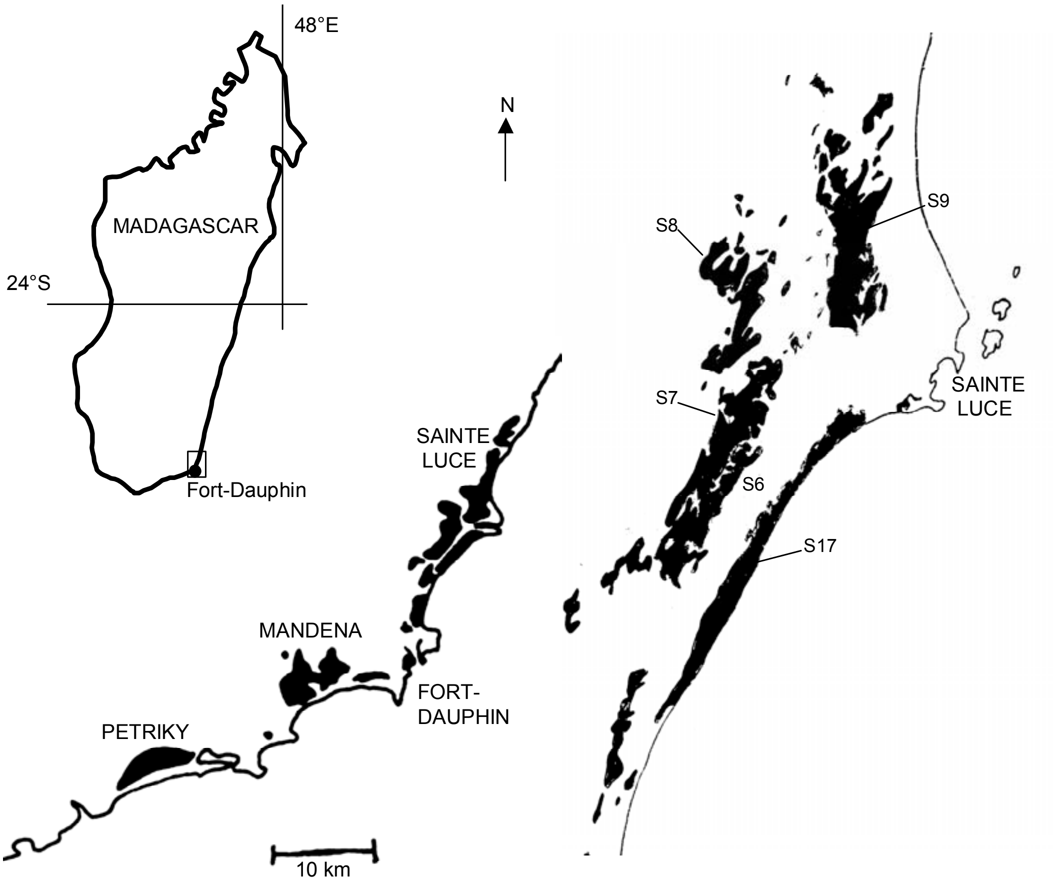

Fig. 1. On the left Madagascar is shown with indication of the south-eastern zone. In the middle a detail of the littoral forests (Sainte Luce, Mandena and Petriky) is given together with a detail of the main forest fragments of Sainte Luce on the right.

METHODS

Plant species studied

Ripe fruits were collected in the study area throughout the research period. Consequently morphological characteristics were measured in the field station and biochemical components were analysed in the lab. In this chapter only plant species are included, which have their fruits or seeds consumed by at least one vertebrate species. The non-zoochorous fruits were left out. Therefore the dataset used here is a subset of the complete one (N =175) used elsewhere (Bollen and Van Elsacker 2002, Chapter 3a;

Bollen et al. in press, Chapter 4). The full dataset is available from the first author by request.

Herbarium specimens of all taxa were collected and deposited at the Missouri Botanical Garden of Antananarivo (Madagascar). Local research assistants provided *Antanosy* names. Scientific names were obtained after determination of voucher specimens at herbaria of Antananarivo (FOFIFA, Tsimbazaza) with the help of botanists from Missouri Botanical Garden (App. I).

Morphological characteristics

Discrete variables used to characterise fruits were:
Growth form: large tree (>6m), small tree (<6m), shrub, vine, epiphyte and herb;
Fruit type: berry, drupe, capsule and others;
Pulp type: juicy soft, juicy fibrous, dry fibrous, aril, no pulp;
Colour: yellow-orange, red, purple, brown, green, other (including black, white);
Odour: absent, present (as perceived by the first author);
Fruit protection: dehiscent, indehiscent with thin husk, indehiscent with thick husk;
Seed protection: no seed protection, thick lignified seed coat.

Continuous variables included fruit and seed weight and length, and seed number per fruit. Fresh fruits and seeds were weighed using spring or electronic balances and measured using scales and callipers with 0.01g and 0.01mm precision, respectively. These measures were taken from a set of 10 samples per plant species and average values are presented. All characterisations were based on the original classifications by Gautier-Hion et al. (1985) and Lambert and Garber (1998). A reference collection of seeds was used for identification of seeds within fruit traps and faecal samples.

Chemical characteristics

Water content was calculated by comparing fresh and dry weight of the fruit pulp after three days of drying in an oven. The pulp of ripe fruits were dried in the sun and in a drying oven, ground to pass through a 2mm sieve and dried again overnight at 50-60°C prior to analyses. Samples were analysed for neutral (NDF) and acid (ADF) detergent fibre (Goering and Van Soest 1970; Van Soest 1994; modified according to the instructions for use in an ANKOM FIBRE ANALYZER). Total nitrogen was determined using the Kjeldahl procedure. Extractable or soluble proteins were assessed with BioRad after extraction of the plant material with 0.1N NaOH for 15h at room temperature. Soluble carbohydrates and procyanidin (condensed) tannins were extracted with 50% methanol. Concentrations of soluble sugar were determined as the equivalent of galactose after acid hydrolization of the 50% methanol extract. Sugars (glucose, fructose, saccharose) are oxidized by sugar-specific enzymes. Concentrations of procyanidin tannin were measured as equivalents of quebracho tannin (Oates et al. 1977; Porter and Hemingway 1990). Lipids were determined by the Soxleth method. Biochemical analyses were carried out at the Institute of Zoology, Department of Ecology and Conservation, University Hamburg, Germany.

Animal species studied

Thirteen fruit eating vertebrate species occur in the littoral forest of Sainte Luce (Table 1). Diets of frugivore animal species were assessed by direct feeding observations through tree watches (36h watches at 27 tree species, one individual per tree species) and casual observations, as well as by more indirect methods such as macroscopical faecal analyses and analyses of fruit trap contents (78x1m² traps under 29 tree species) (Bollen and Van Elsacker 2002a, Chapter3a; Bollen et al., Chapter 2). For *Pteropus rufus* faecal droppings were collected weekly under the roost site year-round. Dietary data on the rodents resulted mainly from identifying gnawing marks on seed remains collected at feeding sites. Since *Eulemur fulvus collaris* was studied intensively in parallel to the present study (Baldi 2002; Donati 2002; Morelli 2002), fruits eaten by this species may be more thoroughly sampled than other species. The con-generic species *Cheirogaleus medius* and *C. major* could not always be distinguished during observations and are treated as *Cheirogaleus* spp. in the analyses. The same applies to rodent species, *Eliurus webbi* and *Rattus rattus* (introduced), as not all gnawing marks could be attributed to a single species. Details of the diets of the various species are given in Appendix I. For the frugivorous bird species, diets are treated separately, but for feeding selection *Alectroenas madagascariensis, Treron australis,* and *Hypsipetes madagascariensis* were combined, as they are the only seed dispersing birds at our site.

Dietary overlap was calculated among pairs of frugivores using Sørensen's similarity index (Krebs 1989). This index generates a value ranging from 0 to 1, with 0 representing no overlap and 1 representing complete overlap. The dataset comprises accounts of fruit species consumed by different frugivore consumers along with the impact they have on the seeds. Based on this, frugivores can be classified into the following categories: seed dispersers or fruit consumers (D), neutral or pulp consumers (N) and seed predators (P) according to Gauthier-Hion et al. (1985) and Debussche and Isenmann (1992). The first group disperses intact seeds by endozoochory through droppings or synzoochory through regurgitation, while the second group eats fruit pulp but drops the seeds under the parent plant. The last group eats and destroys the seeds. It is difficult to assign a certain frugivore to one category only, as one species may have different impacts on the same and on different plant species. The stage of ripeness of the consumed fruits was scored as well. To differentiate between unripe and ripe fruits changes in size, colour and consistency were looked at.

Data analyses

Most of the variables measured have highly skewed distributions so the median value is given instead of the mean. For the same reason non-parametric statistics were used. Chi-square analyses were conducted to compare discrete fruit traits in the diet with those in the overall dataset, whereas Mann Whitney U tests were carried out to control for feeding preferences when comparing continuous traits between food and non-food items. Afterwards sequential Bonferroni corrections were performed on the significance levels (Rice 1989). To understand which factors influence the diet of the different frugivores separately a logistic generalised model was applied in which morphological and biochemical variables were included as fixed factors. Dietary data were used as binomial response variables (0=non-food, 1=food item) in a generalised mixed linear model with logit link (glimmix procedure in SAS 8.1.) with forward procedure retaining significant variables. As *Cheirogaleus* spp. and *Microcebus rufus* go into torpor in austral winter, comparison of their diet and total dataset available were restricted to the fruits that were present during their active period. Statistical significance was accepted for $\alpha \leq 0.05$ for all tests. All statistical tests were carried out according to Siegel (1956) with the statistical software SAS for Windows.

Table 1. List of frugivorous vertebrate species at Sainte Luce, with indication of their diet (F: frugivorous, G: granivorous, O: omnivorous), their activity budget (D: diurnal, N: nocturnal, C: cathemeral), feeding height (A: arboreal, T: terrestrial), body mass and length. ND: no data available.

Family	Scientific name	English name	Diet	Activity	Feeding height	Group size (N individuals)	Body [1] mass (g)	Body [1,2] lenght (cm)
AVES								
Columbidae	*Treron australis* L.	Malagasy Green Pigeon	F	D	A	3-8	215	32
	Alectroenas madagascariensis L.	Malagasy Blue Pigeon	F	D	A	3-12	ND	28
	Streptopelia picturata Temminck	Madagascar Turtle Dove	G	D	T	1-2	190	28
Pycnonotidae	*Hypsipetes madagascariensis* Müller	Madagascar Bulbull	F	D	A	5-15	45	24
Psittacidae	*Coracopsis nigra* L.	Lesser Vasa Parrot	G	D	A	3-15	218	35
	Coracopsis vasa Shaw	Greater Vasa Parrot	G	D	A	3-15	ND	50
MAMMALIA								
RODENTIA								
Muridae	*Rattus rattus* L.	Black Rat	O	N	AT	1-2	100	15-23
Nesomyinae	*Eliurus webbi* Ellerman	Webb's Tuft-Tailed Rat	G	N	AT	1-2	88	10-16
CHIROPTERA								
Pteropodidae	*Pteropus rufus* Tiedemann	Madagascar Flying Fox	F	N	A	250-300	500-750	23-27
PRIMATES								
Lemuridae	*Eulemur fulvus collaris* E. Geoffroy	Collared Brown Lemur	F	C	A	3-10	2000-2300	40-47
Cheirogaleidae	*Microcebus rufus* E. Geoffroy	Brown Mouse Lemur	O	N	A	1	42	12,5
	Cheirogaleus major E. Geoffroy	Greater Dwarf Lemur	O	N	A	1-3	443	25
	Cheirogaleus medius E. Geoffroy	Fat-tailed Dwarf Lemur	O	N	A	1-3	119-282	20

[1] Data from Langrand (1990), Fietz and Ganzhorn (1999), Goodman et al. (1997b), Goodman et al. (in press), Ganzhorn et al. (1999a), Donati (pers. comm. 2002).

[2] Body length is total length for birds and bats but head/body length for lemurs and rodents.

RESULTS

Lemurs fed on most fruiting species, their diet comprised 119 plant species. Birds, rodents, and *Pteropus rufus* consumed 55, 50, and 39 plant species, respectively. Different methods of collecting dietary data influenced the outcome of diet lists (Table 2). In general direct observations (systematic or opportunistic) resulted in the largest numbers of feeding records. However, five species were difficult to observe. Due to hunting pressure, observations of *P. rufus* at night with a headlight were not routinely possible. Both rodent species could be observed only rarely as they detect the observer by smell. As explained in the methods, this bias could be limited by systematically collecting faecal droppings and identifying gnawing marks year-round. *Treron australis* and *S. picturata* were very shy and flew away upon detecting the observer. Moreover droppings of these bird species as well as of *Hypsipetes madagascariensis* were found only rarely. For *Alectroenas madagascariensis* and *E. f. collaris* faecal droppings could be collected more easily, but much less often for the smaller nocturnal lemurs. Characteristic feeding marks were helpful in particular to identify food species of *Coracopsis nigra*, both rodent and all lemur species.

Table 2. Number of consumed plant taxa scored per consumer species is given with indication of the different methods (O:observations, F: faecal analyses; T: traces). 'Ripeness' indicates the stage of ripeness (R: ripe, UR: unripe) at which fruit species were consumed. The effect on seeds by the consumer species is indicated (D: dispersal, N: neutral seed dropping, P: predation, ?: unknown).

	Dietary diversity			Sampling effort			Ripeness		Effect on seeds			
	N species	N genera	N families	O	F	T	R	UR	D	N	P	?
Treron australis	9	9	9	7	4	0	9	0	9	0	0	0
Alectroenas madagascariensis	18	17	14	16	13	0	18	0	18	1	0	0
Streptopelia picturata	13	13	11	13	0	0	13	0	0	0	0	13
Hypsipetes madagascariensis	21	20	17	21	1	0	21	0	21	2	0	0
Coracopsis nigra	37	32	22	36	2	9	26	24	4	8	36	0
Eulemur fulvus collaris	111	76	43	93	67	21	111	25	100	36	27	0
Cheirogaleus spp.	39	31	20	37	7	24	39	0	28	24	0	0
Microcebus rufus	41	33	24	33	6	25	41	0	27	20	0	4
Pteropus rufus	39	27	21	7	34	5	39	0	37	12	0	1
rodents	50	37	31	3	1	47	50	0	4	2	49	0

Morphological Characteristics

The complete data set of all food species involved mainly large canopy tree species (59%). Most common plant families are Rubiaceae (10%), Euphorbiaceae (5%), and Flacourtiaceae, Myrtaceae, Annonaceae, and Areceae (each with 4%). Berries and drupes were the most common fruit types (83%) with a soft and juicy pulp (62%). Dull coloured fruits (green, brown, yellow-orange 68%) with odour (65%) made up the majority of the fruits. Other dominant features were indehiscent fruits with a thin husk (77%) and seeds could be either protected (54%) or not (46%). The median number of seeds per fruits was 2 (quartiles 1-4) and median fruit weight was 1.23g (0.49-5.23g), fruit length was 15.43mm (0.49-5.23mm), and seed length was 8.36 mm (4.85–14.42mm).

Taxonomically, Rubiaceae was the dominant plant family in most diets and Euphorbiaceae, Areceae, and Annonaceae were important as well but to a lesser extent. There appeared to be no clear taxonomic preferences within the diet of all frugivores. The dominant plant families seemed to be represented in the diets as represented in the overall sample. The same is true for growth form (Table 3). Most consumers favour berries and drupes, but for rodents there was a trend for selecting drupes. Even though soft and juicy fruit made up most of the sample, nocturnal lemurs and flying foxes selected this pulp type significantly more often than other pulp types. The latter also favoured arillate fruits (Table 3). For colour a selection was noticed towards red and purple fruits by all frugivore bird species, whereas mammals ate whatever colour was available. Most fruits in the littoral forest had an odour and were probably selected in this way, except for *Coracopsis nigra*, which fed mainly on odourless fruits (Table 3). For the nocturnal lemur species fruits with a thin husk were favoured. The other consumers did not seem to avoid the few dehiscent and thick-husked fruits present (Table 3). In all animal species no difference in seed protection could be found between diet and the overall dataset (Table 3). The few preferences indicated above appeared to be non-significant after correction by sequential Bonferroni.

Flying foxes were the only consumer species, which preferred multi-seeded fruits, while the diet of the other animals did not differ from what was available (Table 4). Initially many significant preferences could be found related to fruit and seed size and weight. However after sequential Bonferroni adjustment, only the frugivorous birds seem to select significantly smaller and lighter fruits. *Coracopsis nigra* also prefers lighter fruits and *Pteropus rufus* smaller seeds. Contrarily the rodents clearly favour heavier fruits and larger seeds. (Table 4).

Biochemical Characteristics

Water was the dominant constituent of fresh pulp (median 76.0%). On a dry mass basis, both acid (22.6%) and neutral (32.0%) detergent fibre contents were high. The median sugar content was 19.2%. Median lipid content of fruits was 3.1%, total nitrogen 0.9%, and extractable protein 2.8%. Tannin values were very low in our dataset with a median value of 0.2%. Enzymatic analyses of all fruits yielded median values of 3.6% saccharose, 1.8% glucose, and 1.8% fructose.

As for fats, frugivorous birds seemed to select fruits with a high lipid content, while the opposite was true for *E. f. collaris* and *P. rufus* (Table 4). Neither total nitrogen nor extractable protein seemed to influence fruit choice for any of the consumer species, nor did water content or acid detergent fibre. *Cheirogaleus* spp. and *Microcebus rufus* selected fruits with high sugar content but this trend was not significant (*Cheirogaleus* spp. P=0.06, *M. rufus* P=0.19). However when looking at saccharose, glucose, and fructose concentrations separately, preferences were significant for *Cheirogaleus* spp. (Table 4). The same trend existed for *M. rufus* (saccharose P=0.17, glucose P=0.11, fructose P=0.056). Tannins were consumed as present in the overall database but *Coracopsis nigra* included fruits with significantly higher tannin content. In the diet of *M. rufus* neutral detergent fibre was significantly lower than in fruits, which were not consumed (Table 4). None of these preferences remained significant after sequential Bonferroni adjustment.

Table 3. Chi-square results comparing fruit and seed traits in the diets of the different consumer species to the overall data set. Significant differences are in bold (* P<0.05, ** P<0.01). After sequential Bonferroni adjustment, no value remained significant.

Parameters	Frugivorous birds: *Treron australis* *Alectroenas mad.* *Hypsipetes mad.*	*Coracopsis nigra*	*Eulemur fulvus collaris*	*Cheirogaleus* spp.[1]	*Microcebus rufus*[1]	*Pteropus rufus*	rodents
Growth form	X^2 = 3.99 df = 2	X^2 = 2.23 df = 2	X^2 = 2.95 df = 2	X^2 = 0.88 df = 2	X^2 = 3.43 df = 2	X^2 = 1.68 df = 2	X^2 = 0.13 df = 2
Fruit type	X^2 = 3.39 df = 2	X^2 = 3.50 df = 2	X^2 = 1.67 df = 3	X^2 = 0.26 df = 2	X^2 = 0.98 df = 2	X^2 = 3.20 df = 2	X^2 = 4.58 df = 2
Pulp type	X^2 = 3.01 df = 2	X^2 = 2.63 df = 2	X^2 = 1.45 df = 3	X^2 = 9.34 df = 2 ** soft & juicy pulp	X^2 = 7.43 df = 2 * soft & juicy pulp	X^2 = 8.24 df = 2 * juicy soft, aril	X^2 = 1.84 df = 3
Colour	X^2 = 19.33 df = 4 * red, purple, black	X^2 = 3.13 df = 4	X^2 = 0.32 df = 4	X^2 = 2.53 df = 4	X^2 = 2.69 df = 4	X^2 = 1.69 df = 4	X^2 = 1.19 df = 4
Odour	X^2 = 0.50 df = 1	X^2 = 5.84 df = 1* no odour	X^2 = 0.26 df = 1	X^2 = 0.14 df = 1	X^2 = 0.02 df = 1	X^2 = 0.60 df = 1	X^2 = 1.05 df = 1
Fruit protection	X^2 = 3.22 df = 2	X^2 = 2.14 df = 2	X^2 = 1.06 df = 2	X^2 = 9.09 df = 2 * thin husk	X^2 = 6.29 df =2 * thin husk	X^2 = 2.76 df = 2	X^2 = 0.42 df = 2
Seed protection	X^2 = 0.01 df = 1	X^2 = 0.32 df = 1	X^2 = 1.68 df = 1	X^2 = 1.22 df = 1	X^2 = 0.04 df = 1	X^2 = 0.43 df = 1	X^2 = 1.71 df = 1

[1] For *Cheirogaleus* spp. and *Microcebus rufus* we did not use the complete dataset of characterized fruits but those fruits that are available when lemur are active.

Table 4. Morphological and biochemical characteristics of food and non-food items of the different frugivore species. For comparison of fruit selection by *Cheirogaleus* spp. and *Microcebus rufus* only those fruits were considered that were present during the months when the lemurs were not in torpor. Values are medians, quartiles and sample size. Z-values are based on Mann Whitney U tests (* P<0.05, ** P<0.01, *** P<0.001). Values that remained significant after sequential Bonferroni adjustment are **in bold.**

Parameters	Frugivore birds			*Coracopsis nigra*		
	Food	Non food	Z	Food	Non food	Z
Seed number	1.00 1.00-3.00 29	2.00 1.00-4.25 96	-1.37	1.00 1.00-3.75 34	2.00 1.00-4.50 91	-1.08
Fruit weight	0.30 0.15-0.65 28	1.79 0.75-5.87 99	**-5.14*** **	0.55 0.23-1.05 35	1.69 0.71-5.99 92	**-4.13*** **
Fruit length	10.60 6.33-12.44 29	17.60 12.45-27.33 104	**-4.44*** **	12.28 7.97-17.20 36	16.67 11.42-29.22 97	-2.92**
Seed length	6.71 3.25-9.65 28	9.79 5.77-15.39 96	-3.07**	6.86 3.95-10.35 33	9.94 5.35-15.33 91	-2.40*
Lipid	4.51 2.78-12.65 27	2.51 1.62-4.96 69	3.03**	3.12 2.12-4.82 29	2.82 1.83-6.92 67	-0.44
Total nitrogen	0.99 0.68-1.19 28	0.83 0.60-1.16 72	0.99	0.86 0.60-1.09 29	0.85 0.63-1.19 71	-0.74
Extractable protein	2.85 1.84-3.71 28	2.65 1.57-4.29 72	0.30	2.86 1.79-4.25 29	2.69 1.58-4.21 71	0.56
Sugar	32.61 4.97-46.37 28	18.26 8.32-34.39 72	1.04	18.18 12.63-41.38 29	21.27 6.59-36.27 71	0.77
Tannin	0.24 0.00-0.63 28	0.19 0.00-0.51 72	0.46	0.39 0.10-0.96 29	0.18 0.00-0.44 71	1.94*
NDF	28.19 22.86-38.42 24	33.42 25.40-47.91 66	-1.39	33.26 25.83-45.14 27	31.85 23.77-47.74 63	0.06
ADF	19.74 16.67-29.52 24	24.67 17.55-35.66 66	-1.32	22.51 17.85-33.31 27	24.54 17.09-35.65 63	-0.20
Water content	79.71 71.50_84.00 19	74.52 66.50-82.00 72	1.24	72.00 65.00-79.71 21	77.00 70.00-84.00 70	-1.42
Saccharose	4.89 0.56-20.78 22	3.51 1.41-11.09 34	0.04	3.80 1.12-21.08 24	3.20 0.62-12.69 32	1.03
Glucose	1.77 0.23-10.62 22	1.67 0.46-3.99 34	0.28	1.87 0.37-7.00 24	1.37 0.42-4.96 32	0.72
Fructose	3.95 0.08-14.68 22	1.56 0.70-5.07 34	0.31	2.37 0.61-12.61 24	1.43 0.23-7.05 32	0.83

Table 4 Continued

Parameters	*Eulemur fulvus collaris*			*Cheirogaleus* spp.		
	Food	Non food	Z	Food	Non food	Z
Seed number	2.00 1.00-5.00 105	1.50 1.00-2.25 20	-0.70	1.50 1.00-3.00 38	1.00 1.00-4.00 74	-0.09
Fruit weight	1.46 0.56-5.86 103	0.72 0.21-157 24	-2.65**	0.66 0.32-1.63 39	1.79 0.79 73	-3.16**
Fruit length	15.5 10.52-25.18 109	13.95 9.13-21.76 24	-1.02	12.34 9.22-16.42 39	19.10 12.42-30.59 78	-3.29**
Seed length	8.36 5.31-15.05 104	7.90 3.37-10.91 20	-1.15	8.19 4.39-11.96 36	10.27 5.35-18.27 75	-2.07*
Lipid	2.77 1.73-5.17 84	6.73 3.74-21.27 12	2.65**	2.82 1.87-5.07 35	3.27 1.85-6.01 49	-0.80
Total nitrogen	0.86 0.65-1.17 88	0.83 0.57-1.07 12	-0.28	0.86 0.60-1.12 35	0.85 0.63-1.26 52	-0.68
Extractable protein	2.82 1.59-4.26 88	3.02 1.62-4.01 12	0.21	3.15 1.64-4.65 35	2.78 1.68-4.18 52	0.57
Sugar	18.39 7.52-35.99 88	31.42 10.38-40.64 12	0.99	27.84 13.81-40.68 35	12.84 6.51-33.76 52	1.88
Tannin	0.19 0-0.51 88	0.22 0.12-0.66 12	0.70	0.16 0.00-0.39 35	0.21 0.00-0.58 52	-1.03
NDF	32.73 24.11-47.91 78	30.00 21.75-33.55 12	-1.37	31.22 24.08-41.77 33	34.36 25.62-52.33 48	-1.28
ADF	22.77 17.11-35.68 78	22.30 16.99-27.80 12	-0.77	21.71 16.99-29.93 33	24.95 17.39-37.02 48	-1.45
Water content	76.50 70.00-83.25 76	71.00 65.00-79.00 15	-0.86	75.86 71.00-82.50 31	74.04 63.04-80.75 52	0.69
Saccharose	3.60 0.92-14.10 48	6.54 1.02-15.58 8	-0.06	5.05 2.48-16.27 28	0.99 0.38-7.54 20	-2.33*
Glucose	1.77 0.39-6.25 48	2.15 0.35-5.67 8	-0.37	1.92 1.09-5.75 28	0.39 0.10-2.00 20	-2.60*
Fructose	1.75 0.58-7.71 48	1.90 0.09-7.52 8	-0.44	2.41 1.22-7.05 28	0.53 0.07-1.45 20	-2.58*

Table 4 Continued

Parameters	*Microcebus rufus*			*Pteropus rufus*		
	Food	Non food	Z	Food	Non food	Z
Seed number	2.00 1.00-3.00 37	1.00 1.00-3.00 75	0.26	3.00 1.00-30.50 39	1.00 1.00-2.00 86	**3.39*****
Fruit weight	0.63 0.30-1.64 38	1.94 0.82-6.43 74	-3.16**	0.98 0.43-3.82 38	1.37 0.54-5.85 89	-0.91
Fruit length	12.28 9.59-15.15 38	19.69 12.70-28.75 79	-3.22**	13.59 9.94-21.09 39	16.56 10.64-25.41 94	-1.10
Seed length	7.46 3.79-10.58 37	11.83 5.98-17.75 74	-2.87**	6.31 3.74-8.38 38	10.30 6.77-15.78 86	**-3.67*****
Lipid	3.12 2.19-5.60 32	2.69 1.79-5.17 52	-0.48	2.52 1.94-3.90 36	3.79 1.84-8.50 60	-2.07*
Total nitrogen	0.83 0.58-1.12 32	0.86 0.64-1.18 55	-0.74	0.79 0.52-1.14 37	0.87 0.67-1.18 63	-1.62
Extractable protein	2.90 1.72-4.18 32	2.86 1.65-4.58 55	-0.18	2.86 2.18-3.96 37	2.53 1.55-4.39 63	0.79
Sugar	21.60 10.66-41.88 32	15.37 6.59-33.5 55	1.29	18.18 8.12-37.23 37	20.98 7.76-37.53 63	-0.36
Tannin	0.20 0.00-0.42 32	0.18 0.00-0.52 55	0.27	0.28 0.10-0.78 37	0.16 0.00-0.52 63	1.05
NDF	27.77 23.27-41.92 31	34.36 27.56-51.56 50	-1.99*	35.06 27.04-47.91 34	31.35 22.97-44.34 56	1.25
ADF	20.10 17.08-31.04 31	25.98 18.85-36.56 50	1.70	25.84 19.08-35.99 34	22.45 16.71-32.81 56	1.46
Water content	76.00 71.75-83.25 32	73.00 63.00-81.00 51	1.54	78.24 71.75-83.00 32	74.00 64.77-83.5 59	1.14
Saccharose	3.95 2.34-20.22 23	1.15 0.61-11.52 25	1.38	3.56 0.96-13.66 29	3.95 0.91-17.74 27	0.38
Glucose	1.91 1.07-5.68 23	0.50 0.17-3.50 25	1.60	1.70 0.45-5.66 29	1.91 0.36-5.86 27	0.07
Fructose	1.97 1.19-9.17 23	0.79 0.10-5.42 25	1.91	1.57 0.64-6.16 29	1.93 0.13-9.77 27	0.04

Table 4 Continued

Parameters	Rodents		
	Food	Non food	Z
Seed number	1.00 1.00-3.00 48	2.00 1.00-5.00 77	-0.92
Fruit weight	3.16 0.82-8.03 50	0.92 0.29-2.90 77	**3.53*****
Fruit length	19.04 13.29-30.38 50	13.20 8.08-21.82 83	3.24**
Seed length	12.06 7.77-18.89 48	6.90 3.89-11.73 76	**3.99*****
Lipid	2.85 1.75-6.92 35	3.22 2.12-5.12 61	-0.01
Total nitrogen	0.86 0.68-1.21 35	0.86 0.59-1.15 65	0.77
Extractable protein	2.53 1.84-4.06 35	2.83 1.57-4.34 65	-0.09
Sugar	18.23 6.98-32.66 35	21.27 10.15-40.02 65	-0.95
Tannin	0.18 0.00-0.44 35	0.20 0.00-0.65 65	-0.95
NDF	33.70 24.03-47.45 33	31.22 23.90-46.24 57	0.58
ADF	23.03 17.21-35.68 33	22.51 17.08-33.87 57	0.49
Water content	73.69 65.00-81.25 40	77.00 70.50-84.00 51	-1.20
Saccharose	3.51 0.75-7.37 20	5.22 1.05-15.75 36	-0.85
Glucose	1.27 0.41-2.27 20	2.33 0.39-6.30 36	-1.01
Fructose	1.34 0.56-3.57 20	2.37 0.37-11.93 36	-0.95

Besides testing feeding selection for each variable separately, we additionally aim to understand which factors influence the diet of the different frugivores. According to the final significant model of *Eulemur fulvus collaris,* growth form ($F_{2,\ 120}$= 5.75, P=0.004) and seed protection ($F_{1\ 120}$=6.66, P=0.011) seem to determine most whether a fruit is eaten. Their diet is characterised by fruits from large trees with a hard kernel (Table 5). For *Cheirogaleus* spp. fruit length ($F_{1,\ 115}$= 10.15, P=0.002) is the only significant determinant, whereas for *M. rufus* this is seed length ($F_{1,\ 109}$= 8.84, P=0.004). Obviously smaller fruits and seeds determine the diet of both lemur species (Table 5). Conspicuous colours ($F_{5,\ 89}$=3.25, P=0.009) and large fat contents ($F_{1,\ 89}$= 6.33, P=0.013) determine whether frugivore birds eat a certain fruit. *Coracopsis nigra* prefers odourless ($F_{1,\ 128}$=6.54, P=0.012) and small fruits ($F_{1,\ 128}$= 6.45, P=0.012). Fat content ($F_{1,\ 87}$= 6.97, P=0.009) and seed length ($F_{1,\ 87}$=15.11, P=0.0002) seem to determine the presence of fruits in the diet of *P. rufus*. In particular fruits with low lipid content and small seed length are most abundant. Finally, the diet of rodents is characterised by a significant interaction between seed length and seed protection ($F_{1,\ 114}$=5.73, P=0.018), indicating that large seeds, which often have a hard kernel predominate their diet (Table 5). The goodness-of-fit of the different model is significant (X^2_{Efc}=92.41; X^2_{Ch}=134.49; X^2_{Mr}=130.51; X^2_{fb}=82.85; X^2_{Cn}=136.04; X^2_{rod}=128.19; P<0.001).

Table 5. Parameter estimates for the logistic regression models determining the probability that a fruit species is included in the diet of different frugivores. Un-transformed values are given

Species	Model			
	Parameters	Classes	Parameter estimate	SE
Eulemur fulvus collaris	Growth form	Large tree	3.44	1.60
		Small tree-shrub	1.47	1.54
		Herbs-vines-epiphytes	1.81	0.76
	Seed protection	None	0.38	1.30
		Hard seed coat	1.81	0.76
Cheirogaleus spp.	Fruit length		0.43	0.02
Microcebus rufus	Seed length		0.28	0.04
Frugivore bird spp.	Colour	Green	-1.98	2.52
		Yellow orange	-2.26	2.55
		Red	-0.06	2.51
		Brown	-3.48	2.69
		Purple	-1.01	2.55
		Others	0.06	1.22
	Fat		0.16	0.04
Coracopsis nigra	Odour	Odourless	1.48	0.87
		Odoriferous	-0.41	0.45
	Fruit length		-0.47	0.02
Pteropus rufus	Seed length		2.08	0.06
	Fat		2.11	0.07
rodents	Seed length* seed protection	SL*no seed protection	-2.78	0.83
		SL*hard seed coat	-2.98	0.75

Diet overlap

Frugivorous animal species shared between 2 and 42 plant species. This corresponds to a Sørensen's similarity index of 0.08 to 0.67 (Table 6). Bird and lemur species had more fruit species in common than flying foxes and rodents. The highest similarity index was found between *M. rufus* and *Cheirogaleus* spp. (Table 6), followed by *P. rufus* and *M. rufus.* The lowest index was found between *Treron australis* and the rodents. In general, dietary overlap among mammals was larger than among birds or between mammals and birds (Table 6). These results have to be interpreted with caution in particular for those species which dietary diversity is underestimated, such as *T. australis* and *S. picturata.* Both inter- and intra-specific interactions as well as polyspecific feeding associations were observed.

Table 6. Diet overlap between each pair of consumer species. The number of species consumed by each frugivore is shown in italics. Above diagonal is the number of species shared between pairs, below the diagonal is the dietary overlap values calculated according to Sørensen's similarity index.

	N	Hm	Am	Ta	Sp	Cn	Efc	Ch^1	Mr	Pr	Rod^1
N		*21*	*18*	*9*	*13*	*37*	*111*	*39*	*41*	*39*	*50*
Hypsipetes madagascariensis (Hm)	*21*		10	5	5	11	14	8	10	9	3
Alectroenas madagascariensis (Am)	*18*	0.51		7	4	10	14	9	8	9	8
Treron australis (Ta)	*9*	0.33	0.52		2	5	6	5	4	4	3
Streptopelia picturata (Sp)	*13*	0.29	0.26	0.18		8	10	7	7	5	2
Coracopsis nigra (Cn)	*37*	0.38	0.18	0.22	0.32		27	18	16	14	10
Eulemur fulvus collaris (Efc)	*111*	0.21	0.21	0.10	0.16	0.36		35	35	35	42
Cheirogaleus spp. (Ch)	*39*	0.27	0.32	0.21	0.27	0.47	0.47		27	20	18
Microcebus rufus (Mr)	*41*	0.32	0.27	0.16	0.26	0.41	0.46	0.67		23	19
Pteropus rufus (Pr)	*39*	0.30	0.32	0.17	0.19	0.37	0.47	0.51	0.57		14
Rodents (Rod)	*50*	0.08	0.24	0.02	0.06	0.23	0.52	0.40	0.42	0.31	

[1] Congeneric species are treated together, as well as both rodent species which could not always be attributed to a single species

Dispersal and predation role

The 'true' frugivorous bird species *Alectroenas madagascariensis, Treron australis,* and *Hypsipetes madagascariensis* dispersed seeds of most of the species they fed on. Ripe fruits were nearly always swallowed and thus dispersed (Table 2). *Streptopelia picturata* was considered a seed predator feeding on seeds on the ground but due to its shy nature, feeding behaviour could not be observed in detail and thus the fate of consumed seeds remains unclear. *Coracopsis nigra* occasionally dropped fruits under the parent plant or flew away with intact fruits but for the majority of their food resources, they acted as seed predators, either destroying seeds directly with their beak or feeding on unripe fruits (Bollen and Van Elsacker, Chapter 3b). In contrast, *E. f. collaris* is an important seed disperser for a large number of plant species. During feeding this species was messy, swallowing numerous seeds while dropping others under the parent plant and this happened for a third of their consumed plant species (Table 2). Furthermore, for some plant species it ate unripe fruits, thus destroying the seeds this way. *Cheirogaleus* spp. and *M. rufus* as well as *P. rufus* act as seed dispersers for smaller seeds and as seed droppers for larger ones. *P. rufus* may participate in dispersal at short distances as they carry larger fruits to nearby feeding roost and drop the seeds there. Rodents often tear off and do not consume the fibrous flesh, which surrounds nuts. Both rodent species clearly preyed on seeds of numerous species, but intact and even germinated seeds of four species were found at feeding sites. No secondary seed dispersal through caching could be detected (Table 2).

DISCUSSION

Food selection based on taxonomy, morphology, biochemistry and phenology

Even though in the literature numerous examples exist of plant families that are typically consumed by birds such as Lauraceae Myristicaceae, Areceae, Burseraceae, and others (McKey 1975; Snow 1981; Corlett 1998; Oliveira et al. 2002) or by flying foxes such as Moraceae, Anacardiaceae, Guttiferae, Myrtaceae, Areceae, and Sapotaceae (Marshall 1983; Banack 1998; Corlett 1998) no clear dominant plant families could be found within the diets of any of the consumer species. The families best represented correspond with the dominant plant families of the littoral forest. This may be linked either to the fact that Madagascar has a high percentage of endemic plant species which may alter the overall floral composition compared to other tropical forests (Schatz 2001) or that the depauperate guild of frugivores does not discriminate its diet taxonomically.

