Behavioural ecology of sympatric lemur species *Lemur catta* and *Eulemur* sp. in forest fragments, South-eastern Madagascar

by

Josia Razafindramanana

Degree awarded by Oxford Brookes University

Thesis submitted in partial fulfilment of the requirements of the award of
Doctor of Philosophy

April 2011

Acknowledgements

First of all, I thank Lord God who gave me health, strength, courage and happiness for the achievement of my thesis.

I gratefully thank the moral, technical and financial support of Sir Richard and Lady Alison Jolly for the fullfilment of this thesis. This study and project would not have been possible without their help, particularly Dr Alison Jolly.

I acknowledge my supervisors Prof. Simon Bearder, Dr Giuseppe Donati and Dr Anna Nekaris, for giving me the opportunity to realize my dream and for believing in me. Many thanks to Simon and Giuseppe for your precious guidance, tireless instruction, invaluable assistance, kindness and generosity throughout this Ph.D. Many thanks to Anna for providing constructive comments and advice on grant applications.

I express my profound gratitude to the 'École Supérieure des Sciences Agronomiques' University of Antananarivo,particularly Pr Bruno Ramamonjisoa et Jeannin Ranaivoasy, and the 'Ministère de l'Environement et des Forêts' for preparing and giving research permission to work in Ambatotsirongorongo forests, for providing a malagasy student assistant: Andoniana Rakotoarisoa and for arranging the capture of animals to attach radiocollars. I am grateful to the RioTinto/QMM Madagascar, in particular Manon Vincelette and Jean Baptiste Ramanamanjato, for offering support and field equipment throughout my fieldwork in this site.

I am thankful to the de Heaulme family who gave me the possibility to work in their lovely private parks: Bealoka and Berenty Reserves. I also thank all the Berenty staff and guides who helped me during the long fieldwork since 2008.

I would like to thank Prof. Jorg Ganzhorn for his collaboration and advice during the fieldwork. Big thanks to the following people for information and advice before, during and after the project; for answering my many questions; for overall discussions and exchange of ideas; for sharing publications; and/or for their collaboration: Dr Anne Mertl-Millhollen, Dr Lisa Gould, Pr Robert Sussman, Dr Sinichiro Ichino, Dr Takayo Soma, Pr Jonah Ratsimbazafy, Dr Hanta Rasamimanana, Kathryn Blumenfeld-Jones and Susan Pinkus.

I would like to express my appreciation to the students from the ‘École Normale Supérieure Antananarivo’, including Fetra, Fefy, Donald, Nirina, Ainga and Rio, who helped me doing the vegetation study in Bealoka and the lemur population survey in Berenty in 2008 and 2009. I also thank the volunteers from Azafady NGO for their assistance in data collection in Bealoka forest. Many thanks to Amber, Vicky, Josh, Flavia and Thiago for their cooperation in data collection and their friendly atmosphere in the field. A big thank to Luca Santini who helped collecting data in Bealoka forest during the rainy season.

I am grateful to Nancy Gladstone and Fali Andriatahiana who always welcomed me to their house, and for their hospitality and generosity during my stays in Oxford. I also thank Ann and Anthony Gladstone for their hospitality during my write-up phase.

I owe special thanks to my lovely husband Rija Rasamimanana for always being there, unconditional love and unfailing support. He taught me to be courageous and strong, and he helped me in so many different ways in order to achieve my thesis. And last but certainly not least, thanks to my parents, my grandparents and sisters who always encouraged and prayed for me throughout my life. Sincere thanks for all my families who forgave me for missing important family events and for sharing only little time for their care.

The study was funded by RioTinto, British Federation for Women Graduates, The Aspinall Foundation and Dr Alison Jolly. Fieldwork was supported by National Geographic Society, IdeaWild, Primate Conservation Inc., Primate Society of Great Britain, Cleveland Metropark Zoo and QMM Madagascar. Conservation International Madagascar offered airplane tickets to England and funds to attend the International Primatological Society Congress in Japan during the studies.

Table of contents

List of figures

List of tables

1. General introduction

1.1 Project goals

The principle aim of the present study is to examine the behavioural ecology and interactions between sympatric lemur species, ring-tailed lemur, Lemur catta, and hybrid Eulemur rufus x E. collaris, herein after called brown lemurs, or collared brown lemur, E. collaris, in two localities near Fort-Dauphin, Madagascar. In particular, I investigate the extent of niche partitioning between native ring-tailed lemurs and an introduced hybrid population of brown lemurs in Berenty reserve, in comparison with the sympatric population of ring-tailed and collared brown lemurs in Ambatotsirongorongo forest. The objective is to study the impact of the introduced brown lemur population at Berenty reserve on the behaviour and distribution of native ring-tailed lemurs. A third study site, the Bealoka forest, served as a control by indicating the behavioural ecology of allopatric ring-tailed lemurs. The work has been accomplished with the help of students from the Ecole Normale Supérieure who assisted in vegetation study and lemur population survey in Berenty and Bealoka reserves, and a student from the Ecole Supérieure des Sciences Agronomique at the University of Antananarivo, Madagascar, who assisted in data collection in Ambatotsirongorongo forest. Inter-Observers Reliability Measurements tests were conducted during the first month of observations and these data were discarded from the analyses.

1.2 Rationale and research questions

Multi-species studies of Malagasy lemurs to date reveal patterns of ecological equilibrium as they consistently demonstrate niche partitioning along dimensions such as habitat type, food type and temporal separation (Ganzhorn, 1989; Schoener, 1974). Ring-tailed and brown lemurs are naturally sympatric in part of their natural ranges, about 300km northwest of Berenty reserve (Sussman, 1972). Brown lemur species ranges extend from dry forest in the north into tropical rainforest, while ring-tailed lemurs' range extends south into arid habitat (Goodman et al., 2006; Sussman, 1972, 1977b). This suggests that Lemur catta and Eulemur sp. used their same respective niches (diets, forest strata) both in sympatry and in allopatry, indicating adaptation to different environments before becoming sympatric species (Sussman, 1974).

Dominated by tamarind trees, Tamarindus indica, Berenty reserve is one of the few protected fragmented gallery forests that remains; it contains native ring-tailed lemurs and an introduced brown lemur population (Jolly et al., 2006b). Berenty reserve is amongst the densest forests in terms of canopy coverage, identified in satellite images (Sussman et al., 2006). Berenty is similar, in resource availability, forest composition and seasonality, to forests in which both lemur species are naturally sympatric, and has the same species of predators and other sympatric primates (Sussman, 1972; Pinkus, 2004). Tamarindus indica, a preferred food for both species in natural sympatry, is abundant in Berenty. This plant constitutes the keystone food source for ring-tailed lemurs and they are dependent on its ripe fruits particularly during their birth/lactation seasons (Rasamimanana and Rafidinarivo, 1993; Sauther, 1998a; Soma, 2006). Recent research in Berenty demonstrated that, tamarind canopy coverage at the riverfront has dropped from 50.7% to 20.9% cover, with little recruitment of seedlings and saplings (Blumenfeld-Jones et al., 2006). At Berenty, ring-tailed lemurs occasionally travel out of their range for tamarind fruit when it is not available within their range. However in the last decade, it has been reported that gallery forest troops were foraging away from closed canopy forest (Jolly et al., 2006c; Mertl-Millhollen et al., 2006; Soma, 2006). The brown lemur population was released at Berenty by accident (O'Connor, 1987). Around 1975, up to 17 brown lemurs of two species, Eulemur rufus and Eulemur collaris, were introduced into Berenty Reserve (Tanaka, 2007; Pinkus et al., 2006). The brown lemurs have hybridized and their population has grown exponentially (Jekielek, 2004). Although, the brown lemur density might not be as high as it could be in natural sympatry with ring-tailed lemurs (Sussman, 1974), it added to the already high ring-tailed lemur density (Jolly et al., 2002; Jolly et al., 2006c). Because brown lemurs adopt similar feeding behaviour as ring-tailed lemurs, and they also feed on green tamarind fruits, they deplete the abundance of ripe fruits. This foraging strategy may also impact recruitment of tamarind seedlings (Mertl-Millhollen, pers. comm.). Schoener (1974) explained that in many species assemblages, niche partitioning appears to have evolved if coexistence is possible. Closely related sympatric species potentially capable of competing with each other regularly show ecological differences in one or more niche dimensions.

To interpret the ecological and behavioural contrasts between ring-tailed and brown lemurs at Berenty reserve, the following major questions are addressed:

- Do ecological and behavioural factors permit the ring-tailed lemur and hybrid brown lemur population at Berenty reserve to overlap sustainably?
- What are the limits of the niche separation and ecological differences between both lemur species at Berenty reserve and anywhere else where they live in natural sympatry?
- What are the effects of the introduced hybrid population of brown lemurs on the behaviour and distribution of native ring-tailed lemurs at Berenty reserve?
- Is feeding competition with brown lemurs among the reasons of forest declining and changes of ring-tailed behaviour?
- How does the niche of ring-tailed lemurs at Berenty compare with that in an area where they occur in the absence of brown lemurs?

To answer these questions, the following strategies that might elucidate the interactions of the two populations are examined. Three study sites were chosen to conduct the project. (1) Berenty reserve where native ring-tailed lemurs occur with introduced brown lemurs, reaching high population density, predicted to be threatening the population of ring-tailed lemurs and the forest. (2) Bealoka forest which is another area of fragmented gallery forest near Berenty that contains only ring-tailed lemurs and other primates in natural sympatry such as Propithecus verreauxi. This forest seems similar to the original situation in Berenty reserve as both of them look similar in terms of structure (Jolly et al., 2006b; Sussman et al., 2006). This site serves as comparison for changes in vegetation parameters and in ring-tailed lemur behaviour after the introduction of brown lemurs at Berenty reserve. (3) Ambatotsirongorongo fragmented forest, a transitional forest between dry and wet zones covered by plant species common in both littoral and dry forests (Andrianarimisa et al., 2005; Ramananjato et al., 2002). Within this unusual ecosystem, Lemur catta and Eulemur collaris occur in natural sympatry. This site was chosen to describe the ecological differences in behaviour of both lemur species in natural sympatry and then to compare with that of Berenty. From this study between the three sites, we will define the possible impacts of the introduced brown lemurs at Berenty on ring-tailed lemurs and on its forest. The niche partitioning between both lemur species is described for each forest. Propithecus verreauxi is present in each study site as a sympatric lemur species inhabiting with ring-tailed and brown lemurs, but this lemur species in not included in our study as it adopts a different ecology from our lemur study species.

1.3 Background on study sites

The main study site is Berenty reserve, but part of the study has been conducted in a nearby forest called Bealoka reserve (Figure 1.1.a). Both reserves are private forests owned by the de Heaulme Family. Berenty, a 200-ha forest, has been a protected private reserve since 1936 (Jolly, 2004); Bealoka, a 100-ha forest, has been protected from outside destruction from 1990 (Crowley, 1995). Berenty and Bealoka reserves are located in the southeastern part of Madagascar along the Mandrare River at 25°0.590'S 46°18.517'E and 24°57.655'S 46°16.051E respectively. Berenty reserve is divided into three parts: Malaza gallery forest, the xerophytic spiny forest and Ankoba secondary forest (Figure 1.1.b). A forth part called tourist front is defined by Jolly et al. (2002) as an open-canopy habitat located in the west forest edge and has intensive food provisioning, permanent standing water through the year and many introduced tree species (see chapter 2). Ankoba forest, located in the north-west of Berenty, is described to be a re-grown closed canopy forest dominated by the introduced plant species Pithecelobium dulce with the presence of other exotic and fruit trees as well as endemic Tamarindus (Jolly et al., 2006b; Rambeloarivony, 2009). Bealoka reserve is one of the largest areas of gallery forest in the south of Madagascar and has been exploited by indigenous people for forest products prior to 1990. The two forests are approximately seven km apart (O'Connor, 1987). Bealoka has an area of 90 ha and is isolated from other riverine forest by the sisal fields and the river. The main 100 ha Malaza forest of Berenty is part of a larger reserve system of 200 ha. Bealoka lies on the outside bend of the river and Malaza on the inside; a difference which undoubtedly affects their flooding patterns. At Berenty reserve, native ring-tailed lemurs (Lemur catta) occur in sympatry with introduced brown lemurs, hybrid between Eulemur rufus and Eulemur collaris (Figure 1.2). The brown lemurs were first introduced in 1975 in the gallery forest with about 8 individuals and about another 7 added during the following years to 1985. Native population of Lemur catta and Propithecus verreauxi coexist peacefully at Bealoka forest.

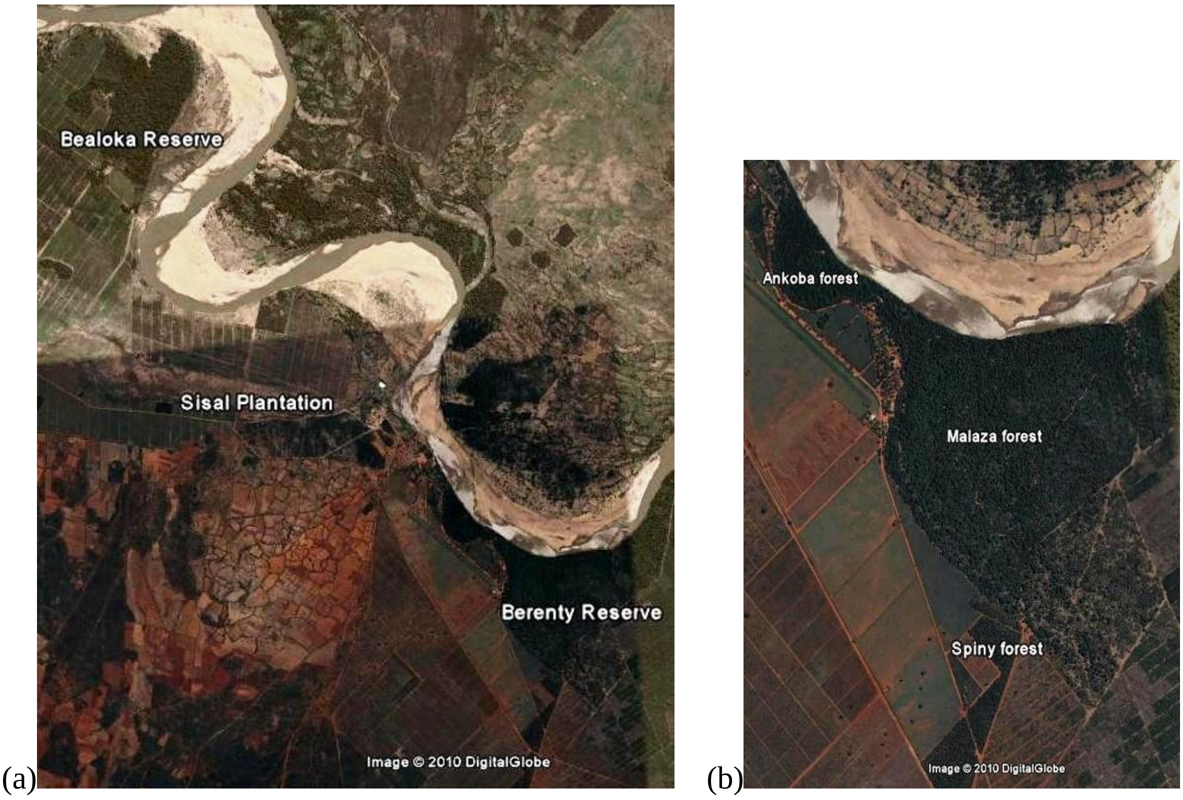


Figure 1.1 Aerial photos of the study sites (a) Bealoka and Berenty reserves, showing their position relative to each other and (b) Berenty reserve, showing three of the distinct habitat types.

Figure 1.2 Photos of a ring-tailed lemur (left) and a female brown lemur (right)

1.4 Community ecology and primate niche

Community ecology is defined as the study of interactions between organisms that live together in the same place (Patterson et al., 2003; Raven and Johnson, 1999). Primatologists have focused their investigations on interactions between species of primates sharing the same habitat. Such research has examined mixed-species associations and competitive interactions between primate species (Boinski et al., 2002; Boinski et al., 2000; Burton and Chan, 1996; Butynski, 1982; Cheney and Wrangham, 1987; De Ruiter, 1986; Eisenberg et al., 1972; Kappeler, 1995). The existing research into primate community ecology has shaped our understanding of how selective pressures such as resource competition and predation influence primate distribution and abundance, primate sociality and primate feeding ecology (Charles-Dominique, 1977; Cheney and Wrangham, 1987; Dunbar and Dunbar, 1979; Gautier-Hion, 1978). One of the organizing principles in ecology is that competition among sympatric species plays a significant role in structuring communities (Hutchison, 1978; MacArthur and Levins, 1964; Schoener, 1983). Competition for shared resources that are limited in abundance will regulate species diversity and population sizes in an ecosystem (MacNally, 1995; Raven and Johnson, 1999). Much of competition and niche theory in community ecology derives from the basic assertion that perfect competitors cannot exist in nature (Gause, 1934). Species pairs or sets of related animals that do share habitats tend to demonstrate some form of ecological divergence. Hutchinson (1957) first proposed a minimim of size ratio that permits related sympatric species pairs to avoid competition. As the number of potential competitors increases in a community, species will tend to segregate on multiple dimensions (e.g., food type choices, horizontal and vertical habitat preferences, and activity schedule; Schoener, 1974).

One of the first concepts developed to address competition was that of the niche. This term refers to the habitat occupied by an organism, its physical adaptations to its habitat and its behaviours (Grinnell, 1904), no two species can have precisely the same niche because the best-fit will survive to the exclusion of any less fit species. Niche separation in sympatric species should mediate interspecific competition for limited resources, thus ecological character displacement may arise through the coevolution of sympatric competitors (Strong et al., 1979). A niche was defined as the total of all of the ways that an organism utilizes the resourves of its environement and n=all of the interactions between an organisms and its environment (Hutchison, 1957; Pianka, 1994). The n-dimensional hypervolume is known as the fundamental niche which is the entire niche that an organism may theoretically be capable of using (Hutchison, 1957; Pianka, 1994). The realized niche is the actual niche in the community, the portion of the niche that does not overlap with the niches of other organisms (Odling-Smee et al., 2003). As a result, an organism's realized niche is part determined by the pressure exerted by symptraic species that share the local resources (Hladik, 1981). The fundamental niche implies that an organism has an equal chance of persistence in all areas within its niche, and a zero probability of persistence in the space outside of its niche (Hutchinson, 1978). Primate species' niche can be studied in areas where the species are sympatric and areas where they are allopatric (Connell, 1980; Peres and Dolman, 2000). Partitioning of niches by sympatric species can be examined by gathering data on resource use and calculating the degree of dietary niche overlap (Connell, 1980). The primary tactic allowing primates to separate their niches is the exploitation of different resources (Charles-Dominique, 1977; Dunbar and Dunbar, 1979). When using the same resources, niches are partitioned in two ways. Primates may forage in different portions of their shared habitat (Charles-Dominique, 1977). For example, Charles-Dominique (1977) found that although Galago demidovii and Arctocebus calabarensis consume an insectivorous diet, they avoid competing for the same resources by utilizing different forest strata. When foraging on a similar diet in the same habitat, primates consume different parts of the same plant or consume insect prey of different size classes (Charles-Dominique, 1977). Different factors may influence the niche such as animal body size which may affect the diet of an organism (Fleming, 1982). This relationship has critical implications for food choice. Niche overlap may also be diminished by foraging at slightly different times or at different heights within the forest canopy.

The community structure and feeding behaviours of primates found in diverse habitats appear to reflect niche partitioning: Africa (Gautier-Hion, 1978; Gonzalez-Kirchner, 1996; Struhsaker and Oates, 1975; Tutin et al., 1997); Neotropics (Chapman, 1988; Mittermeier and van Roosmalen, 1981; Norconk and Kinzey, 1994;

Terborgh, 1983; Terborgh and Janson, 1986; Tomblin and Cranford, 1994); Asia (Raemakers, 1979; Rodman, 1973). Primates may respond to competition for limited resources by adopting different diets, ranging patterns, activity schedules, time budgets and microhabitats (Sussman, 1974; Waser, 1987). A high degree of dietary overlap among sympatric primates may indicate current competition, and clear niche separation is viewed as evidence for the prevalence of past competition shaping the ecological patterns in the community (Waser, 1987). The Malagasy strepsirhines also exhibit divergent feeding and foraging strategies in sympatric species (Ganzhorn, 1988; Sussman, 1977a; Sussman, 1974; Wright and Randrimanantena, 1989; Freed, 1996; Overdorff, 1991; Overdorff, 1993; Overdorff, 1996; Powzyk, 1997; Rasmussen, 1999; Tan, 1999; Vasey, 1997; Vasey, 2000a; Vasey, 2002), and interspecific competition apparently plays a significant role in structuring lemur communities. According to Fox’s assembly rule, communities tend to include a balance of guilds or functional groups (e.g., frugivores, folivores, etc.); if new species are added to the community, they tend to do so in a cycle according to available functional niches (Ganzhorn et al., 1997). The details of dietary niche patterns among sympatric Malagasy primates vary across habitats and taxa. In some cases, dietary differences are marked.

Niche separation also varies according to seasonal shifts in food abundance, although energy demands for reproductive females also have important effects on species’ diets (Vasey, 2000a). Ganzhorn (1988) noted subtle and diverse mechanisms of niche partitioning in both eastern rainforests and western deciduous forests. At Andasibe and Ampijoroa, he found that sympatric lemur species often vary in chemical composition of their diets (including protein concentrations, condensed tannins and alkaloids). This variation is sufficient to segregate the communities into species pairs, with each pair significantly different from the others (i.e., pairs or close competitors). Subsequently, the two species within pairs can be distinguished by divergent activity rhythms. These two factors combine to significantly reduce niche overlap (Ganzhorn, 1988). In the only other study of sympatric brown and ring-tailed lemurs, at the western site of at Antserananomby, Sussman (1974; 1977) found red fronted brown lemurs have highly restricted, folivorous diet in dry forest habitats, while similar-sized ring-tailed lemurs pursue a more diverse foraging strategy. Sussman equated these dietary differences with microhabitat preferences: ring-tailed lemurs use the ground frequently, while brown lemurs are restricted to an arboreal environment. As a possible consequence of this spatial separation (and/or competition) with ring-tailed lemurs, brown lemurs may be confined to fewer food resources. Sussman (1974) did not find variation in either of these species' diets in areas of allopatry vs. areas of sympatry. This, the dietary divergence is not attributed directly to the interaction of the species in their shared environment. Instead, both lemur species appear to demonstrate adaptations to dissimilar allopatric environments. Nonetheless, this ecological separation still may minimize direct competition and facilitate sympatry. This study was conducted 30 years ago and has not been evaluated in environments where one of these species was introduced. Moreover, a comparison of this association with that of natural cohabitation of both lemur species at the other end of the ring-tailed lemur range from Sussman's study in Antseranomby might be of interest to understand the evolution of ecological niches between sympatric species.

1.5 Cathemerality and its role in niche partitioning

Cathemerality was defined by Tattersall (1987) as follow: "the activity of an organism can be regarded as cathemeral when it is distributed approximately evenly throughout the 24 h of the daily cycle, or when significant amounts of activity, particularly feeding and/or travelling, occur within both the light and dark portions of that cycle" (Tattersall, 1987, p. 201). This temporal distribution of activity stated as a distinct primate activity pattern, is recognized mainly in Madagascar lemurid genera. Cathemeral behaviour has been reported in all Eulemur ssp. (Tattersall, 1982, Tattersall, 1987; Overdorff and Rasmussen, 1995; Donati and Borgognini-Tarli, 2006; Donati et al., 1999, Donati et al., 2001; Rasmussen, 1999; Curtis et al., 1999; Curtis and Zaramody, 1999; Rasmussen, 1999; Andrews and Birkinshaw, 1998; Colquhoun, 1998; Wilson et al., 1989; Freed, 1996; Overdorff, 1988; Overdorff and Rasmussen, 1995) and in Hapalemur (Mutschler et al., 1998). Cathemeral behaviour has also been clearly documented in owl monkeys inhabiting highly seasonal forests in Paraguay (Wright, 1989) and Argentina (Fernandez-Duque, 2003). Outside Primates, cathemeral activity has been recorded in a variety of Indonesian mammals, including both small and large bodied carnivores and various ungulates (van Schaik and Griffiths 1996; Curtis and Rasmussen, 2006). Variation in activity patterns has been described to be controlled by a variety of environmental factors including temperature, day length, rainfall, predation, food resource availability (Curtis and Rasmussen, 2006; Donati et al., 1999; Donati et Borgognini-Tarli, 2006; Hill, 2006), by quality (Wright, 1989; Tarnaud, 2006) and by varying nocturnal light levels (Donati et al., 2009; Donati and Borgognini-Tarli, 2006). Social behaviours may also affect activity patterns (van Schaik and Kappeler, 1996; Ostner and Kappeler, 1999).