The main food preferences for all consumers are related to morphological fruit traits. Worldwide in studies on fruit-frugivore interactions size, colour, and fruit protection seemed to be the most important traits in fruit selection. Among these, fruit and/or seed sizes were found to be most significant and related to the body size of the consumers. The gape size of frugivorous birds limits the maximum seed diameter of fruits they can swallow, while mammals have teeth and have other means to eat larger fruits (Fleming et al. 1987; Dowsett-Lemaire 1988; Corlett 2002). For this reason, in our study, as in most studies, birds seem to select significantly smaller fruits than mammals (Snow 1981; Janson 1983; Knight and Siegfried 1983; Gautier-Hion et al. 1985; Wheelwright 1986; Herrera 1987; Debussche 1988; Debussche and Isenmann 1989; Jordano 1995; Corlett 1996; Lambert 2002; Pizo 2002; Carlo et al. 2003). *Eulemur fulvus collaris* in this respect is very important in the local community as it is the only seed disperser of the larger fruit species. Nevertheless fruit size distinction is weakened by the fact that some bird species can pick up broken parts of fruits and eat larger soft fruits in a piecemeal fashion (Kitamura et al. 2002; Pizo 2002). As a result some studies did not find a significant difference in size of bird and mammal consumed fruits (Gautier-Hion et al. 1985; Voigt 2001; Poulsen et al. 2002).

As for fruit protection, mammals are able to feed on fruits with a thick husk (Birkinshaw 2001; Kitamura et al. 2002; Lambert 2002), whereas birds select more frequently those with a thin husk or dehiscent fruits (Janson 1983; Gautier-Hion et al. 1985; Kitamura et al. 2002). However, it seems that not all mammals eat thick-husked fruits. In our study *E. f. collaris* and *P. rufus* did, whereas the *Cheirogaleus* spp. and *M. rufus* nevertheless preferred thin-husked fruits. Another important trait for feeding selection is supposed to be represented by the external colour of ripe fruits, though little agreement exists on this topic. One consistency throughout all studies, including this one, is that birds eat many red and black fruits (McKey 1975; Charles-Dominique et al. 1981; Janson 1983; Knight and Siegfried 1983; Gautier-Hion et al. 1985; Debussche 1988; Dowsett-Lemaire 1988; Horvitz et al. 2002; Kitamura et al. 2002; Poulsen et al. 2002; Voigt et al. 2001). For primates in particular, different results have been found which is likely related to their different visual acuity in different parts of the world. Lemurs have no or limited colour vision, whereas New World primates have dichromate and Old World primates trichromate vision (Jacobs 1995; Dominy and Lucas 2002; Surridge et al. 2003). Nevertheless in many studies dull coloured fruits such as green, brown, yellow, and orange are eaten by mammals and/or primates (Janson 1983; Knight and Siegfried 1983; Terborgh 1983; Gautier-Hion et al. 1985; Dowsett-Lemaire 1988; Birkinshaw 2001; Kitamura 2002; Poulsen et al. 2002) but at some sites, including ours, these species do not avoid bright colours either (Janson 1983; Knight and Siegfried 1983; Gautier-Hion et al. 1985; this study). Few studies include odour in their dataset, as this is a subjective measure. Nevertheless it is common knowledge that birds forage upon visual detection whereas mammals make use of olfactation. For the remaining morphological fruit traits scored, there does not exist a general understanding in literature, nor a clear food preference for certain consumer species in our dataset.

While most studies on fruit preferences concentrate on morphological traits, biochemical characteristics are rarely considered (Janson et al. 1986; Herrera 1987; Ganzhorn 1988; Jordano 1995; Izhaki 2002; Pizo 2002). The most common finding is that mammals in general avoid lipid-rich fruits whereas birds may favour them (McKey 1975; Debussche and Isenmann 1989; Jordano 1995). This differential preference for lipids corresponds indeed with our findings of frugivorous birds, *E. f. collaris,* and *P. rufus*. The only other trend found was that nocturnal lemurs that go into torpor favour sugar-rich fruit pulp. For *Cheirogaleus medius* this preference during prehibernation fattening was already described by Bonnaire and Simmen (1994) and Fietz and Ganzhorn (1999). In Sainte Luce, fruits are relatively low in tannin values (as elsewhere in Madagascar: Iaconelli and Simmen 2002) and the consumer species did not seem to avoid fruit species with high tannin content. Bairlein (1996) mentioned that tannins in general seem to be less detrimental for avian frugivores than others, which seems to be true for *Coracopsis nigra* at our site. Besides the differences mentioned above, the remaining chemical components varied little among consumer species and did not seem to determine their feeding selection as was shown by other studies (Corlett 1996; Pizo 2002).

As mentioned in the results, several of these food preferences do no longer remain significant after sequential Bonferroni adjustment. There has been a great deal of discussion on whether to apply these adjustments or not. Recently Moran (2003) has come up with some arguments for the rejection of this adjustment. All the same, we believe that several of our initial significant findings, which are no longer significant after rigorous adjustment for increasing type I errors, do represent biological meaningful results which are confirmed by similar results from several other studies.

Selection criteria of granivores ought to differ from those of frugivores based on other traits, such as seed length and protection as granivores target the seed instead of the pulp. To look for their nutritional preferences, biochemical analyses of seeds are necessary. The finding that drupes dominate the diet of rodents may indeed indicate a protection of the large seeds against seed predation.

Besides the obvious fruit traits phenology further has a strong impact on food composition. During bottlenecks, feeding preferences are probably not as prevalent as when fruit is abundant. Therefore frugivores have to be flexible in their dietary strategy by enlarging their home range and/or modifying their activity pattern (such as *E. f. collaris,* Donati 2002), leaving the study area (like *Coracopsis vasa*), foraging outside the littoral forest (like *P. rufus*) (Bollen and Van Elsacker 2002a, Chapter 3a) or going into torpor when food is scarce (such as *Cheirogaleus* spp. and *M. rufus*). Goodman and Ganzhorn

(1997) already pointed out that frugivores in Madagascar might have adapted to lean periods by having broad diets (parrots and lemurs) and moving considerable distances in search of food (*P. rufus* and fruit pigeons). For post-dispersal granivores food availability is less problematic as seeds are available much longer than fruits.

Thus in general few traits consistently determine food selection of the thirteen consumer species in the littoral forest. There may be several reasons for this. First, most frugivores in Sainte Luce seem to be flexible to eat what is available. Secondly, the large dietary overlap among frugivores at our site indicates diffuse mutual relationships between plant and consumer species, which is similar to most other study sites (Terborgh 1983; Gautier-Hion et al. 1985; Dowsett-Lemaire 1988; Debussche and Isenman 1989; Kitamura et al. 2002; Carlo et al. 2003). In this respect, Fleming (1979) pointed out that in the Paleotropics dietary overlap is generally higher than in the Neotropics. This is probably linked to the higher spatio-temporal patchiness of fruit resources here that favours dietary generalisation, higher inter-specific dietary overlap, and fewer coexisting species if food levels become critically low. This may indeed be true for the littoral forest where high inter and intra-annual differences can be found in ripe fruit availability (Bollen and Donati, Chapter 1). This might represent one of the reasons why Madagascar's guild of frugivores is depauperate (Fleming et al. 1987; Langrand 1990; Ganzhorn et al. 1999b; Wright 1999) and has higher levels of dietary overlap than found at other sites.

Diet of frugivores and their role in seed dispersal and/or predation

E. f. collaris has a highly frugivorous diet at Sainte Luce (74.0% ripe fruits, 5.4% unripe fruits) (Donati 2002), which corresponds with findings from other studies on *Eulemur* species (Overdorff 1993a,b; Rigamonti 1993; Curtis 1997; Birkinshaw 1999, 2001). *E. f. collaris* can be considered a sequential specialist, feeding on a wide array of endemic fruit species (111 species) but with only two to three dominant fruit species each month (Donati 2002). Their relatively large home range (up to 100ha) and extensive day range lengths (1500-3500m) (Donati 2002) indicate that long distance seed dispersal within a fragment is likely. Furthermore, being the largest frugivores they represent a large proportion of the frugivore biomass in this ecosystem. They eat high amounts of fruit throughout the year and are the only ones that are able to swallow larger seeds. All these aspects suggest that indeed *E. f. collaris* is one of the most important seed dispersers in this ecosystem. The only limiting factor is that this species is reluctant to cross the grassland between fragments and thus rarely disperses seeds across the boundaries of the fragment. This important role in seed dispersal has been found for other *Eulemur* and lemur species (Ralisoamalala 1996; Scharfe and Schlund 1996; Dew and Wright 1998; Ganzhorn et al. 1999a; Birkinshaw 1999, 2001; Britt 2000).

The smaller nocturnal lemurs seem to have a less diverse fruit diet and can be considered more omnivorous (Martin 1973; Petter et al. 1977; Hladik et al. 1980; Tattersall 1982), even though several studies in different forest types found that a high proportion of fruit is included in the diet of *Microcebus rufus* (Wright and Martin 1995; Atsalis 1999). Fietz and Ganzhorn (1999) recorded 25 fruit species in the diet of *Cheirogaleus medius* in the western dry deciduous forest of Kirindy (CFPF). Atsalis (1999) scored 24 fruit species of *M. rufus* in the mid-altitude humid forests of Ranomafana. Compared with these numbers our list of food items likely represents the bulk of their diet in the littoral forest. These lemurs are smaller in body size, eat less, occupy limited ranges (1-4ha, Fietz 1999; Atsalis 2000), and have a rather limited gape size. Furthermore in Sainte Luce as in other Malagasy forests (Fietz and Ganzhorn 1999;

Schmid 2000) *Cheirogaleus* spp. and *M. rufus* go into torpor from May through October, which restricts their feeding and thus also dispersal activity to austral summer. These species are often found at forest edges and in secondary forest throughout Madagascar (Petter et al. 1977) as well as in Sainte Luce. This makes them important seed dispersers for small-seeded plant species that fruit during austral summer. So far, few data are available on the dispersal role of these nocturnal lemurs but Wright and Martin (1995), Ganzhorn and Kappeler (1996), Dew and Wright (1998), and Atsalis (1999) have suggested that they are indeed possible seed dispersers for small and medium sized fruits, which are found intact in their droppings.

Pteropus rufus feeds on a wide array of endemic plant species in Sainte Luce and is the most important long distance seed disperser in the littoral forest. A colony of 300 *Pteropus rufus* eats high quantities of fruit each night, defecates during flight, and covers great distances between sleeping and feeding roosts (up to 50km) (Bollen and Van Elsacker 2002a, Chapter 3a). By bridging isolated forest fragments *P. rufus* helps to ensure genetic exchange between plant populations and forest fragments and even regeneration in clearings. Passage through the gut does not seem to destroy the seeds (Bollen and Van Elsacker 2002a, Chapter 3a).

Few data exist on the diet of both Malagasy fruit pigeon species. However, other studies in the Paleotropics recorded a frugivorous diet for seed dispersing fruit pigeons (Van der Pijl 1969; Corlett 1998; Dowsett-Lemaire 1988; Oliviera et al. 2002), even though Snow (1981) described *Treron australis* as a seed predator of *Ficus* seeds. Goodman et al. (1997b) mentions as well that a large component of the diet of *T. australis* ate *Ficus* fruits. Fruit pigeons have large home ranges and can wander daily 10-12km from their roost (Dowsett-Lemaire 1988; Fleming 1992). In Sainte Luce, they feed on ripe fruits only and always swallow the entire fruit, digesting only the fleshy parts and defecating the seeds, as observed by Van der Pijl (1969), Corlett (1998) and Oliveira et al. (2002). In the littoral forest fruit pigeons seem to be efficient seed dispersers of numerous plant species because they have wide gapes (Corlett 1998), cover great distances and use secondary and disturbed habitats dispersing also seeds from pioneer and heliophil species from perches in a range of habitats. Both short and long-distance seed dispersal occurs. Preliminary results of germination trials demonstrate that passage though the digestive tract of *Alectroenas madagascariensis* does not have a negative impact on germination (Bollen unpubl. data).

Hypsipetes madagascariensis is an important seed disperser as well, feeding at lower heights than fruit pigeons and parrots. This species swallows ripe fruits entirely and defecates the seeds unharmed (Birkinshaw 2001; Bollen unpubl. data). Bulbuls are very tolerant to disturbance and often the most common frugivores and dispersal agents in degraded tropical and subtropical forests including urban areas (Corlett 1998). In Sainte Luce this species could be encountered in intact forest as well as on forest edges.

Only limited data are available on the diet of *Coracopsis nigra* (Goodman et al. 1997a; Hampe 1998; Dowsett 2000), thus the 37 food species that were recorded in Sainte Luce seem to be quite representative. Most data are from *C. nigra*, which is present at the site year round, whereas *C. vasa* is encountered less frequently and during certain periods of the year only. *Coracopsis nigra* destroys seeds of many endemic plant species. They can be considered pre-dispersal seed predators in this ecosystem. Occasional seed dispersal may occur but for few species and on rare occasions only. Even though substantial differences occur between the numerous parrot species present worldwide, they are often referred to as granivores (Janzen 1981; Jordano 1983; Clout

1989; Galetti 1993; Saini et al. 1994; Pizo et al. 1995; Corlett 1998; Renton 2001). For Madagascar Goodman et al. (1997a; 1997b) observed seed predation of *Ficus* seeds by *Coracopsis* spp., while Böhning Gaese et al. (1999) described *C. nigra* as an occasional seed disperser for *Commiphora guillaumini*.

According to the literature most *Streptopelia* spp. feed largely on dry seeds and fruits and destroy most of the seeds they swallow in their muscular gizzards (Corlett 1998). However, *S. decaocto* is said to regurgitate some large seeds (Corlett 1998). *S. picturata* was most often seen feeding on the ground but no details on its feeding behaviour could be obtained at our study site. Nevertheless this species is suspected to be a post-dispersal seed predator destroying most seeds, which is confirmed by Goodman et al. (1997b). Obviously our list of food items sampled for this bird is largely underestimated compared to their actual diet.

Before humans settled, the only seed predators in Sainte Luce were *Coracopsis* spp., *S. picturata,* and *Eliurus webbi*. The latter now has to contend also with a non-native rodent species (*Rattus rattus*) even though there are no indications for food or habitat competition between these two rodent species (Ramanamanjato and Ganzhorn 2001; Ganzhorn 2003). Evidence of post-dispersal predation by rodents destroying the seeds of fifty plant species was found, but Goodman and Sterling (1996) and Ganzhorn et al. (1999a) suggested that native Malagasy rodents may store seeds in their burrows but no evidence has been found so far for *Eliurus webbi* in the littoral forest. Goodman (1994) describes a burrow of *E. webbi* in Andringitra containing 20 seeds of *Cryptocarya* sp. of which only half were eaten. In Sainte Luce a few seeds were observed to escape total destruction when germinating from the rodents’ food piles. This diet list can serve as a first indication on the rodents’ food species in the littoral forest, taking into account that completely digested seeds are missing here. Nevertheless by targeting seeds of selected species, rodents can significantly alter forest composition (DuPuy 1996; Spehn and Ganzhorn 2000).

Besides the described frugivores (Table 1), there are also other animal species in Sainte Luce that occasionally feed on fruits. Bird species such as *Coua caerulea* (Cuculidae) and *Zosterops maderaspatana* (Zosteropidae) (also observed by Goodman et al. 1997a) could be seen feeding on fruits in Sainte Luce, as well as the terrestrial mammal *Tenrec ecaudatus* (Tenrecidae) and the fruit bats *Rousettus madagascariensis* and *Eidolon dupreanum* (Pteropodidae), but the latter species were very difficult to track. Local people may also act as seed dispersers when collecting several fruit species (n=12, App. I). As secondary seed dispersers *Pheidole* spp. (Myrmicinae) seem to be important and they were observed to transport intact seeds of at least 20 species to their ground nests, thus matching the important role of ants in other forests of Madagascar (Voigt et al. 2002; App. I).

As mentioned above, the dispersal quality of the frugivores differs substantially. Frugivores are active at different times of the day and year, forage at different heights, have distinct feeding behaviour, gut passage rates, and seed shadows. While birds may defecate from nearby or far away perches either within primary forest or in the clearings, flying foxes defecate during flight or under feeding or sleeping roosts, rodents concentrate seeds at burrows or feeding sites and lemurs move seeds within the forest fragment only. In the end, the combined action of a variety of fruit-eating vertebrates with distinct seed shadows produces a very heterogeneous transport of seeds, which is very important in the severely fragmented and degraded littoral forest to ensure regeneration of most plant species within and outside forest fragments. So even though dietary overlap among consumers based on species partitioning is high in Sainte Luce, the different frugivore species are not ecologically redundant due to their differential impact. Moreover, the actual diet overlap may be lower than described here because proportional use of diet items should be included (Poulsen et al. 2002). In terms of conservation *E. f. collaris* is of crucial importance for the dispersal and regeneration of large seeded plant species, *P. rufus* for long distance dispersal across fragment boundaries and frugivore bird species for enhancing succession and regeneration of plants in degraded areas.

Although our dietary records for each consumer species are not exhaustive, it is assumed that the interactions reported here are an unbiased sample and thus that the patterns found provide an accurate picture of how interactions are organized in the littoral forest on a species-specific as well as on a community level. On the one hand, species-specific fruit choice is to a limited extent determined by a particular set of morphological, biochemical, and phenological traits. However, on the other hand, there is substantial dietary overlap among species. Unpredictable food availability in the littoral forest may have led to this diet generalisation and to a species-poor frugivore guild as well. However, each frugivore has its own particular impact in the seed dispersal of plant species. As the littoral forests become more fragmented, the remaining patches become increasingly isolated, and heterogeneous seed transport within and between forest patches becomes more critical for long-term species survival.

ACKNOWLEDGEMENTS
We are very grateful to QMM (QIT Madagascar Minerals) for providing logistics and infrastructure at the study site. In particular we thank Manon Vincelette, Jean-Baptiste Ramanamanjato, and Laurent Randrihasipara of the QMM Environmental and Conservation Team. Special thanks go to Giuseppe Donati, Nicoletta Baldi, and Valentina Morelli from the University of Pisa (Italy) for making their data on fruit eating by *Eulemur fulvus collaris* available. This draft benefited greatly from suggestions of Steve Goodman, for which many thanks. This study was carried out under a Collaboration Agreement between the Department of Animal Biology and Department of Anthropology of the University of Antananarivo and the Institute of Zoology of Hamburg University and QMM. The first author is supported by a grant from the Belgian Fund for Scientific Research, Flanders (FWO). We thank the Flemish Government for structural support to the CRC of the RSZA.

Appendix I. All plant species that are included in the diet lists of the consumer species with indication of the method how these data were gathered (O:observation, T: feeding marks; F: faecal droppings). Abbrevations of the species are Efc for *Eulemur fulvus collaris, Ch* for *Cheirogaleus spp., Cm* for *C. medius,* CM for *C. major,* Mr for *Microcebus rufus*, Am for *Alectroenas madagascariensis*, Ta for *Treron australis, Sp for Streptopelia picturata*, C for *Coracopsis nigra*, Hm for *Hypsipetes madagascariensis,* Pr for *Pteropus rufus,* Rod for both rodent species, Rr for *Rattus rattus* and Ew for *Eliurus webbi*. SD refers to secondary seed dispersal by Pheidole sp. and Hss stands for humans. For certain plant species no *antanosy* names existed, so codes (such as x205, FT62) or other descriptions to distinguish between species were used.

		Vernacular		Lemurs				Birds					Bats	Rats			Other	
Family name	Species name	Antanosy names	Efc	Ch	Cm	CM	Mr	Am	Ta	Sp	C	Hm	Pr	all	Rr	Ew	SD	Hss
?	*?*	fanotabe	F															
?	*?*	sarikafe	O															
?	*?*	vahifotsy be	O															
?	*?*	x205												T				
?	*?*	x209	OF															
Anacardiaceae	*Campnosperma micranteium*	roandria	OF															
	Poupartia chapelieri	sisikandrongo	OF	OT	OT	OT	OT				O			T			O	
	Protorhus cf. *lecomtei*	kangy	F															
Annonaceae	*Monanthotaxis* cf. *malacophylla*	vahimbotany	OF	OT	OT			O						T				
	Polyalthia capuronii	menapeka	OT											T				
	Polyalthia madagascariensis	fotsivavo	OF	OT	OT		OT	OF			O	OF	F	T				
	Polyalthia sp.1	fotsivavo géante	O															
	Polyalthia sp.2	fotsivavo marécage	OF															
Apocynaceae	*Cabucala madagascariensis*	tandrokosy					OT				O						O	O
Araliaceae	*Polyscias* sp.	voatsilana sp2	OF					OF	O	O	O	O	F					
	Schefflera rainaliana	voatsilana sp1	O					O			O	O						
Arecaceae	*Dypsis fibrosa*	boakandambo	OF											T	T	T		
	Dypsis nodifera	raotry	OF	OT	OT		OT						TF					
	Dypsis prestoniana	boakabe	OF	OT	OT	OT		OF		O	O	O	O				O	
	Dypsis saintelucei	telopolombilany	OF															
	Dypsis scottiana	raosy	OF	OT	OT			F	F					T			O	
Bignoniaceae	*Ophiocolea delphinensis*	akondronala	F										T					O
	Phyllarthron ilicifolium	zahambe	OF															
	Phyllarthron sp.	zahambe manongaroa	F															
Burseraceae	*Canarium boivinii*	ramy	O											T		T		
Canellaceae	*Cinnamosma madagascariensis*	vahabatra 3eM	OTF										F					
Capparaceae	*Crataeva obovata*	belataka	OTF											T				
Celastraceae	*Mystroxylon aethiopicum*	voavoantatsimo	OT											O				
	Polycardia phyllanthoides	fandrianakanga	F															
Clusiaceae	*Garcina chapelieri*	haziny tomate	OT															
Clusiaceae	*Garcinia* cf/aff *madagascariensis*	disaky kely	OT											T				
	Psorospermum revolutum	harongampanihy		T			OT					O					O	O
Combretaceae	*Terminalia fatraea*	katrafa	OF	OT			OT	OF			O		OTF	T			O	

Appendix 1 Continued

		Vernacular	Lemurs							Birds			Bats	Rats			Other	
Family name	Species name	Antanosy names	Efc	Ch	Cm	CM	Mr	Am	Ta	Sp	C	Hm	Pr	all	Rr	Ew	SD	Hss
Connaraceae	*Agelea pentagyna*	rehiba									O							
Dichapetalaceae	*Dichapetalum* sp.	vahihazo	OF											T				
Ebenaceae	*Diospyros* sp.1	hazomainty blanc	OT															
	Diospyros sp.2	hazomainty	OTF															
Elaeocarpaceae	*Elaeocarpus alnifolius*[1]	x201	O											T				
	Elaeocarpus alnifolius[1]	sanga	OF											O¯	T	T		
Ericaceae	*Vaccinium emirnense*	tsilantria	OT	OTF	OTF		OTF		OF		O	O	F				O	O
Erythroxylaceae	*Erythroxylum braxifolium*	fangora sp1	F								OF	O						
	Erythroxylum nitidilum	fangora sp2	OF					OF			OF			T				
Euphorbiaceae	*Anthostema madagascariensis*	bamby	OF															
	Euphorbia tetraptera	famanta												T				
	Macaranga perrieri	mocarana	F								O	O						
	Suregada baronii	x225								O	O							
	Uapaca ferruginea	voapaky lahy	OF	OTF	OT	OT	OT						OF	T				
	Uapaca littoralis	voapaky vavy	OF	OTF	OT	OT	OT				OT		OTF	T	T	T	O	
	Uapaca thouarsii	voapaly lahy ZJ	TF	OTF		OT	OTF						F	T		T		
Fabaceae	*Cynometra* cf. *cloiselii*	mampay	O											T				
	Phylloxylon xylophylloides	sotro												T				
Flacourtiaceae	*Aphloia theiformis*	fandramana					O			O		O						
	Bembicia uniflora	bemalemy	OF	O	O						O							
	Homalium louvelianum	ramirisa									O							
	*Ludia antanosarum**	hazofotsy	OT				OT						F					
	*Ludia antanosarum**	zorafotsy	OT	OT			OT				OT		F					
	Scolopia orientalis	zoramena	OT	OT	OT		OT			O			OF	T		T	O	
Grossulariaceae	*Brexia* sp.	kambatrikambatri	OF	OF	OF		F						F	T				
Hamamelidaceae	*Dicoryphe stipulaceae*	zorala												T				
Hippocrateaceae	*Salacia madagascariensis*	voatsimatra	OT											T				O
Icacinaceae	*Apodytes dimidiata*	hazomamy marécage	OF	O	O	O	O	OF	O		T	O		T				
	Apodytes sp. nov.	hazomamy an ala	T											T				
Lauraceae	*Beilschmiedia madagascariensis*[1]	tavolohazo février	F				T							T	T	T		
	Beilschmiedia madagascariensis[1]	resonzo					T						T	T				
	Cryptocarya sp.	tavolohazo novembre	O				T	OF										
	Ocotea sp.	varongy	O					OF					F					
Lecythidaceae	*Barringtonia butonica*	lokaza										O						
Liliaceae	*Dracaena reflexa* var. *nervosa*[1]	falinandro	O				T						F					
	Dracaena reflexa var. *nervosa*[1]	tavolobotroka	O										F					
Loganiaceae	*Anthocleista longifolia*	lendemilahy	OTF	OT			F						F	T				
	Anthocleista madagascariensis	lendemibe											F					
Loranthaceae	*Bakerella ambongoensis*	velomihanto sp.1		OF							O		F				O	

Appendix 1 Continued

		Vernacular			Lemurs					Birds			Bats		Rats		Other	
Family name	Species name	Antanosy names	Efc	Ch	Cm	CM	Mr	Am	Ta	Sp	C	Hm	Pr	all	Rr	Ew	SD	Hss
Loranthaceae	*Bakerella* sp.	velomihanto sp.2		OF			OF	F			O	O	F					
Melastomataceae	*Tristemma mauritianum*	voatrotoky												T			O	O
Meliaceae	*Malleastrum mandenense*	sarigoavy	O															
Menispermaceae	*Burasaia madagascariensis*	faritsaty	F	OT		OT								T	T	T		
Monimiaceae	*Tambourissa castri-delphinii*	amborabe	OF									O					O	
	Tambourissa purpurea[1]	ambora	OF				O	OF				O	F	T		T	O	
	Tambourissa purpurea[1]	amboralahy	O										F	T			O	
Moraceae	*Ficus baroni*	aviavy	O										F					
	Ficus guatteriifolia	fihamy	F										F	T				
	Ficus pyrifolia	nonoka	O	O			O	O	O				O	F				
	Trilepisium madagascariense	berono	OF	O	O													
Myricaceae	*Myrica spathulata*	tsilaka						OF	OF			O						
Myristicaceae	*Brochoneura acuminata*	mafotra sp.1	O											T				
	Brochoneura madagascariensis	mafotra sp.2	O											T				
Myrsinaceae	*Embelia incumbens*	taratasy	O															
Myrtaceae	*Eugenia cloiselii*	ropasy sp.1	OF	OT	OT													
	Eugenia sp.	ropasy sp.2	OF															
	Psidium guayave	guavy		T							O							O
	Syzygium sp.1	rotry ala	OF	O			O							T	T	T	O	O
	Syzygium sp.2	rotry mena	OF	O	O		O	OF		O	O	O	O				O	O
Ochnaceae	*Campylospermum obtusifolium*	hazombato						O	O	O	O						O	
Oleaceae	*Jasminum kitchingii*	vahifotsy kely	OF							O	O							
	Noronhia cf. *lanceolata*	hazondraotry									O	O						
	Noronhia sp.1	belavenoka	O								O			T	T			
	Noronhia sp.2	x236												T				
	Olea sp.	vahabatra	OF	OT		OT	OT				OT			T	T	T	O	
Pandanaceae	*Pandanus* aff. *longistylus*	fandranabo	O															
	Pandanus dauphinensis	vakoanala	OF															
	Pandanus rollotii	fandranabotonboky	O															
Rubiaceae	genus indet.	tainbarika	F										F					
	Canthium sp.	Rubiaceae ZJ					OT											
	Canthium variistipula	fantsikaitramainty	OF	OT			OT				O		F					O
	Ixora sp.	x203	OF	OT									F					
	Mapouria aegialodes	x210a	O									O	F					
	Mapouria sp.	x210	OF				O						F					
	Morinda cf. *umbellata*	vahilengo	O								O							
	Morinda rigida	lehengobe	O								O							
	Peponidium sp.	fantsikaidroka	F											T				
	Plectronia densiflora	fantsikaitra	O	O														

Appendix 1 Continued

		Vernacular	Lemurs					Birds					Bats	Rats			Other	
Family name	Species name	Antanosy names	Efc	Ch	Cm	CM	Mr	Am	Ta	Sp	C	Hm	Pr	all	Rr	Ew	SD	Hss
Rubiaceae	*Psychotria* sp.1	tanatananala	O				T											
	Pyrostria sp.	fantsikaitrafotsy	O															
	Rothmannia mandenensis	taholagna	OTF										F	T				O
	Saldinia littoralis	mangavoa	O	O			O			O		O						
	Tarenna thouarsiana	FT 62	F															
	Tricalysia cf *cryptocalyx*	hazongalala	F				O					O	F					
Rutaceae	*Vepris eliotii*[1]	ampoly	OF	OT	OT		O		F		O		F					
	Vepris eliotii[1]	lahinampoly	OF	O			O							T				
	Vepris fitoravina	fitoravina	OTF	OT	OT		OT				OT			T				
Sapindaceae	*Macphersonia radlkoferi*	sanirambaza	O	O			O											
	Plagioscyphus jumellei	ambirimbarika pionair												T				
	Tina thouarsiana	sanirambavy	O				OT			O	OT			O				
	Tinopsis conjugata	sagnira sp3	OTF								OT							
Sapotaceae	*Mimusops commersonii*	natohetiki	O															
	Syderoxylon beguei	ambirimbarika	O								OT		F					
Sarcolaenaceae	*Leptolaena* sp.	fotombavy	OF	OF	OF	OF	O			O								
	Sarcolaena multiflora	meramaintso	OTF	OT	OT	OT	OT			O	OT		F				O	O
	Schizolaena elongata	fotonday	OF	O						O								
Smilaceae	*Smilax anceps*	fandrikatany	F															
Sphaerosepalaceae	*Rhopalocarpus coriaceus*	tsilavimbinanto	F															
Strelitziaceae	*Ravenala madagascariensis*	ravenala									O							
Taccaceae	*Tacca leontopetaloides*	tavolo	OTF											T				
Theaceae	*Asteropeia multiflora*	fanolafotsy	O				T											
Ulmaceae	*Trema orientalis*	andrarezona						O	O			O					O	
Verbenaceae	*Vitex chrysomallum*	nofotrako	OF															

[1] as indicated by their vernacular name several species correspond to the same scientific name. They could represent different ecotypes of one same species or be different species that have no taxonomic names yet. As this is difficult to affirm at the moment we preferred treating all vernacular names as separate species throughout this paper.

3a

Feeding ecology of *Pteropus rufus* (Pteropodidae) in the littoral forest of Sainte Luce (south-east Madagascar)

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ACTA CHIROPTEROLOGICA 4(1): 33-47 (2002)

ABSTRACT

This paper examines bat-plant interactions by focusing on the fruit diet and food selection of flying foxes (*Pteropus rufus*) in the littoral forest fragments of Sainte Luce, south-east Madagascar. Analyses of faecal samples and opportunistic observations revealed 40 endemic plant species in the diet. The flying foxes mainly eat odoriferous ripe and juicy berries. No particular fruit colour was predominant in their diet. Both multi-seeded and single-seeded fruits are eaten. Small seeds (1–3.5mm seed length) are usually swallowed whole. Passage through the digestive tract of the flying foxes does not reduce the germination rate of seeds nor the percentage of seeds germinated. This study indicates that the role of flying foxes in both short and long distance seed dispersal for a large number of endemic tree species of the littoral forest should not be underestimated when designing reforestation programs in particular or conservation action plans in general.

INTRODUCTION

Pteropus rufus is an endemic flying fox in Madagascar and belongs to the Old World family Pteropodidae (Megachiroptera). The genus *Pteropus* lives mainly on islands (Cheke and Dahl 1981; Banack 1998). Its representatives are almost entirely frugivorous, feeding mostly on fruit pulp, juices, nectar and occasionally also on leaves (Marshall 1983). *Pteropus rufus* occurs predominantly in the humid forests in the east and the north. Most roost sites are found in the coastal lowlands (Racey pers. comm).

Although some fragments of littoral forest can be found along the north-eastern coastline of Madagascar, most of it is situated in the south-east. In this report we concentrate on this south-eastern region and more in particular on the littoral forest of Sainte Luce (Fig. 1). This type of forest has been considerably reduced in size over time (Ramanamanjato 2000). Between 1950 and 1995, 3,400 ha, almost half of what was present in 1950, has disappeared. This represents a deforestation rate of 760 ha every 10 years (Mir Télédétection Inc. 1998). At present only highly degraded forest remnants and very few intact forest fragments remain.

In Sainte Luce a colony of 300–350 individuals of *P. rufus* inhabits the littoral forest fragment 'S6' (225ha) (Lewis Environmental Consultants 1992b). This colony has been located there for at least 10 years and according to the local people even longer. These flying foxes are very easily disturbed when approached as a consequence of severe hunting pressure and frequent bush fires in the area (Bollen pers. obs.). Currently there are at least two other roost sites of flying foxes in the region. The largest one contains 800–1000 individuals and is found in a private reserve, Berenty (25°00'S, 46°18'E; Ramanamanjato pers. comm., Fig. 1). In this gallery forest the flying foxes are more or less protected from hunting. Another roost site is found in a sacred forest 'Enato Anandrano' (24°55'S, 47°00'E) where the flying foxes are protected by the local *fady*, a Malagasy taboo related to the presence of tombs of the ancestors (Ramanamanjato pers. comm.). There is no information on the colony size here and its status as it is forbidden to enter these forests. In the lowland Anosyennes, up north of Sainte Luce, in Marovony and Analalava, two small roost sites, with less than 50 individuals each, were observed in isolated forest remnants (Lewis Environmental Consultants 1992b). The current status of both bat populations and forest fragments however is unknown (Fig. 1).

Due to the high degree of fragmentation and degradation of the littoral forest, long distance seed dispersal is important to ensure genetic exchange between plant communities of different forest fragments. At present not much information is available on the diet of *Pteropus rufus* in these littoral forests. Therefore, the main goal of this research is to investigate whether they act as important seed dispersers in this ecosystem by determining which plant species are eaten by these flying foxes. This study forms part of an extensive ecological research project on the mutual dependence of the frugivorous-granivorous guild and the littoral forest flora, more in particular on seed dispersal and predation. Because of this, the focus of this study is on frugivory only and not on nectarivory, and pollen analyses were not carried out.

METHODS

Research site and study period

The littoral forest of Sainte Luce is located in south-east Madagascar (24º45'S, 47º11'E) and is considered to be dense humid evergreen forest (Koechlin et al. 1974). It corresponds to the same forest type as mountain rain forest but grows on sandy soils and is always found within 2–3km of the coast at an altitude of 0–20m (Lewis Environmental Consultants 1992a). Field research was conducted by the first author between November 1999 and February 2001. During this research period annual precipitation was 2,487mm with a mean temperature of 23°C, ranging between 12°C and 33°C.

The forest fragments of Sainte Luce are considered the least degraded of all. In 1991 they represented a total area of about 1,947ha. A group of 20 fragments can be distinguished, separated by plains of grassland and swamps. The five larger fragments (S6, S7, S8, S9, and S17) range in size from 190 to 377 ha (Lewis Environmental Consultants 1992a). Distances between these five fragments vary from 1.5 to 5km. Most of them have been separated from each other at least since 1950 and have since then systematically declined in size due to human impact on the edges (Lewis Environmental Consultants 1992a). Today S6, S7, and S8 are further degrading by recent *tavy* (slash and burn followed by cultivation), bushfires, and selective logging (Bollen pers. obs.).

Fruit diet: faecal analyses and observations

Most of our data on the fruit diet of *P. rufus* was obtained by collecting and analysing faecal samples. From January 2000 till January 2001 the day roost of the *P. rufus* colony in S6 was visited once a week to collect faecal samples under the roost trees. On each visit as many droppings as possible were collected randomly with a minimum number of five droppings containing seeds. These samples were analysed for seed content, seed number per species and seed viability upon returning at the field station. A reference collection of the seeds gathered from several fragments of primary and secondary forest was made. It should contain the majority of fruits available within the littoral forest during our study period. This reference collection was used to identify the seed species during faecal analyses. For several *Ficus* spp., seeds were too similar to allow identification at species level. For these species identifications were based on the characteristics of the seedlings.

Observations on feeding behaviour were obtained during tree watches and during opportunistic encounters with flying foxes. Because of the difficulty of approaching flying foxes at night these data are limited. The following parameters were scored: visitation length, defined as the time elapsing between arrival of the first flying fox until departure of the last one in the feeding tree, number of individuals feeding and if possible feeding behaviour. Ejecta pellets collected under the tree were described by their characteristic feeding marks.

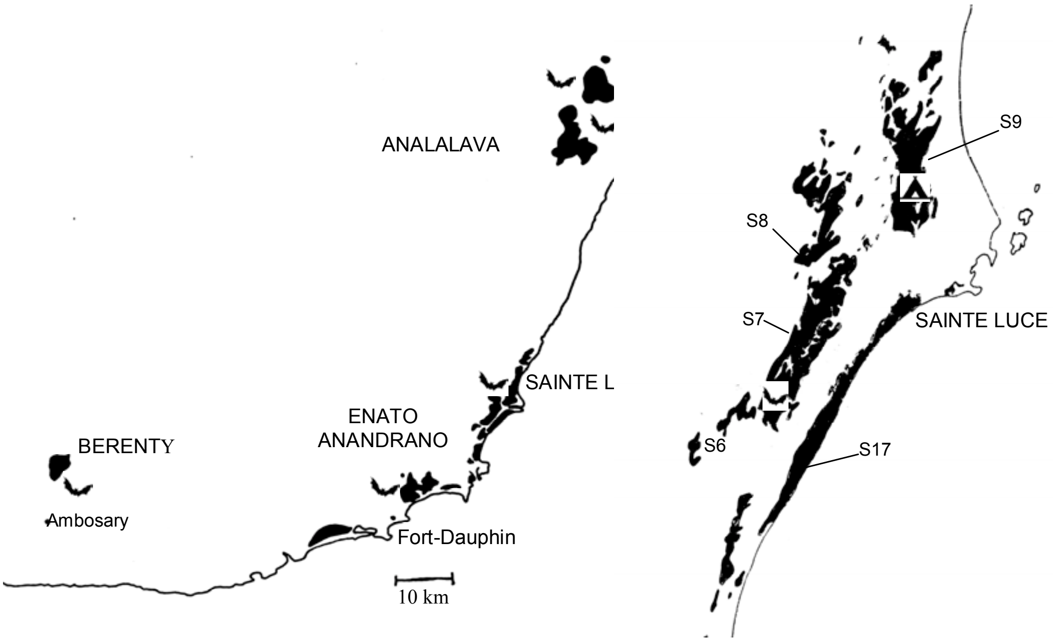

Fig 1. On the left a detail of the littoral forests (Marovony, Analalava, Sainte Luce, Mandena and Petriky) in the south-east is shown with the five *Pteropus rufus* colonies' roost sites indicated and on the right a detail shows the five biggest forest fragments of the Sainte Luce littoral forest with indication again on the bat's day roost (S6) and the campsite (S9).

Food selection: fruit and seed characterisation

The following characteristics of fruits and seeds were noted for a total number of 175 individual plant species available in the forest throughout our research period: growth form, fruit type, external colour at ripeness, odour, pulp type, fruit and seed length and mass, number of seeds per fruit, water content and fruit skin thickness. Large trees (>6m in height), small trees (<6m), shrubs, vines, herbs and epiphytes were the different growth forms considered. Fruit type definitions according to Lambert and Garber (1998) were followed and further lumped into the categories berries, drupes, synconia, capsules and others. External fruit colour could be green, yellow, orange, red or pink, blue or purple, brown, black, white and grey. Odour was scored as absent, present or strong.

Table 1. Overview of the fruit species consumed by P*teropus rufus* with indication of plant family, species or gender name and vernacular name, type of evidence (O: observation,F: faecal analyses, M: gnawing marks), growth form, fruit type, colour at ripeness, odour (S: strong; P: present, A: absent), pulp type, fruit length (mm) and weight (g), seed length (mm) and weight (g), number of seeds (NS) and percentage of watercontent (H2O). Fruit skin thickness was identical for all taxa (easily opened by nail) except for *Rothmannia mandenensis* (by knife only).

Family	Taxon	Vernacular name	Evid	Growth form
Annonaceae	*Polyalthia madagascariensis*	fotsivavo	F	large tree
Araliaceae	*Polyscias* sp.	voatsilana	F	large tree
Arecaceae	*Dypsis prestoniana*	boakabe	OFM	large tree
	Dypsis nodifera	raotry	MF	small tree/shrub
Bignoniaceae	*Ophiocolea delphinensis*	akondronala	M	small tree/shrub
Canellaceae	*Cinnamosma madagascariensis*	vahabatra	F	large tree
Combretaceae	*Terminalia fatraea*	katrafa	OMF	large tree
Ericaceae	*Vaccinium emirnense*	tsilantria	F	small tree/shrub
Euphorbiaceae	*Uapaca ferruginea*	voapaky lahy	OF	large tree
	Uapaca thouarsii	voapaky lahy ZJ	F	large tree
	Uapaca littoralis	voapaky vavy	OMF	large tree
	Ludia antanosarum [1]	hazofotsy	F	small tree/shrub
	Ludia antanosarum [1]	zorafotsy	F	large tree
Flacourtiaceae	*Scolopia orientalis*	zoramena	OF	large tree
Lauraceae	*Beilschmiedia madagascariensis*	resonzo	M	large tree
	Ocotea sp.	varongy	F	large tree
Liliaceae	*Dracaena reflexa* var. *nervosa* [1]	falinandro	F	small tree/shrub
	Dracaena reflexa var. *nervosa* [1]	tavolobotroka	F	small tree/shrub
Loranthaceae	*Bakerella ambongoensis*	velomihanto sp.1	F	epiphyte
	Bakerella sp.	velomihanto sp.2	F	epiphyte
Loganiaceae	*Anthocleista madagascariensis*	lendemibe	F	large tree
	Anthocleista longifolia	lendemilahy	F	small tree/shrub
Monimiaceae	*Tambourissa purpurea* [1]	ambora	F	small tree/shrub
	Tambourissa purpurea [1]	amboralahy	F	small tree/shrub
Moraceae	*Ficus baronii*	aviavy	F	large tree
	Ficus guatteriifolia	fihamy	F	large tree
	Ficus pyrifolia	nonoka	F	large tree
Myrtaceae	*Syzygium* sp.2	rotry mena	OMF	large tree
Rubiaceae	*Canthium variistipula*	fantsikaitramainty	F	large tree
	Tricalysia cf. *cryptocalyx*	hazongalala lahy	F	small tree/shrub
	Tricalysia sp.	hazongalala vavy	F	small tree/shrub
	Rothmannia mandenensis	taholagna	F	large tree
	genus indet.	tainbarika	F	large tree
	Ixora sp.	x203	F	small tree/shrub
	Mapouria aegialodes	x210a	F	small tree/shrub
	Mapouria sp.2	x210	F	small tree/shrub
Rutaceae	*Vepris elliotii*	ampoly	F	large tree
Sapotaceae	*Sideroxylon beguei* var. *saboureaui*	ambirimbarika	MF	large tree
Sarcolaenaceae	*Sarcolaena multiflora*	meramaintso	F	large tree
Saxifragaceae	*Brexia* sp.	kambatrikambatri	F	small tree/shrub

[1] as indicated by their vernacular name in three cases we found two plant species corresponding to the same scientific name. They could represent different ecotypes of the same species or they might be different species that have no taxonomic names yet. As this is difficult to affirm at the moment we preferred including all vernacular as separate units in our diet list and the 40 plant species are also treated as separate species throughout this paper

Table 1 Continued

Fruit	Colour	Odour	Pulp	Fruit		Seed		NS	H_20
type			type	length	weight	length	weight		(%)
berry	orange	A	soft & juicy	12.2	0.3	7.8	0.12	1	72
drupe	green	A	jiucy & hard	5.0	0.1	3.6	<0.01	1	73
berry	orange	P	soft & juicy	14.9	0.6	12.9	0.34	1	80
berry	yellow	A	soft & juicy	9.7	0.3	8.3	0.12	1	72
berry	purple	S	soft & juicy	192.9	-	7.6	0.15	150+	74
berry	brown	S	arillate	22.0	0.2	8.4	0.14	3-13	79
drupe	purple	A	juicy & fibrous	13.2	0.4	8.1	0.13	1	76
berry	red	A	soft & juicy	11.5	0.8	1.4	<0.01	100+	74
drupe	brown	S	soft & juicy	13.6	1.4	10.7	0.19	3 (4)	81
drupe	brown	S	soft & juicy	12.5	1.7	9.6	0.22	3	83
drupe	brown	S	soft & juicy	23.6	4.9	15.0	0.52	3	78
berry	red	A	soft & juicy	14.0	1.5	2.8	<0.01	6-8	93
berry	green	S	soft & juicy	12.5	1.0	3.2	3.00	2-11	62
berry	purple	S	soft & juicy	10.5	0.5	3.8	0.02	2-4	65
drupe	yellow	S	soft & juicy	27.7	8.5	20.1	5.70	1	78
berry	green	S	soft & juicy	25.0	1.4	15.3	0.57	1	70
berry	orange	S	soft & juicy	9.1	0.5	5.7	0.07	1-2-3	82
berry	orange	S	soft & juicy	15.5	0.9	5.8	0.08	(1)-2-3	88
berry	green	A	soft & juicy	8.0	0.1	4.6	<0.01	1	72
berry	green	A	soft & juicy	15.9	0.7	10.4	0.25	1	69
berry	yellow	S	juicy & fibrous	18.5	3.6	2.7	<0.01	80	76
berry	yellow	P	juicy & hard	30.3	5.9	3.4	0.99	50-84	70
drupe	red	A	arillate	43.8	54.2	11.3	0.29	15-70	80
drupe	red	A	arillate	17.8	5.6	7.5	0.09	6-12	89
synconia	brown	S	soft & juicy	13.0	1.2	-	<0.01	1000+	72
synconia	brown	S	soft & juicy	32.8	14.5	1.6	<0.01	1000+	93
synconia	red	P	arillate	6.3	0.1	1.0	<0.01	1000+	61
berry	purple	P	soft & juicy	9.6	0.5	8.1	0.31	1	86
drupe	brown	A	soft & juicy	7.8	0.3	6.3	0.06	2	68
berry	red	S	soft & juicy	10.9	0.4	4.9	<0.01	7 (5-6)	76
berry	red	P	soft & juicy	11.1	0.5	5.8	0.03	4-5-6	78
berry	brown	S	soft & juicy	40.4	35.3	4.3	0.03	100+	63
berry	brown	S	soft & juicy	15.2	2.1	3.7	<0.01	100+	46
berry	purple	P	soft & juicy	7.4	0.3	4.7	0.06	1-2	83
berry	red	A	soft & juicy	7.1	5.1	6.3	0.09	2 (1)	91
berry	red	A	soft & juicy	6.3	0.2	5.0	0.06	2	56
drupe	green	S	jiucy & fibrous	10.2	0.8	7.5	0.08	4	84
berry	green	A	arillate	28.2	3.9	6.6	0.02	7-30	53
capsular	green	A	soft & juicy	14.1	0.7	2.7	<0.01	4-6	81
drupe	yellow	A	soft & juicy	20.2	1.6	15.1	0.21	1	72

Pulp type could be juicy or arillate pulp, fibrous pulp or pulpless. Fruit and seed length and mass were measured with callipers and an electronic scale ‘Kernbalans NM60’ with respectively 0.01mm and 0.01g precision. These measures along with the number seeds were each subdivided in three classes. The water content of the fruits was calculated by comparing fresh mass and dry mass, after three days of drying in an oven. The fruit skin thickness was divided into the following categories; easily cut by fingernail, by a knife or by a secateur.

We used X^2-analyses to compare the flying foxes’ food selection with the overall fruit availability. A herbarium of all fruit species collected during our study was made in the field and identified by Dr. Johny Rabenantoandro at Missouri Botanical Garden in Antananarivo.

Germination trials

The seed viability after passage through the digestive tract was tested by simple germination trials, in which three different treatments were used; defecated seeds, control seeds and control fruits. Ripe control seeds and fruits were collected on or under the parent plant within a restricted time frame. All seeds were sown at 1cm depth in plastic pots filled with 8cm sterile sand and a 1.5cm humus layer on top. Pots were placed under a shed for protection from direct sunlight. The faecal seeds were still surrounded by their faecal matrix, when sown. For each treatment sowing was done at the same time and under the same overall ecological conditions in order to standardize procedures. The germination rate, defined as time to first germination, and percentage germinated seeds were scored weekly over a period of at least six months.

RESULTS

Fruit diet: faecal analyses and observations

Over a 13-month period at least 40 fruit species (27 genera, 21 families) were eaten by *P. rufus* (Table 1). The flying foxes were observed to eat six fruit species while evidence of 38 species was found in the faecal samples. Eight species were identified as eaten by flying foxes based on the marks on the ejecta pellets found under fruit trees. At least five seed species remained unidentified in the faecal samples and therefore are not shown in Table 1. The family Rubiaceae, including genera *Canthium, Rothmannia, Tricalysia, Mapouria, Ixora,* and one unidentified genus, was predominant, representing eight fruit species and thus 20% of the plant species in the diet of the flying foxes. Of the remaining 20 families, eleven were represented by only one species, six by two species and three by three species. The cumulative distribution curve shows that at the end of the 12-month period the curve starts to level out ending in a record of 40 species eaten (Fig. 2). January was sampled the second time after completing a year cycle, which did not result in a higher number of species sampled.

Five particular plant species, *Ficus guatteriifolia, Syzigium* sp.2, *Terminalia fatraea, Uapaca thouarsii*, and *Uapaca littoralis* were found to be important food sources for the flying foxes during the study period. This importance was based on the larger number of droppings found containing their seeds, the evidence on ejecta pellets, multiple feeding observations or because these species were eaten for at least four successive months, often much longer (Table 2).

Typically one seed species per dropping was found. Out of the 410 faecal samples collected only four samples had two different species of seeds. No sample contained a larger number of species. Twenty-three plant species (61%), from a total of 38 food species identified by faecal samples were represented only by one or two seeds per of dropping. More than 50 seeds per dropping were found for 13% of the food plant species. The remaining 26% of the plant species had two to eight seeds in droppings.

Most of the direct encounters occurred from April through June while the flying foxes were feeding mainly on fruits of *Terminalia fatraea, Dypsis prestoniana* and *Syzigium* sp.2, and on flowers of *Ravenala madagascariensis*. Out of a total of 47 independent observations (Table 3), the median number of individuals feeding together was 1 (range 1–15) and the median visitation length was 2 minutes (range 1–48min). Sometimes feeding animals would take off carrying one or more fruits to a neighbouring tree, eat them and then return to the original fruit tree. On other occasions individuals would remain eating in the fruit tree itself. The longest visitation length (48min) and largest group size (N=15) were recorded in *T. fatraea*. During observations it was also clear from the falling seeds and ejecta pellets that flying foxes most often only suck out juices from the pulp and then systematically drop or spit out the remaining pulp fraction and seeds. This feeding behaviour was noticed for *T. fatraea, D. prestoniana*, and *Syzigium* sp.2.

Only few data of feeding on flowers were recorded. On one occasion flower petals of *Ludia antanosarum* (Flacourtiaceae) were noticed to be abundantly present in the faecal samples during May while this tree species is blooming. Furthermore the flying foxes were observed feeding on the nectar of *Ravenala madagascariensis* (Strelitziaceae) flying from one tree to another on several occasions.

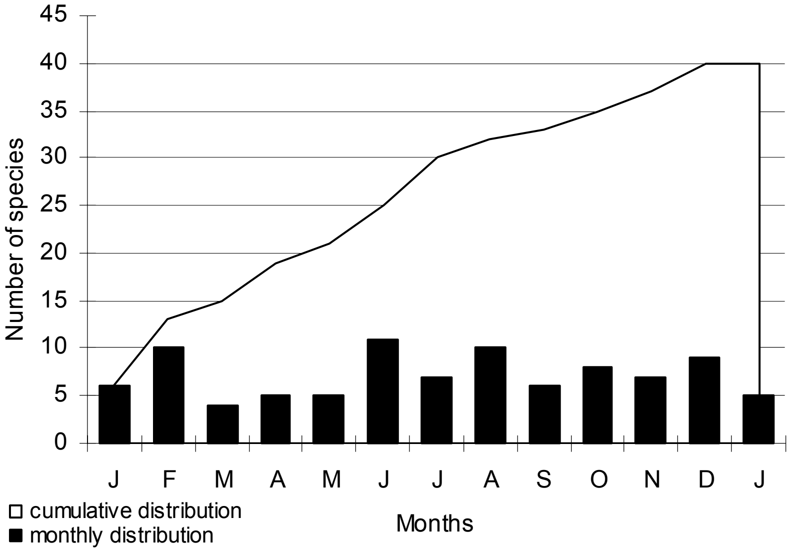

Fig. 2. The monthly and cumulative distribution of the number of plant species eaten by *Pteropus rufus* over a 13-month period.

Table 2. Temporal distribution of feeding patterns of the bats per plant taxon per month from January 2000 to January 2001 with indication of type of evidence (F: faecal samples, O: observation, M: recognizable feeding marks on ejecta pellets) per month. Number of droppings per taxon is also given. The five most important species are highlighted.

Taxon	'Feeding' months													Faecal samples	Number of seeds/dropping		
	J	F	M	A	M	J	J	A	S	O	N	D	J	(N)	Median	Min	Max
Dracaena reflexa var. *nervosa* 'falinandro'						F								2	1	-	-
Dracaena reflexa var. *nervosa* 'tavolobotroka'							F	F						4	1	-	-
Polyalthia madagascariensis						F								1	1	-	-
Polyscias sp.										F				2	6	4	8
Dypsis prestoniana					OM					F				1	1	-	-
Dypsis nodifera					MF									1	1	-	-
Ophiocolea delphinensis		M												-	ND	ND	ND
Cinnamosma madagascariensis							F	F	F					11	1	1	3
Terminalia fatraea				M	OI	OM	M							3	1	1	3
Vaccinium emirnense		F												1	100+	-	-
Uapaca ferruginea								O	F	OF	OF	F	F	34	1	1	3
Uapaca thouarsii											F			43	2	1	2
Uapaca littoralis							M	F	F	F	F	OF	OF	9	1	1	2
Ludia antanosarum 'hazofotsy'		F				F								2	2.5	1	4
Ludia antanosarum 'zorafotsy'	F													1	8	-	-
Scolopia orientalis				O				O				OF		1	4	-	-
Beilschmiedia madagascariensis												M		-	ND	ND	ND
Ocotea sp.												F		1	1	-	-
Bakerella sp.		F												1	1	-	-
Bakerella ambongoensis				F		F		F						3	9	2	11
Anthocleista madagascariensis											F	F	F	36	50+	27	50+
Anthocleista longifolia	F	F												4	4	1	10
Tambourissa purpurea 'ambora'						F								1	1	-	-
Tambourissa purpurea 'amboralahy'						F								1	1	-	-
Ficus baronii	F													12	100+	-	-
Ficus guatteriifolia	F	F	F	F	F	F	F	F	F	F	F	F	F	148	100+	5	300+

Table 2 Continued

Taxon	'Feeding' months													Faecal samples	Number of seeds/dropping		
	J	F	M	A	M	J	J	A	S	O	N	D	J	(N)	Median	Min	Max
Ficus pyrifolia										F				25	100+	-	-
***Syzygium* sp.2**					OI	OF	F	F	F	F	F	F	F	44	1	1	2
Canthium variistipula									F	F	F			10	2	1	4
Tricalysia cf. *cryptocalyx*	F													1	1	-	-
Tricalysia sp.		F												1	1	-	-
Rothmannia mandenensis	F	F	F			F								5	1	1	7
Tainbarika		F				F								1	2	-	-
Ixora sp.							F	F						4	1	1	2
Mapouria aegialodes				F										1	1	-	-
Mapouria sp.								F						1	1	-	-
Vepris elliotii			F											1	5	5	5
Sideroxylon beguei var. *saboureaui*		MF												3	1	3	1
Sarcolaena multiflora			F											1	9	-	-
Brexia sp.												F		1	1	-	-

Table 3. The number of observations (N) per tree species with indication of the median, range, and average deviation (AD) of the number of individuals feeding in the tree. Visitation lengths (in min) are also shown.

	N	Visitation length			Number of individuals		
		Median	Range	AD	Median	Range	AD
Dypsis prestoniana	9	5.00	1-15	7.01	1.00	1-2	0.19
Terminalia fatraea	7	3.00	1-48	14.16	1.00	1-15	3.38
Ravenala madagascariensis	5	1.00	1-2	0.32	1.00	1	-
Syzygium sp.	20	2.50	1-15	2.12	1.00	1-7	1.44
Uapaca ferruginea	2	2.00	1-3	1.00	1.00	1	-
Uapaca littoralis	2	2.00	1-2	0.50	1.00	1	-
Scolopia orientalis	2	2.00	1-3	1.00	1.00	1	-
All species together	47	2.00	1-48	5.44	1.00	1-15	1.31

Table 4. Comparison of morphological characteristics of fruits (with the corresponding sample size and frequency distribution) in the diet of *P. rufus* and the overall fruits available (n=152-175)

Fruit parameters	Total fruit availability		*Pteropus rufus'* diet		Statistics		
	N	%	N	%	X^2	df	P
Growth form							
Larger trees	94	54	23	58	1.42	2	NS
Small trees and shrubs	62	35	15	37			
Others	19	11	2	5			
Fruit type							
Berry	83	50	25	63	4.64	3	NS
Drupe	51	30	11	27			
Capsule	21	13	1	2			
Others	12	7	3	8			
Colour of ripe fruits							
Yellow	22	13	5	13	6.00	6	NS
Orange	10	6	4	10			
Red, pink	29	17	9	23			
Puple, blue	16	9	5	13			
Brown	44	25	9	23			
Green	39	22	8	20			
Others	14	8	0	0			
Odour							
Absent	59	35	16	39	3.30	2	NS
Present	47	28	6	15			
Strong	63	37	18	44			
Pulp type							
Juicy	124	72	35	88	12.56	3	<0.01
Fibrous	9	5	0	0			
No real pulp	29	17	0	0			
Arillus	11	6	5	12			
Fruit length (mm)							
<10	42	25	10	25	0.80	2	NS
10-30	97	57	25	63			
>10	30	18	5	12			
Fruit weight (g)							
<1	69	43	20	51	1.08	2	NS
1-10	79	48	16	41			
>10	15	9	4	10			
Seed length (mm)							
<10	92	57	33	83	10.71	2	<0.01
10-20	51	32	6	15			
>20	18	11	1	2			
Seed weight (g)							
<0,1	58	38	24	60	10.11	2	<0.01
0.1-1.0	56	37	13	32			
>1	38	25	3	8			
Number of seeds							
1-2	97	56	17	43	5.57	2	NS
2-50	56	32	14	35			
50+	20	11	9	22			
Water content (%)							
0-60	28	19	3	8	3.44	1	NS
>60	114	81	37	92			
Fruit skin thickness							
Cut by nail	150	86	39	97	4.30	2	NS
Cut by knife	23	13	1	3			
Cut by cutter	1	1	0	0			

Food selection: exploited versus available food items

In order to gain some insight into the flying foxes' food selection, the different variables of several fruit and seed parameters were compared for the 175 available and 40 exploited food species (Table 4). Focusing on exploited food species only, it was apparent that mainly large trees and to a lesser extent small trees and shrubs are exploited for their fruits. No herbs and vines occur in the diet list. Berries are the fruit type most represented in the diet followed by drupes. Fruits with a strong odour are predominant in the diet, while all colours are present in approximately similar percentages. Fruits with many tiny seeds as well as one- to two-seeded fruits are well represented. In general fruit skin thickness is minimal and most fruits have a water content over 60%. Furthermore juicy fruits with a length between 10–30mm are most common in the list, but no particular fruit mass was most abundant. Seed length is often smaller than 10mm and seed mass less than 0.1g. The threshold for seed swallowing at our study site is as much as 10mm, with 4.4mm being the median diameter (N=38).

Much of the differential use of fruits can be explained by a differential availability. There is only a significant difference between observed and expected values for the parameters pulp type, seed length and seed mass (Table 4). Fruits with juicy pulp are clearly preferred. Fibrous fruits and fruits without pulp, even though available, are not consumed by the flying foxes at all. Fruits with seed length smaller than 10mm are preferred to longer seeded-fruits. The most preferred seed mass is under 0.1g, but the 0.1–1.0g category still makes up one third of their food choice, while seeds heavier than 1g seem to be avoided. After sequential Bonferroni adjustment (Rice 1989 but see Moran 2003) none of these preferences remained significant.

Germination trials

Our faecal analyses show that seeds of at least 38 plant species pass through the digestive tract. Due to the scarcity of simultaneous presence of defecated seeds, control seeds and fruits, it was not always possible to obtain the same number of duplicates or the same number of seeds for all treatments.

None of the defecated seeds looked damaged. Only five species provided enough seeds and fruits at the same time to start a germination experiment (Table 5). Passage through the digestive tract had neither a negative nor a positive impact on the germination rate and percentage of seeds germinated. It appears that seeds from intact control fruits take more time to germinate than seeds of faecal samples and control seeds. Numbers were too small, however, to allow statistical comparison.

DISCUSSION

Fruit diet

Quantitatively

The diet of *P. rufus* studied at Sainte Luce consists of 40 endemic plant species of the littoral forest. Even though our data set represents the most complete information available on the fruit diet of *P. rufus* in littoral forests today, it is probably an underestimation of their overall fruit diet for several reasons. First, by focusing mainly on faecal sample content, larger seeds, that are often spat out and less commonly eaten food species can be missed. Secondly, exotic species that are neither important nor typical for the littoral forest were omitted from our study. It is likely that the five seed species that could not be identified may represent seeds from such exotic species. They may also be fruit species eaten in other forest types and were as such not present in our reference collection. It cannot be excluded that the mountain rain forest, with a different floral composition (Koechlin et al. 1974) lies within the foraging range of the colony studied. Finally, there might also be an important temporal bias since a number of tree species in these littoral forests do not fruit annually but bi-annually or even less often (Randrihasipara pers. comm.; Bollen and Donati, Chapter 1). One year of sampling is not enough to establish the complete fruit diet of *P. rufus*. Nevertheless, our species accumulation curve indicates that a large proportion of the diet is indeed already known. Long-term studies are needed to further complete the diet list.

Table 5. The number of weeks needed for the first germination (a) and the percentage of germinated seeds (b) for the three treatments: faecal seeds, control seeds, and control fruits. The values given here are median, average deviation (AD), and sample size (N).

a)	Germination rate								
Species	Faecal seeds			Control seeds			Control fruits		
	Median	AD	N	Median	AD	N	Median	AD	N
Ludia antanosarum	2.5	-	1	3.5	0.5	2	7	-	1
Terminalia fatraea	25	-	1	22	0.9	3	26	1.2	5
Syzygium sp.	7	-	1	6	0.9	3	10	6.8	3
Ficus guatteriifolia	3.5	2.9	8	7	-	1	15.5	2.5	2
Rothmannia mandenensis	8	-	1	23	-	1	[2]	-	0

b)	Percentage germinated								
Species	Faecal seeds			Control seeds			Control fruits		
	Median	AD	N	Median	AD	N	Median	AD	N
Ludia antanosarum	25	-	1	62.5	12.5	2	33	-	1
Terminalia fatraea	60	-	1	30	15.6	3	30	8.0	5
Syzygium sp.	50	-	1	80	11.1	3	60	13.3	3
Ficus guatteriifolia	16	9	8	[1]	-	1	[1]	-	2
Rothmannia mandenensis	50	-	1	40	-	1	[2]	-	0

[1] as these seeds are very tiny and numerous in fruits it is impossible to know exactly which percentage had germinated in both control seeds and control fruits.

[2] ripe fruits fall apart in small pieces and therefore we could not sow complete fruits for comparison.

Quantitative data on the diet of *P. rufus* in other parts of Madagascar are limited. In the gallery forest of Berenty the diet of *P. rufus* contains only 13 plant species, both flowers and fruits included (Long and Racey submitted). This much lower number can probably be best explained by the lower plant diversity of the much drier gallery forest. Racey et al. (in prep) have studied *P. rufus* in Madagascar for several years at different sites in Madagascar and their data on feeding ecology resulted in a diet list of 38 plant species for *P. rufus* with two thirds of these being fruit resources. Racey and Nicoll (1984) mention a fruit diet of 18 species for *Pteropus seychellensis* in the Seychelles and Parry-Jones and Augee (1991) found 22 fruit species in the diet of *Pteropus poliocephalus*. An extensive literature survey by Marshall (1983) resulted in a list of 62 plant genera consumed for their fruits by all *Pteropus* spp. (N=67) together. All these numbers demonstrate that our diet list including 40 species belonging to 28 genera is quite extensive.

As for the quantitative data of our observations, we believe there may be a bias on the visitation length scored, as flying foxes would fly away when they detected our presence. On the other hand, visitation length could indeed be relatively short because of a particular feeding behaviour of these flying foxes to consume fruits in 'dining roosts' and not in the fruit tree itself on some occasions. This behaviour was also observed for other frugivorous flying foxes (Marshall 1983) and for Neotropical frugivorous bat species (Morisson 1980; Kalko et al. 1996), even though Kalko et al. (1996) mention a rather sedentary feeding mode for Afrotropical flying foxes, which could also be observed in Sainte Luce on other occasions.

Taxonomically

Of the five plant species mentioned in the results, *Ficus guatteriifolia* (Moraceae) is likely to be the most important one in the diet of *P. rufus.* This species is available year-round due to intra-specific asynchrony in flowering and fruiting and faecal analyses show it was consumed the whole year. It forms a staple food and is likely to be a keystone resource (definition according to Mills et al. 1993) for these flying foxes. *Ficus* spp. are also the food taxon that is most frequently regarded as important in literature on the diet of the flying foxes (Pteropodidae) in the Paleotropics (Cheke and Dahl 1981; Marshall 1983; Fujita and Tuttle 1991; Banack 1998) and of fruit bats (Phyllostomatidae) in the Neotropics (Heithaus et al. 1975; Fleming et al. 1977; Morrison 1980; Kalko et al. 1996).

By the same token, *Syzigium* sp.2 (Myrtaceae) could be considered a keystone fruit species as well. It is a very common and widespread tree species, which provides food from May up to January. The fruiting cycle of an individual tree is only about two to three months long but since the fruiting pattern in the different forest fragments shows a delay of a few months, the fruits are available in the area for as long as nine months. In this way certain plant species are accessible only to flying frugivores for extended periods.

Terminalia fatraea (Combretaceae) is a highly preferred food item and one of the plant species of which most observations were recorded and large amounts of macerated fruit pulp were found under the trees in the morning. From April to July *T. fatraea* is eaten in very large quantities. There may be a parallel between *Terminalia catappa* consumed in the Masoala Peninsula (Hutcheon 1994) and *T. fatraea* eaten in Sainte Luce. Both act as important food species during times of fruit scarcity and therefore play a crucial role in the diet of *P. rufus*. *Terminalia catappa* has also been regarded as an important food species for *Pteropus* spp. by Cheke and Dahl (1981), Fujita and Tuttle (1991) and Banack (1998).

Several authors mention that fruit bats feed on a taxonomically non-random subset of fruits. These so-called 'bat fruits' are mainly plant species of following plant families Moraceae, Myrtaceae, Sapotaceae, Arecaceae, Piperceae, Solanaceae, Anacardiaceae, Guttiferae, Leguminosae, and Combretaceae (Marshall 1983; Fleming 1987; Banack 1998; Corlett 1998). Our data set contains several of these families. Surprisingly the family Rubiaceae, not mentioned by any author, is taxonomically represented by the highest species number in our diet list. On the contrary, the plant families Guttiferae and Anacardiaceae, both considered 'bat families' by Marshall (1983) and Corlett (1998), are not eaten by *P. rufus* in Sainte Luce even though available. Certain plant families might indeed be considered 'bat families' but the actual diet may still vary greatly according to forest type and fruit availability within.

Food selection

Growth form

A closer look at fruit characteristics for both eaten and available species seems to point at certain food preferences, although at the same time other, non-significant, results were rather unexpected. For example according to the analyses the flying foxes did not prefer to eat in large trees, which was unexpected as bats were most often observed and supposed to feed in large trees (Fleming et al. 1987). The often larger fruit crop available at the same time in large trees, the more accessible position and the more easily detectable resources both for bats and researchers are probably responsible for this result. All important food resources in our diet list involve large trees, but shrubs and smaller trees still account for almost 40%. The latter occur in larger numbers in secondary forest and are more easily detected and eaten there. Old World pteropodids are known to be primarily canopy feeders (Fleming et al. 1987) and prefer primary forest to secondary forest (Banack 1998). In our data set most of the fruit species eaten grow in intact and primary forest. Both pioneer plant species as well as species from a later successive phase were exploited.

Fruit type versus pulp type and water content

The flying foxes eat mainly juicy berries with a high water content. Observations, ejecta pellets, and literature (Marshall 1983) confirm that fruit juices dominate the diet of flying foxes. As indicated in Table 4, only for the parameter 'pulp type' a difference was found between eaten and available fruits, not for fruit type and water content but these parameters are often inter-correlated. In most tropical forests 50–90% of the plant species depend on animals for their dispersal (Howe and Smallwood 1982; Fleming et al. 1987) and among typical endozoochorous fruits juicy berries with a high water content form a large proportion, which stands also for the majority of available fruits in the humid littoral forest of Sainte Luce.

Odour and colour

Most fruits eaten have an odour and even a strong one, which can be related to the bats' well-developed olfactory senses especially used for locating food (Marshall 1983; Kalko et al. 1996). Odour was a feature of most (65%) of the fruits available in the forest, which may explain why analyses revealed that there was no significant preference for this trait. This abundance of odoriferous fruits is probably because a large amount of the available fruit species are dependant on mammals for seed dispersal and scent in general is also of major importance for mammals when locating and selecting ripe fruits. Besides good smell, the flying foxes have also developed large eyes and thus good vision which might further help them to locate fruits at night (Marshall 1983). Obviously colour is of little relevance since they feed and forage at night and all nocturnal mammals are colour-blind (Corlett 1998). This is confirmed by the fact that selection of fruits in favour of a particular colour was not observed.

Size versus mass

Based on the number of seeds per dropping we presumed that tiny seeds of multi-seeded fruits with a length up to 1–3.5mm are likely to be automatically swallowed together with the fruit pulp. As for larger one- to two-seeded fruits, with seed length between 3.5–20mm, fruit skin and seeds are most often spat out. This feeding behaviour of dropping larger seeds and swallowing tiny seeds together with fruit juices was also mentioned by

Marshall (1983). Occasionally some seeds (up to 15mm length) are swallowed as well. For all three *Uapaca* sp., with seed length over 9.6mm, seeds were often swallowed but this is probably due to the pulp texture and slippery seeds. The threshold for swallowing seeds is reported as being less than 3.2mm diameter for a 600g *Pteropus* sp. and between 3–5mm for flying foxes in general (Corlett 1998; Shilton et al. 1999), which is smaller than the 10mm recorded at our study site.

Our analyses showed no particular fruit mass preference. The fact that *Pteropus* spp. may transport fruits of over 200g (Marshall 1983) means that they are probably not limited by masses up to 50g, being the maximum fruit mass that was scored.

'Bat fruits'

According to Fleming (1979), Marshall (1983), Stashko and Dinerstein (1988), Thomas (1988) and Korine et al. (1998) 'bat fruits' can be morphologically characterised as variable in size with a green or dull colour, a strong and musty odour, high water content, pendant position or held away from the foliage. This description corresponds with our results meaning that the flying foxes' food species in Sainte Luce include fruits of all size, having no particular conspicuous colour, a strong odour and high water content. However, compared to the overall database of available fruits in this forest several of these variables are simply characteristic for the majority of fruits. Thus real food selection or clear preference cannot be established. Therefore it is important that future studies also focus more on all available food resources in an ecosystem rather than studying the diet of the bat species only. This way it will be possible to draw broader conclusions on real food preferences and typical 'bat fruits' compared to the wide array of fruits available.

The exclusive role of flying foxes in seed dispersal

Quantitatively important short and long distance seed dispersal

Pteropus rufus feeds on a huge variety of fruits, which makes this species potentially an important seed disperser for a large number and diverse set of endemic plant species in the littoral forest. Compared to other frugivores in the littoral forest it is the only one capable of long distance seed dispersal since foraging may occur up to 50km away from the roost site (Thomas, 1988) thereby bridging isolated forest fragments. This ensures genetic exchange between plant populations of different forest fragments, and for very small fragments no longer inhabited by other mammal seed dispersers, only flying foxes can disperse these fruits. Long distance seed dispersal happens mainly between successive feeding trees (0.3–8.3km apart) or even further away between foraging areas and roost sites (up to 50km apart) for all ingested seeds (Morrison 1978; Korine et al. 1999).

Gut passage rate in flying foxes is often only about 30 minutes (Morrison 1980), although there is also evidence for gut retention of food for large periods (>12h or >18h) in Pteropodidae (Shilton et al. 1999), which increases the possibility for long distance seed dispersal. As digestion can be rapid, large quantities of food can be processed every night. This is necessary because being flying mammals, these flying foxes have rather high-energy requirements and may eat at least the equivalent of their own body mass each night (Marshall 1983; Shilton et al. 1999). In addition, they are very numerous in the area. All this probably leads to a massive consumption of fruits and possible dispersal of seeds every night by a large number of animals.

Germination experiments

Izhaki et al. (1995) noted a positive effect of passage through bats' guts on germination rate of the ingested seeds. Nevertheless, Palmeirim et al. (1989), Kalko et al. (1996), Iudica and Bonaccorso (1997), Korine et al. (1998), Shilton et al. (1999) as well as this study did not find such a relation. There seemed to be no positive or negative impact on germination rate and germination percentage of defecated seeds. The results on percentage of plants that finally germinated after 6 months are difficult to interpret and appear very variable. More extensive experiments under more controlled ecological conditions and with more replicas should be carried out to confirm these first preliminary data. But, even if germination itself does not profit from the digestive process, more important to consider is the distance covered by the flying foxes during gut passage.

Threats and conservation options

Unfortunately in Sainte Luce not only the fragmented habitat is at risk, but its inhabitants among which the flying foxes, are seriously threatened as well. During our field research the whole colony moved once from their original roost site to another one, five kilometers west, where they remained from February through May 2000. Afterwards the colony returned to the first roost site. At both roost sites, rocks, long sticks and injured patagia were indications of severe hunting pressure. Several bush fires in the nearby area perturbed the colony even more. Too much harassment might cause the colony to divide into smaller groups, and settle elsewhere, leaving the littoral forest deprived of its only capable long distance seed disperser.

ACKNOWLEDGEMENTS

We would like to acknowledge QMM (QIT Madagascar Minerals) for providing logistics and infrastructure at the campsite. In particular we thank Manon Vincelette, Jean-Baptiste Ramanamanjato, Laurent Randrihasipara of the QMM Environmental and Conservation Team and Prof. Dr. Jörg Ganzhorn (University of Hamburg) for their support in this research. We are very grateful to Dr. Johny Rabenantoandro of Missouri Botanical Garden (Antananarivo) for assistance with the identification of the plant species. We also thank Prof. Paul A. Racey (Univ. Aberdeen) for providing important literature and for his extensive revisions and useful suggestions. Finally we owe great thanks to Giuseppe Donati and the Malagasy assistants in the Sainte Luce campsite, without them this research would have been a lot harder. This study was carried out under a Collaboration Agreement between Department of Animal Biology and Department of Anthropology of the University of Antananarivo and the Institute of Zoology of Hamburg University and QMM. First author is supported by a Research Assistantship of the Belgian Fund for Scientific Research, Flanders (FWO). We thank the Flemish Government for structural support to the CRC of the RZSA.