Cathemeral activity can play an important role in minimizing competition, which is intrinsically linked to niche differentiation (Curtis and Rasmussen, 2006). Schoener (1974) ranked three resource partitioning dimensions in order of importance, concluding that habitat dimensions were more often important than food-type dimensions, which in turn were more often important than temporal dimensions. Variation in activity cycle may have been important in maintaining sympatry in a variety of habitats since the potential for competition is expected to be strong among species that are morphologically and ecologically similar (Tattersall and Sussman, 1998). Every forest econiche can accommodate two sympatric species if one is adapted for diurnality and the other for nocturnality (Charles-Dominique, 1975). A long-term study on sympatric species of mongoose lemurs (Eulemur mongoz) and common brown lemurs (E. fulvus) in seasonal dry forest in northwestern Madagascar, described an overlap in core home ranges, preferred sleep trees and diet in these cathemeral congeners, indicating a potential for interspecific competition that could be mitigated by their different patterns of cathemerality (Rasmussen, 1999; Curtis and Rasmussen, 2002). Cathemerality can be considered as an extra dimension that contributes to the temporal niche separation in lemurs. Ganzhorn (1989) reported that microhabitat structure and food chemistry were suffi cient to separate 7 species of sympatric lemurs in eastern rainforest. However, the two cathemeral species occurring in the area E. fulvus and Hapalemur griseus, exhibit little overlap in diet. Being able to initiate activity bouts over the entire 24-hour period, versus only a 12-hour period of day or night, has potential advantages (Curtis and Rasmussen, 2006). The co-occurrence of pairs of Eulemur species in Madagascar that exhibit dietary overlap, but different cathemeral patterns, suggests that a variation on this activity cycle may also contribute to niche separation (Curtis et al., 1999; Tattersall and Sussman, 1998; Rasmussen, 1999). In Lemuridae, cathemerality contributes towards niche separation through partial temporal separation from diurnal and nocturnal competitors, as well as through variation in the cathemeral activity pattern to reduce competition with other cathemeral species. Although it has been documented that Lemur catta exhibits some nocturnal behaviour (Pereira et al., 1999, Curtis and Rasmussen, 2006), Eulemur sp. is considered as a dominant cathemeral species monopolizing and profiting the best time period (e.g., Halle and Stensteth, 2000; Ziv and Smallwood, 2000; Marcelli et al., 2003). This cathemeral behaviour can already play an important role in niche partitioning between both species. In the present study, I report the diurnal dichotomy of the ecological niches of both species in fragmented forests in south-eastern Madagascar.

1.6 Research and conservation issues

The conservation significance of this study is that it provides data to explain the niche separation between two closely related sympatric species and its evolution 30 years after a similar study was conducted in Antserananomby (see (Sussman, 1977b; Sussman, 1974). It elucidates the habitat requirements of both lemur species to allow their coexistence (Schoener, 1974; Vasey, 2000a). That will help us to protect endangered forest types such as gallery forest and transitional forest, as well as lemur populations within their forests. These data will be used to address two major issues in primate conservation. First, we will collect data suggesting whether overpopulation by lemurs in forest fragments can cause interspecific competition and second, whether this interspecies competition can cause the decline of sympatric congeners. This assessment will enable decisions regarding the appropriate management of each study site.

1.7 Thesis structure

This thesis was prepared as a series of manuscripts for submission to international peer-reviewed journals that may be read independently of each other. Papers are presented in the general format required for journals. Although a background of the study is presented in the general introduction, there might be still some overlap and repetition of some details between chapters. All references are reported at the end of the thesis.

In Chapter 2, vegetation and habitat structure in Bealoka and Berenty reserves are described. In Chapter 3, I present the population and distribution interactions of ring-tailed and brown lemurs at Berenty reserve. In Chapter 4, I describe the ecological niche partitioning between native ring-tailed and introduced brown lemurs at Berenty reserve in terms of diet, habitat preferences and social interactions. In Chapter 5, I report the behavioural ecology of sympatric lemur species in Ambatotsirongorongo forest, Lemur catta and Eulemur collaris. In Chapter 6, the behavioural ecology of allopatric ring-tailed lemurs in Bealoka forest is described. In Chapter 7, I summarize the most relevant findings of this thesis and discuss the implications of the ecological niches of sympatric species of ring-tailed and brown lemurs.

2. Vegetation structure and habitat characteristics of gallery forests in south-eastern Madagascar

Abstract

In this study, vegetation structure and habitat types in Berenty and Bealoka gallery forests in Southeast Madagascar are described in order to understand plant diversity and the structural models of these endangered forests for conservation priorities. Fieldwork was conducted from september to november 2008 in Berenty gallery forest called Malaza and in Bealoka forest. Data on forest variables such as plant species, number of young trees and saplings, tree height, tree diameter, canopy width and bole height were recorded in fifteen belt transects (10 X 10 m) (10 in Malaza , 5 in Bealoka). A total number of 557 trees ≥ 10 cm dbh were censused in the 1 ha area surveyed in Malaza gallery forest of Berenty and 280 trees ≥ 10 cm dbh in the 0.5 ha area surveyed in Bealoka forest. Using Principal Component Analysis, three different habitats were identified: the gallery closed-canopy forest, the transitional forest and the scrub habitat. Tree diameter and canopy width were significantly greater in Bealoka. Forest regeneration and survival in Berenty was poorer than in Bealoka. On the other hand, Berenty had higher species diversity. These results might be due to the greater degree of disturbance in Malaza from flooding, human influences and lemur population as well as the early advanced stage of succession. Transitional forests offered the best conditions for forest regeneration thanks to increased light availability due to gaps in canopy cover. Regeneration was obstructed in scrub due to the presence of invasive liana species. We could not discern appreciable differences in plant communities between habitat types, which suggested an overlap of tree species in the different types. This study suggested that these remaining fragments suffer from isolation which may lead to their disappearance if not appropriately conserved.

2.1 Introduction

To fully understand the ecological consequences of the rapid destruction of the tropical forests in general, it is necessary to learn more about their structure and composition (Blumenfeld-Jones et al., 2006; Ganzhorn, 1995; Sauther, 1998b; Sussman and Rakotozafy, 1994). Better conservation priorities can be established by understanding plant diversity, distribution patterns and structural models of the forests (Tomimatsu and Ohara, 2010; Ganzhorn et al., 1997; Reed and Fleagle, 1995). These issues are necessary to comprehend the interactions between animals and its environement in order to seek better conservation practices. For example, the survival for most of the prosimian primates in Madagascar depends mainly on the quality of their typical habitat. Habitat destruction and loss of species diversity threaten largely the diversity of the lemur species (Green and Sussman, 1990; Mittermeier et al., 2010). One of the typical habitats of lemur species in Madagascar is the dry forest in the south and west of the island. These ecosystems are unique and possess an abundance of plant and animals species (Sussman et al., 2006). The dry forests of the south and west in Madagascar, including the deciduous and spiny forests, are considered as the most endangered habitats, and few research has been conducted on them till now (Dirzo and Sussman, 2002; Janzen, 1988; Smith, 1997; Sussman et al., 2006; Sussman et al., 2003).

Berenty and Bealoka reserves are rare remnants of dry semi-deciduous gallery forests in the South of Madagascar (Jolly et al., 2006b; O'Connor, 1987). Berenty reserve has been intensively studied for lemur ecology and social behaviour, particularly in its gallery forest called Malaza (Goodman et al., 2006). Studies on vegetation in Berenty were accomplished by Blumenfeld-Jones (2006), who described different habitat types based on canopy maps. These microhabitats types include: closed canopy tamarind, open Neotina-Tamarind, open Tamarind parkland, open Acacia-scrub, bush and scrub and a small transition spot. Prior to that, three different forest types have been distinguished by qualitative judgments of the extent of canopy cover (Budnitz and Dainis, 1975). Bealoka is a nearby gallery forest, interconnected with Berenty 50 years ago but separated from the latter due to sisal farming. One vegetation study using point quarter sampling was conducted in Bealoka in 1987 (O’Connor, 1987), reporting lower species diversity and reduced plant regeneration in this site, though microhabitat types were not distinguished. In order to update recorded habitat characteristics from a conservation perspective, this study describes and maps the vegetation structure of the different habitats in Berenty and Bealoka forests.

For vegetation studies using a systematic sampling such as transects or quadrants, forest type is often analysed by ordination or classification (Ganzhorn et al., 1997; Sussman and Rakotozafy, 1994). Ordination of vegetation has been performed for the analysis of vegetation that changes continuously according to environmental factors such as canopy, density, or rainfall. This approach generates a classification of forest communities and enables patterns to be detected (Jongman et al., 1995; Økland, 1990) The goal of this study is creating an objective vegetation map by using the scores of principal component analysis. We will also analyse tree density, floristic diversity and regeneration pattern in relation to different habitat types and other forest variables such as canopy coverage, undergrowth and diversity of liana species. We assess the relative importance of these variables to our comparisons of different habitats, in both forests and in other gallery forests in order to determine the conservation priorities for each site (Petrik et al., 2010).

2.2 Methods and study sites

2.2.1 Study site

Please refer to the study sites section in the general introduction for full details.

2.2.2 Data collection

This study was carried out in September and October 2008 and is part of a long-term study on ecological interactions between sympatric lemur species. Data were collected with the assistance of three malagasy students from the Ecole Normale Superieure d'Antananarivo. This study used the belt transect method to describe habitat characteristics (Ganzhorn, 2003; White and Edwards, 2000). Ten belt transects (10 m x 100m each) were set up in Berenty reserve to represent the different habitat types in the site (Figure 2.3a). Five belt transects were located in Bealoka to describe its vegetation structure (Figure 2.3b). Each transect was divided into ten (10 x 10 m) quadrats to facilitate the data collection. Only trees with a diameter greater than or equal to 10 cm dbh (at breast height of 1.3m) were identified and enumerated by this method. We recorded the height of the tree (estimated by eye or by triangulation), tree diameter, canopy width and the bole height (the height of the first branch of the tree). Bole height is a useful way to clarify the forest community structure as each tree species has its own particular structure in each habitat type (Mortelliti et al., 2010). For every quadrat, we also counted the number of young trees (tree with dbh < 10 cm and height ≥ 1m), saplings (1 m > Height ≥ 30 cm). We identified the species of lianas presented in each quadrat, we estimated the percentage of undergrowth (bushes and grasses) occupying each quadrat by visual estimation based on the surface covered. Canopy coverage was estimated using 1 x 1 m imaginary squares every 5 m along the middle of transect (Ganzhorn, 2003). I collected these data to reduce the bias in estimating the canopy cover. Dead trees and dead branches fallen to the ground were counted for each quadrat to evaluate the level of damage in each forest.

2.2.3 Data analysis

We made a systematic census of trees, and used the principal component analysis to differentiate among vegetation types. Principal Components Analysis (PCA) is an ordination technique (Pielou, 1984), which partitions a data set resemblance into a set of orthogonal axes or PCA ‘components’ (Dytham, 2007). The first few PCA components explain the largest percentage of variance in the data set. The ordination of the sampling units describes relationships among environmental variables in order to describe the habitat types and ecological relationships among tree species in different habitat types (Dytham, 2007; McGarigal et al., 2000).

Data were processed into Microsoft Excel and SPSS 17 for statistical analysis (Field, 2005). PCA analysis was conducted to describe the habitat types in both sites. We used each transect as unit of analysis and five variables included tree density, tree species diversity, structural diversity (tree height and tree DBH) and canopy cover to run the PCA. Analyses of these variables on fifteen transects yielded five component factors such that the first two factors combined explained 81% (presented as a cumulative percentage) of the variation in the data. ArcGIS was used to create the vegetation maps of both forests. Data were tested for normality before using parametric statistical tests. We ran a two-way ANOVA to test the differences in ecological variables between the two sites and the different habitat types (Field, 2005; Dytham, 2007). Shannon index was used to measure botanical diversity and calculated using the formula:

Diversity $H' = - \sum^{s}_{i=1} p_i \ln p_i$

where ln = log base n

$$p_i = \frac{N_i}{N_t}$$

s = the number of species, N_i = the number of the trees for each species, N_t = the total number of trees for each species

We assessed the similarity or dissimilarity of species composition between the two sites. The similarity of flora has been expressed in terms of an index of similarity. Sorensen's index (Kent and Coker, 1992) was chosen as it was used in the previous studies of Berenty and Bealoka. Sorensen's index considers theoretically that each species has an equal chance of being present in the two areas (Mueller-Dombois and Ellenberg, 1974; O'Connor, 1987). The index of similarity according to Sorensen, therefore, measures the actual coinciding species that occur in both forests (Mueller-Dombois and Ellenberg, 1974). It is expressed in the following way:

$S_s = C/ [1/2(A+B)]$

Where A = the number of species in Malaza, B = the number of species in Bealoka and C = the number of species in common.

2.3 Results

2.3.1 Site and habitat differences

A total number of 35 tree species were identified from the 837 adult trees recorded in the 15 transects in both sites. We identified 33 species of lianas on all the transects. The first two factors described variables that contributed most to the differences between the habitat types and the two forests. 'Component 1' showed a high positive weighting for tree density, tree height and canopy cover, whereas 'Component 2' gave a high positive weight to "DBH" and a high negative weight to "Plant diversity" (Table 2.1). Visual inspection of the data (Figure 2.1) suggested that Malaza and Bealoka are similar but are slightly different in Component 2 (DBH size and plant diversity). Habitat types (Figure 2.2) are well separated by Component 1, indicating that habitats are differentiated by tree height and density. Ordination by PCA resulted in three main habitat types in Malaza and Bealoka forests: gallery forest, transitional forest and scrub. One more habitat type was distinguished in Malaza forest: the tourist front. This is very similar to the scrub habitat type in terms of component 1 (tree height and density). Based on these results, we created updated maps of Bealoka and Berenty forests showing the different habitat types with detailed transitional zones between them (Figure 2.3).

2.3.2 Patterns of abundance, regeneration and structural diversity

A total of 557 trees ≥ 10 cm dbh were censused in the 1 ha area surveyed in Malaza forest and 280 trees ≥ 10 cm dbh in the 0.5 ha area surveyed in Bealoka forest. In Table I, the relative density of the adult trees ≥ 10 cm dbh is slightly different between both sites and between habitats, particularly for scrub and transitional habitats, though the difference is not statistically significant for either habitats or sites (Site x Habitat effect: two-way ANOVA, $F = 1.19$, $N = 15$, $df = 2$, $P = 0.34$). The density of saplings in Bealoka is double that seen in Malaza forest indicating that regenerative plant growth and survival in Malaza is poorer than in Bealoka (two-way ANOVA, $F = 14.20$, $df = 1$, $N = 15$ transects, $P = 0.004$). However, there is no significant difference in sapling density between habitats although regeneration is low in the scrub habitat found furthest from the river. The survival of saplings, manifested in the density of young trees, is relatively higher in the gallery forests and decreases with distance from the river (Table 2.2). There is a negative correlation between canopy coverage and presence of undergrowth within the different habitat types (Spearman rank-order correlation, 2-tailed, $r = -0.65$, $N = 15$, $P = 0.008$). Conversely, canopy coverage correlates positively with the abundance of saplings and bole height (Spearman correlation, 2-tailed, $r = 0.66$ and $r = 0.77$ respectively, $N=15$, $p = 0.007$ and 0.001 respectively). The canopy coverage does not differ significantly between the two forests (two-way ANOVA, $F = 3.06$, $N = 15$, $df = 1$, $P = 0.11$).

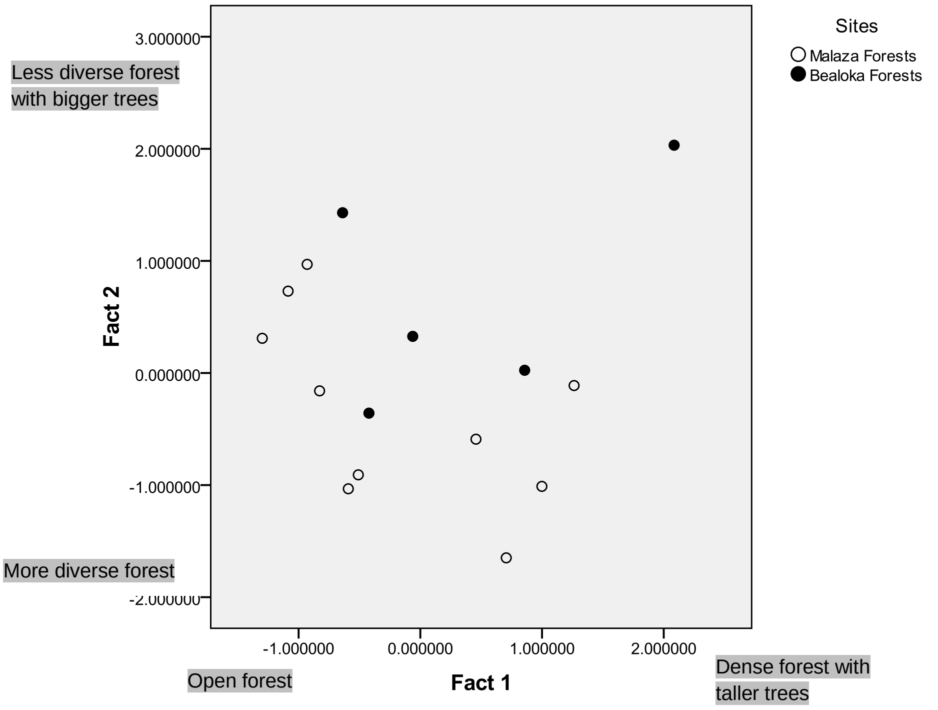


Figure 2.1: Plotting Malaza and Bealoka forests according to their principal components
There is no obvious pattern on axis 1 (tree size diversity and density). On axis 2 (DBH size and plant diversity), the PCA reflects a strong tendency of difference between the two forests in terms of DBH and species diversity, though this is not statistically significant (Site effect: two-way ANOVA, F = 4.613, N = 15, df = 2, P = 0.06). The slight difference in component 2 suggests that Bealoka has somewhat larger DBH and less diversity. The outlining point represents part of the closed gallery forest of Bealoka composed of taller and bigger trees.

Table 2.1 Loadings of two components extracted from principal component analysis of five variables from the transect

Variables	**Loadings of Components/Facts**	
	1	**2**
Tree height	0.835	0.455
Tree density	0.788	-0.237
Canopy cover	0.911	0.202
DBH size	-0.035	0.881
Plant diversity	-0.189	-0.873

When the data from all trees counted in systematic samples are pooled with respect to habitat types and study sites, tree diameter and width of canopy are significantly greater in Bealoka (two-way ANOVA, df = 1, F = 5.15, N = 15, P = 0.04 and F = 18.02, P = 0.002 respectively). The dbh does not differ between habitats in contrast with canopy diameter (two-way ANOVA, F = 8.04, N = 15, df = 2, P = 0.01) which is a lot wider in gallery and transitional forests than in scrub and tourist area. The total canopy cover of the three general habitat types appears qualitatively different with more than 50% coverage in gallery closed canopy area and less than 20% coverage in driest habitat (two-way ANOVA, F = 19.21, N = 15 transects, df =2, P = 0.001). There is a high degree of variance in the height of adult trees in the different habitats (two-way ANOVA, F = 8.61, N = 15, df = 2, P = 0.008). Trees in scrub are much shorter (6.6m ± 4.8) (Table 2.3). Mean bole height in the gallery forests is higher than in scrub and transitional forests (two-way ANOVA, F = 4.90, N = 15, df =2, P = 0.03) (Table 2.2).

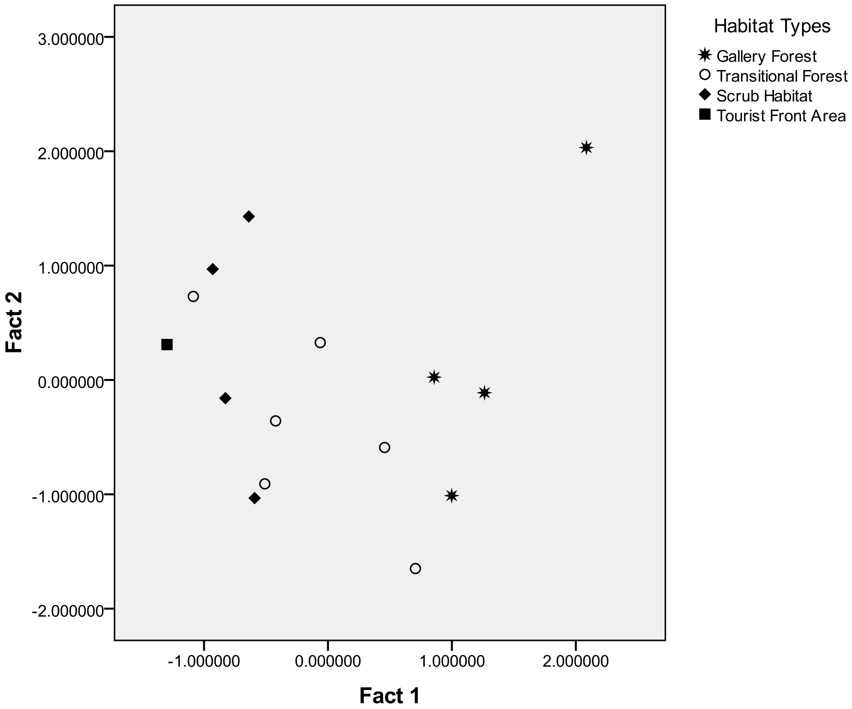
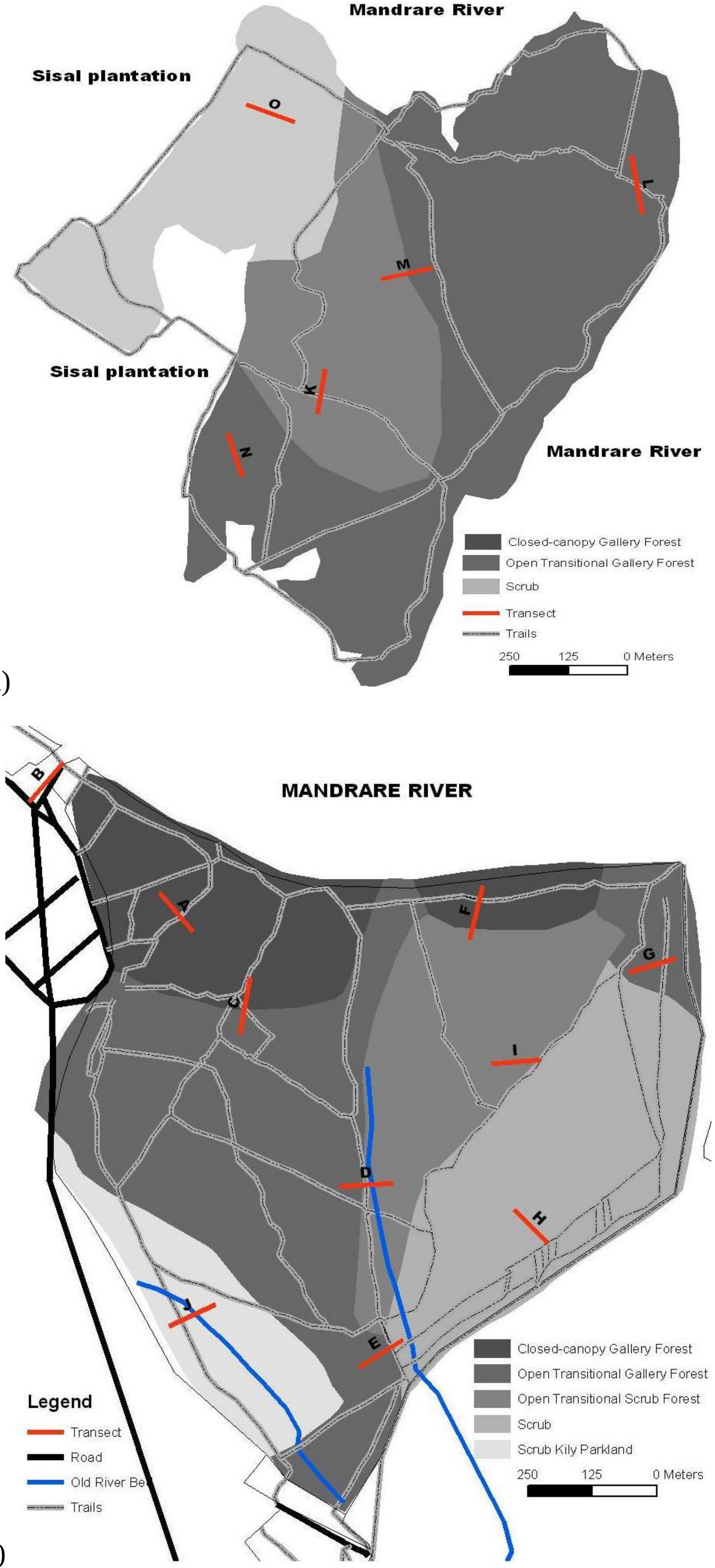


Figure 2.2: Plotting habitat types according to their principal components
This figure provides the evidence of two disticnt habitats in both forests: gallery and scrub linked by the transitional forest. The tourist area is similar to the scrub habitat. This division is shown on component 1 which combines tree density, tree height and canopy cover. These variables show highly significant differences between the four habitats (Habitat effect: two-way ANOVA F = 8.85, N = 15, df = 3, P = 0.006). The tourist front area exists only in Malaza.



a)

b)

Figure 2.3. Vegetation maps (a) Bealoka and (b) Malaza forests.

Table 2.2 Tree densities (total number of individuals), species diversity, undergrowth and canopy cover percentages in different habitats in Malaza and Bealoka forests

	Malaza forest				Bealoka forest		
	Gallery	Transitional	Scrub	Tourist area	Gallery	Transitional	Scrub
Plot size sampled (ha)	0.2	0.4	0.3	0.1	0.2	0.2	0.1
Number of adult trees	145	228	148	32	131	86	63
Number of young trees	1380	1313	537	53	1241	273	221
Number of saplings	322	1005	367	161	603	1211	351
Number of tree species	10	21	19	9	11	12	5
Number of liana species	8	14	13	1	7	12	13
Undergrowth %	0	28	54	10	0	69	43
Canopy cover %	60	27	20	2	90	30	12

Table 2.3 List of tree species enumerated in each habitat type.

Scientific name	Density/ha	Canopy diameter (m)	Height (m)	Bole height (m)	RBA %
a) Closed-canopy Gallery Forest					
Tamarindus indica	25	14.5±7.9	20.4±4.4	4.7±1.9	27.8
Albizzia polyphilla	8	9.3±5.2	13.1±4.1	3.8±2.5	23.1
Acacia rovumea	10	13 ±8.7	16.4±4.9	5.5±4.2	17.9
Cordia caffra	10	5.2±2.2	11.2±2.6	3.5±2.4	8.8
Crateva excelsa	45	3.9±0.1	8.9±0.0	3.6±1	3.2
Antherospermum	3	9.0	8.0	2.0	3.0
Grewia sp.	3	5.0	6.5	0.2	2.4
Rinorea greveana	370	4.2±0.8	8.8±2	3±1.5	2.3
Celtis phillippensis	113	4.7±0.8	10±1.6	4.6±1.4	2.1
Hazuntha modesta	3	5.2	5.4	0.0	1.5
Celtis bifida	75	3.3±0.2	10.4±0.1	5.9±1.2	1.4
Azima tetracantha	18	6.3±1.7	4.8±1.9	0.3±1	1.3
Neotina isoneura	3	3.0	10.0	2.1	1.1
Lawsonia sp.	15	5.3±2.3	8.1±4.1	1.4±1.5	0.8
b) Open-canopy Transitional Forest					
Tamarindus indica	38	12±1.7	15.5±1.6	2.6±1.8	23.3
Acacia rovumea	15	9±1.8	13.2±1.8	3±1.9	10.9
Azima tetracantha	53	4.8±1.1	4.2±1.1	0.5±0.5	6.9
Ximenia perrieri	5	4.5±0.1	4.0±5.0	0.3±0.3	6.3
Quisiviante papinea	3	7±2.8	14.1±4.1	4.2±1.2	5.6
Rinorea greveana	168	3.7±0.7	6.5±2.	1.3±0.9	5.0
Neotina isoneura	22	5.1±2	10.7±4.8	2.9±2.2	4.9
Albizia polyphilla	5	6.5±0.7	9.7±11.0	3.9±0.8	4.9

Scientific name	Density/ha	Canopy diameter (m)	Height (m)	Bole heigth(m)	RBA %
Unidentified sp. 1	2	4.0	6.8	0.1	4.7
Flacourtia ramantalu	2	6.2	6.0	0.0	2.9
Commiphora trifolii	3	5±2.8	5.7±4.8	1.3±1.7	2.6
Tina sp.	2	4.0	5.0	0.4	2.5
Cordia caffra	2	7.0	8.5	4.0	2.4
Opuntia vulgaris	5	0.8±1.0	3.0±1.2	0.2±0.5	2.3
Crateva excelsa	43	37±0.5	7.3±2.4	2.8±2.3	1.9
Grewia sp.	18	4.0	8.0	0.3	1.9
Strichnos madagascariensis	13	2.8±1.3	5.1±3.0	0.6±0.8	1.8
Hazonta modesta	7	4.4±0.8	4.7±1.4	0.4±0.3	1.8
Euphorbia stenoclada	43	3.4±1.0	3.3±2.4	1.0±0.5	1.8
Celtis bifida	17	3±1.6	8±3.8	3±2.8	1.7
Euphorbia leucodendron	12	4.0±0.3	6.1±1.1	2.9±0.8	1.4
Celtis phillippensis	37	3.5±0.8	9.6±1.8	3.9±2.2	1.3
Euphorbia encoclada	8	3.4±0.5	6.7±0.7	2.1±0.4	1.1
c) Scrub					
Tamarindus indica	25	16.3±1.9	22.3±6.8	2.7±0.7	37.8
Acacia rovumea	8	4.9±3	14.3±1.1	4.7±5.4	9.6
Salvadora angustifolia	23	4.7±0.6	4.7±1.2	0.8±0.8	6.8
Quisiviante papinea	8	4.2±0.2	11.5±0.7	1.1±1.4	6.2
Talinella grevei	23	4.9±2.4	3.5±1.7	0.1	6.1
Azima tetracantha	183	3±1.3	3.2±1.1	2.3±3.6	5.2
Celtis bifida	3	1.0	5.0	0.4	3.6
Alluaudia procera	48	2.3±1.0	9.5±2.5	3.0±1.1	3.5
Rinorea greveana	8	1.9±0.5	4.5±0.7	0.2±0.2	3.0
Anterospermum sp	3	5.0	4.2	0.3	2.5
Grewia sp.	4	3.0	5.0	0.5	1.9
Commiphora trifolii	50	3.2±0.3	6.4±0.4	1.1±0.5	1.8
Ximenia perrieri	8	4.1±0.1	3.8±5.0	0.4±0.3	1.8
Croton meridionalis	13	1.9	3.7	0.2	1.6
Euphorbia leucondendron	28	3.5±1.3	5.3±1.3	2.1±0.6	1.5
Urera sp.	13	1.9	3.2	3.8	1.4
Cadaba virgata	8	1.5±1.6	1.8±2.0	0.1±0.5	1.4
Strichnos madagascariensis	8	2.5±0.9	5.2±1.8	1.0±0.4	1.2
Marytenus fasciculata	3	2.5	2.5	0.3	1.2
d) Tourist Area					
Pithecelobium dulce	90	7.2	9.2	0.5	45.8
Albizia polyphilla	20	7.0	11.3	0.4	16.4
Azadirachta indica	20	3.6	5.6	0.3	9.8

Scientific name	Density/ha	Canopy diameter (m)	Height (m)	Bole heigth(m)	RBA %
Salvadora angustifolia	30	3.8	7.1	0.2	9.8
Rinorea greveana	30	2.3	3.0	0.2	8.0
Fernandoa madagascariensis	100	2.5	6.0	1.2	3.1
Acacia rouvinae	10	7.2	15.0	2.1	2.5
Euphorbia leucodendron	10	2.3	2.5	0.1	2.5
Tamarindus indica	10	2.0	5.0	0.1	2.2

RBA (%): relative basal area. Tree species are listed in the order of RBA. Measurements of canopy diameter, height and bole height are shown by the means with their standard deviation.

In table 2.3, emergent trees over 20m in height are rare and only seen in a few tree species, such as Tamarindus indica, Albizzia polyphila and Acacia rovumea. These species form the upper canopy and are fully deciduous whereas the lower canopy (or middle stratum) includes evergreen species such as Neotina isoneura and Azima tetracantha. Tamarindus indica is the most dominant tree species with the largest total basal area in all three habitats, except in the tourist area in Berenty Malaza where the introduced Pithecelobium dulce constitutes the most dominant tree species. The most abundant tree species in both gallery and transitional forests is Rinorea greveana. Azima tetracantha is most abundant in scrub.

2.3.3 Species diversity and similarity between sites

The tree species diversity of Malaza and Bealoka, as expressed by the Shannon Diversity Index H’ (1.8 and 1.3 respectively) is statistically different, showing that the flora in Berenty is more diverse than that of Bealoka (two-way ANOVA, F = 6.45, N = 15, P = 0.03). We could not discern appreciable difference between habitat types, which suggests an overlap of tree species diversity in the different habitat types (Table 2.3). There is an apparent slight difference between the liana species in the different habitats, but this is not statistically significant, and liana diversity did not differ between the two forests. Sorensen’s index is used to express the similarity of flora between the two locations. The I_s for plant species community in Malaza and Bealoka from the systematic samples is 55.3%.

2.4 Discussion

2.4.1 Habitat types and plant communities in Berenty and Bealoka forests

Our findings describe four habitats from closed-canopy gallery forest along the river bank to dried scrub habitat further from the river and the tourist area. Earlier studies show similar patterns. Blumenfeld-Jones (2006) classified vegetation types in Malaza using canopy maps and described plant species communities by recording data along forest trails. Neotina isoneura can be classified as a transitional forest species due to its high density in transitional scrub compared to the other habitats; Acacia rovumea has similar density in gallery and transitional forest (Table 2.3). Tamarindus indica is confirmed as conspicuous component of both forests, due to the large canopy width of its trees (Table 2.3). Higher density of this species was seen in the transitional forest which constitutes half of the Malaza forest surface area. Lower density was seen in the scrub except in the tamarind parkland. Similar plant communities are found in Beza Mahafaly, another remnant gallery forest (Sussman et al., 2006). In comparison with Beza Mahafaly (Sussman and Rakotozafy, 1994), Malaza and Bealoka have relatively low tree density and tree species richness (trees ≥10 cm dbh). Tree densities in both forests are similar with those found in studies of dry tropical forests elsewhere in Africa as well as in neotropical wet forests, although the Malaza and Bealoka forests have lower species diversity (Gentry, 1988; Gentry, 1993; Webb and Peart, 2000).

Our study suggests that bigger transects strips can generate better vegetation data such as floristic composition and forest structure than tree species census by counting and identifying trees on both sides along forest trails (Ganzhorn, 2003; Hashimoto et al., 1999). As canopy coverage was demonstrated by the PCA to be one of the key ecological factors in habitat characterization, canopy mapping should also be considered as an important method in this field. It is also an important factor in hot dry climate allowing for preserved soil moisture and less stress on undergrowth plants (Zanne and Chapman, 2005).

2.4.2 Adaptation and regeneration

Remnants of gallery forests such as Malaza and Bealoka are part of the typical vegetation historically occurring along major rivers in the south of Madagascar

(Blumenfeld-Jones et al., 2006; Sauther et al., 1999; Sussman and Rakotozafy, 1994). These are considered as valuable natural resources and a number of animal and plant species depend on them for their survival (Hughes, 1988). Malaza and Bealoka are fragmented forests whose flora and fauna have remained relatively intact. They were connected less than fifty years ago (O'Connor, 1987), suggesting that differences between them discovered in this study are due to environmental changes or are human-induced. Other factors such as local edaphic variation and the level of the water table may also influence the direction of changes.

All of the trees less than 10 cm dbh, regardless of their height and their species, are considered forest regeneration in this study. They constitute an essential part of the forest community structure. Prior to 1984, seedling survival and growth in Bealoka was poorer compared to Malaza due to livestock herbivory, overgrazing and human disturbances prior to 1984 (O'Connor, 1987). This contrasts with the findings of this study, in which Bealoka appeared to have much higher recruitment of saplings, especially in gallery and transitional forests (Table 2.1). As Bealoka has been protected from human disturbance since 1985 and no serious management has been implemented in the site, perhaps our study results reflect the reappearance of natural regeneration processes following protection. That said, small-scale goat-browsing and firewood collection are still ongoing in Bealoka and people are using the trails in the forest as a shortcut to bring cattle to the Mandrare River to drink. This activity may lead to further fragmentation of this forest due to human and livestock disturbance. Levels of recruitment in Berenty may also have changed since 1987, because the forest is being eroded by the inside bend of the Mandrare River (Jolly pers. comm., Razafindramanana, pers. obs.), as the water flow is undercutting the bank and washing away rather than depositing soil and minerals, a condition which is not favourable for seedling survival in the gallery forest. Also, variations in the water table are likely to influence the vegetation (Mertl-Millhollen et al., 2006). The extent of a complex groundwater supply may differ between the sites. The water table supply may be present for all seasons in Bealoka whereas this may not be the case for Berenty particularly during dry season (Mertl-Millhollen and Jolly, pers. comm.). More research is needed on this.

The highest rates of recruitment in Berenty occur in the transitional forest, which also appears to be the good spot for forest regeneration in terms of growth and survival as shown by density of saplings and young trees. This confirms Sussman (1994), who reports that regeneration is much denser in drier habitat rather than in wet soil. Along with the more stable water table level and soil, the increased light availability due to gaps in canopy cover allows for improved germination, growth and survival (Schnell, 1971). This proved that forest regeneration does not only occur in the lower river bank (Blumenfeld-Jones et al., 2006) but indeed in transitional gallery forests. However, regeneration in scrub is low due to the lack of water and the likely lower level of water table. Gaps in the canopy are also important in rainforest communities in maintaining regeneration and forest structure (Putz and Milton, 1982). Yet, despite the open canopy, there is relative paucity of regeneration in the Malaza scrub. This can be explained by the presence of two species of lianas: Cissus quandragularis and Capparis sepiaria which obstructs this process of regeneration.

Malaza has been far more affected by human management than Bealoka (at least since 1980 for Bealoka) over the last four decades, with a high degree of tourism and research as well as introduction of exotic tree species (Jolly et al., 2006b; Rambeloarivony, 2009). This may explain the relatively greater tree density in Bealoka compared to Malaza as the level of human disturbance has been shown to reduce tree density. We also should report the high density of lemur populations in Berenty reserve (Razafindramanana, 2007), that may also negatively affect regeneration there. Overall, regeneration is a complex variable as it is known to be affected by fire (Schnell, 1971), intra- and interspecific competition, predators and seed-dispersers (Ganzhorn et al., 1999; Opler et al., 1980). In addition, all of these factors can be affected by different processes such as human activities or natural phenomena, such as storm damage. Conservation of Malaza forest will require reforestation in the transitional forest as well as stabilizing the lower riverbank from erosion.

2.4.3 Species richness pattern: towards extinction or conservation?

Species richness and composition of plant communities can be discussed from either an evolutionary or ecological point of view (e.g., Ganzhorn et al., 1997; Hanley et al., 2007; Petrik et al., 2010). Here, the evolutionary histories of plants in Berenty Malaza and Bealoka forests are assumed to have been similar because of the proximity of the forests. Thus, variation in plant diversity is most likely due to ecological factors, either recent or historical. In Malaza, 55 species of plant were identified during this study, whilst 39 species were found in Bealoka. Twenty-six plant species are common to both sites: 16 tree species and 10 liana species (Appendice 1). More than 100 tree species were known from Malaza and Bealoka (O'Connor, 1987; Simmen et al., 2006b). However, only 32 and 19 species of tree were counted within our study transects in Malaza and Bealoka respectively. This discrepancy is partly due to the rarity of many tree species with only one or two individuals occurring in the whole forest and partly because some tree species did not reach the sampling limit of 10cm diameter.

Pattern of species diversity could be affected by environmental biotic and abiotic factors and even the process of data collection (Petrick et al., 2010). Even though we could not demonstrate the difference in species richness in different habitats, which is reported to be greater in drier habitat at Beza Mahafaly (Sussman, 1994), our evidence shows that Berenty is more diverse than Bealoka. It has been reported that species diversity is associated with the level of disturbance (O’Connor, 1987), i.e. those at earlier stages in succession have higher species diversity. This would match the fact that secondary succession in Malaza is more advanced than in Bealoka. Disturbance has also been seen to increase forest productivity elsewhere in Madagascar (Ganzhorn et al., 1997). Nevertheless, Bealoka’s actual succession has more large trees and canopy crowns than Malaza. This suggests a slight trade-off between both forests: The forest is more diverse where smaller and denser stems are present.

This pattern may be also tied up with the history, structure and composition of late successional forests with a component of secondary growth. The difference of species richness in both forests is linked with the natural variation in environmental conditions that a distance of seven km causes, and that the natural history of the forests is very different from each other. The theory of “peninsular effect” (Stiling, 2001) can also describe the species diversity in the two locations: A larger area that can support bigger population contains more species. Bealoka suffers from severe fragmentation; however, Malaza is interconnected with the Analamarangy and Kaleta forest complex. This has made the negative effects of forest isolation more severe in Bealoka (e.g., Tallmon and Mills, 2003). The extent of this effect might include faster extinction rates in the smaller and isolated forest of Bealoka, a reason for the lack of regeneration of major canopy trees in the Tana River Forest of Kenya (Hughes, 1988).

There is a geographical difference between Malaza and Bealoka in terms of flooding patterns, whereas soil properties are similar at both sites (soil composition analysis has done by O'Connor in 1987). Soil properties have been shown to influence tree species richness (e.g., Laughlin, 2007; Weiher, 2003). Although soils appear similar, the alluvial deposits are different: floods bringing nutrient rich sediments would inundate Malaza forest quicker than Bealoka. The proximity of the river differentiates the water table and sedimentation history as well. This raises the issue as to whether the high regeneration of young plants and undergrowth in Bealoka is only a short-term development of rebound from the cessation of grazing 25 years ago. In addition, smaller and more fragmented plant populations exhibit lower reproductive success (Tomimatsu and Ohara, 2010). Overall, complete protection of vegetation from disturbances and degradation can lead to a uniform and floristically poor environment (Stuart et al., 1990; Stiling, 2001), although heavy disturbances can have the same result. In conclusion, the desired long-term effect of conservation and management should be considered before manipulating forest environments.

3. Population composition and distribution of brown and ring-tailed lemurs at Berenty reserve.

Abstract

In this paper, I report on the population structure and distribution of native ring-tailed (Lemur catta) and introduced brown lemurs (Eulemur rufus x E. collaris) at Berenty reserve, Madagascar. Population data from 2005 to 2009 were recorded using a complete and direct census of all troops of ring-tailed and brown lemurs within the reserve. Group size, birth rate, sex ratio and juvenile recruitments were analyzed per species and per habitat. The distribution patterns of brown and ring-tailed lemurs at Berenty reserve were evaluated using the locations recorded for each group sighting. These data were then plotted into ArcGIS program and were analysed spatially. Brown lemur population in Malaza forest increased till 2006, giving a density of 683 individuals/ km^2 in gallery and 258 individuals /km^2 in the scrub. The population started decreasing in 2007 when water provisioning in the forest was stopped. This decrease was considerable in scrub. Fluctuations have been seen in ring-tailed population though it was described as stable. Decrease coincided particularly with the post-drought seasons but the population recovered slowly the years afterwards. The density of ring-tailed lemurs from 2006-9 averaged 108 individuals/km^2 in gallery and 177 in scrub. The presence or absence of water provisioning did not affect the growth or the decrease of this population in different habitats. In gallery habitat, brown lemurs had larger groups (9 individuals, range between 4-15) compared to ring-tailed (6 individuals, range between 4-9). Brown lemur troop density in gallery forest increased from 23 to 36 troops within 5 years. Nevertheless, this high density did not affect the groups of ring-tailed lemurs which remained stable. The sex-ratio of both species in different habitats was similar except in Ankoba where theh number of ring-tailed females in troops was higher. There was a significant higher recruitment in brown lemurs compared to ring-tailed lemurs. GIS analysis of the distribution of ring-tailed lemur population at Berenty reserve in 1995 showed that this population lived in closed canopy habitat. By 2006, ring-tailed lemur distribution had moved into the periphery of the reserve and the scrubby places where their density became higher with a stable group size. Once the water provisioning was stopped in 2007, the distribution of both species changed. Ring-tailed lemurs were then displaced into the marginal habitat and the very scrubby places where they conduct most of their vital activities such as feeding and resting, however, brown lemurs occupied the closed canopy forest in Berenty reserve. This separation was maintained during 2009 and may affect the long-term viability of the closed canopy forest and the ring-tailed population.

3.1 Introduction

Spatial distribution and population composition are a crucial part of the social organization of gregarious primates (Atsalis, 2000; Sussman, 1999). Assessing density and distribution are also important parameters for conservation biology and community ecology (Cowlishaw and Dunbar, 2000; Ganzhorn et al., 1999) and estimating the density of even one species of lemur can predict the overall ecological space exploited by a lemur community (Reed and Fleagle, 1995). There have been extensive studies of the population dynamics of different species of lemur and the factors influencing their population growth (Erhart and Overdorff, 2008; Gould et al., 1999; Gould et al., 2003; Jolly et al., 1982a; Jolly et al., 1982b; Lehman et al., 2006), and many studies on social patterns of ring-tailed lemurs in Berenty have been published (e.g., Jolly et al., 2002; Jolly et al., 1982a; Jolly and pride, 1999; Mertl-Millhollen et al., 1979). However few population studies have been done on the introduced brown lemurs (Eulemur rufus X Eulemur collaris) (Jolly et al., 1982b; Pinkus, 2004). The present study describes the interactions between native ring-tailed and introduced brown lemurs in terms of population growth and spatial distribution for long-term conservation and forest management purposes.

Both ring-tailed and brown lemurs occur in natural sympatry (Sussman, 1972; 1974). Although, these species have similar life histories, morphology, reproductive biology and seasonality, gestation period and juvenile development (Pereira, 1993; Sussman, 1972); the only known study on both species in the wild by Sussman (1974) described high interspecific differences in terms of population structure, diet and habitat utilization. This has also been confirmed by Ganzhorn (1985, 1986) in his behavioural study on these species in large enclosures at Duke Primate Center. In Berenty Reserve, ring-tailed population size and troop ranges remained stable from 1963 till 1980 (Jolly et al., 1982b; Jolly and pride, 1999; Mertl-Millhollen et al., 1979). However, this stability was disrupted by the introduction of brown lemurs (Jolly et al., 1982b) as well as the loss of habitat quality (Blumenfeld-Jones et al., 2006; Mertl-Millhollen et al., 2006). Though the number of brown lemurs has been increasing since 1998 when water provisioning was first introduced to Malaza forest, the number of ring-tailed lemurs within the population prior to 2000 did not decrease (Pinkus, 2004). But some evidence points to the presence of either seasonal or permanent home range shifts in both species, and fluctuations in population composition may be influenced by the interactions between them. Here we analyse the changes in population density, group size, sex-ratio and juvenile recruitment of both lemur species. We describe the interactions between both species in terms of density and spatial distribution. Previous data till 2000 are combined with our data from 2005-2009 to analyse the evolution of the interactions in social organization of both species.

3.2 Methods

3.2.1 Study site

Berenty lies in subdesert southeastern region of Madagascar, where the water table around the Mandrare River maintains the presence of the forest. Berenty is connected with a parcel of degraded forest in the North-East, and both forests are bounded on one side by the Mandrare River and on the three sides by sisal plantations (Jolly et al., 2006b). The detailed description of the study can be seen in the general introduction and in chapter two. The data used in this study were collected from the different habitats in Berenty which are consistent with other demographic studies on ring-tailed and brown lemurs at Berenty (Jolly et al., 2002; Jolly et al., 1982b). This delineating of habitat allows describing the differing spatial arrangements of both lemur species' home ranges.

3.2.2 Census procedures

Complete censuses of ring-tailed lemurs have been conducted by different researchers in Berenty (included gallery forest, scrub and tourist front). The details are presented in table 3.1. I conducted the censuses in 2006-2009 with Jolly and three student assistants within the three habitats of front, gallery and scrub and the Ankoba part. Transitional gallery was grouped with gallery, and transitional scrub with scrub. These censuses followed the methods described by Jolly et al. (2002) where observers walked along trails and transects between trails until they had accounted for all known ring-tailed troops and discovered any unknown troops. It has been reported by Jolly et al. (2002), Mertl-Millhollen (1979), Jolly and Pride (1999) that ring-tailed lemurs in Berenty maintained similar identical home range boundaries over decades and females are individually recognizable and remain in their troops, which makes the direct census easier. New troops resulted from fission of known troops and usually range within or adjacent to the source troop's home range (Jolly and Pride, 1999). The small size of Berenty, the familiarity with the population over decades and the repeated census allow complete censuses. Both ring-tailed and brown lemurs' censuses took place in October and November every year. A complete census for each species took 230 hours per person for four persons.

Complete censuses of brown lemurs at Berenty were performed in 1985 by O'Connor (1987), in 1991 (Davidson, unpublished data) and five censuses between1993-2000 by Pinkus (2004). The censuses in 2005-9 were conducted by myself and Pinkus with the assistance of students assistants, in the whole Berenty reserve (See Table 3.2 for details). The method followed Pinkus (2004), which was adapted from that used to census ring-tailed lemurs. It consists in walking along trails and watching branches and canopies to locate brown lemurs' troops. The area was divided into 4 ha sections where observers walked through it off trail searching for troops. Observations were conducted during the morning and the afternoon peaks of lemur activity. During the period when water basins were still present, observers visited every water points at least every 2 days and spent at least one hour of different period of day watching troops coming to the troughs. After water provisioning was stopped in 2007, sections were divided into smaller areas (2-3ha) to intensify troop search. When observers encountered a troop, they identified it and recorded the location, the habitat type, the age, the sex composition and the number of visible troop members. The first time the troop was sighted, we described 3-4 of troop members by using facial sketches as well as noting distinctive characteristics such as missing limbs or tails, unusual pelage colouration, notched ears or facial scars. Because ranges of brown lemur troops overlap more than ring-tailed lemurs and are less predictable mainly during birth season (Pinkus, 2004; Sussman, 1974); we used black dye-mark on one or two members of the group, either juvenile, adult males or non-lactating females. The dye remained visible for 10-14 weeks. This approach ensured that troop was neither missed nor counted twice. We considered a troop count to be complete when the same age and sex composition were recorded for at least four consecutive independent sightings.

Table 3.1 Previous surveys of ring-tailed lemurs at Berenty reserve

Month	Year	Surveyors	Methods
	1972	Budnitz and Dainis	Full census of all ring-tailed lemur groups in the reserve by walking along trails and transects between trails
	1973		
	1979	Mertl-Millhollen	
September-October	1983	O'Connor	
	1984		
	1985		
October-November	1989 - 2005	Jolly et al.	
October- November	2006	Jolly and Razafindramanana	
October-November	2007 - 2009	Razafindramanana et al.	

Table 3.2 Previous surveys of hybrid brown lemurs at Berenty reserve

Month	Year	Surveyors	Methods
September-October	1985	O'Connor	Complete census of all brown lemur groups in the reserve by walking along trails and transects or forest sections
	1991	Davidson	
August-September	1993	Pinkus et al.	
	1994		
	1996		
	1998		
	2000		
August	2005	Pinkus and Razafindramanana	
October-November	2006 - 2009	Razafindramanana et al.	

3.2.3 Data analysis

The population density was presented as the total of non-infant individuals censused for each species in each habitat. Group size, birth rate, sex ratio and juvenile recruitments were analyzed per species and per habitat. Jolly et al. (2002) and Pinkus (2004) have described the relationship of ring-tailed and brown lemur populations to habitat type. These data have been re-analysed with our five year records and considering the annual census as independent. This was to show the evolution of both lemur population dynamics at Berenty reserve. Data on group size, birth rate and sex ratio was not available from the previous studies on brown lemurs. Data were tested for normality before using parametric statistical tests. Two-way analysis of variance (ANOVA) (Field, 2005) was used to test differences between species population among habitats and water provisioning factor. One-way ANOVA was used to analyse the differences between population size in different habitats. I used two-sample t-test (Dytham, 2007), to compare juvenile recruitment between species and among habitats. Pearson’s product-moment correlation was performed to analyse the density-dependence of the juvenile recruitment in relation to the population size in different habitats after testing the pattern with linear regression. Mean juvenile recruitment was also explained as a function of drought and post-drought years.