3b

The feeding ecology of *Coracopsis nigra* (Psittacidae) in the littoral forest of Sainte Luce (south-east Madagascar)

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OSTRICH (SUBMITTED)

ABSTRACT

This paper describes the diet and feeding ecology of the parrot species *Coracopsis nigra* in the littoral forest of Sainte Luce, south-eastern Madagascar. Forty plant species were recorded being eaten by these parrots over a 14-month study period. *C. nigra* is an opportunistic feeder and eats a large variety of flowers (10%), ripe and unripe seeds (68%) and fruits (22%). Of all fruit species consumed, the majority (70%) of fruits are also eaten in unripe condition, which may lead to an advantage over potential food competitors. Detailed observation of their feeding behaviour shows that generally seeds are destroyed, and as such they are considered primarily as pre-dispersal seed predators. As granivores their role in the ecosystem is rather negative but the impact of this damage seems to be limited due to high dietary overlap with seed dispersing frugivores. Among granivores, the different seed predators seem to have occupied separate trophical niches based on fruit and seed size and weight, feeding height and activity pattern.

INTRODUCTION

Worldwide, frugivorous animals play an important role in forest dynamics in terms of seed dispersal and forest regeneration. In Madagascar, most studies in this field have focused on the dispersal role of lemurs (Ralisoamalala 1996; Scharfe and Schlund 1996; Dew and Wright 1998; Overdorff and Strait 1998; Birkinshaw 1999; Ganzhorn et al. 1999a). At present, hardly any information is available on the potential role of the frugivorous bird species in seed dispersal or predation. The Malagasy frugivore avifauna is strikingly depauperate compared with continental areas and other large tropical islands (Fleming et al. 1987). In the littoral forest of Sainte Luce (south-east Madagascar), there are only six frugivorous bird species being *Streptopelia picturata* or the Malagasy Turtledove, *Treron australis* or Malagasy Green Pigeon, *Alectroenas madagascariensis* or Madagascar Blue Pigeon (Columbidae), *Hypsipetes madagascariensis* or Madagascar Bulbul (Pycnonotidae) and two species of *Coracopsis* (Psittacidae), *C. nigra*, the Lesser Vasa Parrot, and *C. vasa*, the Greater Vasa Parrot. In this study, we focus on one of the largest frugivorous bird species in the region; *Coracopsis nigra* for which little information is available on its feeding ecology (Hampe 1998; Dowsett 2000). Many Malagasy animal species today are under threat of extinction, and this may have a major impact on ecosystems. This is particularly relevant for the littoral forest, as only small forest remnants have survived due to human degradation of this habitat and its subsequent fragmentation. These forest fragments may not be large enough for certain animal species to persist (Ganzhorn et al. 2000) and therefore, it is critical to identify effective seed dispersers in this ecosystem that might aid forest regeneration. Conversely we also want to gain insight into seed predation and the traits that determine food selection of the different granivorous species.

METHODS

Between November 1999 and February 2001, field data were collected by the first author on the feeding ecology of *Coracopsis nigra* in the 377-ha littoral forest fragment of Sainte Luce, called S9 (24º45'S 47º11'E), located in extreme southeast Madagascar. For a detailed description of the study site, I refer to Bollen and Van Elsacker (2002a, Chapter 3a). *Coracopsis* species are naturally forest birds but also inhabit certain degraded areas (Dowsett 2000). Both *C. nigra* and *C. vasa* were observed at our site, mostly in single and occasionally in mixed species formations. However all feeding observations presented in this paper are from *C. nigra,* which is present year-round and in high densities. *C. vasa* was only observed on few occasions during austral summer (December 2000 - January 2001) and seems to migrate into the area sporadically.

Diets were assessed by direct feeding observations through tree watches (36h-watches) and more casual observations while walking along transects. Feeding and handling behaviour were described in detail in order to determine the role of *C. nigra* in seed dispersal and/or predation. More indirect methods such as faecal analyses and identifying fruit trap contents further contributed to the completion of the diet list (for details on methodology, see Bollen et al*.,* Chapter 2). Parrots' bill marks on the rejected fruit parts are easily recognizable and analyses of *Coracopsis*' faecal samples enabled us to evaluate the condition of seeds after gut passage.

All fruiting species encountered during the study site were characterised according to the following variables; fruit type (berry, drupe, capsule, other), pulp type (juicy, fibrous, none), seed protection (none, hard seed coat), seed number, fruit and seed length and weight. The latter were measured with callipers and a 'Kernbalans NM60' scale with a precision of 0.01mm and 0.01g respectively. Fruits were considered ripe when seeds were fully developed, often coinciding with a change in colour, odour or texture.

Most of the variables measured have highly skewed distributions so the median value is given instead of the mean. For the same reason non-parametric statistics were used, such as Spearman rank correlation, Kruskal Wallis test and Contingency tables. Statistical significance was accepted for $\alpha \leq 0.05$ for all tests. All statistical tests were carried out according to Siegel (1956) with the statistical software SAS for Windows.

RESULTS

C. nigra was recorded feeding on 40 plant species (36 genera, 25 families; Table 1), of which 39 are endemic and one, *Psidium guajava*, is exotic. Three plant species, *Symphonia* sp., *Rhopalocarpus coriaceus* and *Eugenia* sp. are exploited for their flowers only, while both the flowers and fruits of *Polyscias* sp. are eaten. All other plant species listed in Table 1 are visited for their fruits or seeds. Summarizing, 68% of the food species served as a seed source, 22% are eaten for seed and pulp and 10% for flowers (Table 1).

The range of plant species consumed by *C. nigra* includes berries (31%) and drupes (47%) as well as capsules and other fruit types (22%). Most consumed fruits have a juicy fruit pulp (70%) but the parrots also consume fibrous (8%) as well as fruits without pulp (22%). The majority of fruits is one-seeded (57%), but several multi-seeded fruits are consumed as well. Fifty-four percent of all species have a hard kernel to protect the seed, while 46% has none. The median fruit length is 12mm (quartiles: 8-17mm) and median fruit weight is 0.6g (quartiles 0.2-1.0g). For seeds, median length is 7mm (4-11mm) and weight 0.1g (0.0-0.3g). Of all the fruit species consumed (N=37), 13 (35%) are taken both ripe and unripe, 13 (35%) in an unripe state only, and 11 (30%) only when ripe.

Tina thouarsiana (N obs.=13; Sapindaceae) and *Macaranga perrieri* (N obs.=8; Euphorbiaceae) are important food items that are eaten from November through January, when overall fruit resources are abundant in the littoral forest (Table 1, Fig. 1). On the contrary, *Bembicia uniflora* (N obs.=28; Flacourtiaceae) fruits during the period of fruit scarcity and is probably the main food source within the diet of *C. nigra.* The parrots consume both ripe and unripe seeds of this plant species for at least six consecutive months. Another essential food source for numerous frugivorous species among which *C. nigra* is *Syzigium* sp.2 (N obs.=18; Myrtaceae), which also fruits when fruit availability is low. This plant species is very common and abundantly present in the littoral forest and may be considered a keystone species for numerous frugivores in this ecosystem. When comparing the phenology of *C.* nigra's food items with the overall phenology of the forest, they are not at all correlated (r_s=-0.22, P=0.48, N=13). Thus the patterns of fruit abundance and scarcity within the ecosystem are not reflected within the diet of the parrots. The monthly dietary diversity of *C. nigra* (median 18 species/month) seems to be quite stable throughout the year with a little less species eaten from June through October 2000.

Our observations revealed that in general *C. nigra* is a very wasteful eater: it eats quickly and drops a considerable quantity of consumable food. Fruits are generally held by one foot and cut in half with the bill. Seeds are often only partially eaten, while pulp or fruit husks are discarded. Bill marks on discarded pulp show that only the seeds are eaten. In the few faecal samples collected (N=6), only parts of the seed coat could be recovered. The seed itself was digested entirely.

Of all selected fruit items, the majority (N=33) is consumed by seed dispersers as well (Table 1). The four remaining species are actually not even zoochorous but rather autochorous fruits. Nearly half (N=17) of the food species are consumed by other seed predators as well such as *Streptopelia picturata, Rattus rattus* and *Eliurus webbi* (Table 1). When comparing fruit and seed sizes within the diet of turtledoves, parrots and rodents, there is a significant size effect that separates these three groups of seed predators (Table 2). *S. picturata* selects significantly smaller and lighter fruits and seeds than *C. nigra,* which in turn eats fruits that are smaller than those consumed by the rodents. The number of seeds does not differ among these species. Apparently all granivorous species select mainly one-seeded fruits. Other traits determining food selection for granivores may be fruit type, pulp type and seed protection. There is no significant difference for any one of these traits however certain trends are clear (Table 2). For example *S. picturata* eats more berries while *C. nigra* and the rodents clearly select more drupes, which then further explains the high proportion of fruits with seed protection in their diet. As far as pulp type, *C. nigra* eats several fruits with no pulp while this is rarely the case for the other seed predators.

Table 1. Diet list of *C. nigra* with indication of the plant part eaten (S: seed, P: pulp, fl: flower), the condition when eaten (UR: unripe, R: ripe), month when observed eaten (ME; 1: January, 2: February , etc.) and months when available (MA) as food source. 'Evid.' refers to the method by which data were obtained (S: systematic tree watches, O: opportunistic observations, T: feeding marks, F: faecal droppings). Other consumer species are also indicated for each plant species, subdivided in seed dispersers and seed predators (L: lemurs, Pr: *Pteropus rufus,* Am: *Alectroenas madagascariensis*, Ta: *Treron australis*, Hm: *Hypsipetes madagascariensis*, Sp: *Streptopelia picturata*, R: rodents, Ew : *Eliurus webbi*, Rr: *Rattus rattus*). The following fruit traits are given as well; fruit and pulp type, seed protection, seed number (NS), fruit and seed length (in mm) and weight (in g).

Family name	Scientific name	Part eaten	Ripeness	ME	MA	Evid.
Anacardiaceae	*Poupartia chapelieri*	S	UR	4	11-4	SOT
Annonaceae	*Polyalthia madagascariensis*	S	R	4	11-5	SOT
Apocynaceae	*Cabucala madagascariensis*	S	UR	2	whole year	OT
Araliaceae	*Polyscias* sp.	fl,PS	R	8	7-9	SO
	Schefflera rainaliana	P,S	R	5	4-5	O
Arecaceae	*Dypsis prestoniana*	S	UR & R	3	2-5	ST
Clusiaceae	*Symphonia* sp.	fl		12	12-3	O
Combretaceae	*Terminalia fatraea*	P,S	UR & R	3	2-6	ST
Connaraceae	*Agelea pentagyna*	S	UR	1	12-1	OT
Ericaceae	*Vaccinium emirnense*	P,S	R	1	10-3	OT
Erythroxylaceae	*Erythroxylum buxifolium*	P,S	UR & R	5	2-5	OF
	Erythroxylum nitidulum	P,S	UR & R	8	8	O
Euphorbiaceae	*Macaranga perrieri*	S	R	11-1	11-2	S
	Suregada baronii	S	UR	5,7	4-11	O
	Uapaca littoralis	S	UR	3,8-11	whole year	ST
Flacourtiaceae	*Bembicia uniflora*	S	UR & R	4-9	4-11	O
	Homalium louvelianum	S	UR & R	6,8	6-11	OT
	Ludia antanosarum	S	UR	1-2	12-3	SOT
Icacinaceae	*Apodytes dimidiata*	S	R	4	3-4	ST
Loranthaceae	*Bakerella ambongoensis*	S	UR	4	3-4	O
	Bakerella sp.	S	UR	12	12-3	O
Myrtaceae	*Eugenia* sp.	fl		12	11-12	O
	Psidium guajava	P,S	R	1	1-2	O
	Syzygium sp.2	P,S	R	4,6	4-7	SOT
Ochnaceae	*Campylospermum obtusifolium*	P,S	UR & R	2	11-8	O
Oleaceae	*Jasminum kitchingii*	S	R	6,9	3-6, 9-11	O
	Noronhia cf. *lanceolata*	S	UR & R	8	8-11	O
	Noronhia sp.	S	UR	7,10	4-1	OT
	Olea sp.	S	R	12	11-1	ST
Rubiaceae	*Cantium variistipula*	S	UR	8,12	4-9	OT
	Morinda cf. *umbelluligera*	S	UR & R	7	3-7	O
	Morinda rigida	S	UR & R	1	12-1	O
Rutaceae	*Vepris elliotii*	S	UR	4	whole year	SO
	Vepris fitoravina	S	UR & R	2	2-3	ST
Sapindaceae	*Tina thouarsiana*	S	UR & R	11-1	6-3	SOTF
	Tinopsis conjugata	S	UR & R	12	10-3	OT
Sapotaceae	*Sideroxylon beguei* var. *saboureaui*	S	UR	11	11-3	OT
Sarcolaenaceae	*Sarcolaena multiflora*	S	UR	3-4	12-5	OT
Sphaerosepalaceae	*Rhopalocarpus coriaceus*	fl		3-4	2-5	O
Strelitziaceae	*Ravenala madagascariensis*	S	R	4,8	4-9	O

Table 1 Continued

Other consumer species		Fruit	Pulp	Seed	NS	Fruit	Fruit	Seed	Seed
Dispersers	Predators	type	type	protection		length	weight	length	weight
L	R	drupe	juicy	hard coat	1	15.43	0.54	15.24	0.36
L, Pr, Hm, Am	R	berry	juicy	hard coat	1	12.22	0.30	7.80	0.12
L	-	drupe	juicy	hard coat	3	9.16	0.10	37.97	1.11
L, Pr, Am, Ta, Hm	Sp, R	drupe	juicy	none	1	5.03	0.04	3.64	0.01
L, Am, Hm	-	drupe	juicy	hard coat	2	4.73	0.08	2.85	0.01
L, Pr, Am, Hm	Sp	berry	juicy	hard coat	1	14.85	0.59	12.92	0.34
L, Pr, Am	R	drupe	fibrous	hard coat	1	13.19	0.37	8.12	0.13
-	-	other	no pulp	none	1	16.89	1.05	12.58	0.32
L, Pr, Ta, Hm	-	berry	juicy	hard coat	100	11.51	0.84	1.45	0.00
L, Hm	-	drupe	juicy	hard coat	1	7.29	0.07	6.86	0.03
L, Am	R	drupe	juicy	none	1	10.97	0.28	8.25	0.09
L, Hm	-	drupe	no pulp	hard coat	1	4.55	-	3.06	0.03
-	Sp	capsule	no pulp	none	4	9.47	0.40	3.95	0.04
L, Pr	R, Ew, Rr	drupe	juicy	hard coat	3	23.63	4.86	15.03	0.52
L	-	capsule	no pulp	none	1	5.34	0.01	-	-
-	-	capsule	no pulp	none	1	2.35	0.02	-	-
L, Pr	-	berry	juicy	none	6	12.47	1.04	3.22	2.98
L, Am, Ta, Hm	R	drupe	juicy	hard coat	1	12.34	0.45	10.61	0.23
L, Pr	-	berry	juicy	none	1	8.03	0.14	4.61	0.01
L, Pr, Am, Hm	-	berry	juicy	none	1	15.86	0.66	10.35	0.25
L	-	berry	juicy	none	-	24.25	4.60	-	-
L, Pr, Am, Hm	Sp	berry	juicy	none	1	9.55	0.55	6.56	0.31
Am, Ta	Sp	drupe	juicy	none	1	28.87	0.25	-	-
L	Sp	berry	juicy	none	1	6.49	0.20	4.07	0.07
Hm	-	drupe	juicy	hard coat	3	7.06	0.21	3.39	0.02
L	R, Rr	drupe	fibrous	hard coat	1	20.53	1.79	18.28	-
L	R, Rr, Ew	drupe	juicy	hard coat	1	16.98	0.90	15.85	0.80
L, Pr	-	drupe	juicy	hard coat	2	7.80	0.31	6.30	0.06
L	-	berry	juicy	hard coat	20	11.94	1.75	5.31	0.01
L	-	berry	juicy	hard coat	100	26.97	9.30	7.23	0.04
L, Pr, Ta	-	drupe	fibrous	none	4	10.20	0.82	7.46	0.08
L	R	drupe	juicy	hard coat	2	8.47	8.15	6.76	0.16
L	Sp, Rr, Ew	other	no pulp	none	1	17.88	0.74	3.79	0.03
L	-	other	no pulp	none	1	20.01	1.79	12.02	0.66
L, Pr	-	berry	juicy	none	18	28.15	3.92	6.57	0.02
L, Pr	Sp	capsule	juicy	hard coat	5	14.11	0.67	2.73	0.01
-	-	capsule	no pulp	hard coat				6.93	0.25

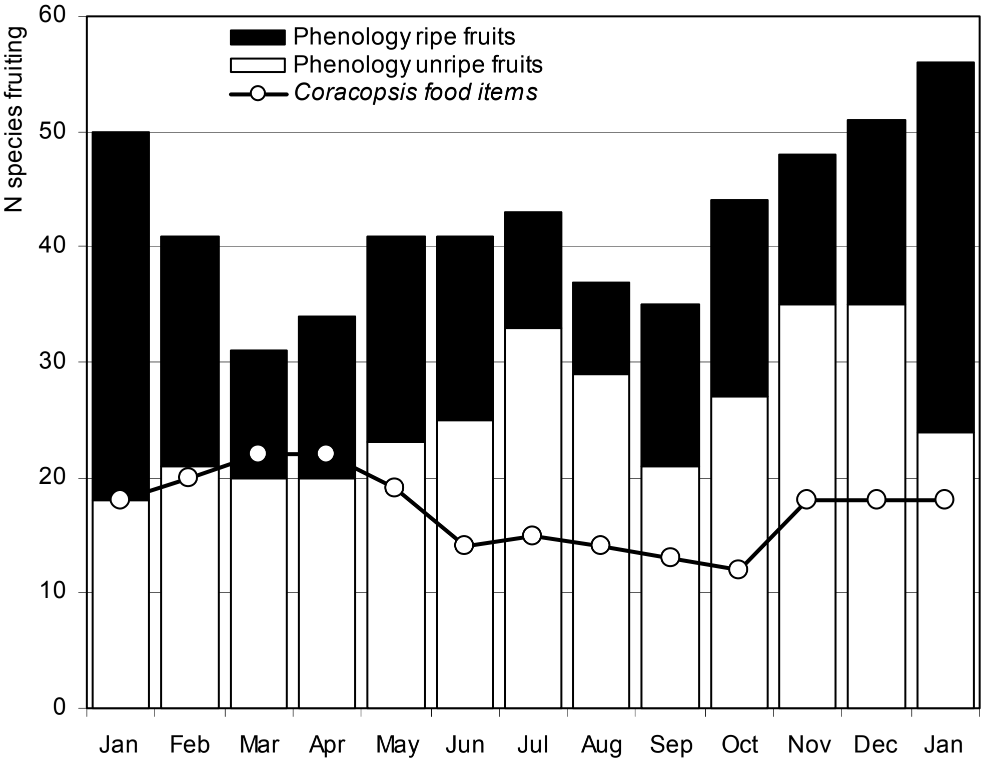


Fig 1. An overview of the overall phenology at Sainte Luce is given for the period January 2000-January 2001. The number of species with ripe and unripe fruits is given per month. The number of C. nigra food species fruiting is also shown.

DISCUSSION

To date, little information is available on the diet of the Vasa Parrots. The work of Dowsett (2000), mostly on *C. nigra,* is the most extensive study of *Coracopsis* carried out at ten different Malagasy study sites, involving humid low-altitude and mid-altitude rainforests in the east, dry deciduous forest in the west and spiny forest in the south. Their feeding data include more than 30 species from 23 plant families, mainly endemic species. As in our study, most (60%) of the food species are exploited for seeds, 20% for flowers and 8% for pulp. The remainder are eaten for young leaves and plant buds. Their dietary list from humid eastern forest sites shows some taxonomic resemblance with ours at genus level (*Uapaca, Psidium, Macaranga, Dypsis,* and *Poupartia*) and at species level (preying on seeds of *Ravenala madagascariensis*). Similarity was found as well with the observations of Goodman et al. (1997b) of *C. nigra* feeding on *Macaranga* sp., *Sarcolaena multiflora*, buds of *Symphonia* sp., blue pericarps of *Ravenala madagascariensis* and the seeds of *Ficus* sp. and *Uapaca* sp. in the South-eastern Marosohy forest. Hampe (1998) observed *C. nigra* for one month in the western dry deciduous forest of Kirindy. Eight food species were recognized; four involved flowers, three fruits and seeds, and one young leaf shoots. Two more studies (Ratsirarson and Silander 1997; Böhning-Gaese et al. 1999)

Table 2. Morphological variables within the diet of *Coracopsis nigra* , *Streptopelia picturata* and the rodents (including *E. webbi* and *Rattus rattus*) are shown. A comparison is made for the continuous variables through Kruskal Wallis test and for the class variables through contingency tables.

	C. nigra	*S. picturata*	rodents	Kruskal Wallis		
	median (N=37)	median (N=13)	median (N=50)	H	df	P
Number of seeds	1	1	1	0.13	2	0.93
Fruit length	12.28	9.55	19.04	22.35	2	<0.0001
Fruit weight	0.55	0.40	3.16	30.23	2	<0.0001
Seed length	6.86	3.75	12.06	24.89	2	<0.0001
Seed weight	0.08	0.02	0.51	24.28	2	<0.0001

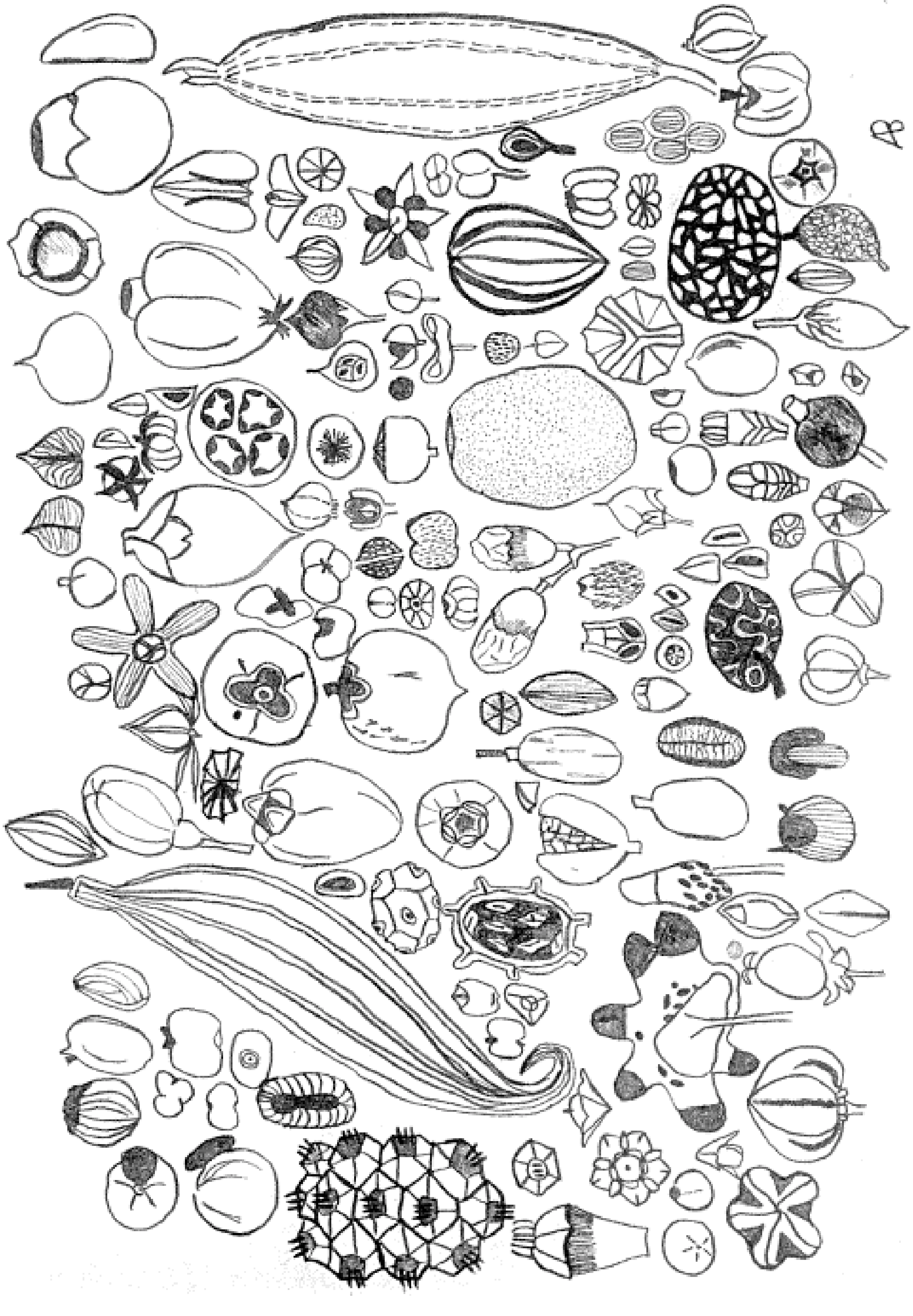
	C. nigra	*S. picturata*	rodents	Contingency Tables		
	(N=37)	(N=13)	(N=50)	X^2	df	P
		Fruit type				
Berry	12	6	17	5.66	4	0.23
Drupe	17	2	24			
Capsule & others	8	5	8			
		Pulp type				
Juicy	26	10	33	6.11	4	0.19
Fibrous	3	1	12			
No Pulp	8	2	5			
		Seed protection				
None	17	7	31	2.58	2	0.28
Hard kernel	20	6	18			

focused on one particular plant species, *Dypsis decaryi* (Arecaceae) and *Commiphora guillaumini* (Burseraceae) respectively, and observed *C. vasa* and *C. nigra* among the seed consumers. Even though our diet list of 40 plant species is probably still incomplete, it represents the most complete information on their feeding ecology in the littoral forest.

C. nigra appears to be a flexible and opportunistic feeder in Sainte Luce. This species consumes a considerable variety of seeds of both ripe and unripe fruits. Parrots worldwide are known to eat both unripe and ripe fruits and to be able to digest unripe fruits that contain toxic alkaloid substances (Janzen 1981; Jordano 1983; Pizo et al. 1995). In Bollen et al. (Chapter 3) it was shown that the fruits eaten by *C. nigra* contained a high proportion of tannins. Eating a high diversity of fruits, including unripe ones, could be to the advantage of *C. nigra* to avoid feeding competition. Intra-specific competition was not observed during our study, nor was competition between *C. nigra* and *C. vasa*. Our observations reveal that *C. nigra* feeds mainly on seeds, but for some plant species, the pulp is also partly consumed. Böhning-Gaese et al. (1999) describe *C. nigra* as an occasional seed disperser of *Commiphora guillaumini* (Burseraceae) and this only when the parrots take off from a tree with a seed in their bill. Hampe (1998) mentions that *C. nigra* swallows the entire fruit of *Breonia perrieri* (Rubiaceae), suggesting that it might be a seed disperser. However, without data on stomach content or faecal analyses, seed fate and thus seed dispersal cannot be confirmed in these cases. Even though for a few plant species pulp appears to be ingested, the data obtained from the majority of our observations and from the literature (Dowsett 2000), in combination with feeding marks on ejected pellets and faecal analyses, indicate a predominantly granivorous diet. Integrating these findings into a broader ecological context and focusing on the feeding behaviour of parrots worldwide, many authors agree on their role as seed predators (Janzen 1981; Jordano 1983; Clout 1989; Galetti 1993; Saini et al. 1994; Pizo et al. 1995; Corlett 1998; Renton 2001). *C. nigra* and possibly also *C. vasa* can certainly be considered as granivores in Sainte Luce rather than frugivores, as they are so often referred to in literature. As such they vary from other seed predators in many different aspects. *C. nigra* is a pre-dispersal seed predator, which feeds in the tree crown only during daylight on both ripe and unripe fruits, which are medium in size. It can further tolerate high tannin contents and eats non-zoochorous fruits as well without any fruit pulp at all. *S. picturata* is a post-dispersal seed predator which eats small seeds of juicy fruits on the ground only, either with a protective seed coat or not. The rodents both feed on the ground as in the tree at night, but most often carry seeds away to a feeding site. They eat the largest seeds of mostly drupes and may occasionally be involved in secondary seed dispersal as well. Nevertheless they can be mainly considered as post-dispersal seed predators for the majority of consumed fruit species. As shown in Figure 1 *C. nigra* has an almost constant year-round food availability as unripe fruits in particular stay long periods on the tree before ripening. On the other hand seeds stay longer periods available on the ground than in the tree, which is favourable for both the rodents and *S. picturata.* So, apparently there is a good niche separation among all seed predators in this ecosystem, which is mainly based on fruit and seed size, feeding height and activity pattern.

In conclusion, *C. nigra* destroys seeds of numerous endemic plant species in Sainte Luce and should therefore be considered a seed predator in this ecosystem. In general, they split and thus destroy the seed with their bill, eat it and reject the surrounding pulp. Seed dispersal does occasionally occur when parrots fly away from the parent plant, dropping several intact fruits or the remains of soft and juicy berries. Zoochorous tree species have evolved phenological, morphological and biochemical flower, fruit and seed characteristics to attract efficient pollinators and seed dispersers, which can assure successful plant regeneration. However, the behaviour of granivorous animals offers the plant no apparent advantage. Nevertheless, most food species consumed by these parrots are also eaten by other frugivores, which act as seed dispersers. Dietary overlap among granivores is limited and the different seed predators seem to occupy separate trophical niches in this ecosystem.

ACKNOWLEDGEMENTS
We would like to thank QMM (QIT Madagascar Minerals) for providing logistics and infrastructure at the study site. We are very grateful to Steve Goodman and Jörg Ganzhorn for their extensive revisions and useful suggestions. This study was carried out under a Collaboration Agreement between the Department of Animal Biology and the Department of Anthropology of the University of Antananarivo, the Institute of Zoology of Hamburg University and QMM. The first author was supported by a grant from the Belgian Fund for Scientific Research, Flanders (FWO). We thank the Flemish Government for its structural support for the Centre of Research and Conservation (CRC) of the Royal Zoological Society of Antwerp (RZSA).



’Isavasavana ny tahony,
tiana hahitana ny fotony’

If someone explores the trunk of a tree,
it means he wants to see the roots

Malagasy proverb
Drawing of fruits from Sainte Luce © An Bollen 2003

4

Fruit characteristics in a dry deciduous and a humid littoral forest of Madagascar: evidence for selection pressure through abiotic constraints rather than through co-evolution with lemurs as seed dispersers.

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FRUITS AND FRUGIVORES (L DEW, J-P BOUBLI)
(IN PRESS)

ABSTRACT

Fruit and seed characteristics are compared between a dry deciduous forest in the west and a humid littoral forest in the south-east of Madagascar to discriminate between the role of abiotic factors (humidity, climate, soil characteristics) and frugivorous vertebrates for the evolution of morphological and biochemical fruit characteristics. The sites differed in abiotic conditions but contain very similar communities of frugivorous vertebrates. Fruit selection by two lemur species (*Eulemur fulvus* and *Cheirogaleus medius*) that are important for seed dispersal and that are present at both study sites, was compared between sites to examine fixed selection criteria that could give rise to possible co-evolution between frugivores and their fruit species on the one hand or to dietary flexibility of the frugivores on the other hand. Our results show that most fruit characteristics differ significantly between study sites. Food selection by both lemur genera in relation to morphological and biochemical fruit characteristics co-varies closely with their representation at a given site. These results indicate that morphological and biochemical characteristics are more likely the result of abiotic conditions rather than of interactions between frugivorous lemurs and their food.

INTRODUCTION

The study of interactions between fruits and their vertebrate consumers has generated a great deal of interest in recent decades, especially in tropical forests where most plant species depend on frugivorous animals for dispersal of their seeds (see Willson et al. 1989 for a review). Attracting frugivores is crucial for these plants in order to ensure reproduction by seed dispersal (Howe and Smallwood 1982). Morphological fruit characteristics, such as colour, pulp richness, hardness of the shell, seed size, and patterns of spatio-temporal distribution have been interpreted as co-adapted features that govern animals' choice of fruit species.

Most seed dispersal studies and reviews of correlations between frugivore food selection and fruit characteristics have produced little empirical support for tight co-evolutionary relationships (Howe and Smallwood 1982; Herrera 1984; Howe 1984; Gautier-Hion et al. 1985; Fisher and Chapman 1993; Chapman 1995; Erikkson and Ehrlen 1998; Lambert and Garber 1998), as most plant species do not depend on one single species of disperser. In most cases a range of taxonomically distinct frugivores may consume and disperse the seeds of the same fruiting species (Gautier-Hion et al. 1985; Herrera 1986; Ganzhorn 1988; Chapman 1995; Chapman and Chapman 1996; Bollen et al., Chapter 2, 3). Fruit traits are likely to evolve in response to other selection pressures or may perform more than one function (Willson and Whelan 1990). Data from the fossil record suggest that morphological fruit traits often have remained relatively constant for millions of years (Fisher and Chapman 1993; Chapman 1995).

Primates represent a major group of mammalian seed dispersers in the tropics. Studies have demonstrated that many primate species rely heavily on fruit and that they represent a large component of the frugivore biomass (25-40%, Terborgh 1983; Bourlière 1985; Chapman 1995; Julliot 1996; Chapman and Onderdonk 1998; Lambert and Garber 1998). In Madagascar, lemurs have been postulated to be important seed dispersers (Ralisoamalala 1996; Scharfe and Schlund 1996; Dew and Wright 1998; Overdorff and Strait 1998; Birkinshaw 1999, 2001; Ganzhorn et al. 1999a) in particular since the guild of frugivorous birds and bats is depauperate in this island as compared to other continents (Fleming et al. 1987; Wright and Martin 1995; Goodman and Ganzhorn 1997; Wright 1997a; Böhning-Gaese et al. 1999; Ganzhorn et al. 1999*a)*.

In this study, we investigate whether morphological and biochemical fruit characteristics can be linked to abiotic conditions or whether there is evidence for co-evolution between these fruit characteristics and the main consumers that are involved in seed dispersal, i.e. *Eulemur fulvus* and *Cheirogaleus medius*. We selected two types of forest in Madagascar growing under very different climatic and edaphic conditions: evergreen littoral wet forest and dry deciduous forest. Both sites had a similar complement of frugivore species, having six genera and five species in common.

The following predictions were tested:

1. If fruit characteristics evolved mainly in response to abiotic conditions we expect different morphological and biochemical fruit characteristics at the two sites
2. If fruit characteristics co-evolved in response to selective pressure of consumers we expect that characteristics of food items at both sites do not differ, as the guild of frugivorous vertebrates is very similar at both sites.
3. The second prediction listed above requires that selection criteria of frugivores are species-specific. We therefore predict that these consumers will have a specialised diet irrespective of fruit availability, as is supposed by co-evolution.

Fig. 1. Location of the study sites.

METHODS

Study Sites

Data were collected at two sites: Sainte Luce (STL) and Kirindy/CFPF (KIR).

In STL the study site is a 377-ha fragment of humid littoral forest located in south-eastern Madagascar, 50km north of Fort-Dauphin/Tolagnaro at 24º45'S 47º11'E. Data collection was carried out by AB and GD between November 1999 and February 2001 (Fig. 1, Donati 2002). From January 2000 through December 2000 annual rainfall was 2,480 mm with four distinct seasons; hot-wet (December-February), hot-dry (March-May), cold-wet (June-August) and transitional-dry (September-November) (Donati 2002), but substantial inter-annual variation has been recorded (QIT Madagascar Minerals, unpubl. data). Mean temperature is about 23°C and ranges from 12°C to 33°C. The littoral forest of STL is characterised by a relatively open or non-continuous canopy, which is 6 to 12m in height with emergents of up to 20 m (Lewis Environmental Consultants 1992a). The diameter at breast height (DBH) of trees rarely exceeds 30-40cm (Rabevohitra et al. 1996). Littoral forest grows on sandy soils and occurs within 2-3km of the coast at an altitude of 0-20m (Dumetz 1999).

The forest of Kirindy/CFPF is a forestry concession of the Centre Formation Professionnelle Forestière de Morondava at 20°04'S 44°40'E, some 60km north of Morondava in west-Madagascar). It consists of 12,000ha of dry deciduous forest. Annual rainfall averages about 800 mm with a long distinct dry season from April to October when most trees lose their leaves. Most rain falls between December and February.

Mean temperature is around 24.7°C and relative humidity varies between 58% and 67% with an average of 63% (Rakotonirina 1996; Sorg and Rohner 1996). The canopy reaches 10-12m in height. Trees with DBH<30 cm predominate (Ganzhorn and Sorg 1996, Ganzhorn et al. 1999b). The forest grows on sandy soils with a narrow band of vertisols along the seasonal Kirindy River about 20km east of the coast at an altitude of 18-40m (Sorg and Rohner 1996). Here, studies were carried out by GD, JF, DS and JG between 1987 and 1997.

Frugivore guild

Ten fruit-eating vertebrate species occur at STL, nine at KIR (Table 1). Some of these species are strictly frugivorous, while others are more frugi-granivorous or omnivorous. However, for the latter the majority of their diet (>50%) consists of fruits and/or seeds so they may be considered as possible seed dispersers. Two lemur species were studied in more detail for this study. These were *Eulemur fulvus rufus* in KIR and *E. f. collaris* in STL and *Cheirogaleus medius* at both sites. These species, particularly *E. fulvus,* are supposed to represent very important, if not essential, seed dispersers in Malagasy forests (Ganzhorn et al. 1999a).

Phenology and pluviometry

In STL a phenological transect with a total of 423 individual trees belonging to 95 species and 43 families was set up by AB and GD and monitored between January 2000 and January 2001. Trees sampled for phenology had a DBH>5cm and an effort was made to obtain five individuals per species whenever possible. Twice a month, presence or absence of young leaves, flowers, unripe and ripe fruits were recorded. A Tru-Check Rain Gauge was installed at the campsite in December 1999. It was checked and emptied each morning around 06h00. during the whole study period. For KIR rainfall and phenological data were taken from Sorg and Rohner (1996) involving 80 individual trees of 56 species (26 families) monitored over several years (1978-1987). For the present phenology analysis only large overstory tree species were considered. Small trees, shrubs, vines and epiphytes were left out in order to allow comparison between sites. A subsample of both phenologies (STL: 54 spp., KIR: 32 spp.) was extracted to include only those plant species that had been characterised morphologically (see below).