To analyse the distribution patterns of brown and ring-tailed lemurs at Berenty reserve, the locations data recorded for each group sighting were plotted into arcGIS program and were analysed spatially using kernel density. Each troop of brown and ring-tailed lemurs was assigned to a habitat type in order to examine the relationship between habitat type and lemur population composition. These habitat categories reflect late dry season home ranges. Dry season home ranges are likely similar to wet home range for ring-tailed lemurs (Jolly and Pride, 1999). However, brown lemurs vary their range use considerably among seasons (Overdorff, 1993; 1996). To classify ring-tailed lemur troops, Jolly’s habitat classifications was used, that based on the location of the troop’s home range and primary feeding and resting sites during opportunistic sightings and 12-hour follows (Jolly et al., 2002). For brown lemurs, home range was estimated using grid squares of Berenty maps or GPS, in which the troop was sighted during the census. An average of 6 sightings per group (range 1-10) was collected, in which, each group were followed throughout an entire activity period for 2-3 sightings in order to get location data of the group’s home range. These data were analysed with kernel density on arcGIS to show the spatial distribution occupied by both lemur species in Berenty reserve. All the groups sighted once only were excluded from analyses. The habitat type that brown lemurs occupied was assigned in at least 75% of sightings. If not, the habitat type was assigned as the place where the group fed and rested (Pinkus, 2004). Troops ranging in transitional scrub habitat were grouped with scrub troops and those ranging in transitional gallery were combined with gallery troops.

3.3 Results

3.3.1 Population density

Figure 3.1 shows the dynamic of brown and ring-tailed lemurs' population at Berenty reserve. Brown lemurs started ranging in the scrub in 1991 when water basins were implanted in the site. The population in Malaza forest increased till 2006, giving a density of 683 individuals/ km^2 in gallery and 258 individuals /km^2 in the scrub. The numbers started decreasing in 2007 when water provisioning in the forest was stopped. This decrease was considerable in scrub (132 individuals/ km^2) with a significant higher growth in gallery (884 individuals/ km^2) (2-sample t-test, n=13 years, P = 0.000) and in Ankoba forest (498 individuals/ km^2); though the overall population has decreased in general. The difference in density of brown lemur populations in different habitats is significantly different (F = 16.86, n=11 years, df = 1, P = 0.001). When water provisioning was abolished, brown lemur population became higher in gallery forest and lower in scrub (F = 11.64, n=11 years, df = 2, P = 0.003).

In contrast to brown lemurs, fluctuations have been seen in the ring-tailed population though it was described as stable (Jolly et al., 2002). Decrease coincided particularly with the post-drought years but the population recovered slowly in the years afterwards. The total non infant population of ring-tailed lemurs in Malaza started from 155 in 1975 (Mertl-Millhollen et al., 1979) and rose to 293 in 2005 where it started to decrease in both Ankoba and Malaza. By 2008, the density of population in the gallery and the scrub decreased to 84 individuals/km^2 and 450 individuals/km^2 respectively. In spite of these considerable decreases, population in the tourist front and Ankoba remains higher than in gallery and scrub (F = 14.80, n=13 years, df = 1, P = 0.000) and that the presence or absence of water provisioning did not affect the growth or the decrease of this population in different habitats (F = 15.73, n=13, df = 2, P = 0.000). In 2009, the population rose again in Ankoba, srcub and gallery habitats while it decreased in the tourist front (280 individuals/km^2).

Concerning interactions between brown and ring-tailed population, the brown lemur population does not affect negatively the population of ring-tailed lemur in a whole or vice-versa (Pearson's Product Moment Correlation, n=11 years, r = 0.09, P = 0.07), which indicates that both species could grow normally together without negative influence to each other. Data from 2005-9 shows that the populations in scrub have changed independently from each other (Pearson’s Product Moment Correlation, n=5 years, r = - 0.54,P = 0.05). In gallery, the high density of brown lemurs did not correlate with the decrease in the population of ring-tailed lemurs (Pearson’s Product Moment Correlation, n=5 years, r = - 0.67, P = 0.09).

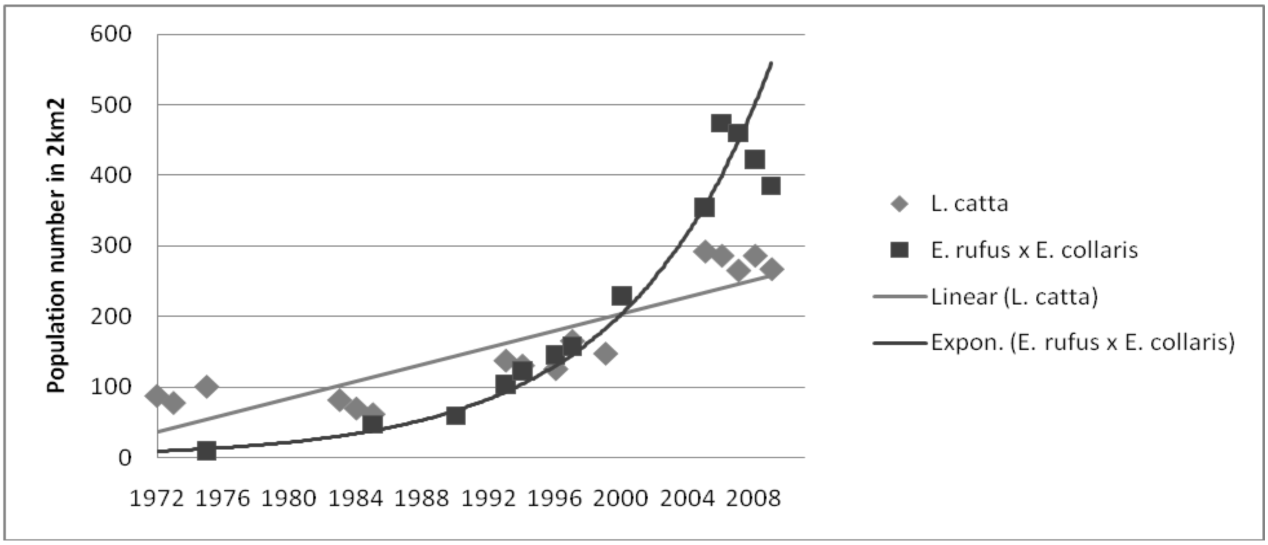


Figure 3.1: Population dynamic of brown and ring-tailed lemurs at Berenty reserve from 1972 to 2009

Data on ring-tailed lemurs from 1972-2005 was from Courtesy of Alison Jolly, data on brown lemurs from 1983-2000 was from Courtesy of Susan Pinkus.

3.3.2 Group size and sex-ratio

Changes in group sizes, sex-ratio and group adult females of brown and ring-tailed lemurs are shown respectively in table 3.3 and 3.4. Table 3.3 suggests that the difference is most marked in gallery, brown lemurs live with larger group of 9 individuals (range between 4-15) compared to ring-tailed with 6 individuals (range between 4-9) (2-sample t-test, n=5 years for brown lemurs and 4 years for ring-tailed lemurs, 2-tailed, P = 0.001). In the other habitats, troop size and number of females is quite similar, or actually higher for Lemur catta in Ankoba.

Brown lemur troop density in gallery increased from 23 to 36 troops within 5 years, due to the movement of groups from scrub to the gallery due to the absence of water provisioning from 2007. High recruitment within the brown lemur population and immigration of groups from Analamarangy forest favoured the high density of this species in gallery. Nevertheless, this high density did not affect the groups of ring-tailed lemurs which remained stable. There is a decrease of brown lemur troops in scrub after the removal of water troughs; however ring-tailed lemurs showed a stable trend. Both species have higher density of population in Ankoba with similar troop size. Even though the Tourist Front has been described as the richest habitat in Berenty (Jolly et al., 2002), ring-tailed lemur population there has decreased since 2006, though they remain composed of the largest troops of females in all Berenty. Change in size of adult female population from one year to the next is noticeable in brown lemurs living in gallery forest where the population is higher. Fluctuations in Ankoba ring-tailed lemurs were synchronous with fluctuations in Tourist Front.

Sex-ratio of both species in different habitats is similar except in Ankoba where there is high number of ring-tailed females in troops (2-sample t-test, n=9, 2-tailed, P = 0.02). There was no significant difference between brown lemur sex-ratios in paired habitats for any census year (paired t-test, n=5, 2-tailed, P = 0.08). Since female brown lemurs tend to remain in their natal troop, it is likely that entire troops moved between different habitats.

3.3.3 Juvenile recruitment of brown and ring-tailed lemurs

Juvenile recruitment (number of one year old per adult female) incorporates both fecundity and survival of infants from birth to 1 year old. It fluctuated from year to year for both species but varied less among years for brown lemurs (Figure 3.2). Even though the coefficient of variation of juvenile recruitment was similar for both species, there was a significant higher recruitment in brown lemurs compared to ring-tailed (2-sample t-test, n=17 for ring-tailed lemurs and 11 for brown lemurs, P = .031). Recruitment in the two species did not vary synchronously. Mean juvenile recruitment by ring-tailed lemurs from 2005-9 varied between habitats, though it is not significantly different (F = 2.68, n=20, 2-tailed, df = 1, P = 0.06). Juvenile survival in gallery (0.24 Juvenile/Female, SD ± 0.18) and Ankoba (0.26 Juv/Fem, SD ± 0.04) was lower than in scrub (0.31 Juvenile/Female, SD ± 0.10) and Tourist Front (0.37 Juv/Fem, SD ± 0.11). Compared to 1990-2000 (Pinkus, 2004), the survival of juveniles in scrub was stable; however the survival in gallery decreased from 0.36 to 0.24 juveniles per female. Mean brown lemur recruitment was the same in scrub and gallery from 2005-9 (0.37 Juv/Fem, SD ± 0.08 in gallery and 0.11, SD±0.13 in scrub), but had dropped down compared to 1990-2000 data (0.57±0.18 in gallery and 0.47±0.14 in scrub). An analyis of density-dependent effects may be assumed to clarify this result.

3.3.4 Density dependence of juvenile recruitment

There is a regression pattern of the juvenile recruitment of ring-tailed as a fonction of the brown lemurs density. An analysis of correlation was performed and showed a negative correlation between the juvenile recruitment of ring-tailed and the density of brown lemurs at Berenty which is not statistically significant (Pearson's Product Moment Correlation, n=11 years, r = - 0.38, P = 0.052, Figure 3.3). Juvenile recruitment of ring-tailed decreased with the increase of brown lemur population; however this did not explain a negative effect of the brown lemur population on ring-tailed lemur survival. The slight decline appeared after the drought year in 2006 and affected the recruitment in the post-drought years. For brown lemurs, there is no significant decrease of recruitment when compared to ringtailed lemur density. However, there was a clear statisitcally significant decline of the juvenile recruitment when all years data from both species were analysed (Linear Regression, R^2=0.73, $F_{1,5}$ = 24.25, P = 0.001; Figure 3.4). In other words, juvenile recruitment by brown lemurs in Berenty declined as the combined population density increased (Pearson's Product Moment Correlation, n=11 years, r = - 0.85, P = 0.001).

There is a strong tendency for correlation between brown lemur recruitment and troop size. From 2000-9, juvenile recruitment of brown lemurs in gallery decreased with increasing of troop size (Pearson's Product Moment Correlation, n=6 years, r = -0.77, P = 0.07). There was a stable trend for juvenile recruitment in Ankoba and scrub habitats. There is no evidence of density-dependent effects at troop level for either ring-tailed and brown lemurs.

Table 3.3 Troop size, sex-ratio and total population of brown lemurs at Berenty reserve

	Gallery				Scrub				Ankoba				Total population Number
Year	Troops counted	Mean troop size	Mean Ad. Fem	Sex-ratio	Troops counted	Mean troop size	Mean Ad. Fem	Sex-ratio	Troops counted	Mean troop size	Mean Ad. Fem	Sex-ratio	2 km²
1985													47
1993													104
2000													229
2005	23	9.25±4.25	3.75±1.64	0.95±0.52	16	8.87±3.83	3.6±1.54	0.98±0.47					355
2006	32	9.58±3.21	4.16±1.31	1.05±0.52	18	9.32±3.83	3.74±1.44	1±0.45	15	9.93±3.61	4.6±1.12	0.91±0.3	623
2007	34	10.03±3.36	4.15±1.15	1.13±0.4	13	9.15±2.73	3.85±0.8	1.18±0.68	22	8.77±3.14	3.5±1.14	1.22±0.67	653
2008	38	8.86±2.88	3.58±0.95	1.19±0.52	9	7.77±2.68	3.22±.97	1.06±0.4	18	11.05±3.63	3.94±1.16	1.41±0.54	621
2009	36	9.14±2.94	3.41±1.22	1.28±0.64	7	8.17±1.6	3±0.63	1.04±1	21	9.9±2.64	3.66±1.06	1.31±0.54	593

Table 3.4 Troop size, sex-ratio and total population of ring-tailed lemurs at Berenty reserve

	Gallery				Scrub				Ankoba				Tourist Front				Total population number
Year	Troops counted	Troop size	Ad. Fem	Sex-ratio	Troops counted	Troop size	Ad. Fem	Sex-ratio	Troops counted	Troop size	Ad. Fem	Sex-ratio	Troops counted	Troop size	Ad. Fem	Sex-ratio	2 km²
2004																	338
2005				0.96				1.04								1.06	492
2006	7	7±3.7	3.71±1.50	1.2±0.42	12	8.75±2.6	3.67±0.9	0.98±0.5	18	10.83±4.91	5±1.85	0.86±0.52	12	11.42±6.37	5.17±2.27	1.14±0.55	482
2007	6	6.83±2.79	3.50±1.94	0.62±0.27	12	8.5±3.26	4.17±2.18	0.86±1.01	17	9.94±4.38	4.94±2.12	0.83±0.73	11	11.45±4.87	5±2.15	0.96±0.76	434
2008	6	6.3±2.34	3.33±2.04	0.90±1.03	14	7.7±3.87	3.57±1.72	1.08±0.64	17	11±5.56	4.17±2.21	0.98±0.33	10	14.6±4.01	6.10±1.25	0.87±0.41	466
2009	7	6.14±1.86	3.29±1.11	0.52±0.58	12	9.3±3.92	3.50±1.68	1.21±0.50	19	10.1±5.34	4.58±1.89	1.03±0.45	9	12.4±4.93	5.44±2.35	0.96±0.36	459

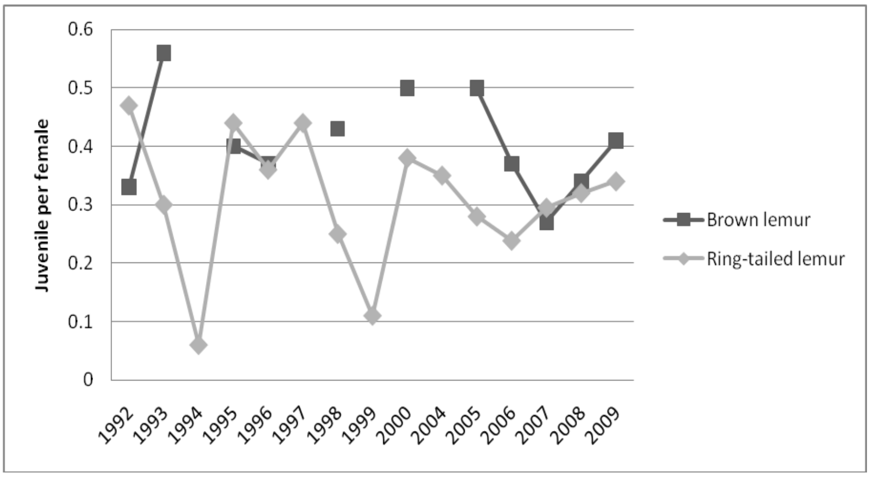


Figure 3.2: Changes of juvenile recruitment of brown and ring-tailed lemurs at Berenty reserve from 1992-2009.

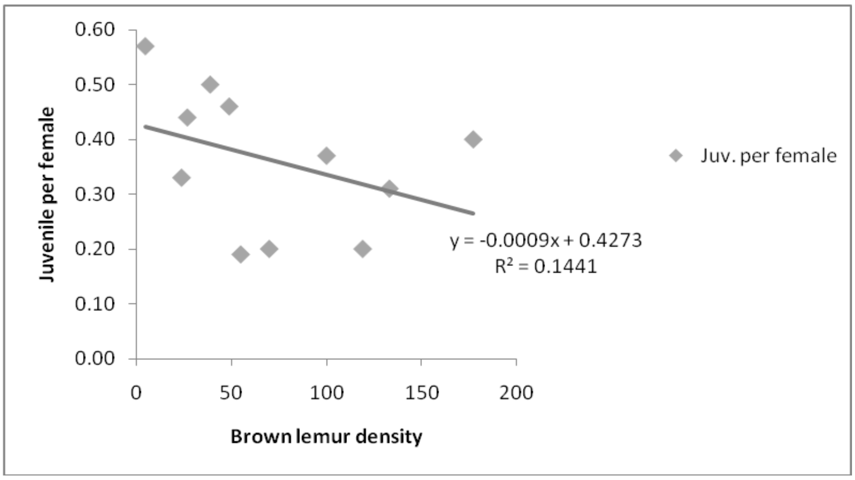


Figure 3.3: Juvenile recruitment of ring-tailed lemurs as function of brown lemur population density

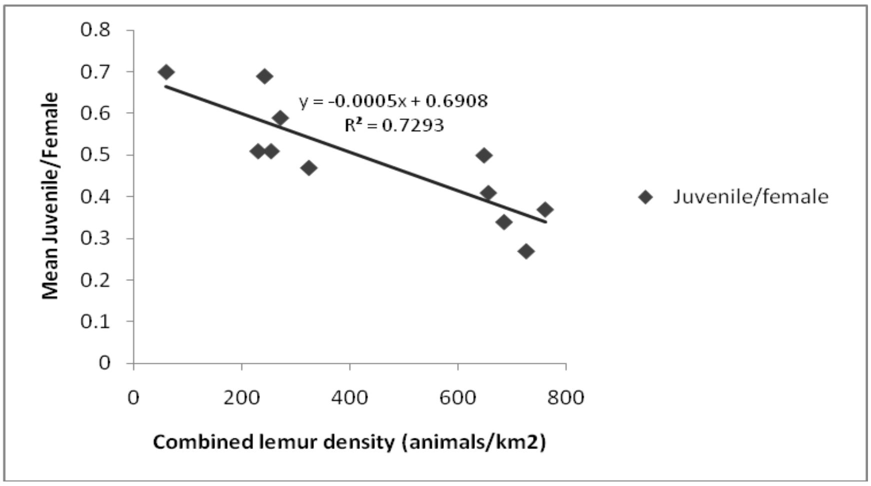


Figure 3.4: Population level density dependence of brown lemur juvenile recruitment Juveniles per female is shown as a function of combined density of ring-tailed and brown lemurs' population per year census.

3.3.5 Distribution patterns of brown and ring-tailed lemurs at Berenty reserve

Maps of the distribution patterns of ring-tailed and brown lemurs at Berenty reserve were created from the locations of group sightings during the census each year, using the kernel density analysis of the ArcGIS program. The distribution of ring-tailed lemur population at Berenty reserve in 1995 shows that this population lived in closed canopy habitat. They also used the scrub habitat as seen in natural sympatric with red-fronted brown lemurs in Antserananomby (Sussman, 1977) (Figure 3.5). This has been demonstrated by the high population of ring-tailed lemurs in gallery forest since 1990 (Jolly et al., 2002) with bigger troop size. Ten years later in 2006 (Figure 3.6), ring-tailed lemur distribution had moved into the periphery of the reserve and the scrubby places where their density became higher with a stable group size. However the density of the population in gallery was decreasing, as did the size of the troops. Meanwhile there was a high increase of the population in the tourist front, with larger groups. There is also high density of ring-tailed lemurs in Ankoba forest. The distribution of ring-tailed lemurs at Berenty reserve was not correlated to the distribution of water troughs.

In contrast, brown lemurs' distribution is strongly influenced by the distribution of water basins (figure 3.6). Following the expansion of water provisioning, brown lemurs' number increased in gallery, reaching four times of that of ring-tails in the same habitat. Since water provisioning began in scrub habitat, brown lemurs have colonised scrub habitat, reaching similar density of ring-tailed lemurs in the closed canopy of Ankoba forest. Once the water provisioning was stopped in 2007, the distribution of both species has changed (Figure 3.7). Ring-tailed lemurs were displaced into the marginal habitat and the very scrubby place where they conduct most of their vital activities such as feeding and resting, while, brown lemurs occupied the core of the closed canopy forest in Berenty reserve. Therefore, the population of ring-tailed in the scrub and tourist front had slightly increased while their number in the gallery has decreased (although the affects of the high density of brown lemurs there has not been verified statistically). This separation was maintained in 2009 (Figure 3.8).

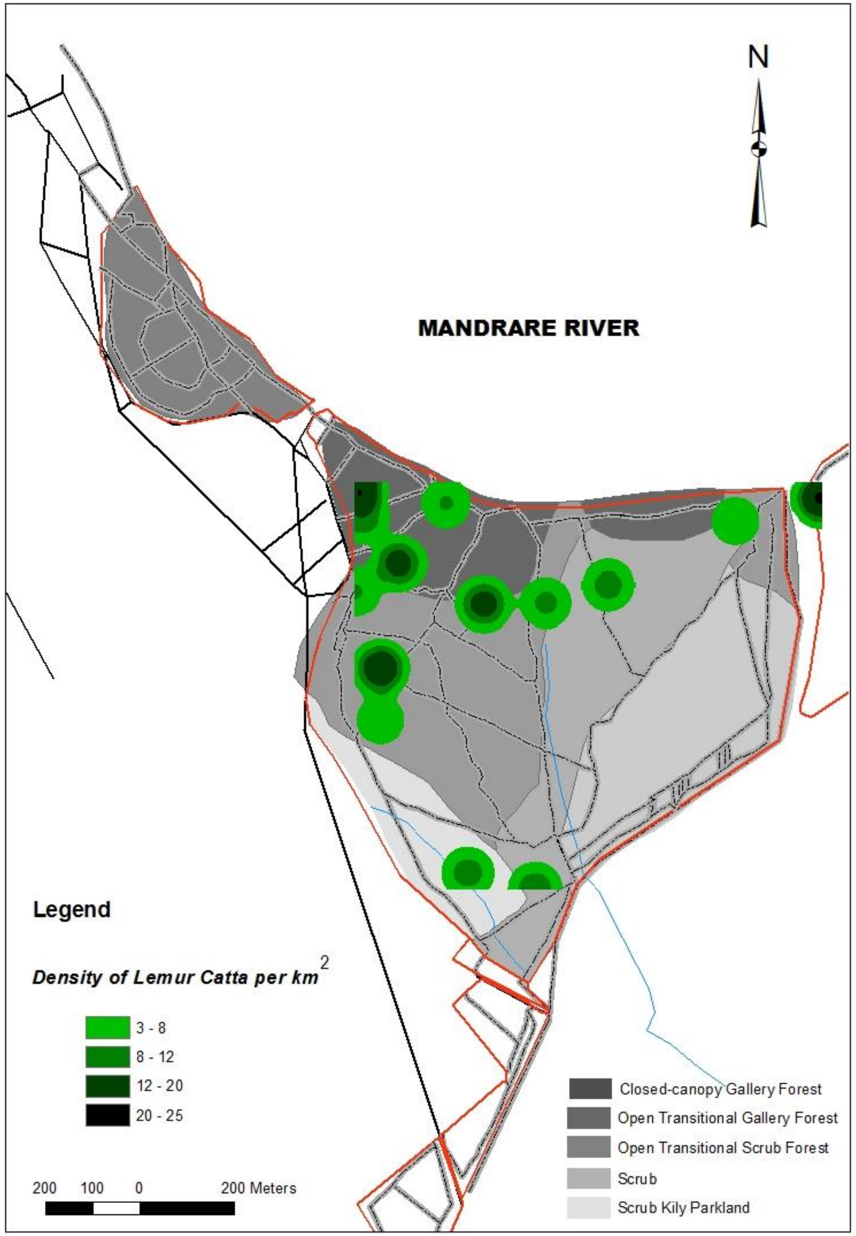


Figure 3.5: Spatial distribution of ring-tailed lemur population at Berenty reserve in 1995.

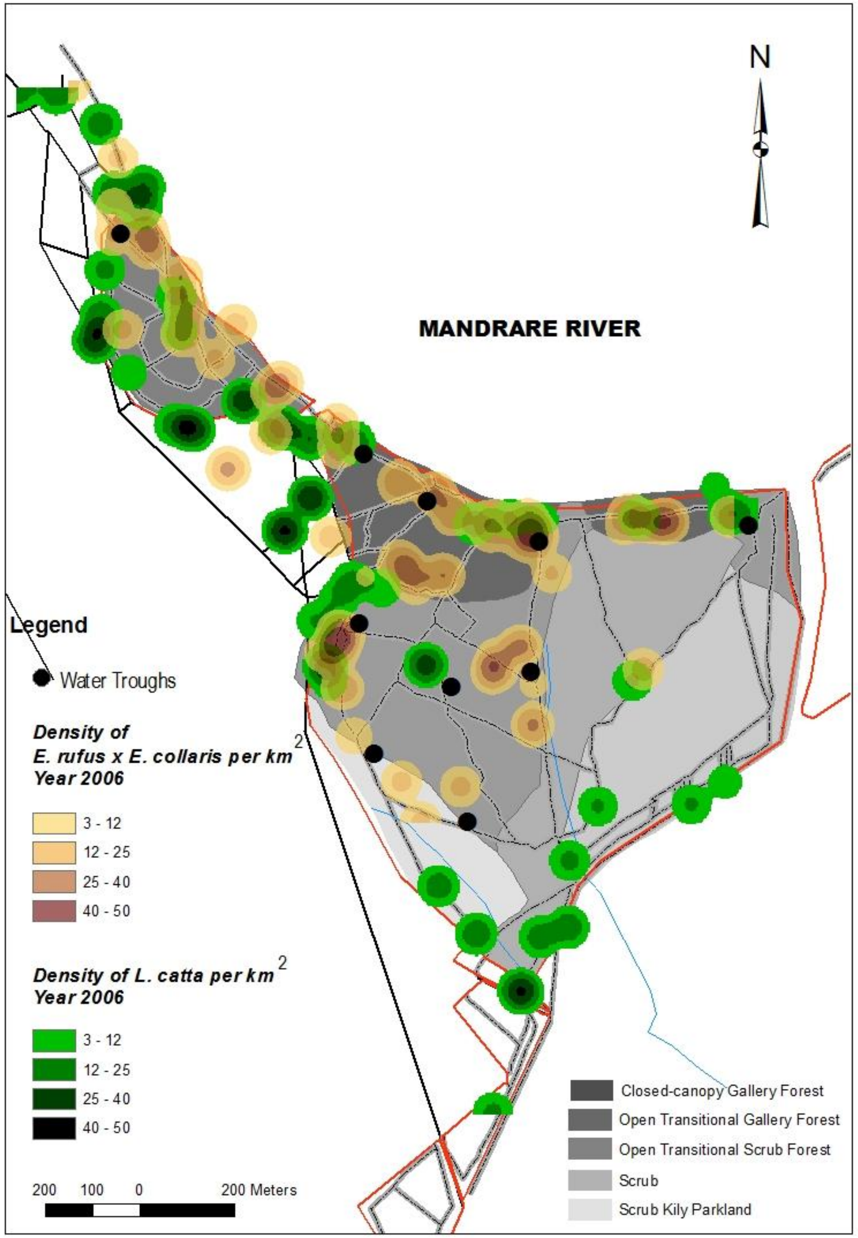


Figure 3.6: Spatial distribution of brown and ring-tailed lemurs at Berenty reserve in 2006 with the presence of water troughs.

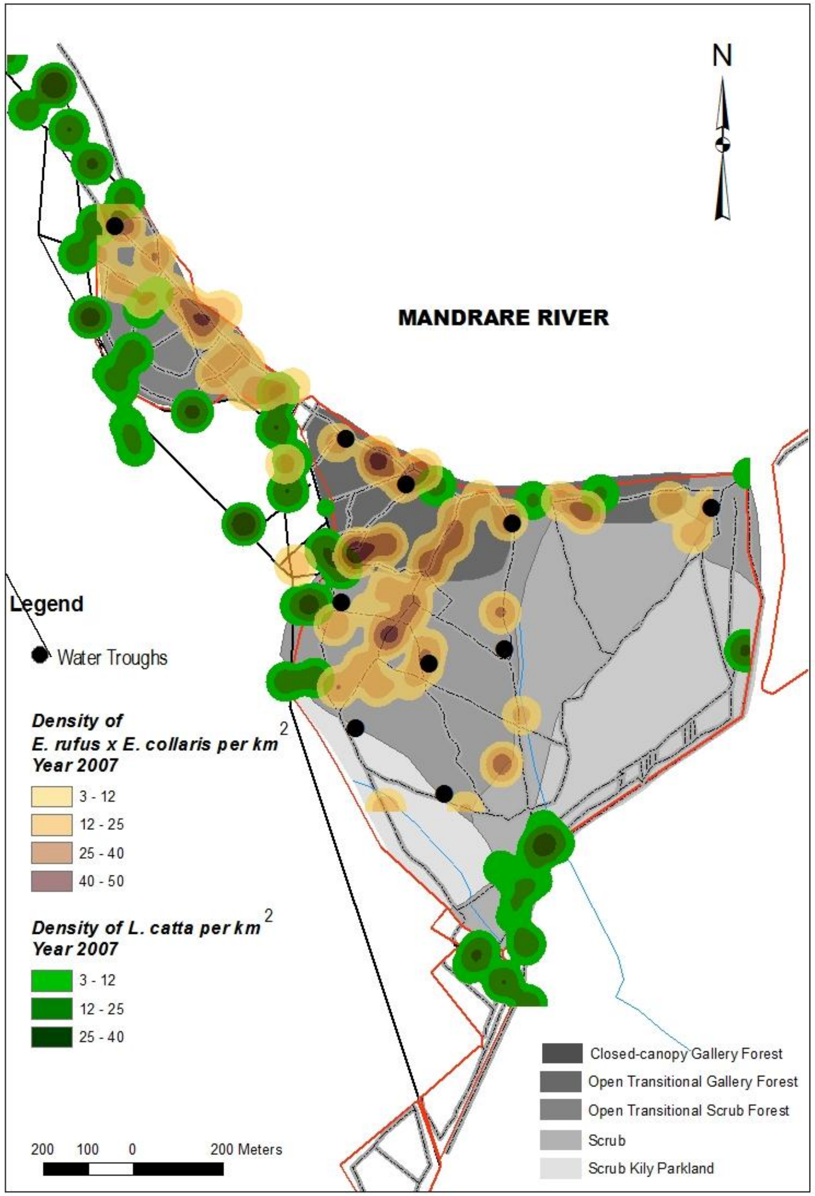


Figure 3.7: Spatial distribution of ring-tailed and brown lemurs in 2007 after stopping the water provisioning.

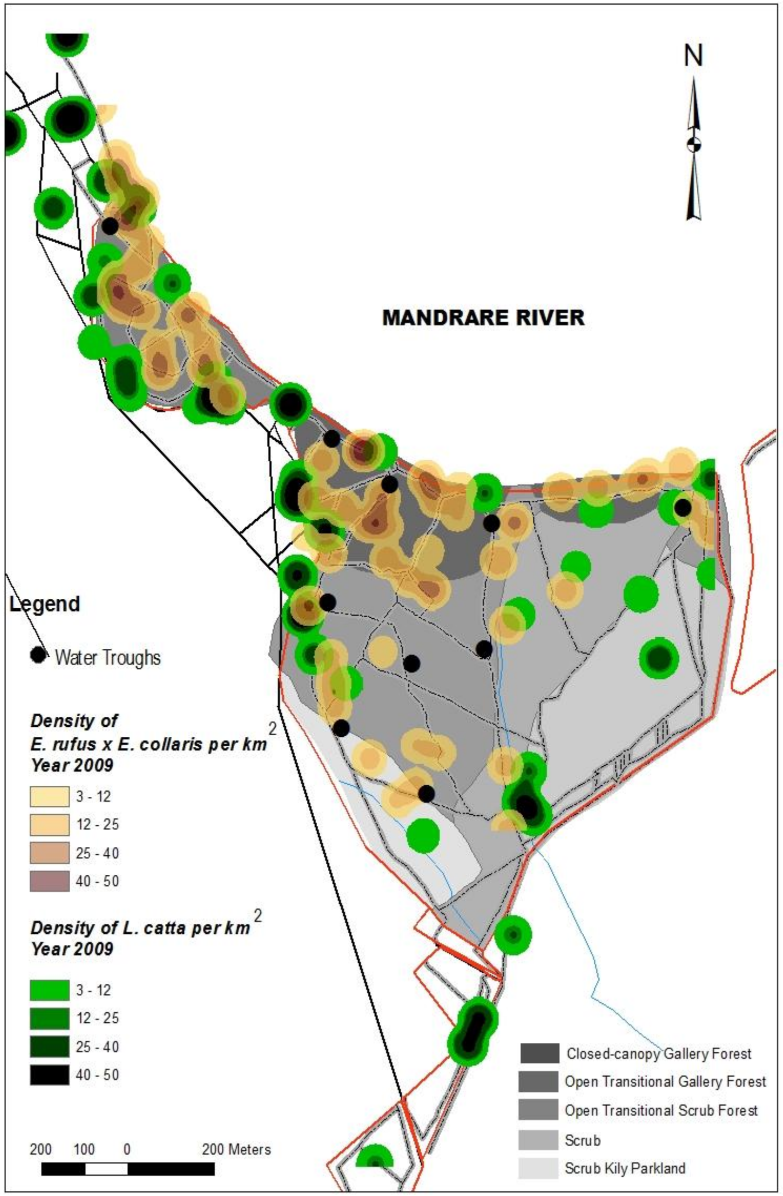


Figure 3.8: Spatial distribution of ring-tailed and brown lemurs in 2009.

3.4 Discussion

3.4.1 Interspecific interactions in density and distribution

Ring-tailed and brown lemur populations increased till the water provisioning was stopped. The density of ring-tailed lemurs did not change markedly when the water provisioning began, particularly in scrub habitat, because ring-tailed lemurs living in scrub can obtain sufficient water by eating succulents and other plants with high moisture contents (Budnitz and Dainis, 1975; Randriamboavonjy, 2003). The high increase of the ring-tailed population in the gallery till 2000 was explained by food availability and habitat quality (Jolly et al., 2002), but also the access of water due to water provisioning. This has correlates with similar large increases in population density in response to food or water provisioning that are common in other primates and vertebrates in general (Fleagle, 1999; Krebs, 1994; Newton, 1989). Standing water does not seem to be a limiting resource for ring-tailed lemurs in scrub, as it was reported that even before water provisioning, their number rarely declined in drought years (Pinkus, 2004). For this reason the population of ring-tailed lemurs in scrub has grown and has been stable even after removal of water troughs, though the overall number of the population has been decreasing since the drought year in 2006. The absence of water provisioning may affect the growth of the ring-tailed lemur population in gallery forest; food competition with higher density of brown lemurs may constitute a different factor. It has been demonstrated that plant species that produce abundant and reliable fruits are keystone resources for frugivorous primates (Overdorff, 1991; Peres and Dolman, 2000; Sauther, 1998b; Tutin et al., 1997). Tamarindus indica fruit, the dominant species in all part of the forest (chapter 2), is a keystone dry season resource for ring-tailed lemurs, and is often the dominant component of their diet (Mertl-Millhollen et al., 2003; Rasamimanana and Rafidinarivo, 1993; Sauther, 1992; Sussman, 1972; Yamashita, 2002; this study). T. indica fruit production varies: it may increase during a minor drought, but plummets during multi-year droughts, then dramatically decrease over the next one to two years (Razafindramanana, pers. obs.; Jolly et al,. 2002; Simmen et al., 2003). For this reason, droughts affect ring-tailed more severely than sympatric species with more folivorous diets (Gould et al., 1999; Richard et al., 2000). In years when T.

indica fruits are scarce, high adult/juvenile mortality and reproductive failure also occur in ring-tailed at Beza Mahafaly (Godfrey et al., 2004; Gould et al., 1999; Jolly et al., 2002).

Brown lemur growth and distribution appears to be affected by the water availability. The water requirements of brown lemurs have been discussed by Scholz and Kappeler (2004) as they may travel considerable distances to reach water. Brown lemurs started colonizing scrub habitat after water provisioning was expanded in scrub. In natural sympatry with ring-tailed lemurs at Antserananomby, brown lemurs were confined to closed-canopy forest (Sussman, 1974; Sussman, 1999). This confirms the distribution movement of the population into the gallery forest after abolition of water troughs, giving such a high density of lemur population exploiting in the closed-canopy forest. Brown lemurs living in dry forest generally have access to a river or a stream (Hawkins, 1999; Scholz and Kappeler, 2004). During the period when Berenty were still provisioned with water in small troughs, brown lemurs were never observed drinking in Mandrare river, though ring-tailed lemurs did so. But this behaviour has been seen occasionally after removal of water provisioning in Berenty. Since then a decrease of the overall population has been recorded. The correlation between brown lemur distribution-growth and water provisioning at Berenty suggests that this population may not range in scrub in the absence of water provisioning. The high recruitment of brown lemurs cannot be explained by the immigration of troops from adjacent forest alone, but it is also affected by the food abundance and adaptation of the species to exploit abundant and uniformly distributed resources during periods of scarcity (Sussman, 1999).

3.4.2 How species distribution and dynamics are influenced by species interactions

Ring-tailed lemurs inhabited closed canopy forest, but most of their territories included large areas of transition forest and scrub habitat at the forest edge (Sussman, 1974; Sussman, 1999) and ring-tailed lemurs outside of sympatry with brown lemurs act in a very similar way to that observed by Sussman (1972) when in sympatry (Sauther, 1992; Yamashita, 2002). Allopatric brown lemurs living in dry and rainforest, exhibit a variety of ecology and are not specialized as seen in natural sympatry with ring-tailed lemurs (Overdorff, 1991; Scholz and Kappeler, 2004). In sympatry with other lemur species (e.g., Varecia variegata or Eulemur rubriventer), they become more vulnerable and weak competitors in terms of population development (Overdorff, 1993). At Berenty, brown lemurs have colonised all parts of the reserve, even the edge habitat normally monopolised by ring-tailed lemurs. But this changed once the water provisioning was stopped, leading to a shift of ring-tailed lemurs range to the marginal habitat and brown lemurs to the closed-canopy forest. Brown lemurs are poorly adapted to edge habitat (Pinkus et al., 2006). Because of their less efficient thermoregulation behaviour compared to ring-tailed (Ganzhorn, 1985; Sussman, 1974), they mainly range in shady habitat and feed on abundant food around them in order to conserve energy and water. Ring-tailed lemurs in sympatry with brown regularly make use of both closed-canopy forest and edge habitat, while Brown lemurs occupy in the forest (Hawkins, 1999; Pinkus et al., 2006; Sussman, 1972; Sussman et al., 2003).

It is a question of definition whether brown lemurs or ring-tailed lemurs are the more specialized species. Brown lemurs clearly prefer closed canopy forests, but Pinkus (2006) characterizes them as “serial opportunists” which can commandier the most rewarding foods in any season. Ring-tailed lemurs have a broader niche, which can use the limited resources present in edge habitats (see Godfrey et al., 2003; Gould et al., 2003; Wright, 1999). The ring-tailed lemurs present a classic case of the “Jack of all trades, Master of none”, who are less good competitors while the browns are masters of the gallery forest, but unable to fully survive in scrub. The brown lemur’s ecological niche is included within that of the ring-tailed lemurs (Hutchison, 1978; MacArthur and Levins, 1964; May and MacArthur, 1972).

After decades of extensive study of the ecology interactions between brown and ring-tailed lemurs in Berenty, the lemur populations have developed a trend toward similar ecology to that in natural sympatry. The ecological interactions were complicated by different human factors such as food and water provisioning, management of the reserve, tourism, in addition to those factors that should have naturally shaped their ecological niches. Ring-tailed lemurs, considered as poor competitors, are adapted to surviving in marginal habitat (Godfrey et al., 2004; Gould and Sussman, 2001), whereas brown lemurs show ecological and behavioural adaptations to being better competitors, but only in rich, shady habitat. Brown lemurs have been reported to have similar ecology to that of some arboreal species of New and Old World monkeys and ring-tailed lemur are comparable to many terrestrial primates living in forest edges (Sussman, 1999).

3.4.3 Conservation implications

At Berenty, ring-tailed lemurs' juvenile recruitment is more erratic than that of brown lemurs, especially in the scrub habitat. The population growth rate for scrub ring-tailed in post-drought years also appears to have decreased since brown lemurs appeared in scrub (Pinkus, 2004). This may be explained with the fact that food competition with brown lemurs in scrub may reduce the high recruitment needed for ring-tailed to recover from post-drought food shortages. Even though the density of brown lemurs at Berenty reserve is lower compared to that in natural sympatry with ring-tailed lemurs (569 vs. 1,000 per sq.km) (Sussman, 1974), a trend for further negative impact of this introduced competitor on native ring-tailed lemurs is seen in this study. Moreover, the combined density of both populations may affect the long-term viability of brown lemur population. Ring-tailed are adapted to rebound rapidly from population declines (Gould et al., 1999; Gould and Sussman, 2001), but their diet and use of edge habitat (Sussman, 1972; Hawkins, 1999) suggest they may be less able to do so while competing for food with brown lemurs. The precaution of removing the access to standing water in the reserve since 2007 will affect the behaviour of brown lemurs at least for a short-term and they may exhibit the more conservative range use seen in other dry forest populations (Ganzhorn, 1985; Ganzhorn, 1986; Donati et al., 1999).

Berenty's forest as a whole is drying out, probably from a combination of causes (Jolly et al., 2006b). Considering the progressive degradation of the forest as well as the decrease of closed canopy area in the forest (Chapter 2), it may be that the pressure of grazing lemurs is beyond the forest's regenerative capacity. While further studies continue, it may be wise to inaugurate a pilot study on birth control of brown lemurs to stabilize this introduced population. Under these conditions, habitat use would be relatively low and the gallery forest would not be subject to the present high pressure of exploitation from the population of brown lemurs.

4. Interspecific ecological niche partitioning between native ring-tailed lemur and introduced brown lemur at Berenty reserve.

Abstract

In this paper, I examine the interspecific patterns of niche partitioning of two sympatric lemur species at Berenty reserve, in southern Madagascar, the native ring-tailed lemur (Lemur catta) and a hybrid brown lemur population arising from E. rufus and E. collaris introduced to the site. The study was conducted from February till December 2009 in the gallery forest of Berenty reserve. Data were collected from two groups of each species, followed up to 9 days a month per species, for 8-12 hours daily. Methods included focal animal 5-min fixed-interval point samples to collect data on diet and habitat use with sex differences, with all occurrences of any interactions of the focal animal with other members of the group. Ring-tailed and brown lemurs shared similar food items and dietary overlap was very high in terms of actual foods eaten. Their niche separation was quantitative rather than qualitative, seen in the proportions of food types consumed, and in patch size use. Ring-tailed and brown lemurs partitioned the environment in other ways including foraging and feeding within a different sized of patches. Ring-tailed lemurs supplemented a diet of varied amount of fruits, flowers, mature leaves and new leaves when available and feed substantially in relatively small food patches particularly during the rainy season; whereas brown lemurs had a more homogeneous diet consisting mainly of fruits and a bit of mature leaves or new leaves depending on the season. Food type differences were relatively small during the dry season compared to the rainy season. Both species exploited similar plant species during the dry season food scarcity period. However, Lemur catta had a more diverse diet which ensured a certain amount of variety for their dietary pattern and brown lemurs had a restricted diet. Even though both species entered all forest sites with quite similar frequencies, the dichotomy in habitat use relied considerably on vertical ranging. Brown lemurs preferred ranging from middle to upper stories and in the canopy trees, whereas ring-tailed lemurs ranged frequently in lower canopy. Generalists' ring-tailed lemurs occurred in wider niche including many habitat types. Brown lemurs' niche was more constrained and might be included in that of the generalists. Ring-tailed lemurs were considered as "Jack-of-all-trades though masters of none", while brown lemurs were masters of the specialized niche of gallery forest. Overall, after decades of cohabitation, both lemur species seemed to have now reached a competitive equilibrium to allow their cohabitation at Berenty reserve.

4.1 Introduction

Sympatric primates are defined as those which are found in the same ecological communities, sharing diverse degrees of space, predators, water sources, and food resources with one another and with other non-primate animals as well (Patterson et al., 2003; Raven and Johnson, 1999). The concept of niche is characterized by all the functions and interactions between an organism and its environment (Hutchison, 1978; Odling-Smee et al., 2003; Pianka, 1994). The concept of competition (Gause, 1934; MacArthur and Levins, 1964a) posits that ecological niches are never identical between two sympatric primates, and that includes every aspect of space, time and resources exploited. There may be overlapping in requirements between different species but interspecific competition will lead, over evolutionary time, to some degree of differentiation or divergence in niches to allow cohabitation, or else to disappearance of one of the competitors (Alley, 1982; Hirzel and Le Lay, 2008). Three major niche dimensions have been reported to be important for the coexistence of primate communities: habitat-type, food-type and temporal separation (Ganzhorn et al., 1997a; Schoener, 1974). Niche separation in worldwide primate communities according to these three variables has been demonstrated in many papers (e.g., Chapman, 1987; Glander et al., 1989; Hladik, 1977; Overdorff, 1993; Overdorff, 1996; Terborgh, 1983). Interactions among vertebrate taxa have been reported to be important in structuring entire vertebrate communities (e.g., Gautier-Hion et al., 1985).

Many studies on lemur communities define niche separation by analyzing niche dimensions (microhabitat use, food-type and temporal separation); but these variables in turn are influenced by body mass, physiology, predation and seasonality in climate, food abundance and food distribution (e.g., Gautier-Hion et al., 1980; Vasey, 2004b). Biotic interactions (like competition, parasitism and mutualism) also affect the fitness and behaviour of co-existing species , and may severely affect their niches (MacArthur and Levins, 1964; Pearson and Dawson, 2003) leading to a bimodal niche (Austin, 1999): the realized niche which is a subset of the fundamental niche (Hirzel and Le Lay, 2008; Hutchinson, 1957). Reproductive stage has also been demonstrated as an important factor in niche separation analysis (Vasey, 2000a). Few studies document sex differences in diet, though these occur especially during gestation and lactation periods (e.g., Boinski et al., 2002; Gautier-Hion et al., 1980; Rasamimanana and Rafidinarivo, 1993; Sauther, 1994). In monkeys, sex difference in diet is thought to result from male dominance, giving males priority in access to food (Clutton-Brock, 1977; Demment, 1983). However, in lemurs, females are dominant and have priority access to protein-rich food particularly during reproductive stages (Clutton-Brock, 1977; Jolly, 1984; Rasamimanana, 2004; Sauther, 1993; Simmen et al., 2010; Simmen et al., 2005). Despite these various studies of sex differences in intraspecific diet, few have focused on how interspecific social behaviour and interactions can affect niche partitioning in different seasons of a year (e.g., Overdorff, 1996). Lemurs are an ideal subject to study the impact of group social interactions on different niche parameters due to their complex social systems (Kappeler, 1993; Pereira and Kappeler, 1997).

Ganzhorn (1997) reveals the presence of consistent niche partitioning along the three major niche dimensions (habitat-type, food-type and temporal separation, Shoener 1974) which indicates an ecological equilibrium among Madagascar lemur communities. Niche separation between lemurs is driven by floristic diversity, physical and chemical properties of food items, food patch size, reproductive stage, and biotic and abiotic factors that may influence niche dimensions (Ganzhorn and Kappeler, 1996; Hladik et al., 1980; Overdorff, 1993a; Sterling, 1993; Sussman, 1974; Vasey, 2000a). This is exemplified by morphological and physiological evolution or adaptation to exploit different food resources for nocturnal lemurs (Charles-Dominique, 1980), or a temporal separation of food plants and microhabitat use for lemur species in evergreen rain forest (Ganzhorn, 1989; Overdorff, 1993), or different energetic requirements between sexes by season and reproductive stage (Clutton-Brock, 1977; Vasey, 2000a). One key study is that of Sussman (1974), which shows that naturally sympatric red fronted brown lemurs and ring-tailed lemurs in his study areas had respective niches and little interspecific overlap in habitat use or diet. These species are rarely observed in interspecific interaction of any sort, which suggests adaptations to different environments both in sympatry and allopatry. Brown lemurs have been described as specialized arboreal folivorous living in closed canopy forest and ring-tailed lemurs as semi-terrestrial generalists exploiting all levels of forest canopy and large areas of scrub and forest edge (Sussman, 1974; Sussman, 1999). Ganzhorn (1985, 1986) studied ring-tailed lemurs (Lemur catta) and brown lemurs (Eulemur fulvus) inhabiting large enclosures at Duke Primate Center and found similar patterns for the ecology of both lemur species. Allopatric ring-tailed lemurs are likely to behave as observed in sympatry (Sauther, 1992; Yamashita, 2002). Allopatric brown lemurs exhibit a variety of ecologies (e.g., Donati et al., 2007; Donati et al., 1999; Overdorff, 1993; Overdorff, 1996; Rasmussen, 2005; Scholz and Kappeler, 2004).

Since the introduction of brown lemurs at Berenty reserve, brown lemurs have increased exponentially in population, and have been acting differently from those living in natural sympatry with ring-tailed lemurs (See chapter 3). Pinkus (2006) found high interspecific diet overlap between both lemur species at least during the late dry season. Both species compete largely for the same food resources, essentially Tamarindus indica fruit, and brown lemurs show dominance over ring-tailed lemurs in terms of food and water resources (Pinkus et al., 2006b; Razafindramanana, 2005). Thus ring-tailed lemur populations are displaced to the peripheral habitats of the reserve which they did not occupy prior to the brown lemur introduction (Jolly, 1966a; Mertl-Millhollen et al., 1979; chapter 3). This suggests a threat to the long-term stability of ring-tailed lemur population. This paper describes the patterns of niche separation in different seasons between these species when living in artificial sympatry in order to propose a model of ecological equilibrium of lemur assemblages and a niche partitioning by lemurs.

Nutrients and energy in ecosystems have a finite availability and there is a loss of energy for an upgrade of trophic level, thus resources are limited in ecosystems (MacNally, 1995). Niche partitioning is defined as the exploitation of different resources by sympatric species due to competition (Gause, 1934; Raven and Johnson, 1999). Dietary partitioning between ring-tailed and brown lemurs at Berenty reserve was tight but there is evidence of dietary niche separation between them based on time spent feeding on different plant parts (Schoener, 1974) and the food patch size used (May and MacArthur, 1972). Similar patterns have been found in western Madagascar between red fronted brown lemurs and ring-tailed lemurs (Sussman, 1977b; Sussman, 1974), between northern populations of E. coronatus and E. fulvus sanfordi (Freed, 1996) and in north-eastern lowland coastal rainforest between Varecia v. rubra and E. f. albifrons (Vasey, 2000a; Vasey, 2004). Diet partitioning varies temporarily in tandem with seasonal food abundance (Bagchi et al., 2003; Feldhamer et al., 1999; Kronfeld-Schor et al., 2001; Waser, 1987; Wrangham et al., 1998).