Plant and fruit characteristics

In STL and KIR fruits of 173 and 171 plant species belonging to 58 and 47 families

Morphological characteristics

Variables used to characterise fruits were:
Growth form of parent plant: large tree, small tree and shrub, others
(including herbs, vines and epiphytes);
Fruit type: berry, drupe, capsule, pod, samara, synconia, others;
Pulp type: juicy soft, juicy fibrous, dry fibrous, aril, no pulp;
(in phenology 'fleshy' fruits are characterised as juicy soft, juicy fibrous or arillate; 'non-fleshy' fruits are dry fibrous or do not have any pulp);
Colour: yellow-orange, red, purple, brown, green, others (black, grey and white), (multicoloured fruits were put in the category of the most conspicuous colour present);
Odour: absent, present;

Table 1. Frugivorous, granivorous and omnivorous vertebrate species possibly involved in seed dispersal in Sainte Luce and Kirindy. Diet: F: frugivorous, FG: frugi-granivorous; Ffo: frugi-folivorous; foF: foli-frugivorous; O:omnivorous; Activity: D: diurnal, N: nocturnal, C: cathemeral; Body mass (in g) and Body length (in cm) and their potential role as seed dispersers (D) or seed predators (P) in these ecosystems.ND: no data available.

Family	Scientific name	English name	STL	KIR	Diet	Activity	Body[a] mass	Body[ab] length	Impact seeds
AVES									
Columbidae	*Treron australis*	Malagasy Green Pigeon	x	x	F	D	215	32	D
Columbidae	*Alectroenas madagascariensis*	Malagasy Blue Pigeon	x		F	D	ND	28	D
Pycnonotidae	*Hypsipetes madagascariensis*	Madagascar Bulbull	x	x	F	D	45	24	D
Psitaccidae	*Coracopsis nigra*	Lesser Vasa Parrot	x	x	G	D	218	35	P
	Coracopsis vasa	Greater Vasa Parrot	x	x	G	D	ND	50	P
MAMMALIA									
CHIROPTERA									
Pteropodidae	*Pteropus rufus*	Madagascar Flying Fox	x		F	N	500-750	23-27	D
PRIMATES									
Indridae	*Propithecus verreauxi*	Verreaux's Sifaka		x	FoF	D	3000	40-47	D,P
Lemuridae	*Eulemur fulvus collaris*	Collared Brown Lemur	x		F	C	2000-2300	40-47	D
	Eulemur fulvus rufus	Red-fronted Brown Lemur		x	FFo	C	1600-2100	45	D
Cheirogaleidae	*Microcebus murinus*	Grey Mouse Lemur		x	O	N	60	12.5	D
	Microcebus berthae	Berthe's Mouse Lemur		x	O	N	30	12.5	D
	Microcebus rufus	Brown Mouse Lemur	x		O	N	42	12.5	D
	Cheirogaleus major	Greater Dwarf Lemur	x		O	N	443	25	D
	Cheirogaleus medius	Fat-tailed Dwarf Lemur	x	x	O	N	119-280	20	D

[a] Data from Langrand (1990), Goodman et al. (1997b), Fietz and Ganzhorn (1999), Garbutt (1999), Ganzhorn et al. (1999a), Donati (2002).

[b] Body length is total length for birds and bats but head/body length for lemurs.

Number of seeds: 1-2, 3-10, 11-50, 50+;
Fruit weight: <1g, 1-10g, 11-50g, >50g;
Fruit length: <10mm; 10-30mm; >30mm;
Seed length: <10mm, 10-20mm, >20mm;
Fruit protection: dehiscent, indehiscent with thin husk; indehiscent with thick husk;
Seed protection: no protection; seed coat or lignified kernel;
Dispersal type: zoochorous (exo- and endo-) or non-zoochorous including anemochorous, hydrochorous, autochorous.

The characterisations were modified based on the original classifications by Gautier-Hion et al. (1985) and Lambert and Garber (1998). Epiphytes, vines, shrubs, large (>6m) and small trees (<6m) but no herbs were considered. Fruits and seeds were weighed fresh using spring or electronic balances and measured using scales and callipers with 0.01g and 0.01mm precision, respectively.

Chemical characteristics

Ripe fruits were dried in the sun or in a drying oven, ground to pass a 2mm sieve, and dried overnight at 50-60°C prior to analyses. Samples were analysed for neutral (NDF) and acid (ADF) detergent fibre (Goering and Van Soest 1970; Van Soest 1994; modified according to the instructions for use in an ANKOM FIBRE ANALYZER). Neutral detergent fibre (NDF) represents the percentage of fibrous material non digestible for herbivores with unspecialised digestive systems. Acid detergent fibre is composed of cellulose and lignin. Total nitrogen was determined using the Kjeldahl procedure. Total nitrogen was not converted to crude protein as the conversion factors for heterogenous samples are unclear (Milton and Dintzis 1981). Extractable or soluble proteins were assessed with BioRad after extraction of the plant material with 0.1N NaOH for 15h at room temperature. Soluble carbohydrates and procyanidin (condensed) tannins were extracted with 50% methanol. Concentrations of soluble sugar were determined as the equivalent of galactose after acid hydrolization of the 50% methanol extract. This measurement correlates well with concentrations obtained with enzymatic analyses of glucose, fructose and galactose (Ganzhorn and Tomaschewski, unpubl. data). Concentrations of procyanidin tannin were measured as equivalents of quebracho tannin (Oates et al. 1977; Porter and Hemingway 1990). Lipids were determined by the Soxleth method. Biochemical analyses were carried out at the German Primate Center (Göttingen) and at the Institute of Zoology, Department of Ecology and Conservation (University Hamburg).

Fruit eating

In STL diets of both lemur species were assessed by tree watches (36h-watches from hides at 30 tree species, 1-2ind/sp), opportunistic observations, faecal analyses and analyses of fruit traps that form part of an extensive ecological study on seed dispersal and seed predation (Bollen unpubl. data). Additional feeding data of *Eulemur fulvus collaris* were also compiled during all-day and all-night follows (Donati 2002; Donati et al. in press). In KIR data on fruit consumption were compiled by several researchers (contrib. to Ganzhorn and Sorg 1996; Donati et al. 1999; Fietz and Ganzhorn 1999; Ganzhorn et al. 1999a, Schwab unpubl. data).

Statistical analyses

Non-parametric tests were applied for comparisons of fruit characteristics. The role of site effects, the impact of frugivorous lemurs and their interactions on biochemical characteristics were analysed with two-way analyses of variance. Data were arcsine transformed for these analyses. Statistical analyses were run according to Siegel (1956) with the help of SAS and SPSS software.

RESULTS

Climate and phenology

Figure 2 shows phenology and annual precipitation for both study sites. Annual rainfall was 2,480mm in STL and 721mm in KIR during the study period. The phenological patterns considered in this study differ slightly from the overall pattern at both sites as published previously (Sorg and Rohner 1996; Donati 2002) because only a subset of the complete phenological dataset was used for comparison.

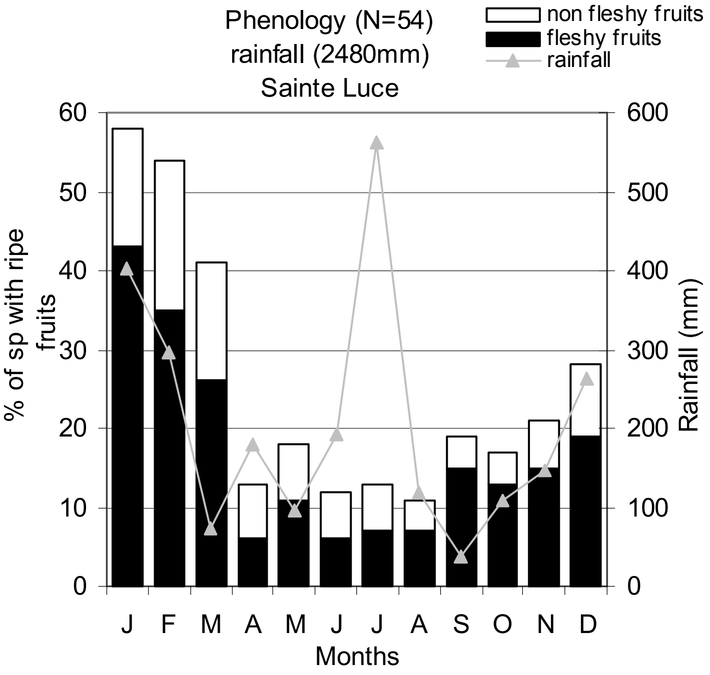
In KIR ripe fruits are available year round with a minimum in April. 'Fleshy' and 'non-fleshy' fruit species are equally (50%) represented in KIR (Fig. 2). During the dry season (May through October) non-fleshy fruits predominate. As indicated before, in STL there are no clearly defined wet or dry seasons. Fruit abundance here is highest from January through March, rather limited from April through October with a lean period from June to August. The majority (81%) of fruit species in STL are characterised as 'fleshy'. In contrast to KIR, the representation of the 'non-fleshy' fruits remains low but fairly constant (4-7%) in STL throughout the year.

Soil conditions

In the upper layer (A horizon) soils are more acid and contain higher concentrations of organic matter, nitrogen and phosphor in STL than in KIR (Table 3). Exchange capacity has not been measured for STL. The situation at STL is similar to the data available for Ranomafana, an evergreen rainforest site at higher altitude (Ganzhorn et al. 1999b). There, growth rate of trees is higher than at Kirindy, probably due to the longer growth season. However, the probability of fruiting is reduced, indicating that fruit production is associated with higher stress for the trees of the evergreen forest. It is unclear how these different constraints affect the type of fruits produced.

Floristics

Both datasets have 30 families (40%) and 19 genera (10%) in common but no tree species (Table 2). In STL the four most important plant families were Rubiaceae (23 species), Euphorbiaceae (8), Flacourtiaceae (6), and Myrtaceae (6). They accounted for 25% of all species. In KIR Fabaceae (16), Euphorbiaceae (14), Tiliaceae (9), Rubiaceae (8), and Combretaceae (6) were the five most important plant families. They accounted for 31% of the species. The representation of these top eight families is not correlated between the two datasets (r_s=0.18; P=0.7, N=8). The representation of large and small trees, shrubs and other growth forms in the samples did not differ between sites (Table 4).



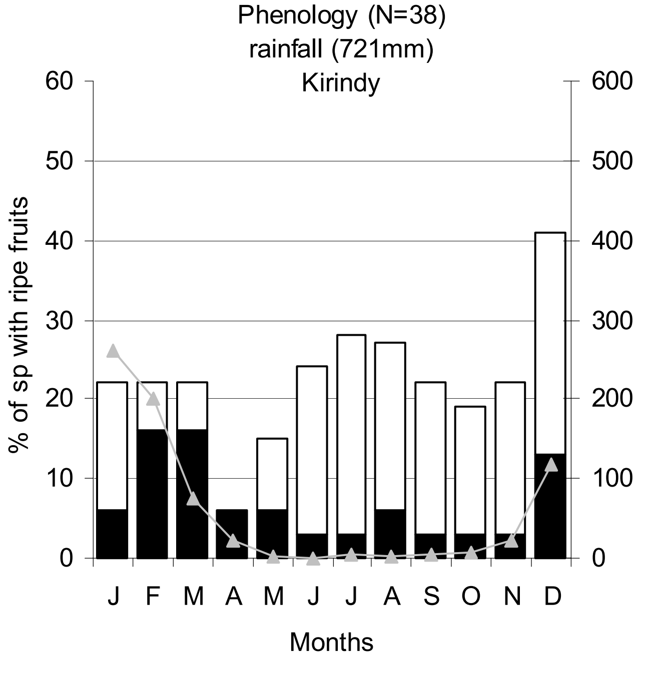


Fig. 2. Monthly fruit availability and rainfall in Sainte Luce and Kirindy. Fleshy fruits are fruits characterised as juicy soft, juicy fibrous or arillate, non-fleshy fruits are dry fibrous or do not have any pulp.

Table 2. Plant families, genera and species sampled in Sainte Luce and Kirindy. In bold the most important plant families per site are indicated. There are 30 plant families in common.

	L	KIR	TOT	COM		STL	KIR	TOT	COM
Families (N = 74)	N	N	N	N	Families	N	N	N	N
	sp	sp	gen	gen		sp	sp	gen	gen
Anacardiaceae	3	4	4	1	Meliaceae	1	4	6	0
Annonaceae	5	0	2	0	Menispermaceae	1	1	2	0
Apocynaceae	1	3	4	0	Monimiaceae	3	0	1	0
Araceae	1	0	1	0	Moraceae	5	3	3	1
Araliaceae	2	0	1	0	Myricaceae	1	0	1	0
Arecaceae	5	1	2	0	Myristicaceae	2	0	1	0
Asclepiadaceae	0	1	1	0	Myrsinaceae	1	0	1	0
Asteraceae	0	2	2	0	**Myrtaceae**	**6**	0	3	0
Asteropeiaceae	1	0	1	0	Ochnaceae	1	1	2	0
Bignoniaceae	3	4	5	1	Olacaceae	1	1	2	0
Bombaceae	0	2	1	0	Oleaceae	5	3	4	1
Boraginaceae	0	1	1	0	Pandanaceae	3	2	1	1
Burseraceae	1	2	2	0	Passifloraceae	0	2	1	0
Buxaceae	0	1	1	0	Pedaliaceae	0	1	1	0
Canellaceae	1	0	1	0	Physenaceae	1	0	1	0
Capparaceae	1	0	1	0	Pittosporaceae	2	0	1	0
Celastraceae	2	1	3	0	Podocarpaceae	1	0	1	0
Guttiferae	5	1	3	1	Ptaeroxylaceae	0	3	1	0
Combretaceae	1	**6**	3	1	Rhamnaceae	0	2	2	0
Connaraceae	1	1	1	1	**Rubiaceae**	**23**	**8**	20	2
Dichapetallaceae	2	0	1	0	Rutaceae	3	2	2	1
Ebenaceae	2	4	1	1	Sapindaceae	4	2	5	1
Elaeocarpaceae	2	0	1	0	Sapotaceae	2	2	3	0
Ericaceae	1	0	1	0	Sarcolaenaceae	4	2	4	0
Erythroxylaceae	3	1	1	1	Saxifragaceae	2	0	1	0
Euphorbiaceae	**8**	**14**	13	1	Scrophulariaceae	0	1	1	0
Fabaceae	3	**16**	17	0	Simaroubaceae	0	1	1	0
Flacourtiaceae	**7**	1	6	1	Solanaceae	0	1	1	0
Hammamelidaceae	1	0	1	0	Sphaerosepalaceae	1	1	1	1
Hernandiaceae	0	1	1	0	Sterculiaceae	0	3	3	0
Hippocrateaceae	1	0	1	0	Strelitziaceae	1	0	1	0
Icacinaceae	2	0	1	0	**Tiliaceae**	0	**9**	1	0
Lauraceae	4	0	3	0	Ulmaceae	1	0	1	0
Loranthaceae	3	0	1	0	Verbenaceae	1	3	2	1
Lecythidaceae	1	1	2	0	Violaceae	1	0	1	0
Liliaceae	4	1	4	0	UNKNOWN	15	37		0
Loganiaceae	3	5	2	1	Sum (N species)	173	171	180	19
Lythraceae	0	1	1	0	Maximum	23	16	20	2
Melastomataceae	1	0	1	0	Minimum	0	0	1	0
					Average	3	1.81	2.46	-

Table 3. Soil characteristics of the littoral forest at Sainte Luce and the dry deciduous forest at Kirindy/CFPF (values are medians and range; N=4 for both sites).

	Depth (cm)	Horizon	pH	C (%)	N (%)	C/N	Organic matter	P (ppm)	K (ppm)
Sainte Luce[1]	10	A	4.6 4.1 – 5.9	11.3 7.2 – 25.5	0.42 0.21 – 0.84	30 23 – 41	18.1 12.4 – 43.9	2.0 1.0 – 3.0	22 17 - 49
	80	B	5.7 5.6 – 7.2	0.6 0.6 – 4.9	0.88 0.14 – 1.46	2.07 0.65 – 4.28	1.1 1.0 – 8.35	0 0 – 3.0	15 0 - 17
Krindy/ CFPF[2]	10	A	6.4 6.0 – 6.5	1.76 0.53 – 2.15	0.13 0.03 – 0.15	14 13 - 21	3.0 0.9 – 3.7	0.55 0.2 – 0.9	25 12 – 35
	80	B	5.2 4.9 – 6.6					0.25 0.2 – 0.3	13 6 – 31

[1] Data come from Razafimizanilala (1996).

[2] Data come from Felber (1984).

Comparison of fruit characteristics between sites

Morphology

Five out of eleven morphological parameters differed significantly between both study sites (Table 4). In STL, berries are the dominating type of fruit followed closely by drupes. In KIR drupes are most abundant followed by berries and capsules. Fruit pulp in STL is mostly soft and juicy. In KIR the majority of fruits has a rather dry and fibrous pulp. Remarkable is the large number of odoriferous fruits in STL while in KIR only one third of the fruits was classified as odoriferous. KIR has more dehiscent fruits and thick-husked indehiscent fruits than STL where 75% of fruits are indehiscent and thin-husked. Concerning dispersal type, zoochorous fruits prevail both in KIR and STL, but KIR has more non-zoochorous fruits than STL. However this difference was no longer significant after sequential Bonferroni adjustment. There is no significant difference between study sites for colour, number of seeds, fruit length, fruit mass, seed length and seed protection.

Chemistry

The chemical composition of mature fruits differed between sites in most chemical variables except for extractable proteins and sugars. Lipid concentrations were significantly higher in STL while NDF, ADF, total nitrogen, and procyanidin tannins were higher in KIR (Table 5). After rigorous adjustment for Type I errors (Rice 1989), there was only a significant difference for NDF, ADF and tannins.

Comparison of diets of Eulemur and Cheirogaleus between sites

Morphology

Fruits eaten by both lemur species at both sites did not differ significantly in growth form, number of seeds, fruit length, fruit mass, seed length or seed protection (Table 4). However significant differences were found with respect to pulp type and the protection of fruits consumed by *Eulemur* and *Cheirogaleus* at both sites. The observed difference corresponds to the differential availability of fruits with different types of pulp and protection at both sites.

Even though significantly fewer berries but more capsules were available in KIR than in STL (Table 4), this difference was not apparent when comparing diets of both lemurs between sites. Both species seemed to prefer berries and drupes even when these are less common and harder to find. In contrast, proportions of fruit colours did not differ significantly between samples eaten by *C. medius,* although *E. fulvus* did eat significantly more brown and green fruits in KIR and more yellow, orange and red fruits in STL. The proportion of odoriferous fruits eaten by both lemur species was higher in STL than in KIR, though the difference is not significant in the case of *C. medius*. KIR also had significantly more non-zoochorous fruits than STL, but still zoochorous fruits dominate the fruit diet of both lemur species at both sites.

Chemistry

Except for higher tannin concentrations in fruits consumed in KIR, none of the concentrations of the plant chemicals differed between fruits eaten by *C. medius* in STL and KIR (Table 6). Fruits consumed by *E. fulvus* contained higher concentrations of fibre and tannins in KIR than in STL. These results correspond with the biochemical differences in overall fruit availability between sites. Only the difference between fibre content remains significant after sequential Bonferroni.

Table 4. Morphological characteristics of fruits collected in Sainte Luce and Kirindy and of fruits eaten by *Cheirogaleus medius* and *Eulemur fulvus* ssp. at the two sites. The X²-values were calculated for comparisons between sites; * P<0.05, **P<0.01, ***P<0.001.
The results that remain significant after sequential Bonferroni adjustment are in bold

	Total database		*Cheirogaleus* diet		*Eulemur* diet	
	STL	KIR	STL	KIR	STL	KIR
Total number of species	173	171	36	36	107	46
Growth form (N)	173	121	36	35	107	44
Large tree	94	69	22	19	69	27
Small trees & shrubs	62	40	11	13	28	15
Vine-herbs-epiphytes	17	12	3	3	10	2
Unknown	*0*	*49*	*0*	*1*	*0*	*2*
X²	0.25; df=2		0.37; df=2		1.64; df=2	
Fruit type (N)	165	159	34	34	103	45
Berry	80	40	18	13	52	17
Drupe	52	58	12	15	39	18
Others	9	13	4	6	12	10
Capsule	21	32				
Pod	3	16				
Unknown	*8*	*12*	*2*	*2*	*4*	*1*
X²	**25.46***; df=4**		1.54; df=2		3.48; df=2	
Pulp type (N) [1]	171	153	36	35	107	44
Juicy soft	103	43	33	15	76	10
Juicy fibrous	24	38	3	20	20	33
Dry fibrous	4	59			11	1
Aril	11	4				
No pulp	29	9				
Unknown	*2*	*18*	*0*	*1*	*0*	*2*
X²	**88.9***; df=4**		**19.30***; df=1**		**43.51***; df=2**	
Colour (N) [2]	172	116	36	31	107	36
Yellow orange	32	14	9	4	22	4
Red	28	10				
Purple	16	6				
Brown	44	41	6	11	25	17
Green	38	35	9	11	24	12
Others	14	10	12	5	36	3
Unknown	*1*	*55*	*0*	*5*	*0*	*10*
X²	10.52; df=5		6.14; df=3		14.14**; df=3	
Odour (N)	167	152	36	33	106	44
Absent	58	104	13	19	33	27
Present	109	49	23	14	73	17
Unknown	*6*	*18*	*0*	*3*	*1*	*2*
X²	**35.30***; df=1**		3.19; df=1		**11.84***; df=1**	

Several categories needed to be lumped if the sample was too small per category:

[1] For pulp type, categories were lumped into juicy soft + aril, fibrous + no pulp for *Cheirogaleus* and juicy, fibrous and no pulp for *Eulemur*

[2] For colour, 'others' included also the red and purple fruits for *Cheirogaleus* and *Eulemur*

Table 4 Continued

	Total database		*Cheirogaleus* diet		*Eulemur* diet	
	STL	KIR	STL	KIR	STL	KIR
Number of seeds (N)	172	151	36	35	107	44
1-2	97	72	22	16	62	17
3-10	43	58	9	15	26	19
11-50	12	9			5	4
50+	20	12			14	4
10+			5	4		
Unknown	*1*	*20*	*0*	*1*	*0*	*2*
X^2	7.02; df=3		2.54; df=2		7.39; df=3	
Fruit weight (N)	161	146	35	33	100	39
<1g	69	75	23	15	40	12
1-10g	77	61			49	24
>10g	15	10			11	3
>1g			12	18		
Unknown	*12*	*25*	*1*	*3*	*7*	*7*
X^2	2.38; df=2		2.83; df=1		1.78; df=2	
Fruit length (N)	167	159	36	36	105	45
<10mm	42	54	12	16	23	10
10-30mm	96	76	22	16	62	28
>30mm	29	29	2	4	20	7
Unknown	*6*	*12*	*0*	*0*	*2*	*1*
X^2	3.63; df=2		2.19; df=2		0.27; df=2	
Seed length (N)	160	148	33	35	101	43
<10mm	91	98	22	24	58	23
10-20mm	51	42			32	17
>20mm	18	8			11	3
>10mm			11	11		
Unknown	*13*	*23*	*3*	*1*	*6*	*3*
X^2	4.52; df=2		0.03; df=1		1.10; df=2	
Fruit protection (N)	173	151	36	35	104	45
Dehiscent	26	39	0	3	10	5
Indehiscent thin husk	130	80			83	26
Indehiscent thick husk	17	32			11	14
Indehiscent			36	30		
Unknown	*0*	*20*	*0*	*1*	*3*	*1*
X^2	**17.68***; df=2**		9.27**; df=1		10.05**; df=2	
Seed protection (N)	158	147	35	34	101	45
None	82	79	14	18	41	24
Lignified kernel/seed	76	68	21	16	60	21
Unknown	*15*	*24*	*1*	*2*	*6*	*1*
X^2	0.10; df=1		1.16; df=1		2.05; df=1	
Dispersal mode (N)	163	150	35	35	103	45
Zoochorous	130	104	34	33	93	41
Non-zoochorous	33	46	1	2	10	4
Unknown	*10*	*20*	*1*	*1*	*4*	*1*
X^2	4.50*; df=1		1.16; df=1		2.05; df=1	

Table 5. Biochemical characteristics of ripe fruits at Sainte Luce and Kirindy. NDF: neutral detergent fiber, ADF: acid detergent fiber; Nitrogen: total nitrogen; Tannin: procyanidin tannin. Z-values are based on Mann-Whitney-U tests; * P<0.05; *** P<0.001.
The results that remain significant after sequential Bonferroni adjustment are in bold

Site		NDF	ADF	Nitrogen	Extractable protein	Fat	Sugar	Tannin
Sainte	Median	31.9	22.6	0.8	2.9	3.0	18.2	0.2
Luce	Quartiles	23.9–47.5	17.1–35.7	0.6–-1.1	1.7–4.4	1.8–5.6	7.8–36.3	0.0–0.6
	N	94	94	104	104	100	104	104
Kirindy	Median	53.3	42.0	0.9	2.6	2.1	10.6	0.4
	Quartiles	34.8–69.4	28.2–50.6	0.7–1.3	1.5–4.0	1.1–3.5	6.2–29.2	0.2–0.9
	N	41	39	45	36	52	36	37
Z		**4.19*****	**4.08*****	2.15*	0.71	2.11*	0.99	**2.31***

Lemur food selection and fruit availability within a site

Morphology

Cheirogaleus medius was observed feeding on 36 fruit species at both sites. The diet of *Eulemur* contained 107 and 46 fruit species in STL and KIR, respectively (Table 4). We compared the lemur food traits with the overall availability of these traits present within a site (Table 7). For the analyses of food selection for *E. fulvus* all fruits were used that had been characterised for the two forests as listed in Table 4. *C. medius* is hibernating for up to 7 months per year. Therefore only those fruits were considered for the analysis of fruit selection that were present during the months when this species was active (not hibernating). This resulted in different numbers than those listed in Table 4.

- *Cheirogaleus medius* -

In STL fruits lighter than 10g and fruits with soft and juicy pulp were over represented in the diet of *C. medius.* They ate only thin-husked indehiscent fruits and 34 of the 35 fruit species were classified as zoochorous (Table 4, Table 6).
In KIR *C. medius* ate more drupes and berries (82%) than would be expected based on the availability of these types (62%) and 33 of the 35 fruit species were classified as zoochorous.

- *Eulemur fulvus* ssp. -

In STL well-protected seeds were eaten more frequently than would be expected based on their representation in the sample, which is correlated with the importance of drupes in their diet (drupes always have a hard seed coat). As frugivores these species target mainly fruit pulp and therefore seed protection is not an important food selection criterion for them. Zoochorous fruits were also over-represented in the diet of *E. fulvus* (Table 4).
In KIR 62% of the fruits weighed between 1-10g and the category ‘indehiscent fruit with a thin husk’ comprise 74% in the diet of *E. fulvus,* compared to 50% in the forest sample. Zoochorous fruit types were also over-represented.

Other morphological fruit characteristics, such as growth form, colour, odour, number of seeds, fruit length and seed length, did not differ significantly between food exploited and the overall fruit availability in both forest types both for *Eulemur fulvus* and *Cheirogaleus medius*.

Table 6. Biochemical characteristics of food and non-food fruits of *Eulemur fulvus* ssp. and *Cheirogaleus medius*. For comparisons of fruit selection by *C. medius* only those fruits were considered that were present during the months when *C. medius* were active (i.e. not hibernating). Values are medians, quartiles, and sample size. Z-values are based on Mann-Whitney-U. * P<0.05, ** P<0.01, *** P<0.001.
The results that remain significant after sequential Bonferroni adjustment are in bold

	Cheirogaleus medius						Difference of food items between sites
	STL			KIR			
	Eaten	Not eaten	Z	Eaten	Not eaten	Z	
NDF	30.6 24.1-41.9 31	33.4 24.4-50.7 58	0.90	49.8 29.8-54.8 21	67.4 52.5-72.8 16	**2.80****	1.85
ADF	22.0 17.1-31.0 31	24.7 17.6-37.6 58	1.13	34.2 21.3-42.3 20	49.5 42.6-53.1 15	**3.12****	1.69
Total nitrogen	0.8 0.6-1.1 33	0.8 0.6-1.1 64	0.38	0.9 0.7-1.2 23	1.0 0.8-1.5 18	1.31	1.30
Extractable protein	3.2 1.5-4.7 33	2.9 1.8-4.3 64	0.01	2.5 1.7-3.1 20	3.0 1.9-4.1 14	0.65	0.69
Fat	2.7 2.1-4.9 33	3.1 1.8-7.5 61	0.82	2.0 1.2-3.6 24	2.3 1.1-3.7 24	0.07	1.19
Sugar	31.2 11.2-41.4 33	14.8 6.6-33.1 64	2.03*	25.2 8.5-53.6 20	8.3 5.0-10.7 14	2.40*	0.16
Tannins	0.2 0-0.4 33	0.2 0-0.6 64	0.70	0.3 0.2-0.7 21	0.6 0.2-1.0 14	0.40	2.09*

	Eulemur fulvus						Difference of food items between sites
	STL			KIR			
	Eaten	Not eaten	Z	Eaten	Not eaten	Z	
NDF	32.0 23.6-47.7 76	31.2 26.6-44.9 18	0.22	52.2 36.1-70.3 19	53.3 34.7-68.9 22	0.14	**2.87****
ADF	22.4 17.1-35.6 76	22.6 20.6-35.3 18	0.75	42.0 25.7-48.1 18	41.6 27.9-52.0 21	0.29	**2.91****
Total nitrogen	0.9 0.6-1.2 86	0.8 0.6-1.0 18	0.80	1.01 0.8-1.2 20	0.93 0.7-1.3 25	0.44	1.86
Extractable protein	2.8 1.6-4.3 86	3.3 2.5-4.5 18	1.24	2.5 1.9-3.6 17	2.7 1.5-4.2 19	0.09	0.22
Fat	2.7 1.7-5.1 82	5.0 2.5-16.9 18	2.33*	2.0 1.5-3.4 22	2.5 1.1-3.9 30	0.23	1.48
Sugar	19.2 8.3-36.6 86	11.0 7.6-24.2 18	1.34	16.4 5.7-26.9 17	10.2 6.3-23.4 19	0.25	0.61
Tannins	0.2 0-0.5 86	0.31 0.1-1.0 18	1.33	0.5 0.2-1.0 17	0.4 0.2-0.8 20	0.62	2.36*

Chemistry

At both sites, fruits consumed by *C. medius* contained higher concentrations of sugar than fruits not consumed (Table 6), but this was no longer significant after sequential Bonferroni adjustment. In KIR, fruits consumed by *C. medius* had lower fibre contents than fruits that had not been consumed. The only significant difference between non-food fruits and fruits consumed by *E. fulvus* consisted of lower fat concentrations in food species consumed at STL. Again this was not significant anymore after adjustment for Type I errors (Rice 1989).

Interactions between lemur food selection and site effects on fruit chemistry

In order to separate possible effects due to site characteristics from effects of lemur food selection on the chemical composition of fruits, two-way analyses were run using 'site' and 'lemur food' as fixed independent factors. The results of these analyses are consistent with the conclusions above. Site-specific effects are significant for the majority of chemicals. According to the two-way ANOVA *C. medius* consistently searches for fruits with high sugar concentrations (Table 8). *E. fulvus* seems to avoid fruits with high fat contents in Sainte Luce only. The site effects persisted once the food items of the two lemur species were pooled and contrasted to the fruits that had not been eaten by neither species. There were several significant interactions between site and the food effects. *Cheirogaleus medius* avoids high fiber content but this clearly depends on the relative availability of fiber content at a certain site, while for *Eulemur fulvus* tannin concentrations in fruits eaten by *E. fulvus* vary differently at the two sites. Finally when both lemur species are pooled together, the lipid content of the consumed fruit species corresponds as well with the site specific availability.

Table 7. The X^2 results of the comparison between morphological traits of lemur food species and the overall representation of these fruit traits within a site; * P<0.05, ** P<0.01. The results that remain significant after sequential Bonferroni adjustment are in bold

	Cheirogaleus medius				*Eulemur fulvus*			
	STL		KIR		STL		KIR	
	X^2	df	X^2	df	X^2	df	X^2	df
Growth form	0.93	2	1.20	2	4.85	2	4.80	2
Fruit type	1.28	3	11.11*	3	5.08	3	6.15	3
Pulp type	**11.44****	2	1.36	2	3.64	3	3.47	2
Colour	3.49	4	4.19	3	3.78	5	6.44	3
Odour	0.04	1	1.54	1	0.66	1	0.75	1
Number of seeds	0.26	2	0.84	2	1.09	3	1.66	2
Fruit mass	8.53*	2	0.78	1	0.52	2	6.77*	2
Fruit length	3.72	2	2.51	2	0.66	2	4.14	2
Seed length	1.97	1	1.35	1	0.03	2	2.84	2
Fruit skin protection	**12.31****	2	3.06	2	2.77	2	10.65**	2
Seed protection	1.62	1	0.47	1	5.16*	1	0.02	1
Dispersal mode	6.58*	1	**8.56****	1	7.49**	1	**10.46****	1

Table 8. Effects of site characteristics and whether or not an item was eaten by lemurs according to two-way analyses of variance. Analyses were performed on arcsine transformed data. Analyses were run separately for *Cheirogaleus medius, Eulemur fulvus*, and for fruits that had been eaten by either one or both species.
Values are F-values; * P<0.05, ** P<0.01, *** P<0.001.

	Cheirogaleus medius			*Eulemur fulvus*			Lemurs in general		
	Site	Food	Site * Food	Site	Food	Site * Food	Site	Food	Site * Food
NDF	19.88***	10.36**	4.20*	19.75***	0.02	0.21	21.58***	2.00	3.12
ADF	16.96**	10.94**	4.29*	16.28***	0.06	0.16	18.14***	3.32	2.63
Nitrogen	8.68**	3.12	0.87	5.67*	0.12	0.02	5.90*	1.26	0.49
Extractable protein	0.21	0.15	0.16	0.50	0.03	0.94	0.10	0.50	0.21
Fat	2.91	0.78	2.20	10.51***	6.09	2.68	11.05***	4.66*	4.57*
Sugar	0.86	9.07**	0.23	0.45	0.67	0.3	0.12	5.49*	0.25
Tannin	6.39*	0.15	0.25	1.45	0.35	4.06*	1.16	0.49	1.73

DISCUSSION

The compared forest types did not have any plant species in common with only few genera represented at both sites (19 out of 181 in our dataset, Table 2). The low similarity even at higher taxonomic levels and the different phenological pattern lead us to conclude that the two datasets are phylogenetically relatively independent. This view is supported by floristic classifications that based on phytogeographic criteria the evergreen forests of eastern Madagascar can be clearly distinguished from the deciduous formations of the west (e.g. Koechlin et al. 1974; Schatz 2001). The difference in plant species composition and phenology can be related to adaptations in response to abiotic conditions that differ substantially between sites, such as severe water stress and a long period of drought in KIR. In contrast, the seed dispersers available at both sites do not differ markedly. Specifically, the same species of frugivorous lemurs, representing some of the most important seed dispersers of Madagascar (Dew and Wright 1998; Overdorff and Strait 1998; Birkinshaw 1999, 2001; Ganzhorn et al. 1999a), occur at both study sites.

Comparison of fruit characteristics between sites

In both forests the majority of plant species depend on animals for dispersal (80% in STL and 69% in KIR). This situation resembles that in other tropical forests where between 60% and 90% of fruits are zoochorous (Howe and Smallwood 1982; Fleming et al. 1987) including typically a high percentage of berries and drupes with soft and juicy pulp (Tiffney 1984; Gautier-Hion et al. 1985; Smith 2001). However, the proportion of zoochorous fruits is unevenly distributed between the two study sites along with other significant morphological and chemical distinctions. In this respect, we find in STL more fleshy zoochorous berries and drupes with thin husks while dehiscent capsules and indehiscent thick-husked drupes are more abundant in KIR. These morphological properties result in higher fibre and tannin concentrations in the fruits of KIR. Most of these traits in dataset of KIR can be interpreted as adaptations against drought and are also characteristic for the Fabaceae. This is a typical plant family of the dry deciduous forest and at the same time the most important plant family present in KIR when considering species number (Table 2). Scharfe and Schlund (1996) also concluded from their study that in the western forests of Madagascar the majority of fruits are autochorous or dispersed by mammals while in the east dispersal by birds (that eat mainly berries and drupes) and mammals prevail. Our results concur with these.

The site-related difference in the representation of fruits with an odour merits further consideration. In Malagasy forests, frugivorous diurnal and thus visually oriented bird species are poorly represented and most mammalian frugivores of Madagascar are cathemeral or nocturnal. Colour is probably less relevant for these lemurs and flying foxes while olfactory clues are likely to be important (Schilling 1979; Barton et al. 1995; Hladik and Simmen 1996; Bollen and Van Elsacker 2002a, Chapter 3a; Dominy et al. 2002; Luft et al. pers. comm.). Since comparative data on fruit odour from other forests are lacking and taste and smell perception differ largely between individuals and species, the present results - which are based on subjective impressions of different human individuals - cannot be further interpreted. A more standardised evaluation of olfactory clues might be worthwhile in future research.

With respect to our predictions we can say that given the almost identical set of frugivores present at both sites, these large differences in morphological and biochemical fruit traits between sites are most likely not a consequence of selection for seed dispersal by animals, as far as the particular lemur species compared. They rather represent the adaptations of a plant community responding to the need for protection against water loss during the long and harsh dry season, typical for dry deciduous forest in Madagascar.

Comparison of lemur diets between sites and lemur food selection within a site

Regarding feeding selection within a given site and comparison of diets between sites several patterns arise from the datasets. First of all, there are several parameters that seem less important for lemur food selection such as growth form, colour, fruit length, seed length, number of seeds, seed protection and extractable proteins. They did not differ at all between sites and did not influence lemurs' feeding selection. On the contrary, clear feeding preferences were found according to fruit and dispersal type. Both lemurs selected almost exclusively zoochorous berries and drupes when fruits with abiotic dispersal were also available at both sites. Finally and most remarkably, both lemur species display a high dietary flexibility for certain parameters, both morphological (pulp type, odour, fruit skin protection) as biochemical (total nitrogen, tannins, ADF and NDF). For these parameters they would select food items in correspondence to what is most available at a given site. This seems to indicate that these species can switch their diet to what is available. This allows them to survive in different forest types on frugivorous diets with different nutrient compositions and different morphological traits.