In this study, I examine interspecific differences in social interactions, microhabitat use and diet by sex and season. Only adult individuals were considered during this study. My initial hypothesis was that niche partitioning would vary over the year with seasonal variation in climate, food abundance, and energetically costly periods in the reproductive cycle. I predicted that niche separation in diet eventually occurs between both species but this may be more emphasized during food scarcity periods and reduced during seasonal food abundance. This pattern follows observation of lemurs living in natural sympatry in north-eastern Madagascar that showed greater niche partitioning during food scarcity and reduced niche partitioning during greater food availability (Vasey, 2000a). I also observed intra- and interspecific variations in niche partitioning of males and females in both lemur species. Females may invest more energy in reproduction, thus the diet could be more similar between species than that of males (Rasamimanana et al., 2006; Soma, 2006a). Social interactions would define a realized niche for each species that is constrained to occupy because of interactions with the other species. As ring-tailed and brown lemurs at Berenty are ecologically and morphologically closely related, I expected that microhabitat use (patch size, forest site, and vertical ranging) would play a large role in niche partitioning. Seasonal differences in microhabitat use and diet were evaluated as to how they are affected by social interactions, such as aggression or affiliation, in each species and interactions between the two. Results of niche separation from this study will be discussed with other studies to evaluate the lemur niche partitioning and its evolution in Madagascar.

4.2 Methods

4.2.1 Study site

The study was conducted from February till December 2009, in the gallery forest of Berenty reserve, southern Madagascar, with the help of three volunteer assistants. The data were collected in Malaza gallery forest which is a 100-ha area composed of front tourist, gallery, scrub and spiny forests. For details on study site and forest composition, see Jolly et al, 2006 and chapter 2.

4.2.2 Rainfall, seasonal food availability and reproductive stages of lemurs

Data on rainfall were recorded daily with an All Weather Rain Gauge, if missed, then data were gathered courtesy of Rakotomalala Alain, the Reserve Manager (Figure 4.1). Two distinct seasons were found: 1) cold and dry season (May –September), 2) hot and rainy season (October – April). September constitutes the late dry season/early birth season, a transitional month between the two seasons, so we consider it as part of the dry season. Figure 4.1 summarizes plant phenology in correspondence with rainfall and reproductive stages of lemur species during our observations in 2009 at Berenty reserve (Razafindramanana, pers. obs.). Phenological data of 31 plant species were recorded from 200 trees in the forest. Abundance of plant parts is rated on relative scale from 0 (none) to 4 (75-100% plant part available) (Soma, 2006). Fruits are almost always available during the year from endemic and introduced tree species. Green fruits from native trees such as Tamarindus indica are more abundant during the dry season, Rinorea greveana from early wet season and then came Neotina isoneura and Crateva excelsa. The late rainy season is dominated by the fruits of the introduced tree species of Azadirachta indica and Cassia sp. Flowers and young leaves are more abundant in the beginning of rainy season. Peaks of flowers are also seen during at the end of the rainy season. These patterns are similar to what has been previously described in Berenty and Beza Mahafaly reserves (Sauther, 1998; Soma, 2006). Reproductive stages of the two lemur species in this study differ slightly. Food availability synchronizes with the birth season but in ring-tailed lemurs from September to October and brown lemurs from October to December. Ring-tailed lemurs mated from end of March till end of April, brown lemurs mated from May till mid-June. These periods correspond to the availability of flowers and fruits. Gestation period occurs when food availability is low from June till August.

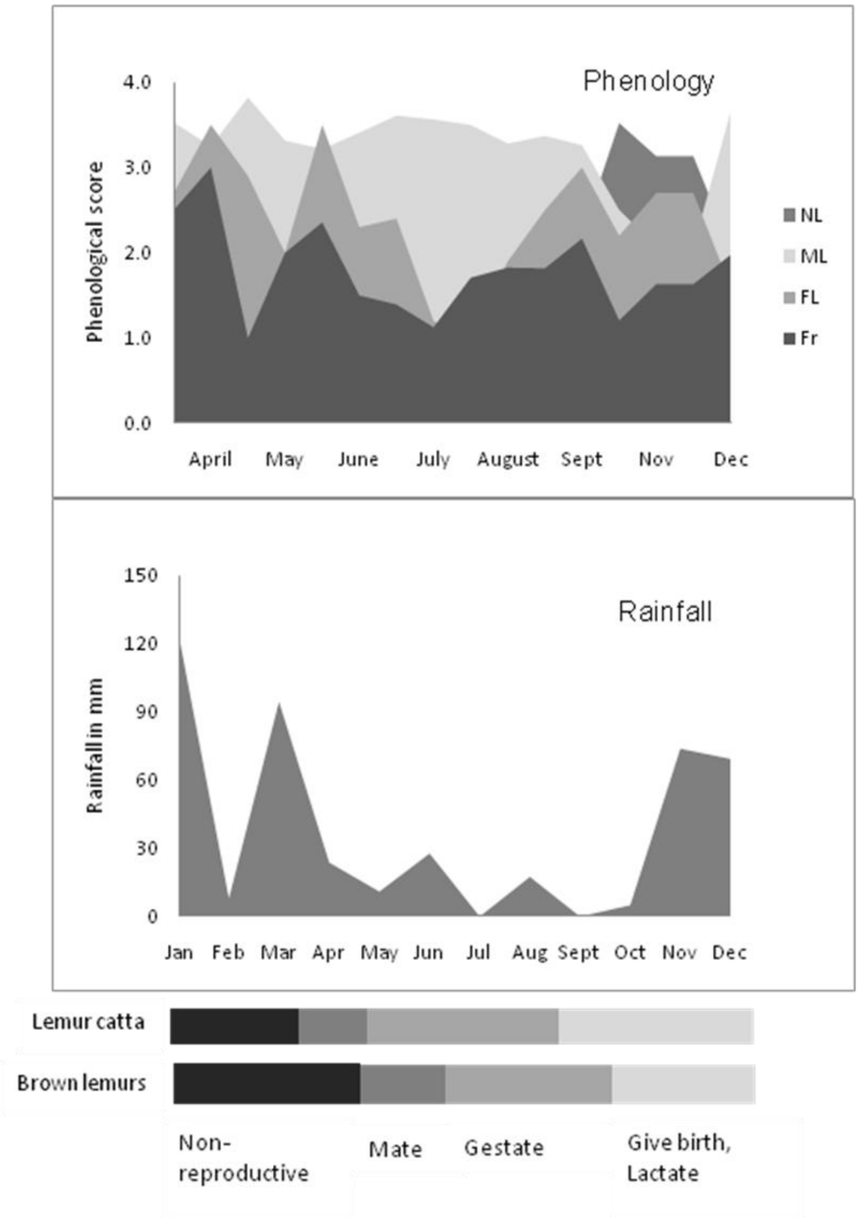


Figure 4.1: Plant phenology and rainfall at Berenty reserve in 2009
with the correspodance with reproductive stages of the lemur study species based on our observations in the field. NL: new and young leaves, ML: mature leaves, FL: flowers and flower buds, Fr: fruits.

4.2.3 Study groups

Two groups of ring-tailed lemurs (A1 and C1) and two groups of brown lemurs (VJs and River) were each followed up to 9 days a month (minimum 4 days) per species, for 8-12 hours daily from 6am to 6 pm, depending on seasonal differences. The composition of study groups is shown on Table 4.1. During our observations, the brown lemur groups ranged from 12 to 15 individuals, while A1 ranged from 15 to 17 individuals. C1 sometimes mixed up with another small subgroup called Moon

Sisters, thus ranging from 10 to 15 individuals. Both species of lemur are multi-male and multi-female (Jolly et al., 2002; Overdorff, 1991; Pereira and McGlynn, 1997). Several births occurred in October 2009. Time point data were collected from representative 6 adults (3 males, 3 females) selected at random for each study group, which reflects the sex-ratio of the species. Observations were conducted with the help from two student assistants. Variables to be measured were tested and standardized before the assistants started full observation; these preliminary data were not used for analyses.

Ring-tailed lemurs are known to conserve their home ranges over decades (Jolly and pride, 1999; Klopfer and Jolly, 1970). However, brown lemurs exploit a bigger home range and may change it through seasons (Overdorff, 1993; Sussman, 1974). To facilitate finding of the brown lemur study groups at the beginning of each observation, one female of each group was fitted with a radio-collar manufactured by Biotrack Ltd. Captures were conducted by specialists from Beza Mahafaly reserve and followed the instructions detailed in (Glander et al., 1991; Setchell and Curtis, 2003), using remote injection of Ketamine (0.3 to 0.4 ml) to anesthetize animals. A 15 mm blowpipe was used to deliver the darts to the animals, using lightweight syringes with Vario stainless steel needles, manufactured by Telinject USA Inc. All members of the study groups, particularly the focal individuals were identified by distinctive characteristics such as missing limbs or tails, unusual pelage characteristics or eye colour, notched ears or facial scars and stripe types, cap hair (Jolly, 2002; chapter 3). These characteristics include age and specific behaviour known from previous study (Ichino and Koyama, 2006; Jolly and Pride, 1999; Koyama et al., 2006; Razafindramanana, 2005).

4.2.4 Data collection

Throughout the study, four data collection methods were used: (1): focal animal 5-min fixed-interval point samples to collect data on diet and habitat use with sex differences, (2) all occurrences of any interactions of the focal animal with other members of the group, (3) all occurrences focal animal sampling of feeding behaviour to analyse the sexual differences in feeding time and feeding bouts and (4) group scan sampling to record the activity and ranging patterns with all occurrences of intergroup social behaviour (Altmann, 1974; Martin and Bateson, 2007). Only data from focal animal sampling are analysed in this paper. The other data will be presented in different papers. Ring-tailed lemur were observed for 672 hours (female: 352 hr; male: 320 hr) during 65 focal animal observation periods. Brown lemurs were observed for 736 hour (female: 404 hr; male: 332 hr) during 71 focal animal observation periods.

Table 4.1 Composition of study groups during observations in 2009

Lemur species	Group	Females		Males		Juveniles	Infants	Peripheral individuals
		A	SA	A	SA			
Ring-tailed lemurs	A1	4	2	5	3	1 (M)	3*	2 (M)
	C1	3	1	3	1	2(M)	2	1 (M)
	Moon Sisters	1		1	1	1 (F)	1	
Brown lemurs	River	5		6		2 (F, M)	3	2 (M)
	VJ's	4*		6		1 (F)	2	2 (M, F)

*1 infant and 1 female were seen died in October 2009. M = male, F = female, A = adult, SA = sub-adult. Moon Sisters which is a subgroup of C1, mixed up with it sometime during the observations

During each observation, quantitative data were collected on each focal animal at five minutes intervals. These data include plant part consumed (fruit, flowers, leaves, young leaves, water, insects, other); species composition of the diet; estimated animal height from ground and forest substrate (ground in open canopy, ground in closed canopy forest, trunk, branches, crown, liana, bushes, buildings), estimated canopy diameter for all feeding trees. Buildings refer to all concrete construction on the edge or outside of the forest; branches refer to the area between trunk and the crown (Vasey, 2000a). All measurements were made visually and estimated in 5 m increments except for first category of height which has been split into 1-2 m and 2-5 m. Affiliative and agonistic interactions of the focal animal with other members of the group were recorded throughout the day to describe the social relationship and social organization of each species. During the follows, the location of the focal animal was noted every 15 min, using GPS or the quadrats unit on the map of the study site; the activity of the animal and the nearest neighbour were also collected; but these data are not presented here.

4.2.5 Data analysis and statistics

Diet, forest substrate and height: Data were compared between species. The proportions of scans were calculated daily, based on number of time points records for each variable category (fruits, flowers, leaves, young leaves, water, insects, other). The number of plant species fed in during each day was counted. The proportions of scans in each forest substrate and height category were calculated daily for each focal individual. These data were later subdivided into sex, season and reproductive stage when possible. Food patch size was estimated based on the crown diameter data. The crown volume constitutes an important measure which indicates the food carrying capacity and productivity of the whole tree (Chapman et al., 1992; Strier, 2007; Vasey, 2000b). The proportions of scans in each canopy diameter category were calculated daily and compared between species according to season. The daily total counts or proportions for each variable were transformed to the log of the values and tested for normality (Fowler et al., 1998). Three analyses were then conducted: (1) Two-way ANOVA was performed to test interactions between species by season or by reproductive stage or by sex. This has been also used to test for interactions by lemur species and seasonality in diet, forest substrate, height and canopy diameter. (2) Three-way ANOVA includes lemur species, sex, and seasonality in the four different variables (diet, forest substrate, height and canopy diameter). (3) Non-parametric test equivalent of two-way ANOVA, the Scheirer-Ray-Hare test (Dytham, 2007), was used to check the interactions in food plant species exploited by both species per season.

Social behaviour: Affiliation of the focal animal was counted throughout the day. The proportion of agonistic behaviour acts of the focal animal and its outcome (lose, win or peaceful encounter) were also calculated daily. Data on social behaviour were too small and did not meet the assumptions for parametric statistics, thus non-parametric tests were performed to test differences. The Kruskall-Wallis test was used to test the differences between affiliative and aggressive behaviour by species across seasons. Differences between peaceful and aggressive troop encounters by species and by season were tested using the same test. The test statistics for two-tailed are reported using a significance level of 5%, (P, 0.05; P, 0.01; P, 0.001);

variability in data is displayed using 95% confidence intervals (Field, 2005; Sokal and Rohlf, 1981).

4.3 Results

4.3.1 Diet and food patch sizes

4.3.1.1 Combined data by season:

Brown lemurs spend more time feeding on fruits (Species effect, F = 12.83, df = 1, P < 0.001), while ring-tailed lemurs exploited varied amounts of other items. Food partitioning varies across seasons and between species (Figure 4.2a): both in the rainy and dry season, brown lemurs relied heavily on fruits whereas ring-tailed lemurs fed significantly on new leaves during the rainy period (Season effect: F = 10.85, df = 1, P < 0.01), and on a higher quantity of mature leaves during the dry season (Species effect: F = 50.12, df = 1, P < 0.001; Season effect: F = 8.49, df = 1, P < 0.01). For both seasons, ring-tailed lemurs fed more on flowers compared to brown lemurs (Species effect: F = 7.16, df = 1, P < 0.01) and they also exploited significant other resources apart from plant parts (Species effect: F = 9.57, df = 1, P < 0.01). Brown lemurs harvested more water than ring-tailed lemurs (Species effect: F = 4.38, df = 1, P < 0.05).

4.3.1.2 Combined data by reproductive stage:

Dietary niche partitioning varies from stage to stage (figure 4.2b). During the mating season, brown lemurs fed almost exclusively on fruits whereas ring-tailed lemurs harvested a good amount of mature leaves and flowers (Species effect: F = 9.45, df = 1, P < 0.01; Reproductive stage effect: F = 5.46, df = 3, P < 0.01). Diets are similar in both lemur species during the non-reproductive phase which is dominated by fruits. For new leaves, there was significant interaction between species and reproductive stage: both lemur species fed more on young leaves during birth and lactation periods than in other stages (Species x Reproductive stage: F = 4.57, df = 1, P < 0.05). During gestation, diets were composed of similar items but only differed by the quantity and feeding time spent on each item: brown lemurs harvested more fruits than ring-tailed lemurs who fed on mature leaves, fruits and flowers with the same amount.

4.3.1.3 Females and males by season:

Diets are similar for every season; but differ in quantity and feeding time partitioning across seasons (Figure 4.2c). Brown lemurs females have a homogeneous diet of fruit and new leaves or fruit and flowers/ mature leaves, while ring-tailed lemurs' females diversify the amount of items fed on during food-rich seasons with either flowers or new leaves. Shifts in males' diet in both species were roughly similar to that of females from season to season (Figure 4.2d). Significant differences between sex by season were not statistically verified which suggests similarity in diet between males and females across season.

4.3.1.4 Feeding patches:

The use of medium patch size with canopy diameter (CD) of 10-15 m, varied among species by season (Species x Season effect: $F = 9.52$, $df = 1$, $P < 0.01$), whereas the use of larger trees for both species (CD 15-20 m) was higher during the dry season (Season effect: $F = 7.88$, $df = 1$, $P < 0.01$). In every season, ring-tailed lemurs fed more on smaller patches (CD < 1m or CD 1-5 m) (Species x Season effect: $F = 58.58$, $df = 1$, $P < 0.001$), whereas brown lemurs exploited bigger feeding trees with CD > 20 m (Species effect, $F = 25.31$, $df = 1$, $P < 0.001$). Differences between species during the rainy season reflected the utilization of bigger patches with CD > 10m for brown lemurs. The use of different patches was roughly similar during the dry season, and only differs by the use of the two extreme patch sizes: CD < 1m for ring-tailed lemurs and CD > 20m for brown lemurs (Figure 4.3). Both species used trees with CD 5-10m in similar ways from season to season (Species x season effect: $F = .68$, $df = 1$, n.s.).

4.3.1.5 Resource type variety:

The degree of diet partitioning or diet breadth per lemur species can be estimated by the number of resource types exploited by lemur species (Krebs, 1999). On average, ring-tailed lemurs fed on more varied food species than brown lemurs particularly during the high availability period (8 vs. 4.40). However, when food was scarce, brown lemurs also exploited fewer resource types compared to ring-tailed lemurs (5 vs 3).

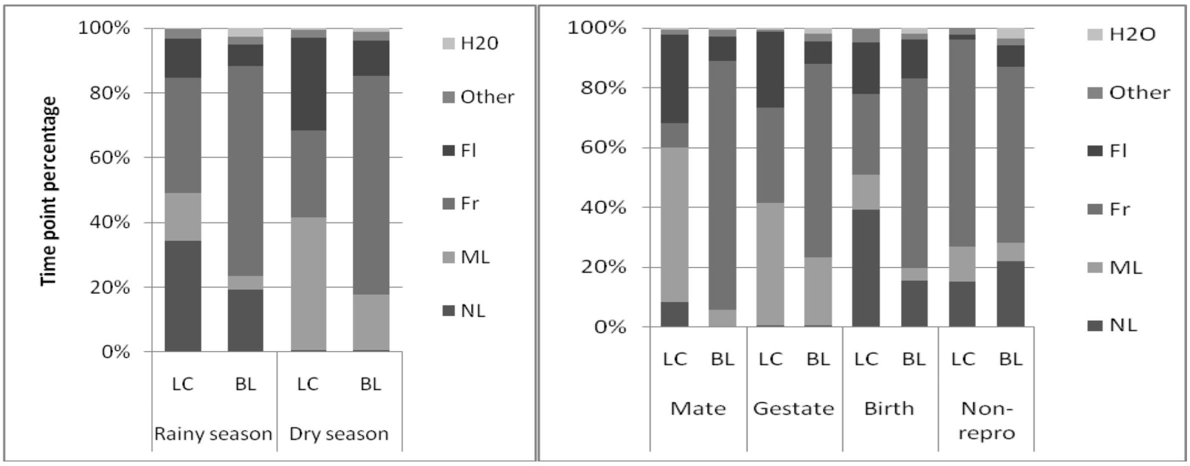


Figure 4.2a. Combined data by season

Figure 4.2b. Combined data by reproductive stage

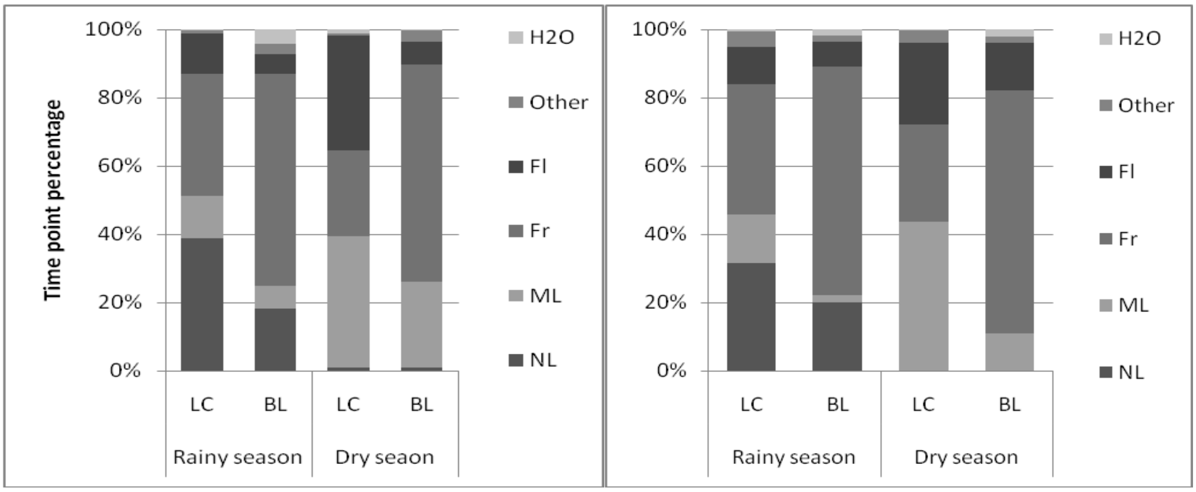


Figure 4.2c. Males by season

Figure 4.2d. Females by season

Figure 4.2: Feeding time on different foods by ring-tailed (LC) and brown lemurs (BL) according to season, reproductive stage and sex.

Fr: Fruits, Fl: Flowers, ML: Mature leaves, NL: New leaves, H2O: water, Non-repro: non-reproductive stage, birth includes birth and lactation periods

(Species x season effect: Scheirer-Ray-Hare test, Statistical value = 0.63, df = 1, $P < 0.05$). These results were gathered from 5-min fixed-intervals time point data, and did not include data from all occurrences samples of feeding data which is presented in a different paper elsewhere. But this gives an estimation of the diet breadth of both species from season to season (figure 4.4).

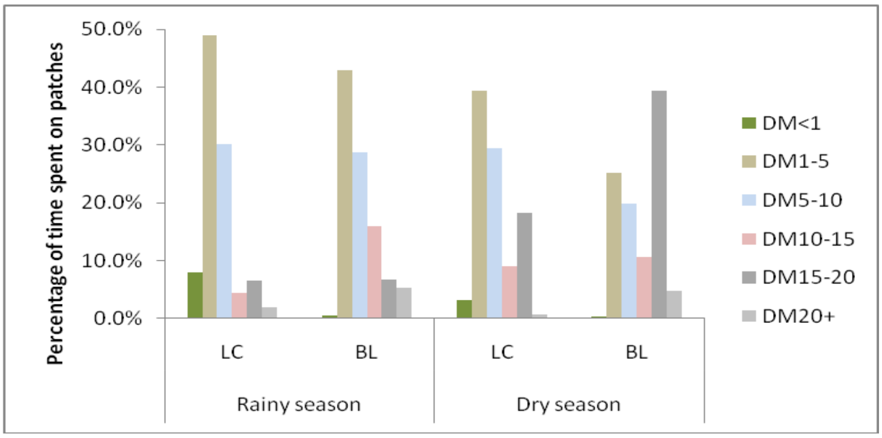


Figure 4.3. Time spent for the use of different patch sizes by ring-tailed (LC) and brown lemurs (BL) across season.
DM: patch diameter

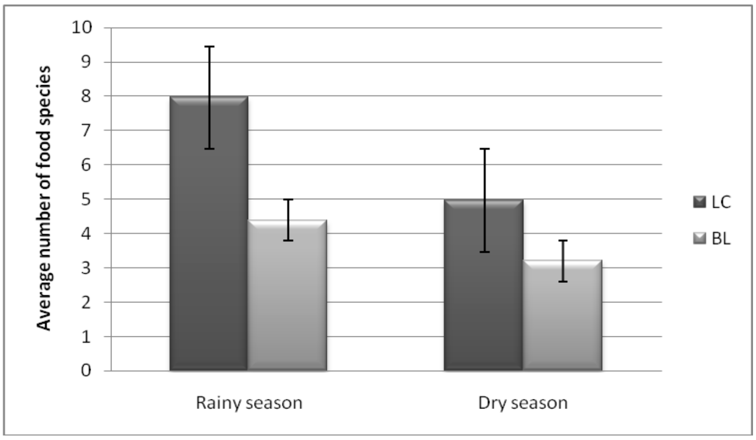


Figure 4.4. Average number of food species varieties exploited by ring-tailed (LC) and brown lemurs (BL) according to season.

4.3.2 Forest substrate

Niche partitioning in forest site use varied across season and between species (Figure 4.5a). Overall, both lemur species used major branches and tree crowns more often than any other forest site. However, there is a difference in the use of tree crowns by brown lemurs, which is much higher compared to that of ring-tailed lemurs (Species effect: $F = 100.09$, $df = 1$, $P < 0.001$), whereas ring-tailed lemurs spent time more often on the ground in open areas or forest edges and on buildings (Species effect: $F = 6.22$, $df = 1$, $P < 0.05$ for concrete constructions; $F = 52.61$, $df = 1$, $P < 0.001$ for ground open areas). Both species entered all forest sites during the hot rainy season, but brown lemurs increased the use of ground in closed canopy forest while ring-tailed ranged on ground outside of the forest. The use of vines was seen in both species across seasons except brown lemurs did not use them substantially during the dry season (Species x season effect: $F = 5.10$, $df = 1$, $P < 0.05$) and ranged more often on the ground in the forest compared to ring-tailed lemurs. Both lemur species used canopy trees and major branches differently according to reproductive stage (Species x reproductive stage x forest site effect: $F = 10.46$, $df = 3$, $P < .001$ for tree crowns; $F = 4.18$, $df = 3$, $P < 0.01$ for major branches).

4.3.3 Height

Significant variation in the use of different forest strata was observed between species (Figure 4.5b): ring-tailed lemurs spent more time on the ground (species effect: $F = 112.18$, $df = 1$, $P < 0.001$), whereas brown lemurs more often used the middle story of 5-10m height (Species effect, $F = 12.89$, $df = 1$, $P < 0.001$). Brown lemurs increased the use of upper story and canopy trees from season to season ($F = 15.41$, $df = 1$, $P < 0.001$ for height 10-15m; $F = 4.17$, $df = 1$, $P < 0.05$ for height 15-20m). During the food scarcity period, ring-tailed lemurs increased the use of lower canopy (below 5m), while brown lemurs used the middle and upper story. This is the only significant interaction between species and season in the use of lower canopy: ring-tailed lemurs ranged more often within 1-2 m height during both seasons ($F = 5.09$, $df = 1$, $P < 0.05$). Although variation was observed between species by season and sex or reproductive stage, no significant interactions occurred between these three variables, which suggests a partitioning of forest site use between species from season to season but similar among sex and reproductive stage as for combined data.

4.3.4 Comparison of social behaviour between lemur species

Even though agonistic behaviour in both lemur species was apparently similar (Figure 4.6), brown lemurs were significantly more engaged in affiliative behaviour such as mutual grooming or approach between each other than ring-tailed lemurs (Kruskall-Wallis: Chi-square = 8.70, $df = 1$, $P < 0.01$). During the dry season, brown lemurs were less aggressive between each other, while ring-tailed were both aggressive and affiliative. During the hot rainy season, in contrast, ring-tails were more affiliate to each other and reduced agonistic behaviour. When data are combined by reproductive stage, brown lemurs were more affiliative during mating and gestation periods; however they increased aggressive behaviour during birth and non-reproductive phases when food was abundant. In contrast to brown lemurs, ring-tailed lemurs were more aggressive during mating and gestation periods and reduced agonistic behaviour during birth and non-reproductive seasons. Agonistic and affiliative differences across season were significant (Kruskall-Wallis: Chi-square = 8.64, df = 1, $P < .01$ for aggression; Chi-square = 7.80, df = 1, $P < 0.01$ for affiliation).

4.3.5 Interpecific social interactions between lemur species

Encounters between brown and ring-tailed lemurs within 10 m radius show that brown lemurs are more aggressive towards ring-tailed lemurs, while this latter is more engaged in peaceful encounters with brown lemur across season, particularly during the food scarcity period (Kruskall-Wallis: Chi-square = 3.78, df = 1, $P < 0.05$) (Figure 4.7). This social behavioural pattern creates equilibrium between intraspecific and interspecific social organizations in each lemur species leading to niche separation (see Discussion). When reproductive stages were examined separately, interspecific patterns of interactions between both lemur species remained similar to seasonally combined data.

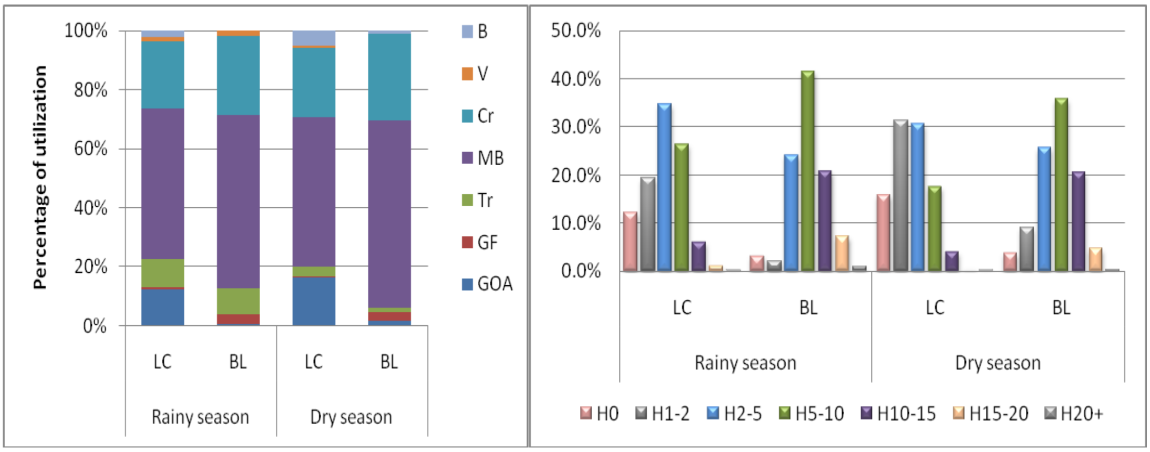


Fig 4.5**a**: Forest site Fig 4.5**b**. Vertical ranging

Figure 4.5: Time spent in different forest sites **(a)** and height **(b)** by ring-tailed (LC) and brown lemurs (BL) according to season. B: Buildings, V: vines, Cr: tree crowns, MB: major branches, Tr: trunk, GF: Ground in closed canopy forest, GOA: ground in open area or outside of the forest, H: height.

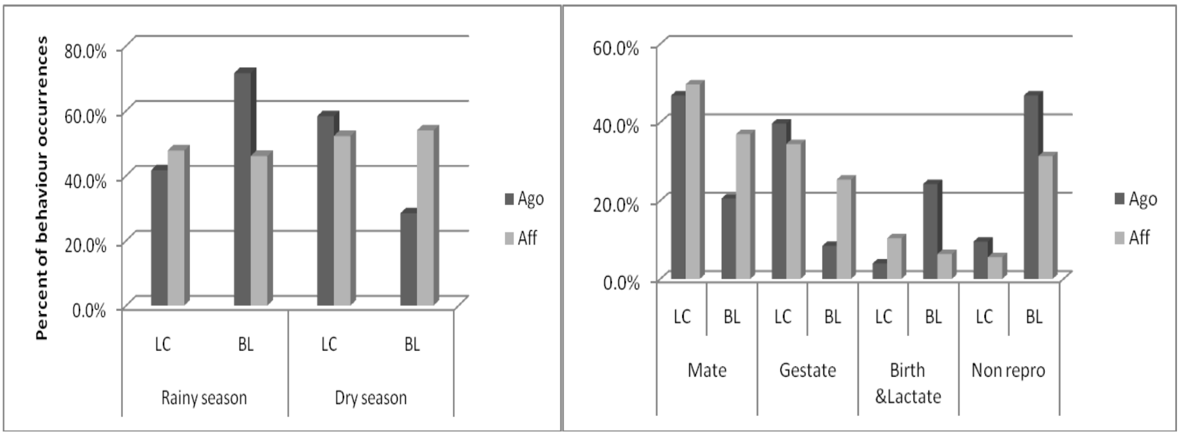


Fig 4.6**a**: Combined data by season Fig 4.6**b**: Combined data by reproductive stage

Figure 4.6: Frequence of occurrences of agonistic and affiliative behaviour in ring-tailed and brown lemurs according to season (**a**) and reproductive stage (**b**). Ago: agonistic behaviour, Aff: affiliative behaviour, Non-repro: non-reproductive stage.

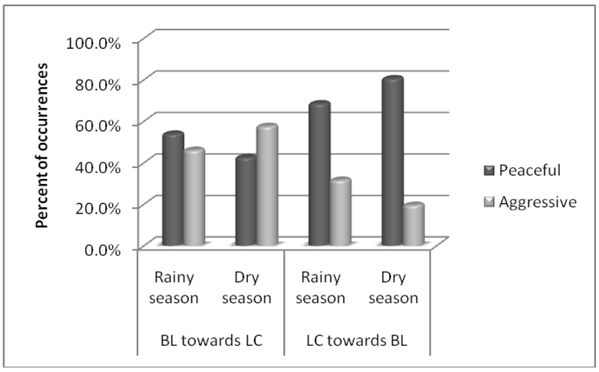


Figure 4.7: Frequence of confrontations between ring-tailed and brown lemurs according to season

4.4 Discussion

4.4.1 Dietary and food patch partitioning

Ring-tailed and brown lemurs share similar food items and dietary overlap is very high in terms of actual foods eaten (Figure 4.2). Their niche separation is quantitative rather than qualitative, seen in the proportions of food types consumed, and in patch size use. Overall, results from this study differ sharply from previous work. At Antserananomby, where ring-tailed and red fronted brown lemurs live in natural sympatry, brown lemurs subsisted mainly on mature leaves for part of the year, particularly during the dry season (Sussman, 1977a; 1977b; 1999). Ganzhorn's (1985; 1986) study of semi-free ranging groups in a natural habitat enclosure at Duke University also found that brown lemurs were more folivorous than ring-tailed lemurs. In contrast, brown lemurs at Berenty ate fruit for the large majority of their feeding time, while ring-tailed ate mainly new and old leaves and flowers. An earlier study by Rasamimanana and Rafidinarivo (1993) found that of a ring-tailed troop that ranged wholly within the gallery forest also spent 60% of time on fruit during both birth and lactation seasons, while a troop on the periphery of the reserve, in the same habitat as our study troops, ate mainly leaves and flowers in all seasons. This may in turn reflects the increasing spatial separation between brown and ring-tailed troops, as browns take the centre of the forest and ring-tailed the periphery (See below and chapter 3). Ring-tailed and brown lemurs partition the environment in other ways including foraging and feeding within different sized patches. Ring-tailed lemurs supplement their diet with varied amount of fruits, flowers, mature leaves and new leaves when available and feed substantially in relatively small food patches particularly during the rainy season; whereas brown lemurs have a more homogeneous diet consisting mainly of fruits and a bit of mature leaves or new leaves depending on the season. During rainy season, brown lemurs feed in small patches like ring-tailed lemurs but differ by also exploiting many larger patches apart from the ones shared with ring-tails. During the food scarcity period, brown lemurs mainly exploit bigger food patches and decrease feeding time on smaller patches that ring-tailed lemurs use.

This diet partitioning between species can also be interpreted by the compromise between metabolic rates and body size. A larger animal requires less energy intake per unit of body weight (Fleagle, 1999; Lambert, 1998). The slight difference in body size between ring-tailed and brown lemurs may have driven a diet partitioning between both species (Lemur catta: 2300 to 3500 g; Simmen et al., 2010; Tattersall, 1982 for captive animals; E. rufus: 2200 to 2300 g; Glander et al., 1992); Razafindramanana pers. obs.). The metabolic rate of brown lemurs is higher and therefore they require high quality food that is rich in energy and nutrients and easy to digest, such as fruits (Pereira et al., 1999; Simmen et al., 2010; Simmen et al., 2003), whereas ring-tailed lemurs feed on lower quality food such as leaves, flowers and fruits (Donati et al., 2009; Jolly, 1966; Sauther, 1998b; Sauther, 1993; Sauther et al., 1999). Simmen et al., (2010) reported a low basal metabolic rate in larger ring-tailed lemurs in comparison with smaller brown lemurs which could be reflect feeding and foraging strategies. These processes are confirmed by the fact that the behavioural thermoregulation of ring-tailed lemurs is more flexible than that of brown lemurs in terms of dietary (Ganzhorn, 1985), thus the former species can live in different environments and habitats and their niche may be wider than that of the brown lemurs (Ganzhorn, 1986; MacArthur and Levins, 1964).

Food type differences were relatively small during the dry season compared to the rainy season. Both species exploited similar plant species during the dry season food scarcity period. However, Lemur catta had a more diverse diet which ensured a certain amount of variety for their dietary pattern and brown lemurs had a restricted diet. This pattern has been reported and by Sussman (1974; 1999) for Antserananomby. At Duke, Eulemur fulvus concentrated their feeding on clumped food resources such as fruits and was considered as a “conservative feeder” (Ganzhorn 1986; (Donati et al., 1999; Rasmussen, 2005). Our results, that are quite similar to others, indicate that ring-tailed lemurs display a consistent dietary pattern from season to season and that they have a generalist behaviour adapted to a variety of environments (Ganzhorn, 1986; Jolly, 1966a; Sussman, 1977a). Eulemur rufus in sympatry with E. rubriventer in southwestern rainforest exhibited a frugivorous diet and diet overlap was also lowest during the food scarcity period though both species relied on the same keystone food (Overdorff, 1993; Overdorff, 1996). This is similar to our finding but contrasts with those from sympatric African monkeys which show low dietary overlap in terms of plant parts during periods of low fruit production (e.g., Gautier-Hion, 1978; Terborgh, 1983; Tutin et al., 1997), however the low dietary overlap during food scarcity period is similar to our finding. Allopatric brown lemurs in the west and south-eastern of Madagascar also exhibit similar frugivory feeding pattern as seen in this study and on other study sites (at Kirindy forest: Donati et al., 1999; at Mandena littoral forest: Donati et al., 2007)

We conclude that, as predicted, niche separation in terms of both diet and feeding patches is much greater during the dry season when food is scarce than in most of the rainy season, and also even higher at the end of the rainy season. Diet differences between sexes in this study were not significant, except that in the dry season female brown lemurs ate more fruit than male brown lemurs. This analysis demonstrates how dietary niche partitioning varies throughout the year, depending on food availability and reproductive stages. Brown lemurs at Berenty are “specialists” (Sussman, 1977a) highly frugivorous and show little flexibility in diet, whereas ring-tailed lemurs are “opportunistic” (Rasamimanana and Rafidinarivo, 1993) frugi-folivores including varied amount of other food items in their diet in every season. These interspecific differences in diet may allow coexistence of both lemur species. These patterns are found in other sites (Ganzhorn, 1986; Pinkus et al., 2006; Sussman, 1977a; Sussman, 1974). This dichotomy is currently under study in depth in terms of plant species, food properties and feeding bouts.

4.4.2 Height and forest sites partitioning

Niche refers not only to the behaviour of an organism but also to the habitat it occupies and its physical adaptation to its habitat (Hutchinson, 1978). In this study, height levels and forest substrate are used to characterize microhabitat use differences in niche dimension between both lemur species (see May and MacArthur, 1972; Schoener, 1983). Brown lemurs range more in terminal branches compared to ring-tailed lemurs, particularly during the dry season. Although both lemur species may use all forest sites but with different frequencies, the dichotomy in habitat use relies considerably on vertical ranging. Brown lemurs prefer ranging from the middle to upper stories and in the canopy trees, whereas ring-tailed lemurs frequently range in lower canopy, mainly during the food scarcity period. Brown lemurs also range on the ground in closed canopy forest more often than ring-tailed lemurs do (at least in this study), though they also visit forest edge and open areas most occupied by ring-tailed lemurs when food is scarce. Both lemur species exploit the middle story level during the rainy season, they timed it differently. In comparison with other studies, our findings follow what has been reported in Antserananomby (Sussman, 1974), that most of the activities of brown lemurs take place above 5 m. The difference is that ring-tailed lemurs are rarely seen above 15 m also found that brown lemurs at Berenty range mainly in middle story (Tanaka, 2007). However, the height levels at Berenty are lower compared to that of E. f. rufus in Ranomafana where they often range above 20 m (Overdorff, 1996) and to that of E. albifrons in Masoala peninsula where they range substantially between 15 – 20 m (Vasey, 2000a; 2004). Thus the use of continuous or closed canopy area either on the ground or higher on the trees is common for the brown lemurs (Donati et al., 2009; Ostner and Kappeler, 2004; Overdorff, 1996b; Pinkus et al., 2006b; Sussman, 1999; Vasey, 2000a). In contrast, the adaptations of ring-tailed lemurs to use all levels of closed canopy area, and also in the forest edges, allow this species to live in a variety of substrate types (Goodman et al., 2006; Gould et al., 1999; Gould et al., 2003; Jolly et al., 2006c; Mertl-Millhollen, 2000; Mertl-Millhollen et al., 2003; Sauther et al., 1999; Simmen et al., 2010; Soma, 2006; Sussman, 1999). These differences suggest that these lemur species may be able to partition food and microhabitat use effectively by feeding or being active in different portions of the tree or with different timing even though in some seasons, they may exploit the same food patches of keystone resources.

Seasonal variation in forest height and substrate also play a role in illustrating specific adaptations for each species (Clutton-Brock, 1973). Microhabitat use partitioning between ring-tailed and brown lemurs can also be based on their circadian activity rhythms. Both lemur species exhibit similar diurnal activity, but brown lemurs are active during the night for up to 10% throughout the rainy season and even more in the dry season (Curtis and Rasmussen, 2002; Curtis and Rasmussen, 2006; Donati et al., 1999; Donati et al., 2001; Jolly et al., 2006c). This may reflect the high cost of energy expenditure required by brown lemurs, met by feeding on high food-quality for longer, and even far away from the troops’ normal home range (Overdorff, 1993; Pinkus et al., 2006; Simmen et al., 2003). However, ring-tailed lemurs meet their energy needs from lower quality food and herbaceous plants (Rasamimanana et al., 2006; Rasamimanana and Rafidinarivo, 1993; Simmen et al., 2003). Ranging for a shorter time and at lower levels reduces costs of horizontal and vertical activities.

Overall, the mechanisms of energy conservation in ring-tailed and brown lemurs are similar to adaptation and socio-biological characteristics in other Malagasy prosimians (Ganzhorn et al., 1999; Simmen et al., 2010; Sussman, 1999). Differences in diet and utilization of microhabitat are related to habitat preferences (Ganzhorn, 1985; Sussman, 1974). The diet specialization of the brown lemurs suggests that they are adapted to exploit abundant and uniform resources but they can change their emphasis as new things come into fruit; thus exhibiting a strict habitat selection for the closed canopy forest (see MacArthur and Levins, 1964; Pinkus et al., 2006). Furthermore, the brown lemurs' habitat requirements for shade and water mean that their niche is more constrained (Scholz and Kappeler, 2004; Razafindramanana, chapter 3). In contrast with brown lemurs, ring-tailed lemurs are adapted to a variety of different habitat types and possess a mechanism of higher water flux in order to conserve water (Simmen et al., 2010). To this extent, they can range from closed canopy forest to arid spiny forest and bush where no Eulemur species lives.

4.4.3 Role of social structure and interspecific interactions in niche partitioning

The Niche concept was developed to address competition (Gause, 1934). Competition constitutes the major force structuring communities (MacNally, 1995). Competition for shared food resources that are limited in abundance will shape species diversity and population sizes in an ecosystem (Ganzhorn et al., 1997b; MacNally, 1995; Raven and Johnson, 1999). It has been also reported that encounters are important in maintaining group cohesion and sociality (Koenig et al., 2006; Sussman, 1999; Sussman et al., 2005; van Schaik, 1996) though few primate studies have demonstrated its role in niche partitioning. When food is scarce, brown lemurs are highly affiliative to each other in order to appease their stress that is related to food scarcity, and also to conserve more energy to cope with mating and gestation periods. Moreover they also exhibit higher active behaviour during the nights of dry season which may need more energy as well (Donati et al., 2009;

Donati et al., 1999). This observation agrees with Sussman and Richard (1974) and (Harrington, 1975) the during mating season, there is an increase of marking frequencies though agonistic encounters are neither intense nor frequent. This behaviour is compensated by the aggressive behaviour that brown lemurs exhibit towards ring-tailed lemurs during the dry season, as they displace ring-tailed lemurs from food patches or from their favourite forest sites so that they can feed peacefully to meet their physical energy demands. However, when food is abundant, brown lemurs remain aggressive within groups and more peaceful towards ring-tailed lemurs. Intra-group agonistic encounters happen when food is abundant, and are often led by females as they have high energetic demands during this period, presumably due to their long lactating period for 14-16 weeks compared to that of ring-tailed lemurs for 10-12 weeks (Harrington, 1978; Klopfer and Boskoff, 1979; Sauther, 1991; Sauther, 1992; Sauther et al., 1999). During this period brown lemurs are seen feeding individually in different patches (Razafindramanana, pers. obs.) to decrease ubiquitous intra-group aggression, thus conserving energy for intra-group social interactions. Ring-tailed lemurs, in contrast, are more aggressive to each other during the food scarcity period, when the strong female hierarchy confers priority of access to certain resources (Ichino and Koyama, 2006; Jolly, 1966b; Kappeler, 1990; Rasamimanana, 1999; Sauther, 1993; Taylor, 1986). They fight to maintain individual and group advantage, defending food patches and territories (Gould, 2006; Mertl-Millhollen et al., 1979; Pride et al., 2006). It can be assumed that social affiliation within ring-tailed lemur groups depends on food availability because when food is abundant the frequency of agonistic encounters is decreased and the group is less aggressive.

Overall, social group structure in ring-tailed lemurs is driven by food availability, territory defence and dominance hierarchy, while in general social interactions with brown lemurs are peaceful. Social group structure and interspecific interactions exhibited by brown lemurs may be driven by higher energetic requirements. This can explain the high tolerance in brown lemur population once each individual meet its energy needs. Brown lemurs are aggressive for some season but are not for other season. This contrasts with ring-tailed lemurs, as they are consistently in the brink of aggression within their group (Koyama, 1991; Pereira, 2006b). This analysis draws a dichotomy of the ecology of both lemur species: individual energy demands for various activity rhythms and social behaviour according to seasons, play a big role in brown lemurs' ecology, whereas food availability, hierarchy and territory are the main niche dimensions that shape ring-tailed lemurs' ecology.

4.4.4 Cohabitation of native and introduced sympatric lemur species: evolution of ecological niches

Brown lemurs, considered as specialists, concentrate on taking the best food from the environment to meet their ultimate energy demands. They also exhibit agonistic encounters towards ring-tailed lemurs to allow them taking their preferred food. This defines them as superior competitors (see Austin, 1999; MacArthur and Levins, 1964b) which prevent the ring-tailed lemurs from occupying some part of their fundamental niche. The inferior competitors, the ring-tailed lemurs, previously inhabited the closed canopy gallery forest at Berenty (Jolly, 1966; Mertl-Millhollen et al., 1979; O'Connor, 1987). They now avoid negative interactions by settling in competitor-free locations (Harrison et al., 1995) where brown lemurs cannot live due to their habitat requirements. This leads to a bimodal niche for ring-tailed lemurs: the forest edges and the gallery closed canopy forest. Forest edges and open area are considered as the realized niche that ring-tailed lemurs were constrained to occupy because of interactions with brown lemurs. This niche evolution shows that the new living conditions do not lie far from the ancestral niche (Bradshaw et al., 2004; Hirzel and Le Lay, 2008) of ring-tailed lemurs which is both the xerophytic forest and bush as well as closed canopy gallery forest (Goodman et al., 2006; Sussman et al., 2006). The brown lemurs, in contrast, once introduced at Berenty reserve, exploited two different habitats: the scrub and gallery forest, though the use of scrub was conditioned by the water provisioning (chapter 3, Pinkus et al., 2006); and higher interspecific overlap in diet and possibly in habitat use was reported in late 90s at least during the late dry season (Jolly et al., 1982b; Pinkus et al., 2006b; Rasamimanana et al., on press). But this has been changing after stopping water provisioning in the scrub (chapter 3) when brown lemurs occupy only the closed canopy gallery forest and ring-tailed lemurs are displaced into the periphery and forest edges. This demonstrates that the global patterns of niche evolution are driven by habitat-dependent fitness (Gilbert and Lechowicz, 2004) and that the sympatric species have evolved using a competitive equilibrium to reduce niche overlap and interspecific competition (Alley, 1982; Holt, 2003).

Susman (1999) reported that differences in diet, habitat use, social structure and interactions are related to habitat preferences and are independent of the presence or absence of the other species. Various studies from different species of primates also reported that there should be differences in diet, activity budget and/or habitat use to allow coexistence by minimizing competition for resources (Crockett and Wilson, 1980; Freed, 1996; Ganzhorn, 1988b; Gittens and Raemaekers, 1984; Hladik, 1977; Janson, 1988; Raemaekers, 1978; Struhsaker and Oates, 1975; Struhsaker, 1981; Sussman, 1977b) Differences reflect phylogenetic adaptations to environmental conditions which occur where the species are allopatric (Donati et al., 1999; Rasmussen, 2005; Ganzhorn, 1985; Ganzhorn, 1986). Generalists' ring-tailed lemurs occur in a wider niche including many habitat types. The brown lemurs' niche is more constrained and might be included in that of the generalists (Hutchinson, 1978). Hence, ring-tailed lemurs are considered as "Jack-of-all-trades though masters of none", while brown lemurs are masters of the specialized niche of gallery forest (MacArthur and Levins, 1964; May and MacArthur, 1972). Overall, after decades of competitive equilibrium between native ring-tailed and introduced brown lemurs, a trend towards their fundamental niches that would reflect the niche separation of both lemur species seen in Antserananomby in long-term (Sussman, 1977a; 1974), is now occurring at Berenty reserve. A comparison with the situation of natural sympatry between ring-tailed and red collared brown lemurs will be described in the next chapter.

5. Sympatric association of *Lemur catta* and *Eulemur collaris* in Ambatotsirongorongo, south-eastern Madagascar: diet, habitat use and social relationship.

Abstract

I report the unique ecological association of ring-tailed lemurs, Lemur catta and collared brown lemurs, Eulemur collaris in the transitional zone of Ambatotsirongorongo forest in south-eastern Madagascar. The study was conducted from March to August and then from October to December 2009. One group of collared brown lemurs and one group of ring-tailed lemurs were followed for a total of 252 hours and 205 hours respectively using group scan sampling of 5 min intervals. Approximately 55% of the collared brown lemur height records were more than 8 meters during the dry season, compared to 6% of the ring-tailed lemurs' records. Ring-tailed lemurs used the middle story for about 64.6% of their time compared to 29% for collared brown lemurs. Both ring-tailed and red collared brown lemurs had similar diet with a resembling dietary diversity in terms of food species. Differences on diet between both lemur species relied on the quantity of food types consumed and feeding time. Red collared brown lemurs conserved their allopatric frugivorous dietary pattern as seen in littoral forest and was confined primarily to the upper regions of the forest especially during the dry season but occasionally foraged on the ground mainly during the wet season. Ring-tailed lemurs conserved part of their ancestral behavioural ecology as generalist in terms of food quantity and quality by feeding on flowers during the high energetic cost period such as the lactation season, and are found throughout the entire vertical range of the forest and exploited all forest sites. In the present study, coexistence of red collared brown lemurs and ring-tailed lemurs is possible by sharing the feeding time on similar food items across seasons; and by exploiting different levels of vertical stratification and forest sites. In summary, the sympatric association between both lemur species is conditioned by seasonality that can be related either to the season or to the energy requirements for each season, or to the seasonal shifts in resource availability.