Overall, from a chemical perspective these lemur species did not show much evidence for fruit selection based on consistent chemical properties once site-specific characteristics were taken into account. In the present analyses *E. fulvus* avoid fruits with high lipid contents and fruits eaten by *C. medius* had lower fibre content than the non-food items. These criteria persist even after site-specific effects have been accounted for (Table 8). Similarly, the preference of *C. medius* for fruits with high sugar content also persists at both sites. This has been linked to their need to accumulate fat reserves for hibernation (Fietz and Ganzhorn 1999). This selectivity however does not result in tight co-evolution, as a lot of less sugary fruits are present as well at both sites because other seed dispersers also occur and do not necessarily select sugary fruits.

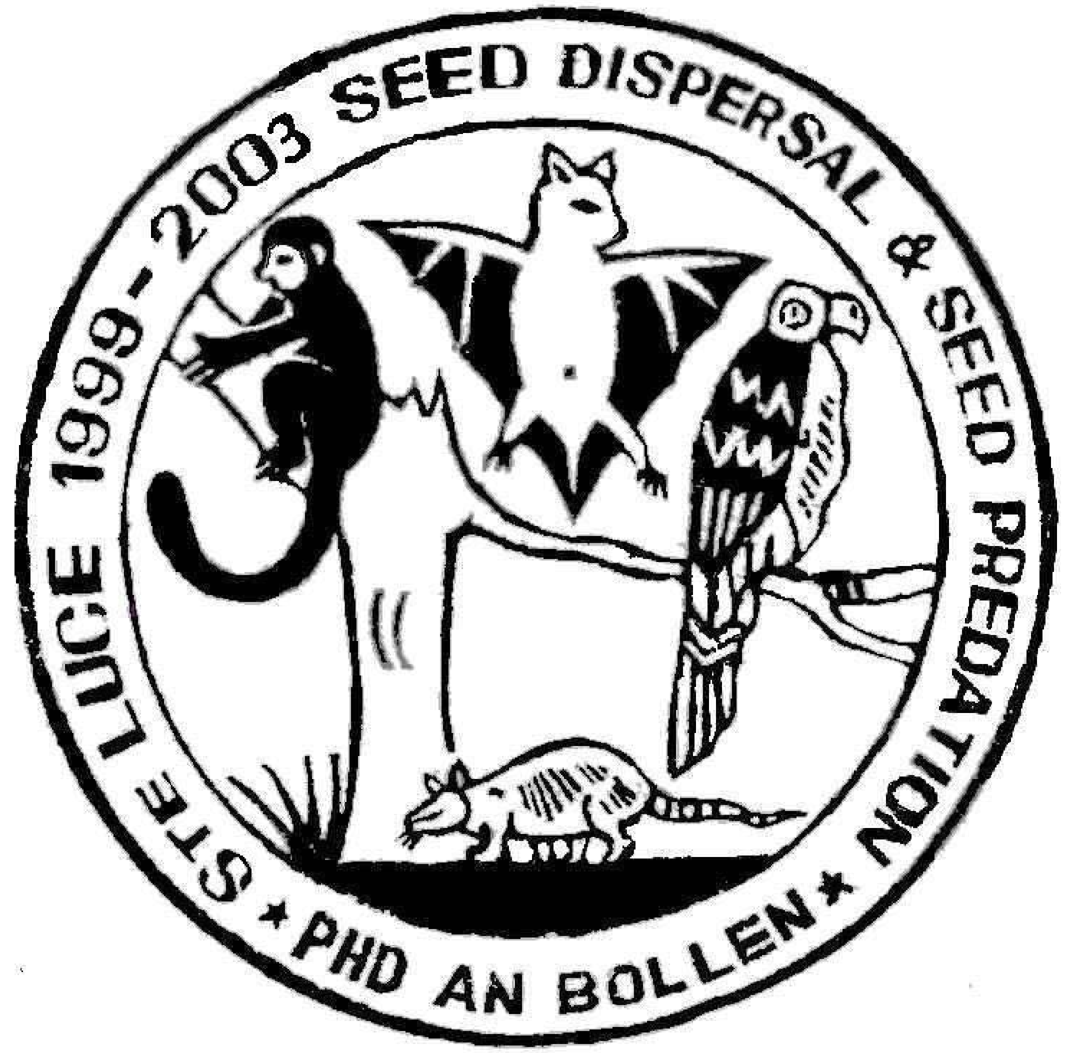
The results of the present study do not support the prediction that morphological and biochemical fruit and seed characteristics result from strong specific interactions and co-evolution with lemurs. Rather they could be the consequence of abiotic conditions and can best be interpreted as the result of an opportunistic and generalist zoochorous dispersal strategy of plants. Chapman (1995) has pointed out that weak selection pressure on fruit traits could result if primates have highly flexible diets and are not the only dispersers available in an ecosystem. Furthermore, large dietary differences between neighbouring primate groups or groups living a few hundred kilometres apart are not uncommon (Chapman 1995). This matches our findings of selection criteria of *Eulemur* and *Cheirogaleus* at STL and KIR, which are located 600km apart. Abiotic factors influence the phenology and taxonomy at a site and may then indirectly also lead to different morphological features and distinct biochemical compositions of food items available at each site.

Considering the predictions outlined above we can summarize our results as follows:

1. Since the frugivore communities are rather similar at the two sites, abiotic conditions rather than specific consumers are more likely to be responsible for the variety of morphological and biochemical features in fruits from different forest types.
2. No evidence for co-evolution between these lemurs and fruit traits could be found as diets of the same lemur species differed substantially between sites.
3. Within fleshy fruits, the lemur species considered did not show any persistent criteria for fruit selection in general besides few biochemical preferences but modified their diet according to fruit availability, even though mutual interactions and dependencies of fruits/seeds and their consumers exist.

ACKNOWLEDGEMENTS

We thank L. Dew and J. P. Boubli for their invitation to participate at the symposium ‘Floristics, Phenology and Frugivore Communities: A Pantropical comparison’ at the ATB Conference in Panama and the ‘Commission Tripartite’ of the Malagasy Government, the Laboratoire de la Primatologie et des Vertébrés de E.E.S.S. d'Antananarivo, the Ministère pour la Production Animale et des Eaux et Forêts, Missouri Botanical Garden at Antananarivo, the CFPF at Morondava, QMM (QIT Madagascar Minerals) and the WWF Madagascar for their collaboration and permission to work in Madagascar. The studies were carried out under *Accord de Collaboration* between the Dept. Animal Biology and Dept. Anthropology of the University of Antananarivo, the University of Tübingen, the German Primate Center, the Institute of Zoology of Hamburg University, the CFPF and QMM. We are grateful to Nicoletta Baldi and Valentina Morelli for providing data on *Eulemur* feeding ecology for STL. B. Rakotosamimanana, C. Ravaoarinoromanga and E. Rakotovao provided important help at various stages of the study. I. Tomaschewski and U. Walbaum helped with plant analyses. Financial support came from the Belgian Fund for Scientific Research, Flanders (FWO) to AB, the University of Pisa to GD, the German Primate Center, DFG and DAAD to JF, DS and JUG. We thank the Flemish Government for structural support to the CRC of the RZSA.


STE LUCE 1999 - 2003 SEED DISPERSAL & SEED PREDATION
* PHD AN BOLLEN *

’Ny valala tsy indroa mandry
eo am-bavahady’

Grasshoppers won’t show up
twice at your doorstep

Malagasy proverb
Personal Malagasy stamp made by a young man on the streets of Antananarivo

5

The Malagasy littoral forest: threats and possible solutions

AN BOLLEN, GIUSEPPE DONATI
(TO BE PUBLISHED)

ABSTRACT

The littoral forest is expected to lose numerous endemic plant and animal species in the near future because of deforestation and resultant habitat changes. A great concern is the disruption of plant-animal interactions. It can be predicted that alterations in the recruitment dynamics of plant species in forest fragments might have unknown consequences for their long-term survival. This paper discusses the characteristics of animal seed dispersal relevant to the regeneration of the littoral forest. Possible management implications are discussed in relation to the existing initiatives. Urgent protection of the largest remaining forest fragments (S9, S17), including a flying fox roost site (S6) is of great importance. Furthermore it is necessary to install corridors to connect the isolated fragments and create plantations to fulfil the need for wood of the local people.

INTRODUCTION

Worldwide, Madagascar is considered a high priority for global biodiversity protection due to high faunal and floral endemism and biodiversity (Mittermeier et al. 1998). The flora of Madagascar is one of the richest in the world in comparison to its area (Dumetz 1999). About 96% of all plant species present are endemic (Schatz 2001). The avifauna is relatively species poor compared to other tropical islands, but the level of endemism is also extremely high (52% Langrand 1990). For mammals, reptiles and amphibians endemism even raises up to 90% (Garbutt 1999), 95% (Ramanamanjato 2000) and even 99% (Ramanamanjato 2000) respectively. At the same time Madagascar is one of the tropical regions where the effects of deforestation are most worrying (Green and Sussman 1990). Ever since humans first reached the island some 2000 years ago, the native forests have provided them with animals for food, land for cultivation and wood for construction and fuel. Humans have thus dramatically changed the island vegetation. According to Kull (2000) dense endemic rainforests cover only 10% of the island, while total forest cover is about 23%. Deforestation is proceeding most rapidly in the east, where 66% of the original rainforest has been logged or irreversibly converted to land for cultivation (Dumetz 1999; Kull 2000). At these rates it is predicted that in the year 2025 rainforest will only remain on the steepest slopes, in remote areas and nature reserves (Kull 2000). Madagascar receives global attention as a hot spot of biological diversity, environmental degradation and conservation action (Mittermeier et al. 1998; Kull 2000), but at the moment only 3% of the island has a protected status (Godfrey et al. 1997).

The littoral forest of south-eastern Madagascar is one of the ecosystems most threatened on this island and is reduced to its vestiges with only 2500ha remaining today, representing at most 10% of the original forest (Ganzhorn et al. 2001; Vincelette pers. comm.). During the last 50 years more than 5000ha have disappeared (MIR Télédétection Inc 1998). This forest type has been severely degraded due to charcoal production, logging, bushfires and shifting cultivation (slash and burn). At the moment it is represented by severely degraded forest fragments, ranging in size from 3 to 377ha. In the Fort-Dauphin area the existing littoral forests on sandy soils are Petriky, Mandena and Sainte Luce (Fig. 1). Sainte Luce has the highest species diversity and can be considered among the most intact littoral forest remaining in eastern Madagascar (Dumetz 1999; Rabevohitra et al. 1996). A botanical study by Razafimizanilala (1996) and Rabevohitra et al. (1996) in the forest fragment 'S9' of Sainte Luce shows that 98% of the 189 plant species monitored are endemic for Madagascar and there are 29 endemic plant species for the south-eastern littoral forest (Lewis Environmental Consultants 1992a).

In order to highlight the importance of the littoral forest before it completely vanishes, we present here our current understandings of frugivore-fruit interactions. We further discuss the causes of habitat loss and forest fragmentation and imply our knowledge on seed dispersal for landscape restoration. Finally suggestions concerning conservation applications as well as priorities for future research are made.

STUDY SITE

In this paper we focus in particular on the situation of Sainte Luce, where first and second author conducted two PhD researches from September 1999 till February 2001. The campsite is located in the 377 ha-large forest fragment, called 'S9' (24º45'S 47º11'E). Littoral forest lies within 5 km of the coast and occurs on sandy soils at an elevation of 0 up to 20m. It is characterised by a relatively open or non-continuous canopy, which is 6 to 8m in height and diameter at breast height (DBH) of trees rarely exceeds 30 to 40cm (Rabevohitra et al. 1996; Dumetz 1999). This forest type is characterised by an average annual rainfall of about 2,690 mm, with a marked rainy season from November through February. No clear dry season could be detected (Bollen and Donati, Chapter 1). Mean monthly temperature is 23°C (QMM unpubl. data). Fruit production is seasonal, with a peak in abundance of ripe fruits in December and January and with periods of fruit scarcity that differ strongly inter-annually (Bollen and Donati, Chapter 1)

THREATS

Three villages, Ambandrika, Ampanasatomboky and Manafiafy lie within close range of the largest forest fragments of Sainte Luce; S6 (225 ha), S7 (206 ha), S8 (190 ha), S9 (377 ha) and S17 (244 ha)(Fig. 1), which make up half of the remaining south-eastern littoral forest. Some 700 villagers depend on the forest for crop growing, timber and non-timber forest products for subsistence and commercial activities. The main causes responsible for degradation and fragmentation in Sainte Luce are clearance by slash and burn, useless bushfires and unsustainable harvesting of logs. Threats in the near future further include charcoal production by the Antandroy people, a southern tribe, and

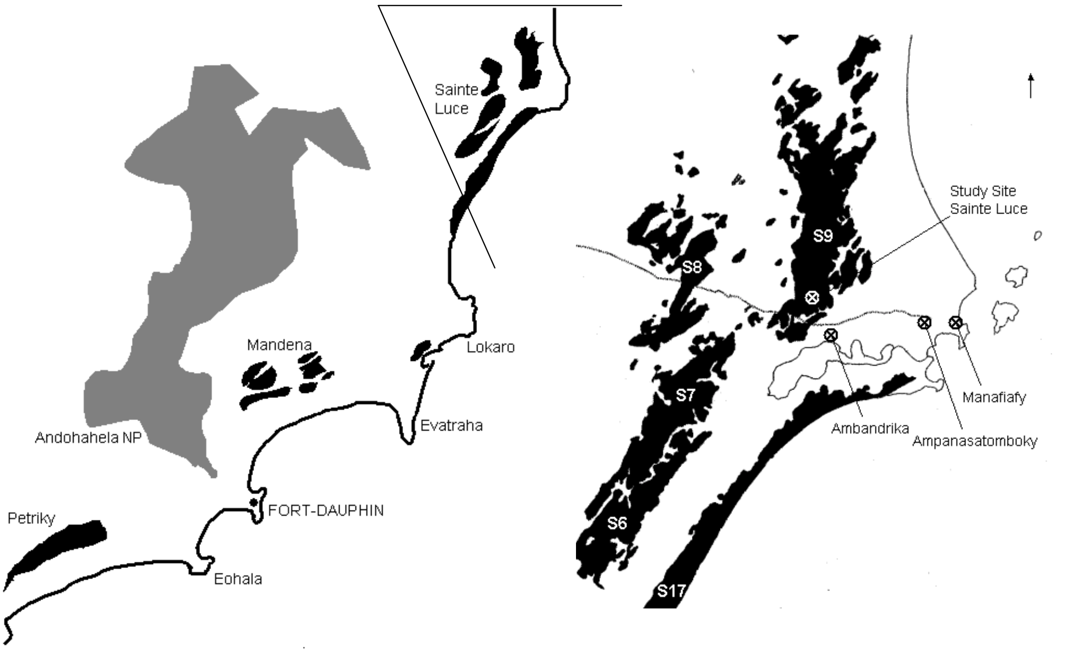


Fig. 1. On the left is a detail of the south-eastern Malagasy region around Fort-Dauphin shown. In black the remaining littoral forests are indicated, while the humid montane rainforest (including Andohahela National Park) is in grey. On the right we zoom in on the largest forest fragments of the littoral forest of Sainte Luce and indicate the *Antanosy* villages in this area and our study site.

ilmenite extraction from the sand by a large Malagasy mining company, QIT Madagascar Minerals (QMM) owned by QIT-Fer et Titane, a subsidiary of Rio Tinto Zinc.

Shifting cultivation through '*tavys*' (slash and burn) contributes directly to the actual dramatic levels of deforestation, in particular for forests on sandy soils. Farmers cut a patch along the forest border, allow the slash to dry and then burn it in preparation for cultivation of maize, manioc or rice. A new patch is created and cultivated every 1-2 years, since extensive rain quickly depletes the bare sandy soil from minerals. This causes a retreat of forest edges and leads to soil sterilisation. After the first clearing, grasslands dominated by invasive heath shrubs *Erica* sp. (Ericaceae) directly replace the natural forest (Lewis Environmental Consultants 1992a). As such the soils become even more acid and less suitable for regeneration of endemic plant species. Farmers rarely monitor their fires allowing them to expand and run their course. As a consequence uncontrolled bushfires further result in an alarming progress of deforestation while not serving any purpose. Even though the people burn throughout the whole year, these activities are more concentrated in periods when winds are stronger (September-October, February-March). Whereas in the dry deciduous forest of West Madagascar bushfires occur naturally, this is less common in the eastern forests (Kull 2000).

There is both subsistence and commercial logging, but on a local scale only. People cut mainly large and mature trees to get fuel, construction and tool wood. Logging here involves mainly unsustainable and wasteful resource use so that many cut logs are partially left behind in the forest. The selective removal of timber species changes their distribution patterns impeding regeneration. Although the logging pressure was considered low up to now in Sainte Luce, some plant species used for fuel were observed at a very low density in apparent pristine area (Donati pers.obs.). Discussions with local people and observations of many cut trunks lead us to the conclusion that some plant species, like *Cinnamosma madagascariensis*, are already rare due to selective logging. At the end of our study period (December 2000) logging intensified and trucks transporting the logs could be observed at night on the national road heading to Fort-Dauphin. This short-sighted commercial logging is even more harmful and a serious threat to all forests in the surrounding area of Fort-Dauphin as needs for construction wood get larger in the city. The only wood people are allowed to take out of the forest by law is 'dead wood'. As such, people have been very inventive in interpreting this law. They cut several trees in the forest, leave the logs there for a month to afterwards collect this 'dead' wood (Donati and Bollen pers. obs.). Nowadays they even circumcise the bark deep enough so eventually trees will die (Hapke pers. comm.).

The villagers take several other products out of the forest. Large palms (*Dypsis prestoniana*) are cut at the base only to collect the nervature of their leaves of which traps for crabs and langoustines are made. The enormous logs are often left behind unused. Canoes are dug out of the largest trees, such as '*ramy*' *Canarium boivinii* and '*vitano*' *Calophyllum* sp. (Table 1) and different vine species serve for fishing gear. People also eat the fruits of several endemic tree species, but no real large-scale harvesting occurs. During famine, people collect and eat the roots of tavolo (*Tacca leontopetaloides*) and via (*Typhonodorum lendleyanum*)(Table 1).

Besides the indirect threat of habitat loss, hunting also has its impact on littoral forest dynamics. However in contrast to sites more inland, such as Andohahela NP, Mandena and Petriky, the impact of hunting in Sainte Luce is rather limited. Fish rather than bush meat make up the largest proportion of animal protein in the daily menu. The majority of villagers are fishermen and catching fish (year-round) and shellfish (langoustines only April-December) represents their most important income. Bush meat is only eaten on rare occasions or during traditional events. Nocturnal lemurs, such as *Cheirogaleus major, Cheirogaleus medius* and the tiny *Microcebus rufus,* that hibernate during austral winter in hollow tree trunks are an easy catch. The larger *Eulemur fulvus collaris* is hunted by a traditional technique called *tandroho* (Randriamanalina et al. 2000). More specifically a strip of forest (50 m^2) is cleared, so that canopies are too far apart for the lemurs to cross. Long logs are then placed between both ends as the only crossover with two snares in the middle. This hunting technique could be at the base of the unbalanced sex-ratio in favour of males reported in S9 (Donati unpubl. data), as in this species females often have progression priority and as such they are more likely to become victims of these traps. *E. f. collaris* was also captured by the use of row slings, a practice particularly frequent in young mans and probably responsible for the cryptic behaviour of these lemurs at the beginning of our study. Hunting pressure on *E. f. collaris* declined drastically in the study area (S9) during the presence of researchers based on several discussions with the local people. Nevertheless traps were still encountered in September 2000 in S17 (Fig. 1). *Pteropus rufus* is very vulnerable to hunting as it roosts communally and can thus be located and killed easily in great numbers. Catapults, long branches and stones were often found under their roost site. The animals were harassed during daylight and even changed their roost site twice in 2000 (Bollen and Van Elsacker 2002*a*, Chapter 3a). Terrestrial birds are trapped using snares or other ingenuous systems on the ground. Fruit pigeons (*Treron australis, Alectroenas madagascariensis*), parrots (*Coracopsis vasa* and *C. nigra*) and bulbuls (*Hypsipetes madagascariensis*) are hunted with arrows or catapults. Alternatively, fruit pigeons get stuck onto small branches covered with sticky latex, which are placed in *Ficus* or other fruiting trees by adolescent men. Tenrecs are hunted with the aid of dogs at dusk. Hunting occurs mainly for food purposes but occasionally the animals are traded regionally as well for pets and this in particular for *Eulemur fulvus collaris* and *Coracopsis* spp. (Bollen pers.obs.).

Charcoal production is an important activity of the people living in the extreme southern *Androy*. At the moment, charcoal pits are regularly found in Mandena and Petriky but not yet in Sainte Luce. It is a very destructive practice. A strip of forest is cleared, branches are stapled in a hole in the ground, covered by vegetation and then burned for several days. Charcoal is used by numerous people as fuel and represents a major income for the *Antandroy*. It can be expected that in the near future these activities will move up north towards Sainte Luce as the forests of Mandena and Petriky get more depleted.

Furthermore QMM represents another threat as mining activities will destroy a large part (76%) of the littoral forest (Lewis Environmental Consultants 1992a). In Sainte Luce, 74% of the remaining forest will vanish (QMM 2001). In November 2001, QMM got permission of the Malagasy government to start the mining. For the coming six year all infrastructure is being prepared to begin extraction of ilmenite in 2009 in Mandena. Petriky and Sainte Luce will be mined respectively 20 and 35 years later. Mining activities will last 45 up to 60 years (Vincelette pers. comm.). Populations of numerous plant species risk disappearing together with the fauna (Lewis Environmental Consultants 1992a). Anthropogenic pressure will then further intensify on the few remaining littoral forest fragments outside the QMM concession zone.

As everywhere, population growth is associated with limited resources. Even though the local people are responsible for most of the degradation and fragmentation of the littoral forest at the moment, there is definitely also willingness from their part to protect the forest. The President of Sainte Luce in 2000-2001, Olaf Abel Isaia has done this by initiating a traditional *dina*. These are local agreements for protection of natural resources (LOI N°96-025, 1996). At the moment, QMM and delegates from the three villages are discussing on a new version of the *dina* for Sainte Luce, which will probably be finalised later this year (Vincelette pers. comm.).

IMPACT ON ECOSYSTEM AND SEED DISPERSERS

Plant-frugivore interactions are important components of complex forest communities. Vertebrate seed dispersal is a key process in the dynamics of natural vegetation and vegetation recovery (Wallace and Painter 2002). Furthermore, frugivores play a vital role in the maintenance of biodiversity in tropical forests, where they constitute a large proportion of the vertebrate biomass (Fleming et al. 1987). In the same way zoochorous tree species make up the bulk of the tropical flora (Howe and Smallwood 1982). Loss of fruit-frugivore interactions may thus have profound consequences for conservation (Corlett 1998).

Many animal species in Sainte Luce rely on fruit as an essential food resource and conversely provide valuable dispersal services to many of these fruit bearing plants (Bollen et al*.,* Chapter 3)(Table 1). As forests become more fragmented the remaining patches become increasingly isolated and less accessible for arboreal lemur species. As a consequence gene flow and seed dispersal between patches becomes more critical for long term survival of many plant species. On the other hand, if fragments get too small or hunting increases, the long-term survival of animal species will not be guaranteed either

Table 1. A list of plant species from Sainte Luce, Indicating if they are endemic (E), abundant (A), common (C) and typical littoral forest (LITT) plant species. The utility of these plant species is given as well; medicinal use (M), firewood (F), construction wood (C) or unknown use (X). 'Special' indicates plant species that are consumed by numerous frugivores (number is given), LS means that these are large-seeded plant species for which *Eulemur fulvus collaris* is the only seed disperser and 'key?' refers to a potential keystone species during periods of fruit scarcity. 'Food' species for the people are indicated as well, with indication of plant part eaten.

Family	Species	Vernacular name	Status^1	Utilitair ^{1}	Special	Food
Anacardiaceae	*Poupartia chapelieri*	sisikandrongo	A	C	7	
	Protorhus cf. *lecomtei*	kangy			LS	
Annonaceae	*Monanthotaxis* cf. *malacophylla*	vahimbotany	C			
	Polyalthia madagascariensis	fotsivavo			8	
	Polyalthia capuronii	menapeka			LS	
Apocynaceae	*Cabucala madagascariensis*	tandrokosy				FRUIT
Arecaceae	*Typhonodorum lindleyanum*	via				ROOT
Araliaceae	*Schefflera rainaliana*	voatsilana sp1		FM		
	Polyscias sp.	voatsilana sp2			7	
Areceae	*Dypsis fibrosa*	boakandambo	LITT		LS	
	Dypsis nodifera	raotry	LITT			
	Dypsis prestoniana	boakabe	LITT		9-key?	
	Dypsis saintelucei	telopolombilany	LITT		RARE	
	Dypsis scottiana	raosy	LITT		6	
Bignoniaceae	*Ophiocolea delphinensis*	akondronala	EC	X		FRUIT
	Phyllarthron ilicifolium	zahambe	E	C		
	Phyllarthron sp.	zahambe manongaroa	E	C		
Burseraceae	*Canarium boivinii*	ramy		MC	LS	
Canellaceae	*Cinnamosma madagascariensis*	vahabatra 3eM			LS-RARE	
Capparaceae	*Crataeva obovata*	belataka	C		LS	
Clusiaceae	*Psorospermum revolutum*	harongampanihy		MF		FRUIT
	Calophyllum sp.	vitano		C		
	Garcina chapelieri	haziny tomate			LS	
	Garcinia cf/aff. *madagascariensis*	disaky kely			LS	
Combretaceae	*Terminalia fatraea*	katrafa		C		
Dichapetalaceae	*Dichapetalum* sp.	vahihazo			LS	
Ebenaceae	*Diospyros* sp.1	hazomainty blanc		F	LS	
	Diospyros sp.2	hazomainy	LITT	F	LS	
Elaeocarpaceae	*Elaeocarpus alnifolius**	sanga			LS	
Ericaceae	*Vaccinium emirnense*	tsilantria		CF	9	FRUIT
Erythroxylaceae	*Erythroxylum buxifolium*	fangora sp.1		F		
	Erythroxylum nitidilum	fangora sp.2		F		
Euphorbiaceae	*Uapaca ferruginea*	voapaky lahy		CF	6	
	Uapaca littoralis	voapaky vavy		CF	9	
	Uapaca thouarsii	voapaky lahy ZJ	LITT	CF		
Fabaceae	*Cynometra* cf. *cloiselii*	mampay	A	C		
	Phylloxylon xylophylloides	sotro	E	C		
	Intsia bijuga	harandrato		C		
Flacourtiaceae	*Aphloia theiformis*	fandramana	C			
	Bembicia uniflora	bemalemy	A	CF		
	Homalium louvelianum	ramirisa		CF		
	Scolopia orientalis	zoramena	C	F	7	
Grossulariaceae	*Brexia* sp.	kambatrikambatri	C			
Hippocrateaceae	*Salacia madagascariensis*	voatsimatra	C		LS	FRUIT

Table 1 Continued

Family	*Species*	Vernacular name	Status[1]	Utilitair [1]	Special	Food
Icacinaceae	*Apodytes dimidiata*	hazomamy marécage	E		9	
	Apodytes sp. nov.	hazomamy an ala	E	X	LS	
Lauraceae	*Cryptocarya* sp.	tavolohazo		X		
	Ravensara acuminata	?		M		
Liliaceae	*Dracaena reflexa* var. *nervosa*	falinandro	LITT-C	FM		
	Dracaena reflexa var. *nervosa*	tavolobotroka	LITT-C	FM		
Loganiaceae	*Anthocleista longifolia*	lendemilahy	C	C		
Loranthaceae	*Bakerella* sp.	velomihanto			6	
Melastomataceae	*Tristemma mauritianum*	voatrotoky				FRUIT
Meliaceae	*Malleastrum mandenense*	sarigoavy	EC			
Monimiaceae	*Tambourissa castri-delphinii*	amborabe		CFM		
	Tambourissa purpurea	ambora		CFM	7	
Moraceae	*Ficus guatteriifolia*	fihamy		M		
	Ficus pyrifolia	nonoka			7	
Myricaceae	*Myrica spathulata*	tsilaka		M		
Myristicaceae	*Brochoneura acuminata*	mafotra sp.1	C	CM	LS	
	Brochoneura madagascariensis	mafotra sp.2	C	CM	LS	
Myrsinaceae	*Embelia incumbens*	taratasy		M		
Myrtaceae	*Eugenia cloiselii*	ropasy sp.1	EC	CFM		
	Eugenia sp.	ropasy sp.2		CFM	LS	
	Syzygium sp.1	rotry ala		C	7	FRUIT
	Syzygium sp.2	rotry mena		C	10-key?	FRUIT
Oleaceae	*Jasminum kitchingii*	vahifotsy kely	C			
	Noronhia cf. *lanceolata*	hazondraotry		M		
	Noronhia sp.1	belavenoka		M		
	Olea sp.	vahabatra	A	M	7	
Pandanaceae	*Pandanus dauphinensis*	vakoanala	A	C	LS	
	Pandanus aff. *longistylus*	fandranabo		C	LS	
	Pandanus rollotii	fandranabotonboky		C	LS	
Podocarpaceae	*Podocarpus madagascariensis*	harambilo		CFM		
Sphaerosepalaceae	*Rhopalocarpus coriaceus*	tsilavimbinanto			LS	
Rubiaceae	*Canthium* sp.	Rubiaceae ZJ		CFM		
	Canthium variistipula	fantsikaitramainty	C	CFM	6	FRUIT
	Ixora sp.	x203	C	X		
	Plectronia densiflora	fantsikaitra		M		
	Psychotria sp.1	tanatananala		F		
	Rothmannia mandenensis	taholagna		X		FRUIT
	Tricalysia cf. *cryptocalyx*	hazongalala		F		
Rutaceae	*Vepris eliotii*	lahinampoly	EC	CFM	6	
Sapindaceae	*Macphersonia radlkoferi*	sanirambaza		X		
	Plagioscyphus jumelei	ambirimarika pionair		X		
Sarcolaenaceae	*Leptolaena multiflora*	fotombavy	C	CF		
	Sarcolaena multiflora	meramaintso	LITT-C	CF	9	FRUIT
	Schizolaena elongata	fotondahy		C		
Sphaerosepalaceae	*Rhopalocarpus coriaceus*	tsilavimbinanto	C	X		
Strelitziaceae	*Ravenala madagascariensis*	ravenala		CM		
Taccaceae	*Tacca leontopetaloides*	tavolo				ROOT
Theaceae	*Asteropeia multiflora*	fanolafotsy		CFM		
Verbenaceae	*Vitex chrysomallum*	nofotrako	LITT	C		

[1] data come from Dumetz (1999), Razafimizanilala (1996), Rabevohitra et al.(1996), Koechlin (1974), Lewis Environmental Consultants (1992a), QIT Madagascar Minerals (2001).

(Ganzhorn et al. 1999a). Madagascar in general, already has a depauperate avian frugivore community (Langrand 1990; Goodman et al. 1997a) and lacks larger frugivores such as ruminants, ungulates and elephants. Moreover one third of lemur species became extinct years ago (Godfrey et al. 1997). Thus emphasizing even more the importance of the remaining seed dispersers here. Large frugivores, such as *E. f. collaris,* are often most vulnerable to habitat fragmentation which is conform findings at other sites (Johns and Skorupa 1987; Kannan and James 1999). The vulnerability of *E. f. collaris* is reflected by the fact that this species is only present in the two largest and most intact fragments, S9 and S17, but absent in all other, smaller fragments in Sainte Luce (Ganzhorn et al. 2000). *E. f. collaris* is in particular important for seed dispersal of numerous plant species and it is the only frugivore present here that is able to swallow and thus disperse larger seeds (up to 16.5mm diameter, Table 1). Therefore, local extinction of this species could ultimately lead to the lack of regeneration of different dependant plant species. Other specialist frugivores, such as *Pteropus rufus, Treron australis* and *Alectroenas madagascariensis,* are very vulnerable as well, in particular when important food sources are selectively logged (Table 1). Frugivorous birds and flying foxes are the most important mobile seed dispersers bringing seeds into grasslands and early succession vegetation. The simple structure of these habitats pose less of a barrier to them than it does for arboreal lemurs. Genetic exchange and long distance dispersal between and among fragments are less likely to occur, if populations of mobile flying dispersers decrease or vanish.

Our studies showed that no evidence for co-evolution could be found, nor were there strong indications for syndromes that attract taxonomic groups by certain morphological and/or nutritional traits (Bollen et al., Chapter 2, 3, 4; Bollen et al. in press). Instead we found that there is great dietary overlap among frugivore species and that dispersal is achieved through redundant systems. Most frugivores seem to eat according to what is available, given the limitation of fruit and seed size and certain feeding preferences. Animal seed dispersers are vital for the regeneration of littoral forests. Especially since losses of ecologically interdependent species will be permanent to an even larger extent here as forest fragments are very isolated. Due to co-dependency of frugivores and tree species, the hunt on frugivores leads to suboptimal or insufficient dispersal and recruitment success of certain plant species (Chapman and Onderdonk 1998; McConkey and Drake 2002) while deforestation, forest degradation and fragmentation has a drastic impact on the food chain of the frugivorous fauna.

PROTECTION OF THE LITTORAL FOREST

Forest

The remaining intact forest fragments, which act as reservoirs from where indigenous floral and faunal species can colonize new habitats are in urgent need for protection. Even though the littoral forest only represents 5% of all forest cover in the south-eastern region (QIT Madagascar Minerals 2001), the importance of its conservation cannot be emphasized enough. At present, Sainte Luce contains the most intact littoral forest fragments on sand, which differ strongly in floristic diversity from the one on laterite and from the inland montane forest (Rabevohitra et al. 1996; Dumetz 1999). Ideally conservation zones should be large enough to encompass the micro-heterogeneity in order to avoid their effective elimination. In this respect, the forest fragments S9 and S17 have the highest conservation priority, representing the two largest and most intact forest fragments, including both inland and coastal littoral forest. S9 has been subject to numerous research projects since 1989 (Vincelette pers. comm.). This fragment contains some recent *tavy* in its northern and north-eastern section (Bollen and Donati pers. obs.). Logging has increased during the last years but 'intact' primary forest with important lemur populations is still present. S17 is a long and narrow forest fragment located on a dune system very close to the coast. The southern part is very degraded (Bollen and Donati pers. obs.) but the northern part can still be considered very pristine, which is probably due to its remote position as it is separated from the villages by a lake and an estuarine system (Fig. 1). The extreme northern part (ca. 60ha) is owned by Mr. De Heaulme and theoretically supervised by local guards. Both fragments, S9 and S17 are very different in appearance and floral composition and include much of the biodiversity present in the littoral forest. The conservation zones proposed by QMM involve 190ha of S9 and almost complete S17. This will be enforced once the *dina* gets accepted by all involved parties. Additionally we believe S6 is of extreme importance due to the presence of the roost site of a colony of flying foxes, which are irreplaceable long distance seed dispersers for numerous plant species. The forest fragment itself is extremely degraded and victim to numerous unregulated forestry activities. All these fragments together comprise about 1000ha of littoral forest. They lie within close proximity to one another and comprise inland and coastal littoral forest, mangroves, dunes and marshes, sandy beaches, a lake and an estuary providing important refuges for a wide variety of plant and animal species (Fig. 1).

Several studies in Madagascar have demonstrated that it is better to protect a few large fragments as opposed to several small ones. Ramanamanjato (2000) found that a series of small littoral forest fragments does not provide the biodiversity of reptiles and amphibians found in one or a few large fragments. The species number declines substantially in fragments smaller than 200-300ha. As for birds, Raherilalao (2001) showed that the number of bird species also decreases proportionally with the size of forests blocks in Ranomafana. In addition, Ganzhorn et al. (2000) found that the number of lemur species present in a fragment is related to its overall size. At the moment, Sainte Luce still provides an important refuge for *E. f. collaris* (S9 density 0.38ind/ha, Banks 2002), which occurs only in the south-eastern region of Madagascar. Protection of the remaining primary forest is of crucial importance in general because Ganzhorn and Schmid (1998) found that even 40 year old secondary dry forests in western Madagascar are unlikely to provide a suitable habitat even for the smallest seemingly least threatened of all lemur species. As for protection measure all logging, hunting and slash and burn practices should be banned from these fragments, so that ecosystems can recover. In theory, the regional division of the Ministry of Water and Forests should control the presence of these activities in the forest but there is a shortage of staff, finances and means and the remoteness of Sainte Luce further contributes to the lack of an accurate control system. The final management plan should clearly indicate what land could still be used for these traditional activities allowing buffer zones close to the main population centres. Ideally slash and burn practices should be replaced by more sustainable land use practices in the zones adjacent to protected areas. Involvement of local people in decision-making for conservation action plans is indispensable. Resource management should be urgently improved and control systems should at least partially come from within the villages.

Animals

The degree of vulnerability of a given species due to forest fragmentation is likely to be related to its tolerance to habitat change and its capability to use or bridge the grasslands around the remaining forest fragments. As for frugivores, the large lemur species *E. f. collaris* is most vulnerable as it is reluctant to cross these grasslands. Due to the spatio-temporal patchiness of its food resources, it needs large home ranges (up to 100ha) and covers long distances daily (1500-3500m, Donati 2002). *E. f. collaris* only occurs in the south-eastern region of Madagascar (Tattersall 1982) and risks to decline severely in numbers as a consequence of fragmentation and degradation of the littoral forest and through hunting practice. *Eulemur fulvus collaris,* or *Eulemur collaris* as debated by some (Djletati et al. 1997; Wright 1999; Wyner et al. 1999; but see also Pastorini et al. 2000) is listed as a vulnerable taxon by IUCN (Hilton-Taylor 2000) and needs to be urgently protected. With respect to this species, there has already been a translocation on several groups of *E. f. collaris* in 1999 in Mandena. Their habitat (fragment M3) was almost completely destroyed by producers of charcoal. Therefore the lemurs were captured and transferred to an actively protected forest fragment (M15-M16, Mandena Conservation Zone). Despite the initial loss of some individuals, the groups seem to have adapted to their new habitat (Ramanamanjato pers. comm.). Translocation and re-introduction of primates, especially in ‘rescue’ situations such as the one in Mandena will become increasingly important as a tool for species conservation (Soorae and Baker 2002). Moreover, this practice has a high popular significance and a very high potential for educational applications. The nocturnal lemurs are still more abundantly present in smaller forest fragments (Ganzhorn et al. 2000) but are restricted to a single fragment as well. Another highly vulnerable species is *Pteropus rufus,* because a population of 250-300 flying foxes has its roost in a severely degraded fragment. Therefore, this roost site should be included in an actively protected zone. Most frugivorous bird species seem to be less threatened and more abundantly present in small, large, intact and degraded fragments.

As frugivores face periods of fruit scarcity it is important to collect long-term data on phenology to understand inter-annual patterns and predict periods of fruit abundance and scarcity. Interesting as well is to identify keystone species that bear fruit during periods of fruit scarcity and supply much of the diet of the frugivores in this forest (Terborgh 1986b). Given the short duration of our studies (Bollen and Donati, Chapter 1) we are unable to asses true ‘keystone species’ (definition according Terborgh 1986b; Mills et al. 1993) at the moment. However, a potential candidate may be *Syzigium* sp. 2 (Myrtaceae) and to a lesser extent *Dypsis prestoniana* (Arecaceae). Both species fruit when fruit availability is low. *Syzigium* sp. 2 is a large canopy tree species that is very common in the littoral forest (Razafimizanilala 1996) with numerous odoriferous purple berries characterised by a soft and juicy pulp and thin husk. These fruits are one-seeded with high sugar concentrations (43%). This species constituted 80% of the diet of *E. f. collaris* in June 2000*. Dypsis prestoniana* is much less abundant as it used to be but can still be find in the more intact parts of S9. This high palm species has a relatively large fruit crop considering its small canopy. Within the diet of *E. f. collaris* fruits of this species constituted 20% in April (Table 1). The overall importance of these potential keystone species increases if we consider that they are eaten by all frugivorous species present in Sainte Luce. Phenology data on important timber species could further be a useful tool to more ecologically sustainable initiatives as well (Wallace and Painter 2002). As they can contribute disproportionately to the diets of certain species, detailed data on food supply are indispensable (Chapman and Peres 2001).

Corridors and plantations

As degradation and fragmentation are quite advanced in the littoral forest, active protection of the remaining intact forest and control of hunting, logging and fires is not enough to conserve and restore this ecosystem. Furthermore, natural regeneration via secondary forests is too slow to counteract the loss of primary forests. Therefore, it is necessary to accelerate the natural recovery process. In this respect, creation of corridors that connect isolated primary forest remnants with thin strips of habitat is considered a prime target for conservation activities (Ganzhorn et al. 1997; Beier and Noss 1998). In this respect, QIT Madagascar Minerals (2001) has installed a corridor in 1999 in between M4 and M5 in Mandena with 20% endemic species and 80% exotic species. Corridors are valuable conservation tools, promoting increased plant and animal movement among patches that will enhance population viability and likelihood of recolonisation, as well as facilitation of pollination and seed dispersal (Beier and Noss 1998; Tewksbury et al. 2002) As some species readily move between fragments, using habitat corridors, others do not (Chapman and Peres 2001). Reasonably, seed of forest plant species will be dispersed at greater distances from their source through continuous forest than through open field or pasture, so corridors should ideally be contiguous with the native forest seed source (Wunderle 1997).

In Sainte Luce, S9, S17, S6 and S7 are not too far apart and could ideally be linked by corridors in the near future so that reforestation can happen from these nuclei. Birds and flying foxes are of great importance during first succession stages dispersing pioneer and heliophil species. After three years the ground is effectively shaded by their canopy that climax species will then predominate in seedling growth, provided the seed source is brought into these parcels by flying foxes, fruit pigeons, bulbuls and in a later phase even mouse lemurs. As the corridor gets more ample dwarf lemurs and eventually *E. f. collaris* will make use of them as well, dispersing certain seeds. If we depend entirely on natural seed dispersal to bring tree species to a site, this may result in a secondary forest dominated by a well-dispersed subset of the forest flora. Unassisted succession has proven to be better at restoring biomass than biodiversity (Corlett 2002). In this respect large-seeded plant species (for example *Canarium boivinii, Diospyros* sp., *Apodytes* sp. nov.)(Table 1) are less easily dispersed than small-seeded trees and because they have fewer dispersers, they require planting in subsequent efforts (Terborgh 1983; Janzen 1988; Wunderle 1997; Kitamura et al. 2002. Ingle 2003).

Besides creating corridors, plantations of both native and exotic species can help regeneration as well while at the same time providing an alternative wood source for the local people. In this respect QIT Madagascar Minerals has carried out experiments in a tree nursery for 10 years with different exotic tree species such as *Eucalyptus, Acacia* and *Casuarina* species (QIT Madagascar Minerals 2001), which were found to be suitable in landscape restoration. They even accelerate natural forest succession by ameliorating harsh soil and understory microclimatic conditions, suppressing dominant grasses, improving soil fertility and nutrient availability and attracting seed dispersers (Wunderle 1997; Holl et al. 2000; Corlett 2002). In the near area of Mandena there are about 1930ha of plantations, either private, state property or installed by QMM. QMM has installed 200ha of plantations in Mandena and 2ha in Sainte Luce. So far there are no plantations in Petriky. QMM intends to grow more plantations every year (Vincelette pers.

comm.). Mixed species plantations in Ampijoroa have proven to be suitable and to offer fairly acceptable habitats for the majority of the extant lemur species. In Mandena *Cheirogaleus medius* and *Microcebus murinus* were observed to feed on the flowers of the exotic *Melaleuca quinquenervia* (Myrtaceae, QIT Madagascar Minerals 2001). In other eastern sites even the larger lemurs, like *Eulemur* sp., were seen to relate on *Eucalyptus* flowers (Ganzhorn 1985; Overdorff 1988). However the floristic diversity of plantations is limited and may thus not provide food year round for all lemur species (Ganzhorn 1987; Ganzhorn and Abraham 1991). Therefore plantations, just as corridors, should ideally border natural forests. This way economic interest can be combined with lemur conservation by planting economically and ecologically valuable trees on presently deforested areas (Ganzhorn and Abraham 1991). Nevertheless one should be careful in selecting appropriate species for this and the corridors or plantation should not be monospecific nor involve dominant invasive species.

Planting important fruiting trees in corridors, plantations or clearings also improves the process of reforestation by attracting frugivores and the seed dispersal they provide. Fruit trees can thus be used to accelerate seed dispersal and enrich biodiversity. As zoochory is the predominant dispersal mode in the tropics (Howe and Smallwood 1982), dietary data on frugivores can influence the choice of fruit species included in planting projects. Otherwise, perches or trees in clearings may further attract bird and flying foxes, which then again bring certain seeds into these open areas (Holl et al. 2000). In this way frugivores can be used to facilitate regeneration, reforestation and vegetation succession of tropical forest.

Development aid

Together with active protection measures for the littoral forest ecosystem, there is great need for an integrated approach combining research, conservation and developmental aid in the area. Madagascar is one of the poorest countries in the world. More than 75% of its human population lives below the poverty level. Conservation of local fauna and flora is a luxury for the Malagasy who struggle to survive from day to day. There is an urgent need for alternative resources necessary to provide the people with fuel, construction and tool wood. For this, plantations of fast-growing non-invasive species are necessary. At the same time conservation management plans and long term integrity of protected areas depend critically upon support from rural communities. Cooperation with local people, as promoted by the first phase of the National Environment Action Plan (1991-1995), is an essential feature to succeed in conservation.

There are several possibilities to provide economical benefits to the Malagasy. First of all, ecotourism may serve as a conservative strategy for extending economic opportunities while safeguarding this unique natural environment. The area of Sainte Luce provides several options for ecotourism, as there are impressive coastal and inland forests, beautiful pristine white sandy beaches, several nearby small islands, gorgeous bays and traditional villages. Several groups of *E. f. collaris* are habituated and can thus easily be observed as well as numerous bird, amphibian and reptile species. The main problem for ecotourism is the difficult accessibility of Sainte Luce because of the poor road system and rough sea conditions during most of the year. Sharing revenues from forest entrance may be one way to fully distribute benefits from tourism to residents. Furthermore local guides can be trained and organisations could support local economy. Mainly small-scale tourism would be advantageous here, so it does not have a negative impact on the ecosystem nor lead to increased habitat disturbance or human immigration.

Ferraro (2001) has noticed that benefits from tourism in Ranomafana are only seasonal and have been captured by a relatively small subset of the population, which are often migrants. This should be avoided by all means. Butterfly farming and beekeeping were proposed as other economical opportunities by QMM and the latter was set up by QMM in Mandena and Sainte Luce. This initiative was welcomed with great enthusiasm by the local people (Vincelette and Ramanamanjato pers. comm.). Different possibilities can be thought of as long as they offer benefits for both the local people and the littoral forest. Exclusively protected areas may have a negative impact on the livelihood of residents that cultivate the land and/or collect and sell fuel and construction wood to the fishermen. They need to be compensated by recruitment as tourist guides, forest guards, workers in the plantations and so on. Compared to sites more inland, this is only a small percentage of the population in Sainte Luce. Another possibility to diminish the locals' impact on the littoral forest in general is to offer alternatives for their fishing gear, such as more synthetic materials (nylon or plastics). By the same token, gas or *Eucalyptus* charcoal may be a better alternative for charcoal and indigenous firewood. Overall, it is very important that ecologically, economically and socially sustainable solutions to the conservation of biodiversity are searched for as well as the wise management of natural resources.

We further believe that environmental education in the villages is of great importance. The first and second author had several meetings with the local authorities and gave presentations in the local school regarding research activities in the forest. We explained the purpose of our studies and the relevance of conserving this ecosystem. These meetings always attracted lots of people and should definitely be continued in the future to include all parties in the process of decision-making and to improve social acceptance of conservation plans.

Future studies

Even though dynamics of the littoral forest ecosystem are slowly revealed, much more data are necessary. First of all, a community wide study on pollination is needed, as no seed setting can occur without it. Secondly there is an urgent need for long-term data on phenology in order to predict periods of fruit scarcity and to define important food species, which can be consequently planted in corridors and/or plantations to facilitate and enhance germination. Thirdly future studies should focus on patterns of seed shadows and post-dispersal survival of seeds and seedlings across the full range of habitats including both intact as well as degraded landscapes. Managers need to be able to predict which species will survive in forest fragments in order to identify which ones are potentially most threatened by deforestation and thus should be given priority for planting (Chapman and Peres 2001). Furthermore, once we get insight on community wide plant-animal interactions, it is necessary to estimate minimum viable population sizes of animals and their tolerance to forest fragmentation, translocation or re-introduction, which will become a necessary tool in the littoral forest due to the future mining plans. Finally a follow up is needed to assess whether they make use of plantations and corridors. Most studies in the past have been carried out in primary and protected forest. This approach may not serve the interests of conservation as we need to be able to evaluate conservation action plans and to reformulate these based on new findings. Future research should be carried out by animal ecologists, plant population biologists and forest managers collaborating closely together in order to find a better balance between timber harvesting, biodiversity conservation and sustainable management. Even though more data are needed we believe this study along with others from the littoral forest provide a conclusive and solid data base to aid in formulating conservation plans now and thus urgent and active protection should no longer be delayed any further in time.

CONCLUSION

The littoral forest is being cleared at an alarming rate while our understanding of its ecology is still incomplete. Multi-disciplinary approach is required in the near future to unravel further interactions and to refine conservation action plans. Forest restoration is a necessary activity but simultaneously efforts should be focused on conserving the integrity of existing primary forests, as there is no guarantee that all species will re-colonize after disturbance. At the moment, less than 3% of Madagascar has a protected status (Wright 1997b) and one third of the lemur species has already gone extinct (Godfrey et al. 1997). Up to date, the littoral forest is not represented in protected areas. This is an important and unique forest type due to its high endemism and biodiversity. Understanding forest dynamics and unravelling plant-animal interactions in degraded tropical ecosystems is essential if we are to conserve existing forests and accelerate the process of reforestation. It is necessary to urgently join forces in order to prevent that our and several other studies were a last testimony of what once was the littoral forest. We owe it to the future generations to protect this ecosystem, so they can take pleasure in exploring it further and so the endemic plant and animal species can persist and thrive here.

ACKNOWLEDGEMENTS

We like to thank Manon Vincelette and Jean-Baptiste Ramanamanjato of the QMM Environmental team for providing detailed information on the environmental policy in the littoral forest and on the current activities of QMM. Many thanks as well to Jörg Ganzhorn, Linda Van Elsacker and Silvana M. Borgognini Tarli for their support in this research. The first author is supported by a grant from the Belgian Fund for Scientific Research, Flanders (FWO). We thank the Flemish Government for structural support to the CRC of the RZSA. The second author was supported by a doctoral grant of the Italian Ministry for Scientific Research (MURST) and the University of Pisa.

GENERAL CONCLUSION

The main purpose of this study was to gain insight into overall fruit-frugivore interactions in the littoral forest of Sainte Luce. It represents the first community-wide approach to primary seed dispersal in a Malagasy forest type from the perspective of both the tree and the consumer species.

Three hypotheses concerning evidence of co-evolution between life history traits of plants, their diaspores and animal consumers were tested by studying the frugivorous vertebrates and the dispersal strategies of 34 tree species. Phenological, morphological and biochemical fruit traits from these species were measured to look for co-variation with their seed dispersers. No evidence was found for **species-specific co-evolution** in this study. The lack of tight co-evolutionary relationships was suggested as well by many other studies (Gautier-Hion et al. 1985; Herrera 1986; Fisher and Chapman 1993; Erikson and Ehrlen 1998). Five large-seeded tree species however did seem to depend critically on the largest lemur, *Eulemur fulvus collaris*, for seed dispersal and recruitment. This strong dependence however does not represent a case of co-evolution in the strict sense but can be interpreted as an indirect consequence of the extinction of the larger frugivorous birds and lemurs, which would also have been capable of dispersing these large fruits. Nevertheless, in terms of conservation these fruit-frugivore interactions are of crucial importance to conserve the integrity of the littoral forest.

The **low-high investment model** (McKey 1975) subdivides tree species into specialists and generalists but again my results do no support this model. McKey's model was originally developed for bird-dispersed trees in the Neotropics and its validity seems to depend largely on the site-specific composition of the frugivore guild (see Wheelwright et al. 1984). It seems that the species-poor guild of frugivores in Madagascar did not lead to specialised dispersal strategies. Most tree species seem to be characterised by rather 'generalist' fruit traits allowing them to attract as many seed dispersers as possible. This way the risk of relying on only one frugivore species is avoided, which may be dangerous in an ecosystem with few frugivores. Furthermore, the low species diversity of avian frugivores resulted in significantly few bird fruits compared to other sites.

Of all three hypotheses, the concept of **dispersal syndromes** (Van der Pijl 1969) was supported most clearly, as there were indeed indications that certain morphological traits correspond to taxonomic groups of dispersers. I found that diaspores dispersed by birds, mammals or both groups (called mixed fruits) differ in their fruit and seed size, fruit shape and seed number, but not in biochemical composition. These results agree with studies on fruit syndromes in other tropical regions with distinct assemblages of plants and animals (Janson 1983; Knight and Siegfriend 1983; Gautier-Hion et al. 1985, Corlett 1996; Pizo 2002). Nevertheless, dispersal syndromes can only partly clarify the variability displayed in tree dispersal strategies at Sainte Luce, while the influence of abiotic factors on fruit traits may serve as an additional explanation along with the phylogenetic heritage of plant taxa. In this respect, Hampe (2003) mentions the importance of temperature, water availability and day length in relation to seed growth, fruit size and sugar or lipid content respectively. As such, there may be similar meaningful correlations that I overlooked. Overall, efficient plant-disperser interactions do exist in Sainte Luce as well as in other sites (Gautier-Hion et al. 1985; Dowsett-Lemaire 1988; Herrera 1995, Corlett 2002; Pizo 2002) without requiring the close co-variation of fruit traits with their dispersers as predicted by the tested models.

To evaluate the relative contribution of the different animal species in relation to seed dispersal and predation, the core part of this study concentrated on plant-animal interactions on a species-specific as well as on a community level. These mutual relationships determine the dynamics of the littoral forest ecosystem. Fruit and seed size appear to be the most determining physical traits in food selection of all consumer species. While birds show a strong preference for specifically coloured fruits (red, purple and black), nocturnal lemurs show clear preference for soft and juicy fruit pulp and thin-husked fruits irrespective of colour. Arillate or soft and juicy fruits are also favoured by flying foxes. Nutritionally, birds prefer lipid-rich fruits whereas certain mammals (*Eulemur fulvus collaris, Pteropus rufus*) avoid those, which may be linked to their differential capacity to digest and assimilate lipids. Mouse and dwarf lemurs select fruits with high sugar content. This allows them to prepare and store fat reserves before going into torpor (see also Bonnaire and Simmen 1994, Fietz and Ganzhorn 1999). These findings are the only indications for diet selection of all frugivores, while for the vast majority of fruit traits, both biochemical and morphological, the frugivores consume whatever is available. This **weak selection pressure** represents another reason for the lack of strong mutual relationships among fruit traits and dispersers.

Compared to other study sites worldwide (Fleming 1979; Gautier-Hion et al. 1985; Kitamura et al. 2002) dietary overlap among frugivores seems to be rather high in Sainte Luce. However, without considering the proportional use of different food items this overlap may be overestimated. Dietary overlap among frugivores may be strongly influenced by phenology, increasing when fruit is abundant and decreasing when it is scarce (Overdorff 1993; Johnson 2002). Phenological data from Sainte Luce show that fruiting is highly seasonal and that lean periods differ substantially inter-annually. The **overall low fruit productivity** and high unpredictability of food resources in Sainte Luce and other Malagasy forests (Overdorff 1996; Goodman and Ganzhorn 1997; Wright 1999) may be the at the base of low feeding selection pressure and thus relatively high dietary overlap. This also corresponds with the theory of Fleming (1979) that high spatio-temporal patchiness in the Paleotropics leads to much higher dietary overlap and at the same time to the **co-existence of fewer frugivore species** as opposed to the Neotropics. In this respect, Terborgh (1986) says that periods of fruit scarcity are crucial to set the carrying capacity of tropical forests for their frugivore community. During bottlenecks frugivores have to switch to other food items (such as young leaves, flowers or insects) to compensate for the lack of fruit and to avoid inter-specific competition. In Sainte Luce and other Malagasy humid forests phenophases are highly inter-correlated in time, which means that alternative diet items are not available either during lean periods. As a result many lemur species remain highly frugivorous even when fruits are scarce but concentrate on a few important food species (Overdorff 1993; Vasey 2000; Donati 2002; Johnson 2002). Some of these plant species may be potential **keystone species** and *Ficus* species are known to often play this role in the tropics for numerous tropical frugivores (Terborgh 1986a; Johnson 2002 but see Gautier-Hion and Michaloud 1989). However Goodman and Ganzhorn (1997) mention that Madagascar in general has a reduced *Ficus* diversity. This is also the case for Sainte Luce, where other plant species are likely to fulfil this role (*Syzigium* sp.2*, Dypsis prestoniana*).

Even though **dietary overlap is high** and most fruit species are eaten and dispersed by several frugivores, the different animal species clearly have a distinct impact on seed dispersal. As such, they do not appear to be ecologically redundant in their role within the ecosystem. While flying frugivores (fruit pigeons, bulbuls, flying foxes) disperse seeds into the clearings and ensure genetic exchange between forest fragments, *E. f. collaris* is the only disperser of large-seeded fruit species. Mouse and dwarf lemurs disperse only small-seeded fruit species during austral summer. On the contrary the granivores (rodents, turtledoves, parrots) prey on seeds of most fruits they eat. Clearly, heterogeneous seed transport is particularly important for a severely fragmented ecosystem such as the littoral forest.

The community-wide and mainly descriptive approach of this study only allowed me to unravel general trends in food ecology and determine the particular importance of the different species within the ecosystem. This study lacks more detailed quantitative data on the animal side of the interactions. Due to this shortcoming niche differentiation of the sympatric frugivores has certainly been overlooked. Frugivore species occupy a species-specific multidimensional niche within the ecosystem, which obviously has its influence as well on food selection. Due to competition and particular life history traits not all fruits may be 'truly' available to all frugivores as was set forward by this study. When understanding niche differentiation, it may be easier to detect which other traits may indeed be more relevant in determining actual diet choice.

To check whether previous results are confirmed at other Malagasy forest types, a comparison on fruit availability and the feeding ecology of two lemurs species was conducted within two completely different forests: the dry deciduous forest in Kirindy (west Madagascar) and the humid littoral forest in Sainte Luce (south-eastern Madagascar). Both sites differ substantially in abiotic conditions and have a distinct plant species composition and phenology. However, the frugivore guild at both sites is comparable. As for fruit traits, Sainte Luce has more fleshy zoochorous berries with thin husks while dehiscent capsules and indehiscent thick-husked drupes are more abundant in Kirindy. Biochemically, lipid concentrations are higher in Sainte Luce whereas fibre, tannin and nitrogen contents are higher in Kirindy. Most of the dominant fruit traits in the dry deciduous forest represent adaptations against water loss during the long and harsh dry season. This stresses once more the importance abiotic factors may have on fruit traits. Other studies comparing fruit traits on a larger geographical scale have found a potential influence of abiotic factors and phylogeny of plant communities (Hampe 2003, Voigt et al. submitted). When comparing feeding selection of two seed dispersers, *Eulemur fulvus* and *Cheirogaleus medius* within and between sites, there are three different trend that can be found. Firstly, there are clear food preferences. Zoochorous berries and drupes are strongly preferred, even though other dispersal and fruit types are present at both sites. As for nutrients, *Eulemur fulvus collaris* avoids lipid rich fruits in Sainte Luce and *Cheirogaleus medius* selects fruit with high sugar content both in Sainte Luce and in Kirindy as preparation for their torpor. Secondly, many traits such as fruit and seed size, growth form, colour, seed number, seed protection and extractable proteins do not differ between sites and do not determine lemur food selection. Finally, for several traits, both morphological (pulp type, odour, fruit skin protection) and biochemical (total nitrogen, tannins, ADF and NDF) the lemur species seem to display a large **dietary flexibility**. For these features, which differ between sites, the animals select according to the overall availability at a given site. These results show that overall there is a **weak**

selection pressure by frugivores on fruit traits and this at both study sites. At the same time these frugivores show remarkable regional dietary variation, a phenomenon that has been found in other studies on primates as well (Richard and Dewar 1991; Richard 1977; Chapman 1995). Thus on a larger geographical scale, the results confirm our previous conclusions that fruit traits are more likely to be the result of abiotic conditions rather than of interactions with their frugivores. In Kirindy, no evidence could be found either for species-specific co-evolution. To summarize there has been no support for tight co-evolution between fruit traits and dispersers in Madagascar (this study), nor in temperate forests (Herrera 1984, 1987; Hampe 2003) or the Neotropics (Janzen 1983; Pizo 2002; Silva et al. 2002) and the Paleotropics (Gautier-Hion et al. 1985; Corlett 2002). There seem to be three main explanations for this. First of all, research has shown that fruit traits are very conservative and **strongly phylogenetically determined** (Herrera 1986, 1989, 1995; Jordano 1995, Hampe 2003). Secondly, fruit selection by dispersers is not consistent in time and space and has shown to be too weak to shape fruit traits in different ecosystems with different frugivore diversity. Worldwide, fruit size seems to be the only common selection cue for dispersers. Finally, many studies, along with this one show that rather **abiotic factors** may shape fruit characteristics (Herrera 1986, 1995; Hampe 2003; Voigt et al, submitted). It seems thus that we need to look beyond co-evolution as it may well be that the ‘conservative’ fruit traits have more strongly influenced frugivore behaviour than the other way around.

As mentioned before, one might question the suitability to study seed dispersal in a site with a depauperate frugivore community. Indeed, Madagascar is characterized by a species poor frugivore guild, with sparsely representation of bird and bat species and the complete lack of larger mammals like elephants and ungulates. Besides the composition and abundance of the frugivore assemblage varies significantly over time as larger lemur species have gone extinct during Holocene and bush pigs and lemur species disappeared locally. On an evolutionary time scale these extinctions occurred recent and it is unlikely that they may have interfered in shaping fruit traits. The main disadvantage of dealing with a **depauperate and incomplete frugivore community** is that it obviously narrows down the chance of finding species-specific co-evolution. Specialized dispersal strategies seem rather unlikely in an ecosystem where few frugivores occur. Nevertheless it does seem that the frugivore composition is reflected in the representation of the different dispersal syndromes (cf. findings Gautier-Hion et al. 1985; Ganesh and Davidar 2000; Hampe 2003; Voigt et al. submitted) as very few ‘bird-fruits’ are present at the study site. Besides, the models that were investigated, were developed in the Neotropics where species-rich frugivore communities are present. Nonetheless no evidence could be found there either, nor elsewhere. So in the end, my results from Sainte Luce do not seem to contradict with findings from other sites with completely different frugivore guilds. The main advantage of this particular frugivore composition is that it allowed me to sample data on all frugivores present and to include frugivory by bats, birds and rats which has only been poorly studied up to now in Malagasy forests. Interesting as well is that following Fleming’s (1979) theory, Madagascar represents an extreme situation for the Paleotropics as it has a significantly low and unpredictable fruit production and few frugivores. Furthermore, the majority of frugivores and fruiting trees studied are endemic, which stresses the importance of providing data on these distinct ecosystems as well to complete our knowledge on the tropics worldwide. Besides, insight in fruit-frugivore interactions in Sainte Luce is crucial to understand forest dynamics here and to provide a solid database on which to formulate conservation plans.

In the closing section of this study, the hazardous situation of the Malagasy littoral forest at the moment is described and suggestions are made as to how my findings can be used in the design of population habitat viability analyses (PHVA), which will further lead to the development of conservation management plans. The littoral forest is expected to lose numerous endemic plant and animal species in the near future because of continuing deforestation and resultant habitat changes. Of great concern is the disruption of plant-animal interactions. Alterations in the recruitment dynamics of plant species in forest fragments might have unknown consequences for their long-term survival. As forests become more fragmented, the remaining patches become increasingly isolated and less accessible for arboreal lemur species, which were found to be important seed dispersers for numerous plant species. Consequently, gene flow and seed dispersal between patches become more critical for the long-term survival of many plant species. Conversely, if fragments get too small or hunting increases, the long-term survival of animal species will not be guaranteed either. As Holocene extinctions have shown, large frugivores, such as *E. f. collaris,* are most vulnerable to habitat fragmentation. We now know that this species is the only remaining seed disperser of large-seeded plant species and its decline and extinction will inevitably lead to a decline and lack of regeneration of large-seeded trees. Frugivorous birds and flying foxes are the most important mobile seed dispersers bringing seeds into grasslands and early succession vegetation. Genetic exchange and long distance dispersal between fragments is less likely to occur if populations of mobile flying dispersers decrease or vanish. It is thus not only the threat of habitat loss but also the hunting in the littoral forest that will disrupt animal-plant dynamics. I believe my findings on seed dispersal can represent a crucial input for underlying PHVA of conservation management plans. They will help to indicate priorities of action and vulnerable animal and plant species, which need special protection efforts. Obviously, it is of crucial importance to urgently protect the largest remaining intact forest fragments, which act as reservoirs from where indigenous floral and faunal species can colonize new habitats. In this respect, conservation zones are being established by QMM at the moment. Furthermore, to accelerate the natural recovery process corridors and plantations are being installed. In addition, environmental education in local schools should be continued as active cooperation with local people is indispensable to the success of sustainable use of land and natural resources and to actively protect the remaining littoral forests.

To conclude, this study provided a survey on fruit availability and its fluctuations in the littoral forest as well as an extensive three-dimensional dataset involving numerous plant species with their corresponding phenological, morphological and biochemical traits. Fruit diets of all frugivore species were obtained as well. Based on my results, I can conclude with great certainty that, in the littoral forest of Sainte Luce, fleshy-fruited plants engage in diffuse mutualisms with their dispersal agents. These interactions are quite generalized, very ancient and extraordinarily frequent in certain communities (Willson and Traveset 2000). High unpredictability and asymmetry of interactions, coupled with an important influence of abiotic factors, signal that mutual selection pressures between plants and seed dispersers are greatly constrained (Levey and Benkman 1999). In Sainte Luce fruit-eating animals tend to consume many fruit species and likewise the fruits of many plants are consumed by a wide range of animals, possibly to minimize the effects of the loss of one dispersal agent. Abiotic factors seem to be more responsible than biotic ones in shaping fruit characteristics. The long-term dynamics of fruits and their dispersers appear to be decoupled and the diet choice of frugivores shows a remarkable flexibility towards variations in the fruit supply. If frugivore preference had influenced the evolution of fruit traits at all it would most probably have acted upon general characteristics, such as fruit size. Clearly, this shows that abiotic variables and phylogeny are much more important in this ecosystem and thus may outweigh the extent of connections between frugivores and fruits.

Future research should concentrate more on the animal side of these interactions, which is essential to understand how niche separation among frugivores is organised in space and time. This will lead to a better understanding of what exactly determines diet choice. Data on the post-dispersal phase are needed as well to complete the dispersal cycle and to comprehend how the assembly and recruitment of plant communities are organised in space and time. As clear patterns in one year may disappear in the next, long-term data on phenology are needed. At present several undergraduate and graduate students are looking at parts of these processes, slowly filling the gaps in our knowledge. Even though there is still a lot to explore and to investigate, now is the time to act in order to preserve the littoral forest, and to prevent the irreversible disappearance of this precious ecosystem.

SAMENVATTING

Dit doctoraat behandelt zaadverspreiding op soort- en op gemeenschapsniveau in het littoraal regenwoud van Sainte Luce in zuidoost Madagaskar. Het tracht bovendien een inzicht te geven in de ecologische relaties tussen enerzijds de gilde van frugivoren en anderzijds bepaalde soorten vruchtbomen kenmerkend voor dit ecosysteem. Meer specifiek wordt aandacht besteed aan de predispersie- en dispersiefase. Zaadverspreiding wordt benaderd zowel vanuit het standpunt van de plantensoorten als dat van de diersoorten. In het eerste deel bestuderen we aan de hand van de temporele beschikbaarheid van vruchten en hun morfologische en biochemische kenmerken de verspreidingsstrategieën van 34 boomsoorten. Een uitgebreid onderzoek wordt hiervoor uitgevoerd naar de algemene vruchtbeschikbaarheid in het littoraal regenwoud. Vervolgens worden bestaande hypotheses, zoals soortspecifieke co-evolutie, het hoge versus het lage investeringsmodel en het concept van verspreidingssyndromen onderzocht. Verder hebben we getracht te achterhalen op basis van welke vruchtkenmerken de verschillende diersoorten hun voedsel selecteren. Hiervoor werden in dit woudtype 173 vruchtensoorten beschreven op morfologie en voedingswaarde. Dertien vruchteneters komen in dit ecosysteem voor. Zij behoren tot de volgende taxonomische groepen: primaten (4 spp.), vleermuizen (1 sp.), vogels (6 spp.) en knaagdieren (2 spp.). Ook bepalen we eveneens de rol die deze verschillende diersoorten spelen in het behoud van deze habitat en de regeneratie van typische woudsoorten door een actieve deelname aan de verspreiding en/of predatie van zaden. Om de geldigheid van deze resultaten binnen een ruimer kader te testen en te interpreteren, vergelijken we vruchtkenmerken en voedselkeuze van twee lemuursoorten in twee totaal verschillende woudtypes. We kunnen besluiten dat dit werk niet alleen aanleiding heeft gegeven tot fundamenteel wetenschappelijke resultaten maar eveneens een bijdrage kan leveren in de onderbouwing van beleidsplannen omtrent conservatie.

Eerst bestuderen we de vruchtbeschikbaarheid in het littoraal regenwoud. Deze wordt aan de hand van twee methodes bepaald, met name *phenological transects* en *fruit trails*. Hoewel dit woudtype een aseizoenaal klimaat kent, blijkt uit de resultaten toch dat er duidelijke seizoenale en jaarlijkse fluctuaties optreden in het vruchtaanbod. Jaarlijks is er een vruchtpiek van november tot en met februari. Anderzijds zijn de periodes van vruchtschaarste minder voorspelbaar, ze verschillen van jaar tot jaar. Frugivoren hebben dus af te rekenen met zowel periodes van vruchtovervloed als van -schaarste. In het littoraal woud zijn, net als in de andere regenwouden in Madagaskar de *phenophases* (bladgroei, bloei en vruchtrijping) onderling sterk gecorreleerd en bereiken ze hun hoogtepunt in de periode van maximale neerslag (november-februari). In droge woudtypes daarentegen zijn de *phenophases* meer gespreid over het hele jaar. Zonlicht fungeert als *trigger* bij fotosynthese en daglengte blijkt sterk gecorreleerd te zijn met alle *phenophases* in Sainte Luce. Variatie in daglengte is een belangrijke factor in dit extreem zuidelijk gelegen tropisch woud in tegenstelling tot evenaarwouden waar daglengte constant is. Daarenboven is de aanwezigheid van rijpe vruchten ook sterk gecorreleerd met temperatuur. Dit verband is hoogstwaarschijnlijk een gevolg van het hoge nutriëntengehalte in de bodem in periodes van hoge temperatuur en neerslag. Deze omstandigheden zijn bovendien ideaal voor de zaadkieming. De resultaten van zowel *phenological transects* als *fruit trails* tonen aan dat beide methodes aanvullend zijn. In tegenstelling tot het noteren van vruchtrijping bij grote bomen in de *phenological transects*, worden in *fruit trails* alle groeivormen (bomen, struiken, kruiden, epifyten en lianen) in rekening gebracht. Uit de resultaten blijkt dat die onderling een verschillende impact hebben op het seizoenaal verloop van het integraal vruchtaanbod in een woud. Bovendien worden in *fruit trails* ook de vruchten op de bodem meegeteld. Door combinatie van beide methodes wordt een inzicht verworven in de temporele variatie in vruchtbeschikbaarheid voor zowel arboreale als terrestrische vruchteneters.

Vervolgens richten we onze aandacht op verspreidingsstrategieën van 34 boomsoorten. Hierbij baseren we ons op enkele basismodellen uit de tropische ecologie, zijnde soortspecifieke co-evolutie, het model van lage versus hoge investering (McKey 1975) en verspreidingssyndromen. Eerst en vooral gaat men er bij co-evolutie van uit dat één bepaalde vruchtensoort verspreid wordt door één enkele vruchteneter. Hierbij zou de wisselwerking tussen beide soorten zo sterk zijn dat ze elkaars evolutie beïnvloeden, wat mogelijk zou leiden tot extreme vormen van wederzijdse aanpassingen. Volgens het model van lage en hoge investering verwachten we dat de lage investeerders of generalisten aan de hand van massale vruchtproductie gedurende een korte periode zoveel mogelijk zaadverspreiders aantrekken met hun waterige en zoete vruchten. De hoge investeerders of specialisten daarentegen produceren minder vruchten maar met een hogere voedingswaarde (hoog vet- en eiwitgehalte) en dit gedurende een langere vruchtperiode. Hierdoor zouden ze slechts enkele maar wel efficiënte zaadverspreiders aantrekken. Uit beide modellen vloeit het meer genuanceerd principe van verspreidingssyndromen voort waarbij bepaalde morfologische co-adaptaties in vrucht en zaad bepaalde taxonomische diergroepen aantrekken. Om deze modellen en principes te testen hebben we aan de hand van *fruit traps* en *tree watches* de identiteit van de vruchteneters achterhaald evenals hun rol als mogelijke zaadverspreiders en/of –predatoren. Fenologische, morfologische en biochemische kenmerken van de vruchtensoorten werden bovendien in rekening gebracht om te testen of er al dan niet co-variatie optreedt tussen deze kenmerken en bepaalde verspreidingsstrategieën. Er werd geen bewijs gevonden voor co-evolutie, noch voor het model van lage en hoge investering. Desalniettemin kan er toch een onderscheid gemaakt worden tussen wat we vogel-, zoogdier- en gemengde (zowel vogels als zoogdieren) vruchten kunnen noemen op basis van vrucht- en zaadgrootte, vruchtvorm en zaadaantal per vrucht. Voedingswaarde kan niet volgens deze categorieën ingedeeld worden. Vijf boomsoorten met grote zaden worden enkel en alleen verspreid door *Eulemur fulvus collaris.* Hieruit concluderen dat dit om co-evolutie gaat is wellicht fout, gezien het eerder een gevolg is van het uitsterven van grote frugivore vogel- en lemuursoorten, die ongetwijfeld ook deze grote zaden konden verspreiden. Niettegenstaande spreekt het voor zich dat deze exclusieve interacties uiterst belangrijk zijn vanuit het standpunt van conservatie. Wat het investeringsmodel betreft, blijkt dat dit model gebaseerd werd op vogelvruchten in de *Neotropics* en de geldigheid ervan blijkt dan ook sterk afhankelijk te zijn van de samenstelling van de frugivore gilde. De soortenarme groep van vruchteneters zowel in heel Madagascar als in het littoraal regenwoud heeft blijkbaar geen aanleiding gegeven tot gespecialiseerde verspreidingsstrategieën. Het is voor een bepaalde boomsoort mogelijk te riskant om afhankelijk te zijn van slechts één enkele vruchteneter. Als gevolg hiervan worden de meeste boomsoorten dan ook gekarakteriseerd door een set van gemengde en veeleer algemene morfologische en biochemische kenmerken. Anderzijds heeft de lage soortendiversiteit van frugivore vogels aanleiding gegeven tot opvallend weinig vogelvruchten hier in vergelijking met andere tropische sites. Tot slot kunnen we dus stellen dat van de drie modellen het concept van de verspreidingssyndromen het meest aannemelijk is in Sainte Luce maar de variatie in verspreidingsstrategieën wordt hierdoor maar gedeeltelijk verklaard.

Het centrale hoofdstuk van dit doctoraat behandelt de vrucht-frugivoor interacties die deel uitmaken van het ecosysteem. Zowel het dieet als de selectiecriteria en de overlapping van voedselsoorten van de 13 verschillende vruchten- en zaadeters wordt beschreven evenals hun respectievelijke rol binnen dit ecosysteem. Vrucht- en zaadgrootte blijken de voornaamste kenmerken te zijn in de voedselvoorkeur van alle frugivoren. Vogels eten vooral kleine vruchten, terwijl voor de verschillende zoogdieren de gegeten vrucht- en zaadgrootte evenredig toeneemt met de grootte van de mondholte en het lichaam. Terwijl vogels voornamelijk rode, paarse en zwarte vruchten selecteren, hebben de nocturne lemuren en een duidelijke voorkeur voor sappige en vlezige vruchten met een dunne schil. Vliegende honden eten eveneens graag vlezige vruchten. Wat voedingswaarde betreft verkiezen vogels vetrijke vruchten terwijl de zoogdieren (*Eulemur fulvus collaris* en *Pteropus rufus*) deze net vermijden. Dwerg- en muislemuren selecteren vruchten met een hoog suikergehalte om vetreserves aan te leggen voor hun torpor. Overlapping van de diëten tussen de verschillende vruchteneters is relatief hoog hier ten opzichte van andere sites, wat mogelijk kan verklaard worden door de onvoorspelbaarheid van het vruchtaanbod in het littoraal regenwoud. Dit zou op zijn beurt een verklaring kunnen zijn voor het lage soortenaantal frugivoren dat Madagaskar en onze site kenmerkt. Ook al is er een grote overlapping van dieet, de impact van de vruchteneters op zaadverspreiding blijkt toch verschillend en hun rol in het ecosysteem evenmin overlappend. Naast de vermelde vruchteneters, telt dit woud ook een aantal zaadeters. Zowel endemische als exotische rattensoorten, een tortelduifsoort en twee papegaaiensoorten zijn duidelijk granivoren daar zij de zaden vernietigen van de meeste vruchten die ze eten. Daarentegen zijn de sterk frugivore duiven en *bulbuls* belangrijke zaadverspreiders voor de verspreiding van soorten in open gebieden waar deze planten deel uitmaken van de eerste successiefase. *E. f. collaris* heeft een zeer soortenrijk dieet en is daarenboven als grootste vruchteneter vooral belangrijk als exclusieve verspreider van grote zaden binnenin een woudfragment. De kleine dwerg- en muislemuren zijn eerder omnivoor en verspreiden vooral zaden van kleine vruchten gedurende de periode waarin ze actief zijn. Tenslotte zijn de vliegende honden uiterst belangrijk voor zaadverspreiding op lange afstand en verzekeren ze bovendien de genetische uitwisseling tussen plantenpopulaties en woudfragmenten. Dit heterogeen zaadtransport is enorm belangrijk in een sterk gefragmenteerd ecosysteem zoals in Sainte Luce. In twee kleinere hoofdstukken besteden we extra aandacht aan de voedselecologie en de rol van de vliegende honden als zaadverspreiders en de zwarte papegaaien als zaadpredatoren omdat over beide soorten tot hiertoe nauwelijks data beschikbaar zijn voor Madagaskar.

Tenslotte vergelijken we vrucht- en zaadkenmerken binnen twee totaal verschillende woudtypes in Madagaskar: enerzijds het littoraal regenwoud van Sainte Luce (zuidoost Madagaskar), anderzijds het droge bladverliezende woud van Kirindy (west Madagaskar). Aan de hand hiervan trachten we de rol van abiotische factoren en vruchteneters in relatie te brengen tot de evolutie van morfologische en biochemische vruchtkenmerken. Beide sites verschillen sterk in abiotische factoren maar hebben een vergelijkbare frugivore gilde. Deze studie laat ons toe te testen of onze bevindingen van Sainte Luce ook opgaan voor andere sites van Madagaskar en ze vervolgens in een ruimer kader te interpreteren. Eerst en vooral is het duidelijk dat de algemene vruchtkenmerken sterk verschillen tussen beide sites. Sainte Luce heeft opvallend meer sappige steenvruchten en bessen met dunne schil terwijl openspringende doosvruchten en steenvruchten met dikke schil meer voorkomen in Kirindy. Biochemisch ligt het vetgehalte hoger in vruchten van Sainte Luce, in tegenstelling tot de hogere concentraties vezels, tanninen en stikstof in Kirindy. De typische vruchtkenmerken in dit droge bladverliezende woud duiden dan ook vooral op aanpassingen tegen watervlies gedurende het lange droge seizoen. Wanneer we kijken naar voedselselectie van *Eulemur fulvus* en *Cheirogaleus medius* binnen en tussen beide sites wordt het duidelijk dat kenmerken zoals vrucht- en zaadgrootte, groeivorm, kleur, zaadaantal, zaadbescherming en eiwitgehalte, die niet verschillen tussen de sites, niet echt relevant zijn voor de voedselselectie van deze lemuren. Anderzijds is er wel een sterke voorkeur voor zoöchore bessen en steenvruchten in beide sites, ook al is er een kwantitatief verschil in de aanwezigheid van deze vruchttypes tussen Kirindy en Sainte Luce. Wat de voedingswaarde betreft, negeert *Eulemur fulvus* vetrijke vruchten in Sainte Luce en selecteert *Cheirogaleus medius* vooral vruchten met een hoog suikergehalte en dit zowel in Sainte Luce als in Kirindy als voorbereiding voor hun torpor zoals eerder vermeld. Tenslotte blijkt dat beide lemuursoorten zich sterk kunnen aanpassen aan de algemene beschikbaarheid wat tal van morfologische (pulptype, geur, vruchtwand) en biochemische kenmerken (stikstof, tannines, ADF en NDF) betreft. Deze vruchtkenmerken verschillen sterk tussen beide sites en de lemuren eten dan ook wat meest aanwezig is in een bepaalde site. Voedselkeuze van beide soorten lemuren wordt dus sterk bepaald door het algemene vruchtaanbod. Aan de hand van deze resultaten kunnen we dus stellen dat vruchtkenmerken wellicht eerder het gevolg zijn van sitegebonden abiotische factoren dan het gevolg van een sterk selectieve impact door interacties met hun vruchteneters. Net zoals in andere onderdelen van deze studie kan ook deze vergelijking tussen sites evenmin bewijsmateriaal leveren voor het bestaan van co-evolutie. Er kan hooguit gesproken worden van een zwakke selectieve invloed van de frugivoren op vruchtkenmerken. De lemuren zijn duidelijk flexibel genoeg om hun dieet aan te passen en te overleven op vruchten met andere morfologische kenmerken en andere voedingswaarde, waarvan het aanbod verschilt per regio.

Uiteindelijk wordt in het afsluitende hoofdstuk de huidige situatie van het littoraal regenwoud toegelicht en worden enkele adviezen geformuleerd die relevant zijn voor conservatie. Het littoraal woud van Sainte Luce bestaat momenteel enkel nog uit sterk gedegradeerde woudfragmenten. Dit woud riskeert dan ook vele endemische planten- en diersoorten te verliezen in de nabije toekomst omwille van ontbossing en verdere habitatdegradatie. Het ontwrichten van plant-dier interacties is dan ook een van de grootste bedreigingen, aangezien veranderingen in de regeneratie van plantensoorten in woudfragmenten belangrijke gevolgen kunnen hebben voor het overleven van deze soorten op lange termijn. *Slash and burn*, nutteloze bosbranden en houtkap vormen de belangrijkste oorzaken voor wouddegradatie en fragmentatie. Daarenboven is er in de nabije toekomst ook nog de bedreiging van houtskool en titaniumontginning in deze regio. Door sterke fragmentatie raken de resterende woudfragmenten geïsoleerd waardoor ze niet langer toegankelijk zijn voor arboreale diersoorten. Genetische uitwisseling tussen fragmenten door vogels en vleermuizen is dan ook van extreem belang om de dynamiek van deze wouden in stand te houden. Daarenboven hebben grote zaden weinig zaadverspreiders en verdienen deze plantensoorten speciale aandacht wat conservatie betreft. Het zijn bovendien ook juist die grote vruchteneters met hoge habitatvereisten die het meest kwetsbaar zijn en bedreigd worden door versnippering van hun habitat. Niet enkel habitatverlies maar ook de jacht op verscheidene diersoorten kan leiden tot het uiteenvallen van plant-dier interacties. Aan de hand van onze resultaten hopen we toch duidelijk een aantal sleutelsoorten, zowel binnen fauna als flora te hebben aangeduid die extra aandacht verdienen in natuurbehoud. De bevindingen van dit proefschrift kunnen dan ook als soliede basis dienen waarop beleidsvoering rond natuurbeheer ter plaatse zich kan baseren. In eerste instantie is het van groot belang de meest intacte en grootste woudfragmenten dringend maar vooral actief te beschermen. Zij vertegenwoordigen de laatste reservoirs vanwaar planten en dieren nieuwe habitats kunnen koloniseren. Anderzijds is het ook noodzakelijk de regeneratie van het woud te stimuleren door het aanleggen van plantages en corridors die herbebossing bevorderen. Actieve deelname van de lokale bevolking is hierbij onmisbaar en van cruciaal belang voor de slaagkans van het natuurbehoud in deze regio. Milieu-educatie in de lokale scholen is in dit verband een ideale manier om de *Antanosy* actief bij deze projecten te betrekken. Alleen zo kunnen wij hen overtuigen dat het belangrijk is voor henzelf en vooral voor de toekomstige generaties om hun wouden te beschermen.

Als conclusie hopen we te kunnen stellen dat dit doctoraat erin geslaagd is een eerste inzicht te geven in de algemene vruchtbeschikbaarheid en haar fluctuaties in het littoraal regenwoud. Eveneens hebben we een driedimensionale dataset van 173 plantensoorten samengesteld met hun respectieve fenologische, morfologische en biochemische kenmerken. Bovendien hebben we het dieet en de voedselecologie van de verschillende vruchteneters beschreven. Uit de resultaten is gebleken dat in het littoraal regenwoud van Sainte Luce sappige en vlezige vruchten eerder diffuus geassocieerd zijn met hun zaadverspreiders. Een hoge onvoorspelbaarheid en asymmetrie in de interacties, die daarenboven sterk beïnvloed worden door abiotische factoren, leggen beperkingen op aan mutuele selectieve druk. Vruchteneters consumeren een grote variëteit aan vruchten, terwijl vruchten daarentegen vaak door verschillende diersoorten gegeten worden. Hierdoor is het risico van te sterke afhankelijkheid beperkt wanneer een welbepaalde zaadverspreider lokaal uitsterft. Abiotische factoren (neerslag, bodem, zonlicht, temperatuur) zijn duidelijk belangrijker in het scheppen van vruchtkenmerken dan biotische factoren (de frugivoren zelf) in het littoraal regenwoud. Bovendien vertonen bepaalde frugivore diersoorten vaak een hoge flexibiliteit wat hun voedsel betreft en passen zij zich aan de algemene beschikbaarheid aan. Toch zijn er enkele duidelijke voedselvoorkeuren van bepaalde taxonomische groepen of soorten, maar die hebben blijkbaar geen sterke impact gehad op de ontwikkeling van bepaalde vruchtkenmerken. Des te meer omdat de samenstelling en grootte van frugivore groepen sterk kan verschillen in de tijd. Dit is zeker het geval in Madagaskar waar talrijke grote vogel- en lemuursoorten uitstierven sinds de komst van de mens. Als er al enige duidelijke impact heeft bestaan van frugivoren op de evolutie van vruchtkenmerken dan heeft dit vooral geleid tot bepaalde algemene morfologische kenmerken. Vooral abiotische factoren overheersen de relatie vrucht-frugivoor. Om de cyclus van zaadverspreiding te vervolledigen zouden toekomstige studies in Sainte Luce het lot van de zaden na zaadverspreiding moeten bestuderen. Zo kan de samenstelling en regeneratie van plantengemeenschappen in tijd en ruimte nog beter begrepen worden. De rol van zaadverspreiders benadrukt het probleem van ‘lege wouden’ waar langlevende bomen als ‘levende doden’ getuige zijn van de ontkoppeling van essentiële biotische interacties ten gevolge van habitatverstoring en jacht.

RÉSUMÉ

Cette thèse de doctorat traite des modalités de dispersion des graines au niveau des espèces ainsi qu'au niveau de la communauté (floristique et faunistique) de la forêt littorale de Sainte Luce au Sud-est de Madagascar. Cette étude tente de mieux comprendre les relations écologiques entre la communauté de frugivores et les arbres fruitiers qui caractérisent cet écosystème. Plus spécifiquement, nous nous sommes concentrés sur les phases de pré-dispersion et dispersion des graines. La dispersion des graines est abordée du point de vue de la flore aussi bien que de la faune. Dans un premier temps, nous avons étudié les stratégies de dispersion des arbres en nous basant sur la disponibilité temporelle des fruits et sur leurs caractéristiques morphologiques et biochimiques. Ensuite, nous avons évalué certaines hypothèses telles que le principe de co-évolution, le modèle d'investissement haut/bas et le concept des syndromes de dispersion. Enfin, nous avons tenté de déterminer, sur base de quelques caractéristiques des fruits, comment les différents frugivores sélectionnent leur nourriture. Pour cela, nous avons décrit et catégorisé 173 espèces de fruits en nous basant sur leur morphologie et leur valeur nutritive. Dans cet écosystème, il existe treize espèces de frugivores appartenant à quatre groupes taxonomiques: les primates (4 spp.), les chauve-souris (1 sp.), les oiseaux (6 spp.) et les rongeurs (2 spp.). Nous avons évalué le rôle que jouent ces animaux dans le maintien de cet habitat et dans la régénération des espèces forestières typiques au travers de leur contribution à la dispersion et/ou à la prédation des graines. Afin de tester la validité de nos résultats de manière plus vaste, nous avons étudié les caractéristiques des fruits et la sélection alimentaire des deux espèces de lémuriens dans deux types de forêts différentes. Finalement, ce travail n'a pas seulement donné lieu à des résultats scientifiques intéressants mais a aussi contribué à l'élaboration de plans de gestion pour la conservation de ce milieu.

Premièrement, nous avons étudié la disponibilité des fruits et ses fluctuations dans une forêt littorale du Sud-est de Madagascar. Afin de faire ce peu, nous avons parcouru des layons phénologiques et réalisé des relevés mensuels au sol. Malgré que la saisonnalité soit peu marquée et qu'une vraie saison sèche soit inexistante dans la forêt littorale de Madagascar, les tendances phénologiques interannuelles peuvent être considérées comme relativement saisonnières. De plus, une variation intra-annuelle se discerne avec des périodes d'abondance et d'autres de pénurie en fruits. Toutes les phénophases (feuillaison, floraison, fructification) sont inter-corrélées et culminent à un maximum durant la période de novembre à février. Ce phénomène a déjà été observé dans d'autres forêts humides malgaches. Cependant, dans les forêts malgaches sèches, les différentes phénophases sont relativement espacées dans le temps en raison d'un climat plus saisonnier. Apparemment, la photopériode exerce un impact important sur les phénophases. La luminosité fonctionne comme un déclencheur pour la photosynthèse et, de manière évidente, il existe une plus grande variation de la durée du jour dans un site situé aussi extrêmement au sud. Par contre, la durée du jour est constante dans les forêts équatoriales. Les précipitations n'ont une importance que pour la feuillaison et la température affecte la présence des fruits et surtout des fruits mûrs. Ceci peut être expliqué par la haute valeur nutritive du sol durant les périodes de plus haute

température et précipitation. Ces circonstances sont par ailleurs idéales pour la germination des graines. Lorsqu'on compare les résultats obtenus par les deux méthodologies que nous avons utilisées, la différence de présence de fruits mûrs peut être expliquée par une contribution différente des types biologiques rencontrés sur le layon phénologique et le relevé au sol. Cette différence de contribution influence clairement les tendances de fructification totale. De fait, lors des relevés au sol, les fruits rencontrés à même le sol sont aussi comptés. La combinaison des deux méthodes met en évidence la variation temporaire dans la disponibilité des fruits pour les frugivores arboricoles ainsi que les frugivores terrestres.

Ensuite, nous nous sommes concentrés sur les stratégies de dispersion de 34 espèces d'arbres. Nous nous sommes basés sur certains modèles de l'Ecologie Tropicale : la co-évolution, le modèle d'investissement haut/bas (McKey 1975) et les syndromes de dispersion. Selon le modèle de co-évolution, une espèce de fruit dépend d'une seule espèce de frugivore pour sa dispersion. Cette interaction est si forte que les deux espèces influencent leurs évolutions réciproquement, ce qui peut mener aux formes extrêmes d'adaptations mutuelles. Selon le modèle d'investissement haut/bas, les moindre investisseurs ou généralistes attirent les espèces disséminatrices grâce une production fruitière importante durant une courte période de fructification. En général, la pulpe des fruits de ce genre d'espèces est succulente et sucrée. Par contre, les grands investisseurs ou spécialistes produisent moins de fruits mais d'une valeur nutritive plus haute avec un taux élevé de lipides et protéines, et ce, pendant une période plus longue. De ce fait, elles n'attirent que peu d'espèces disséminatrices mais ces espèces seront des disséminatrices efficaces. De ces deux modèles découle des syndromes de dispersion qui supposent des co-adaptations morphologiques des fruits et graines attirant certains groupes taxonomiques plutôt que d'autres. Afin de tester ces modèles et principes, nous avons identifié les consommateurs et déterminé leur rôle en tant que disséminateurs ou prédateurs par les méthodes des placettes, des pièges à fruits et par un suivi régulier de quelques pieds de différentes espèces. De plus, nous avons caractérisé les traits phénologiques, morphologiques et biochimiques des espèces de fruit pour tester s'il existait une co-variation de ces traits et de certaines stratégies de dispersion. Les résultats ne soutiennent pas l'hypothèse de la co-évolution ni le modèle d'investissement haut/bas. Néanmoins, il est quand même possible de distinguer les fruits à oiseaux, les fruits à mammifères et les mixtes (mangés par les oiseaux et par les mammifères) sur base de la taille des fruits et graines, de la forme des fruits et du nombre de graine par fruit. Ces mêmes catégories ne se retrouvent pas quand on mesure la valeur nutritive des différentes espèces. Cinq espèces d'arbres à grandes graines ne peuvent être disséminées que par *Eulemur fulvus collaris*. Nous ne pouvons dès lors conclure que ces cas représentent un cas de co-évolution. Il s'agirait plutôt d'une conséquence de l'extinction des grandes espèces de lémuriens et oiseaux qui étaient capables d'aussi avaler ces graines de grande taille. Pourtant ces interactions exclusives sont extrêmement importantes du point de vue de la conservation. Quant au modèle d'investissement différent, il semble qu'il soit basé sur des fruits à oiseaux des Néotropiques et sa validité dépend fortement de la composition de la communauté de frugivores. En règle générale, la communauté de frugivores est relativement pauvre à Madagascar tout comme à Sainte Luce, ce qui semble avoir mené à des stratégies plutôt généralistes de la part des espèces de cette communauté. Il est peut-être top risqué pour une espèce d'arbre fruitier de dépendre d'une seule espèce de frugivore pour sa dispersion dans cette région. Par conséquent, la plupart des espèces d'arbres est caractérisée par des traits morphologiques et biochimiques générales et non spécialisés. D'autre part, la faible diversité des oiseaux frugivores a pu avoir donné lieu au fait qu'il y ait très peu de fruits à oiseaux en comparaison avec d'autres sites. En conclusion, on constate que des trois modèles, celui des syndromes de dispersion semble le plus plausible à Sainte Luce. Cependant, il n'explique que partiellement la variation dans les syndromes de dispersion.

Le chapitre central de ce doctorat traite des interactions fruit-frugivore qui font partie de l'écosystème. On y décrit aussi le régime alimentaire des frugivores que le chevauchement des espèces consommées par 13 différentes frugivores et granivores ainsi que leurs rôles respectifs dans cet écosystème. La taille des fruits et des graines semble être un des facteurs les plus déterminants dans la sélection alimentaire de tous les frugivores. Les oiseaux mangent surtout des petits fruits tandis que pour les différents mammifères, la taille des fruits et graines augmentent proportionnellement avec la taille de leur gueule et de leur corps. Alors que les oiseaux sélectionnent les fruits rouges, pourpres et noirs, les lémuriens nocturnes ont une préférence pour les fruits succulents à enveloppe fine. *Pteropus rufus* se délecte aussi de fruits succulents. Quant à la valeur nutritive des fruits consommés, les oiseaux favorisent les fruits au contenu en lipides très élevé alors que les mammifères (*Eulemur fulvus collaris* et *Pteropus rufus*) évite simplement ceux-ci. *Cheirogaleus* spp. et *Microcebus rufus* sélectionnent des fruits sucrés pour créer des réserves de graisses durant les périodes de torpeur. Le chevauchement des régimes alimentaires entre les différents frugivores est relativement haut comparé aux autres sites, ce qui peut être expliqué par l'imprévisibilité de la disponibilité des fruits dans la forêt littorale et, qui peut être le motif du nombre relativement bas des espèces frugivores à Madagascar. Même s'il y avait un chevauchement important dans les régimes alimentaires, l'impact des différents frugivores sur la dispersion des graines serait quand même différent ainsi que leur rôle dans l'écosystème. Outre les frugivores déjà mentionnés, il y a aussi des granivores dans la forêt littorale (deux espèces de rongeurs endémiques et exotiques, une espèce de tourterelle et deux espèces de perroquet noir) qui consomment et détruisent les graines. Par contre les pigeons et bulbuls sont des disséminateurs importants qui transportent les graines dans les ouvertures de la végétation, là où ces espèces feront partie de la première phase de régénération de la forêt. *E. f. collaris* a un régime alimentaire très divers et, étant le plus grand frugivore, cette espèce est surtout importante en tant que disséminatrice exclusive des grandes graines à l'intérieur d'un seul fragment de forêt. *Cheirogaleus* spp. et *Microcebus rufus* sont plutôt omnivores et dispersent surtout les graines des petits fruits pendant la période où ils sont actifs. Enfin la chauve-souris *Pteropus rufus* est l'espèce la plus importante pour la dispersion des graines à longue distance et assure en plus l'échange génétique entre les populations des plantes des différents fragments de forêt. Ce transport hétérogène des graines est essentiel dans un écosystème aussi fragmenté que celui de Sainte Luce. Dans deux plus petits chapitres, nous attirons l'attention sur l'écologie alimentaire de *Pteropus rufus* et *Coracopsis nigra* et sur leur rôle en tant que disséminateurs et prédateurs de fruits parce que le régime alimentaire de ces deux espèces reste encore très peu connu à Madagascar.

Finalement, nous comparons les caractéristiques de fruits et graines dans deux types de forêt complètement différentes à Madagascar: D'une part, la forêt littorale de Sainte Luce

(Sud-est de Madagascar) et d'autre part, la forêt sèche caducifoliée (Ouest Madagascar). Cette étude nous permet de mieux comprendre le rôle des facteurs abiotiques (humidité, climat, sol) sur les caractéristiques des fruits et l'influence des frugivores eux-mêmes qui exercent une pression sélective sur ces mêmes caractéristiques (interactions faune-flore). Les deux sites diffèrent fortement par les facteurs abiotiques qui y prévalent mais sont occupés par une communauté de frugivores comparables. Ceci nous permet de vérifier si nos constatations et les résultats obtenus lors de cette étude sont valables aussi sur d'autres sites malgaches et de les interpréter dans un cadre plus vaste. Il est clair que les caractéristiques de fruits sont assez différentes entre les deux sites. A Sainte Luce, il y a beaucoup plus de baies et drupes succulentes à enveloppe fine tandis qu'à Kirindy, on retrouve plus de capsules déhiscentes et drupes à enveloppe épaisse. Biochimiquement le taux de lipides des fruits est plus élevé à Sainte Luce. Les fruits de Kirindy ont, quant à eux, un taux plus élevé de fibres, de tannins et de composés azotés. Ces caractéristiques sont typiques d'une forêt caducifoliée et indiquent l'existence d'adaptations contre la déshydratation pendant la longue saison sèche. Quant à la sélection des fruits par les deux genres de lémuriens (*Eulemur* et *Cheirogaleus*) dans un même site ainsi que entre les deux sites, les résultats montrent que les caractéristiques comme la taille de fruits et de graines, le type de végétation dans laquelle le fruit se retrouve, la couleur du fruit, le nombre de graines par fruits, la protection des graines et le taux des protéines qui ne diffèrent pas entre les deux sites, ne sont pas pertinents pour leur sélection alimentaire. Par contre, il existe une claire préférence pour des baies et drupes zoochores dans les deux sites même s'il y a une différence du point de vue de leur disponibilité entre Kirindy et Sainte Luce. Quant à la valeur nutritive, *Eulemur fulvus collaris* ignore les fruits riches en lipides à Sainte Luce, tandis que *Cheirogaleus medius* sélectionne surtout des fruits sucrés à Sainte Luce et Kirindy pour préparer leur torpeur tel que précédemment mentionné. Finalement, nous avons trouvé que pour certaines caractéristiques morphologiques (type de pulpe, odeur, enveloppe) et biochimiques (azotes, tannins, ADF, NDF), ces espèces de lémuriens peuvent s'adapter étroitement à la disponibilité générale des fruits. Ces caractéristiques diffèrent dans les deux sites et les lémuriens mangent ce qui est à leur disposition. Sur la base de ces résultats, il semblerait que ces caractéristiques soient plutôt influencées par les conditions abiotiques spécifiques à chaque site que par les interactions strictes entre lémuriens frugivores et les espèces consommées. Cette comparaison affaiblit les possibilités d'existence de la co-évolution, ce qui correspond à nos constatations précédentes. Nous dirions plutôt qu'il n'y a qu'une faible influence sélective des frugivores sur les caractéristiques de fruits. Les lémuriens sont clairement assez flexibles que pour s'adapter à un régime alimentaire caractérisé par des fruits à morphologies différentes et avec une autre valeur nutritive, selon la disponibilité locale et ponctuelle en fruits de la région.

Enfin, dans le chapitre final, nous commentons la situation actuelle de la forêt littorale et nous nous permettons de formuler certains conseils pertinents pour la conservation. En ce moment, la forêt littorale de Sainte Luce est composée de fragments fortement dégradés. Cette forêt risque donc de perdre beaucoup d'espèces de plantes et d'animaux endémiques dans un futur proche avec pour cause le déboisement et la dégradation progressive de l'habitat. L'interruption des interactions entre les plantes et les animaux est une des plus grandes menaces pour cette région car elle suppose des changements consécutifs dans la régénération des plantes qui peut avoir des conséquences importantes pour la survie des espèces à plus long terme. Les cultures sur brûlis, les feux de brousse et la coupe du bois sont les causes plus importantes de cette dégradation et fragmentation de la forêt. Dans le futur, cette région sera en plus sujette à la fabrication du charbon et à l'extraction d'ilménite, ce qui représentent quelques menaces de plus à long terme. Par une forte fragmentation, les îlots de forêt deviennent de plus en plus isolés et moins accessibles pour les animaux arboricoles. L'échange génétique entre les populations d'oiseaux et de chauve-souris des différents fragments est crucial pour maintenir la dynamique de ces forêts. Les grandes graines ont peu de disséminateurs potentiels et méritent une attention spéciale en matière de Conservation. Par ailleurs, ces grands frugivores nécessitent de grands habitats et sont donc les plus vulnérables face à la fragmentation du leur habitat. Non seulement la perte de l'habitat mais aussi une chasse excessive peut mener à l'interruption des interactions entre les plantes et les animaux. Nos résultats prétendent avoir indiqué certaines espèces-clés de la faune et de la flore qui méritent une attention spéciale et qu'il est urgent de protéger. Certaines constatations de cette étude de doctorat peuvent être intégrées concrètement et appliquées dans les analyses sur lesquelles se base la gestion de la faune et la Conservation. Tout d'abord, il est d'un grand intérêt de préserver activement et urgemment les fragments de forêts les plus grands et plus intacts. Ils représentent les derniers réservoirs où plantes et animaux peuvent coloniser de nouveaux habitats. D'autre part, il est aussi nécessaire de stimuler la régénération de la forêt en installant des plantations et corridors qui stimulent le reboisement. Une participation active de la population locale est indispensable pour la réussite de chaque plan de conservation dans la région. L'éducation environnementale dans les écoles locales est la façon idéale pour impliquer les *Antanosy* dans les projets de protection de l'environment. C'est l'unique manière de pouvoir les convaincre de l'importance d'une conservation de leurs forêts pour eux-mêmes et les générations futures.

En conclusion, nous espérons que ce doctorat soit parvenu à faire mieux comprendre la disponibilité des fruits et ces fluctuations dans la forêt littorale du Sud-est de Madagascar. Nous avons établi un ensemble de données tridimensionnelles de 173 espèces de plantes avec leurs caractéristiques phénologiques, morphologiques et biochimiques respectives. Nous avons aussi décrit le régime et la sélection alimentaire de différents frugivores. Les résultats montrent que dans la forêt littorale de Sainte Luce les fruits juteux et succulents sont associés à leurs disséminateurs de graines de manière diffuse. Une haute imprévisibilité et une asymétrie dans les interactions, qui sont fortement influencés par des facteurs abiotiques, limitent les possibilités de pression sélective mutuelle. Les frugivores consomment une grande variété de fruits et les fruits sont souvent mangés par plusieurs espèces d'animaux. De cette façon, le risque d'une trop forte dépendance est limitée lorsqu'un disséminateur particulier disparaît localement. Les facteurs abiotiques (précipitations, nature du sol, soleil, température) influencent plus les caractéristiques des fruits que les facteurs biotiques (les frugivores eux-mêmes) dans la forêt littorale de Madagascar. Certaines frugivores montrent, quant à eux, une grande flexibilité, notamment, en ce qui concerne leur nourriture et s'adaptent facilement à la disponibilité générale en fruits du site. Néanmoins, il y a des préférences évidentes dans la nutrition de certains groupes taxonomiques mais qui n'ont apparemment pas eu d'impact important sur le développement de certaines caractéristiques de fruits. De même, la composition et diversité d'espèces de frugivores à un site peuvent différer dans le temps. Ceci est certainement le cas à Madagascar où de grandes espèces d'oiseaux et de lémuriens se sont éteintes depuis l'arrivée des hommes. S'il y a eu un impact clair des frugivores sur l’évolution des caractéristiques de fruits, cela a plutôt amené à des traits morphologiques très généraux. Ce sont surtout les facteurs abiotiques qui déterminent la relation fruit-frugivore. Il serait intéressant que les études futures à Sainte Luce se concentrent sur le destin des graines après dispersion pour compléter l'étude du cycle de dispersion. Ainsi la composition et régénération des communautés des plantes dans l’espace et le temps pourraient être encore mieux compris. Le rôle des disséminateurs souligne l’importance des forêts vides où des arbres à longévité élevée sont comme des reliques, les derniers témoins de l'interruption des interactions biotiques mutuelles à cause de la perturbation des habitats et de la chasse.

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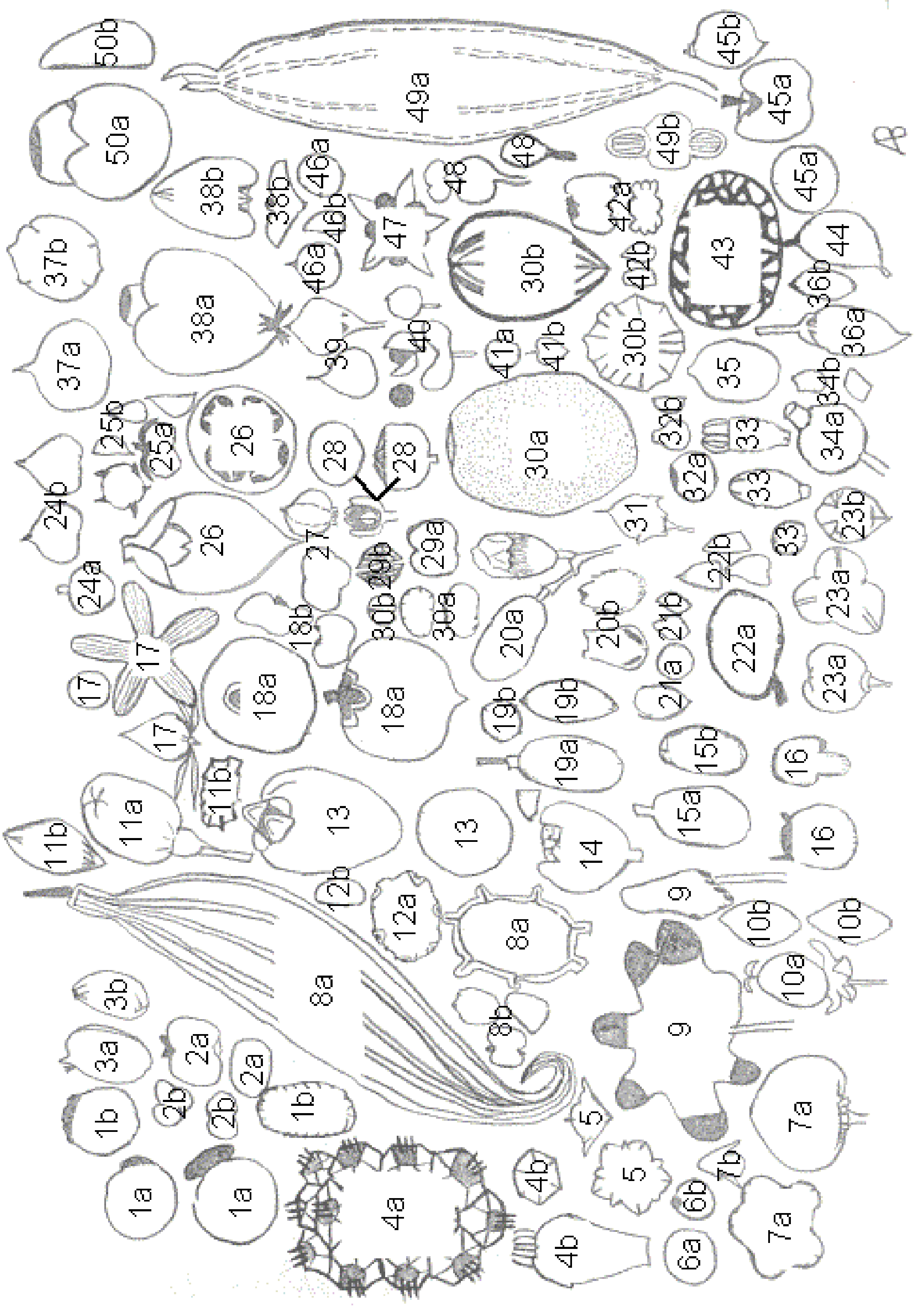
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nr	vernacular name	scientific name	family	**nr**	vernacular name	scientific name	family
1	hazomamy an ala	Apodytes sp. nov.	Icacinaceae	**26**	lendemilahy	*Anthocleista longifolia*	Loganiaceae
2	rotry mena	Syzygium sp.2	Myrtaceae	**27**	falindandro	*Dracaena reflexa* var. *nervosa*	Liliaceae
3	raotry	*Dypsis nodifera*	Arecaceae	**28**	meramaintso	*Sarcolaena multiflora*	Sarcolaenaceae
4	fandranabo	*Pandanus* aff. *longistylus*	Pandanaceae	**29**	ampoly	*Vepris eliotii*	Rutaceae
5	ramirisa	*Homalium louvelianum*	Flacourtiaceae	**30**	ramy	*Canarium boivinii*	Burseraceae
6	fandrikatany	*Smilax anceps*	Smilaceae	**31**	memboloa	*Rinorea pauciflora*	Violaceae
7	fandrianakanga	*Polycardia phyllanthoides*	Celastraceae	**32**	fantsikaitrafotsy	*Pyrostria* sp.	Rubiaceae
8	akondronala	*Ophiocolea delphinensis*	Bignoniaceae	**33**	bemalemy	*Bembicia uniflora*	Flacourtiaceae
9	amboralahy	*Tambourissa purpurea*	Monimiaceae	**34**	FT62	*Tarenna thouarsiana*	Rubiaceae
10	kambatrikambatri	*Brexia* sp.	Grossulariaceae	**35**	sisikandrongo	*Poupartia chapelieri*	Anacardiaceae
11	x219	*Erythroxylum* sp.	Erythroxylaceae	**36**	fangora sp2	*Erythroxylum nitidilum*	Erythroxylaceae
12	vahilengo	*Morinda umbellata*	Rubiaceae	**37**	tavolohazo novembre	*Cryptocarya* sp.	Lauraceae
13	ropasy sp.2	*Eugenia* sp.	Myrtaceae	**38**	voapaky vavy	*Uapaca littoralis*	Euphorbiaceae
14	x202	*Pittosporum polyspermum*	Pittosporaceae	**39**	zoramena	*Scolopia orientalis*	Flacourtiaceae
15	fotsivavo	*Polyalthia madagascariensis*	Annonaceae	**40**	mocarana	*Macaranga perrieri*	Euphorbiaceae
16	hazomamy marécage	*Apodytes dimidiata*	Icacinaceae	**41**	tsilaka	*Myrica spathulata*	Myricaceae
17	fanolafotsy	*Asteropeia multiflora*	Theaceae	**42**	?	*Canthium* sp.	Rubiaceae
18	vahabatra 3e M	*Cinnamosma madagascariensis*	Canellaceae	**43**	tsilavimbinanto	*Rhopalocarpus coriaceus*	Sphaerosepalaceae
19	x201	*Elaeocarpus alnifolius*	Elaeocarpaceae	**44**	mampay	*Cynometra* cf. *cloiselii*	Fabaceae
20	nofotrako	*Vitex chrysomallium*	Verbenaceae	**45**	voavoantatsimo	*Mystrolylon aethiopicum*	Celastraceae
21	fotombavy	*Leptolaena* sp.	Sarcolaenaceae	**46**	hazongalala	*Tricalysia* cf. *cryptocalyx*	Rubiaceae
22	tainbarika	genus indet.	Rubiaceae	**47**	hazombato	*Campylospermum obtusifolium*	Ochnaceae
23	x225	*Suregada baronii*	Euphorbiaceae	**48**	fantsikaitramainty	*Canthium variistipula*	Rubiaceae
24	fitoravina	*Vepris fitoravina*	Rutaceae	**49**	tavolo	*Tacca leontopetaloides*	Taccaceae
25	voatsilana	*Schefflera rainaliana*	Araliaceae	**50**	hazomainty	*Dyospyros* sp.2	Ebenaceae

Each number represent a certain fruit species ('a' refers to the entire fruit and 'b' to the seed). One exception is 4b which referes to a fruitlet.