5.1 Introduction

Behavioural studies of the lemurs in Madagascar have been contributed relevant information and theories about primate ecology and social structure. Sympatric association is of interest to primatologists to understand interaction of two or more reproductively isolated population which inhabit a common or overlapping geographical area (Crook and Aldrich-Blake, 1968; Hutchinson, 1978). Ecologists particularly have concentrated on differences in the way species in the same community utilize resources (Schoener, 1974). The standard way to express sympatric association is mainly competition and/or niche overlapping presented in a variety of studies such as the density compensation in a number of primate communities in South America, Asia and Africa – an increase in the density of one species in response to the decline in abundance of a competing species (Gonzalez-Solis et al., 2001; Peres and Dolman, 2000; Struhsaker and Oates, 1975). Other studies investigate dietary overlap in primate assemblages caused by feeding competition between primate species (Waser and Case, 1981). Gautier-Hion et al. (1983) studied the overlap in foraging heights and diets of Cercopithecus monkeys in polyspecific associations. Numerous studies have focused on feeding and forest level niche partitioning of primate sympatric species (e.g., Charles-Dominique, 1977; Clutton-Brock, 1977; Curtin, 1976; Hladik, 1977; Wroe et al., 2007). There are many behavioural investigations on primates and other animals, such as the recent study on the interpsecific competition of gibbons with other vertebrate frugivores in a Bornean rainforest (Marshall et al., 2006). Ganzhorn (1999) even suggested that competition with non-primate taxa has profound effects on the evolution of primate communities. These different studies converge with the earlier principle of modern primate ecology which is “coexistence of two related species in any area is only possible if their differential exploitation of the environment maintains competition at a minimum. If this is not so, competition will lead to the exclusion of one species from the habitat” (Crook and Aldrich-Blake, 1968). Organisms within ecological communities are linked together by biotic relationships like competition, predation, and mutualism (e.g., Boucher, 1985; Crawley, 1992; Heymann, 2000; Keddy, 1989).

In Madagascar, among the studies on community ecology, some have been conducted with Eulemur ssp. or with Lemur catta, focusing on competition and/or niche partitioning or overlapping of sympatric lemurs. Cohabitation of Lemur catta and Eulemur fulvus rufus has been studied in dry deciduous forest in Antserananomby (Sussman, 1977b; Sussman, 1999); a comparative study of Lemur catta and Propithecus verreauxi has been conducted by Jolly (1982a) in dry deciduous gallery forest at Berenty Reserve; Simmen et al. (2003) studied food intake of three sympatric species of brown, ring-tailed and sifaka lemurs at the same place; Pinkus et al. (2006) focused on feeding competition between ring-tailed and brown lemurs at Berenty Reserve. In the high montane rainforest of Ranomafana, Eulemur rubriventer and Eulemur fulvus rufus are highly frugivorous with very similar diets, though Eulemur rubriventer differs their habitat use by exploiting terminal branches and taller trees more often especially during food scarcity period (Overdorff, 1993; Overdorff, 1996). Sympatric species also decrease their degree of overlap by differentiating their crucial activity times such as feeding (Schoener, 1974). Similar patterns have been observed in western dry deciduous forest populations of Eulemur fulvus rufus and Lemur catta (Sussman, 1974; 1999) and in the northern populations of Eulemur coronatus and Eulemur fulvus sanfordi (Freed, 1996). In a lowland coastal rainforest in northeastern of Madagascar, Varecia variegata rubra use larger trees and feed mainly on fruits throughout the year compared to Eulemur fulvus albifrons who has a varied diet (Vasey, 2000a; Vasey, 2004).

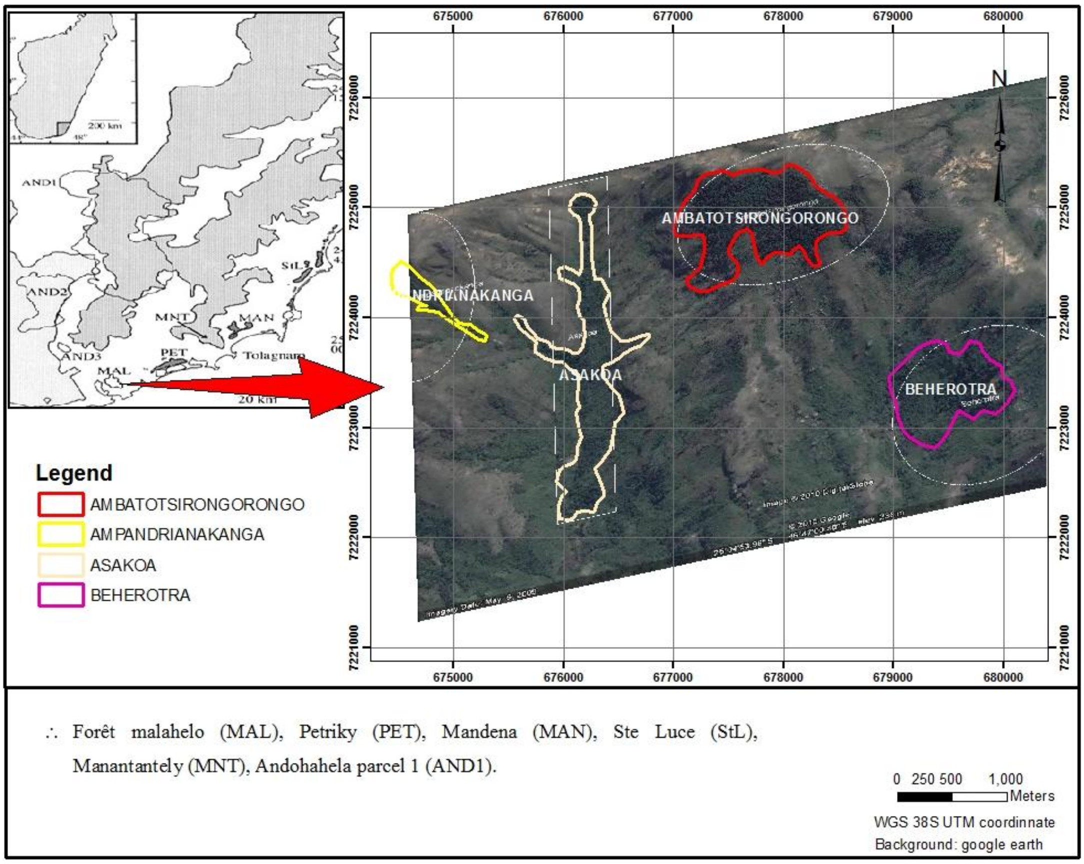
Despite the recent growth of interest in ecological studies of sympatric lemur species in Madagascar, mainly with lemur species living in the same ecosystem; none of them has been conducted on a community of species belonging to different ecosystems, though occurring naturally in the same forest. The three major types of forest occurring in Madagascar, are all found in south-eastern Madagascar: fragments of littoral forest lying along the coast, montane and lowland humid forests on the slopes of Anosyenne and Vohimena chains and the spiny and dry forests lying west and southwest of the Anosyennes chain (Goodman and Ganzhorn, 2004; Goodman et al., 1997). In between these dominant types of forest, lies a small biogeographical transitional forest zone, Ambatotsirongorongo, which has been identified as a high priority conservation zone for southern Madagascar due to the high species diversity of flora and fauna on the site (Andrianarimisa et al., 2005; Ganzhorn et al., 1997; Nicoll and Langrand, 1989; Ramanamanjato et al., 2002). The lemur community comprises species from both dry and humid forests in a combination rarely found elsewhere, and also includes most species found in the littoral forests. This gives the unique natural cohabitation of ring-tailed lemrs, a lemur species whose distribution includes spiny bush, gallery, dry deciduous forests, and anthropogenic savanna (Goodman and Langrand, 1996; Goodman et al., 2006), and red collared brown lemurs, a lemur species whose distribution is restricted to littoral and tropical moist lowland forests on the eastern coast of Madagascar (Donati et al., 2007; IUCN, 2010; Harcourt and Thornback, 1990; Mittermeier et al., 2010). The forests in the south-eastern Madagascar are highly threatened due to human demands for fuel, crop land and pasture (Bollen and Donati, 2006; Ganzhorn et al., 2000), making its unique lemur assemblage under pressure of extinction. Given the potential historical, species diversity and conservation importance of this transitional zone of Ambatotsirongorongo, numbers of ecological studies are needed. These might be of particular biogeographic conservation interest.

In this paper, we present the ecological cohabitation of ring-tailed and red collared brown lemurs in terms of diet, habitat use and social intergroup interactions between those opposed species occurring together in this unique zone between humid and dry ecosystems of Ambatotsirongorongo. We demonstrate how both species live and share ecological niche dimensions such as food resources, forest levels and substrate, and how they interact between themselves. We predict that each lemur species will live the way they do so in their original habitat in allopatry. We will discuss the results in terms of niche partitioning and ecological behavioural evolution with other studies on sympatric association between ring-tailed and brown lemurs as well as with studies on each species in allopatry, and conclude by discussing some possible approaches to protect this unique forest and its lemur population.

5.2 Methods

5.2.1 Description of the study site:

Ambatotsirongorongo forest (25° 4.703’S 46° 47.246’E) also called Malahelo Forest, lies on the western part of the Ambatotsirongorongo Mountain at around 400 m elevation. The whole forest covers less than 20 ha. It is composed of three forest fragments: the fragment of Ambatotsirongorongo itself (Malahelo forest) which is now the smallest fragment of the entity, the Vohisampa fragment and the largest fragment of Lavasoa. Historical land cover maps indicate that these forests have not been directly connected to other forests for more than 40 years (Foiben-taon-tsarin-tanin'i Madagasikara, 1979). Floristic and faunistic inventories have been conducted at Ambatotsirongorongo fragment where our study was carried out (Andrianarimisa et al., 2005; Ramanamanjato et al., 2002). This forest is situated in a block on the top of the mountain, with a narrower strip extended southward downhill toward the valley. The slope near the bottom of the mountain is deforested and surrounded by agricultural fields and cattle pastures. The forest of Ambatotsirongorongo lies on granitic rock outcrops and is characterized by two different vegetation types: the humid closed canopy forest and the thicket bush which is mainly dominated by herbaceous species and invasive plants (Ramanamanjato et al., 2002; WCS, 2005; Razafindramanana, pers. obs.) (Figure 5.1). The typical canopy height of the humid forest is approximately 12-14 m with canopy coverage of 45% from emergent trees such as Carissa sessiflora (Apocynacea) and Macphersonia sp (Sapindaceae). The understory is composed of trees of 4-8 m height and dominated by Canthium sp (Rubiaceae), Trilepisium madagascariensis (Moraceae), Treculia sp (Sapindaceae) and Scolopia sp (Salicaceae). The lower story of 0-4 m height is characterised by herbaceous plants such as Selaginella polymorpha (Selaginellaceae), Dracaena reflexa (Convallariaceae) and Gaertnera macrostipula (Rubiaceae). At the edge of the humid forest, invasive species of Lantana camara surrounds the area, thus formed a bush at the periphery of the forest. The thicket vegetation lies on a ferralitic soil and is located for 600 m south-west outside of the humid forest at 260 m elevation. It is characterized by smaller trees of 5-6 m height with diameter less than 10 cm. Dominant species are Leptolaena pauciflora (Sacolaenaceae), Enterospermum sp (Rubiaceae) and Polycardia phyllantoides (Celastraceae). Other plant species typical of spiny and dry forests have been seen on the site such as Euphorbia enterophora (Euphorbiaceae), Acacia brachypus (Fabaceae), Pachypodium sp (Apocynaceae) and Xerophuta sp (Velloziaceae) which indicates that the site is a transitional zone between humid and dry forests (WCS, 2005). Apart from these two main vegetation types, there is also ragged vegetation in the northwest of Ambatotsirongorongo extended to Asakoa dominated by bush and scrubby vegetation. All of these habitats were visited and exploited by the groups of lemurs we followed during observations. The site is marked with two clear seasons: the wet season from December to June and the dry season from July to November. During our observations in the field, the minimum and maximum temperatures recorded are 17°C and 42°C respectively with an annual average of 24°C. Rainfall is very similar to a nearby transitional forest in Andohahela with 700-800 mm per year (Nicoll and Langrand, 1989; Ramanamanjato et al., 2002).



∴ Forêt malahelo (MAL), Petriky (PET), Mandena (MAN), Ste Luce (StL), Manantantely (MNT), Andohahela parcel 1 (AND1).

Figure 5.1 Map of Ambatotsirongorongo site (Forêt Malahelo), showing the position of the different forest fragments in it.
Ambatotsirongorongo: humid closed canopy forest, Beherotra: thicket bush, Asakoa and Ampandrianakanga: isolated closed canopy forest fragment composed of native and invasive plant species

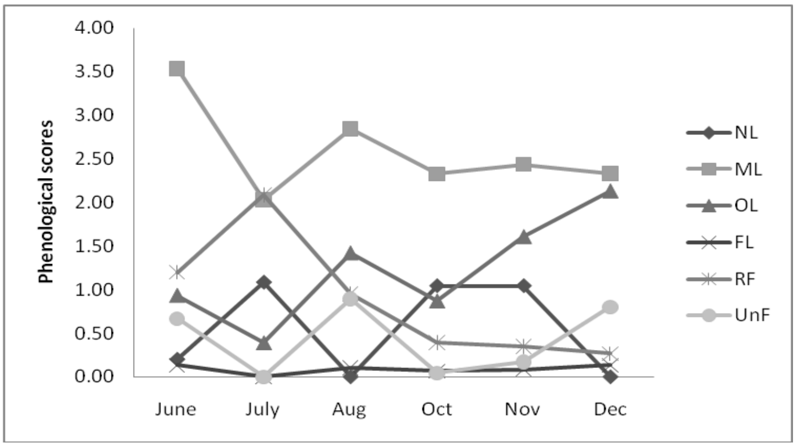


Figure 5.2: Plant phenology at Ambatotsirongorongo forest during our observation in 2009
NL: new and young leaves, ML: mature leaves, OL: Old leaves, FL: flowers and flower buds, RF: Ripe fruits, UnF: Unripe fruits

5.2.2 Methods:

The study was conducted from March to August and then from October to December 2009. Data from the first one month and half were discarded from analysis as it served as group habituation time. The majority of observations were made on two groups of lemurs: one group of red collared brown lemurs and one group of ring-tailed lemurs (see Table 5.1 for group composition). The brown lemur group was observed for a total of 252 hours and the ring-tailed lemur group for 205 hours during group scan sampling of 5 min intervals (Altmann, 1974). The two groups were followed for alternating periods of two to three days each, from dawn to dusk whenever possible. The daily observation duration ranges from 6-14 hours depending on finding the group in the morning (mainly for ring-tailed lemurs) and due to difficulties of walking on the site (with a gradient of approximately 5 in 10 steep slopes). The red collared lemur group was fully habituated, and the ring-tailed lemurs grew increasingly tolerant of the observer’s presence by the end of the study. Every 5-min time, samples were taken of the number of animals in view with their activities, the animal height, and the forest substrate (i.e., ground in the forest or outside of the forest, trunk, major branches, tree crown, liana) the animals were using. Social behaviour and interactions such as aggressive conflict or affiliative behaviour (approach, cuddling, grooming) were recorded instantaneously for all occurrences throughout the day. Whenever the group was observed feeding on a tree or vine, the tree height, its diameter at breast height, the plant species, plant parts consumed and the position of the animals feeding on it were recorded. Specimens of the foliage were taken either to the QMM biodiversity department or to the Parc Botanique et Zoologique d’Antananarivo in Madagascar for identification. Phenological data were recorded every 15 days from 212 trees of 20 plant species. Abundance of plant parts is rated on relative scale from 0 (none) to 4 (75-100% plant part available). Patterns of food availability and abundance on this site are shown on Figure 5.2. Focal animal sampling was also used to study ecological difference between males and females but these results are not presented here. Day ranges and activity patterns are also reported elsewhere.

5.2.3 Statistical analysis:

The frequencies of scans for feeding variables (plant part consumed per plan species, canopy diameter of feeding patches), habitat use variables (height and forest site) and social behaviour such as agonism and affiliation were calculated daily for each lemur group regardless of the number of animals involved in each interaction. Daily proportions of diet, substrate and height were tested for normality and then transformed into log to be able to use parametric statistical tests (Dytham, 2007; McGarigal et al., 2000). Two-way ANOVA was carried out to test interactions by lemur species and seasonality in forest levels, substrates and food consumption. Each day of observation was considered as the unit of analysis, giving a sample size of 19 days for red collared brown lemurs and 17 days for ring-tailed lemurs. Dependent variables included heights, forest site variables, plant part consumed and feeding patch diameters. Independent variables were seasons and lemur species. Other behaviour such as agonism and sociality between species and intra species was tested for differences using Mann-Whitney non-parametric test. Shannon Diversity Index was calcultated to evaluate the dietary diversity between the two lemur species, using the formula:

$$H = \sum_{i=1}^{s} - (P_i * \ln P_i)$$

where:

H = the Shannon diversity index

P_i = fraction of the entire population made up of species i

S = numbers of species encountered

∑ = sum from species 1 to species S

Table 5.1 Study group composition during 2009

Lemur species	Group	Females		Males		Unknown sex	Infants	Total*
		A	SA	A	SA			
Lemur catta	Lc	3		2	3		2	8
Eulemur collaris	Ec	4	2	7	1	3	2	17

*Total without infants number

5.3 Results

5.3.1 Forest level and substrate preference

Both lemur species were active and fed lower in the forest from season to season (Figure 5.3a). Approximately 55% of the collared brown lemur height records were more than 8 meters during the dry season, compared to 6% of the ring-tailed lemurs records (see Table 5.2 for statistical results). Ring-tailed lemurs, in contrast, made the most of the middle story (between 2 to 8 meters) for about 64.6% of their time during the dry season. These differing stratum preferences appeared to be associated with the patterns of substrate utilization (Figure 5.3b). Forest site use varied across seasons and between species particularly for the use of tree canopy, ground and bush. Both species exploited tree crowns almost similarly during the rainy season, but the red collared brown lemurs used them substantially during the dry season. Ring-tailed lemurs ranged mainly on the ground and in bushes during the dry season, while red collared brown lemurs made the most of them during the rainy season. Even though differences were detected between both lemur species in the use of major branches and tree trunks, these were not statistically significant.

5.3.2 Degree of folivory and frugivory

Seasonal variation in the diets of both lemur species was marked. Mature leaves were important food items across the year. Ring-tailed lemurs were less frugivorous but more folivorous than red collared brown lemurs: the former species consumed 33% leaves and 65% fruit, the latter 22% leaves and 73% fruit, although significant differences were not seen in the consumption of fruits, indicating that both species could be considered as frugivorous (> 50% of their feeding time spent on fruits) (see Table 5.2 for statistical results). The consumption of flowers differs between species across seasons: ring-tailed lemurs fed more on flowers during the rainy season, while brown lemurs consumed more of it in the dry season. When the data are separated by season (Figure 5.4), ring-tailed lemurs focused more on mature leaves during the rainy season, while collared brown lemurs fed on a good amount of it in the dry season. Differences on diet between both lemur species relied on the proportions of food types consumed and feeding time.

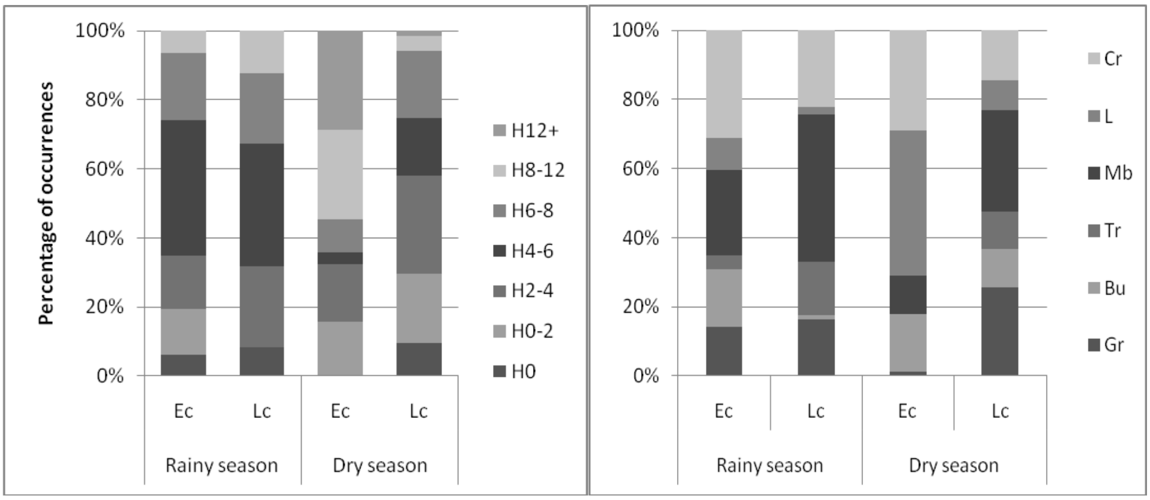


Figure 5.3a Figure 5.3b

Figure 5.3. Percentage of (a) Forest level and (b) forest substrate exploited by Eulemur collaris (Ec) and Lemur catta (Lc) during rainy and dry seasons.

H: Height in meter. Cr: Tree crown, L: Liana, Mb: Major branches, Tr: Tree trunk, Bu: bush, Gr: Ground

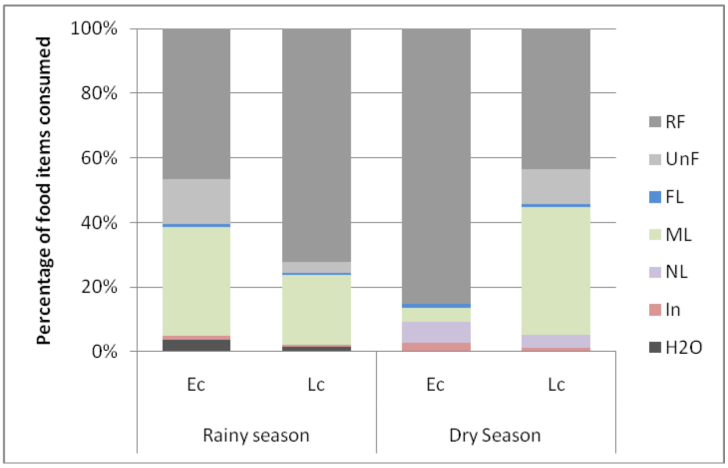


Figure 5.4: Percentage of food items consumed by E. collaris (Ec) and L. catta (Lc) during the rainy and dry season.

RF: ripe fruits, UnF: unripe fruits, Fl; Flowers, ML: Mature leaves, NL: New leaves, In: Insects and other, H2O: water

Table 5.2. Statistical results of the two-way ANOVA analysis

Effect of Independent variables	**Dependent variables**	**F**	**P value**
Species	H 0m	2.05	0.18
	HT 0-2m	4.53	**0.047**
	HT 2-4m	0.74	0.397
	HT 4-6m	1.32	0.261
	HT 6-8m	0.605	0.445
	HT 8m+	6.01	**0.04**
	Bush	4.21	0.055
	Ground	0.098	0.757
	Tree crown	0.98	0.33
	Patch diameter 5-10m	6.91	**0.016**
	Mature leaves	0.83	0.371
	Flowers + buds	21.42	**0.01**
	Fruits	0.424	**0.51**
Season	H 0m	0.002	0.963
	HT 0-2m	7.22	**0.015**
	HT 2-4m	0.014	0.905
	HT 4-6m	6.73	**0.016**
	HT 6-8m	1.7	0.205
	HT 8m+	0.9	0.347
	Bush	2.7	0.117
	Ground	0.628	0.437
	Tree crown	2.69	0.112
	Patch diameter 5-10m	0.98	0.333
	Mature leaves	0.14	0.711
	Flowers + buds	7.71	**0.05**
	Fruits	0.038	0.846
Species x Season	H 0m	4.75	**0.05**
	HT 2-4m	6.83	**0.015**
	HT 4-6m	6.37	**0.019**
	HT 6-8m	3.32	0.082
	HT 8m+	0.42	0.522
	Bush	6.41	**0.021**
	Ground	5.93	**0.024**
	Tree crown	5.39	**0.027**
	Patch diameter 5-10m	6.43	**0.02**
	Mature leaves	689	**0.015**
	Flowers + buds	7.71	**0.05**
	Fruits	1.45	0.236

The statistical results with the other dependent variables not shown in this table are not significant for the three outputs of the two-way ANOVA analysis

5.3.3 Species composition of diet

The variety of food consumed by both lemur species was high: 51 species in 205 hours of observation on ring-tailed lemurs, 47 species in 252 hours of observation on red collared brown lemurs, given a Shannon Index (H) of 3.93 for ring-tailed lemurs and 3.85 for red collared brown lemurs (Table 5.4). Thirty-two percent of the 74 food species recorded during the total observations was shared between both lemur species, but differed, for some plant species, by the food items exploited (Table 5.4). Their main diet was composed of two exotic plant species Melia azedarach and Lantana camara but consumed with different proportions (Table 5.3).

Table 5.3. Top 10 food species exploited by Lemur catta and Eulemur collaris

Lemur catta			Eulemur collaris		
Family	Species	No. of occas.	Family	Species	No. of occas.
Meliaceae	Melia azedarach	197	Verbenaceae	Lantana camara	165
Verbenaceae	Lantana camara	126	Icacinaceae	Pyrenacantha sp.	43
Rubiaceae	Coptosperma sp	37	Meliaceae	Melia azedarach	43
Salicaceae	Flacourtia ramontchi	23	Burceraceae	Canarium sp	32
Linaceae	Hugonia sphaerocarpa	15	hypericaceae	Harongana madagascariensis	29
Linaceae	Hugonia littoralis	13	Ulmaceae	Chaetacne madagascariensis	17
Rubiaceae	Peponidium sp	13	Cannabaceae	Trema orientalis	15
Moraceae	Streblus dimepate	12	Salicaceae	Slocopia madagascariensis	11
Erythroxylacea	Erythroxylum buxifolium	11	Salicaceae	Flacourtia ramontchi	11
Hypericaceae	Harongana madagascariensis	10		Unknown Liana	11

5.3.4 Social interactions

For both lemur species, intra-group agonistic behaviours such as presenting and chasing were more frequent in ring-tailed lemurs than in red collared brown lemurs (Mann Whitney, 2-tailed, U= 4.5, Z=-2.56, P < 0.00). Intra-group aggression were higher during the rainy season (Mann Whitney, 2-tailed, U= 6.5, Z=-1.91, P = 0.05), while affiliative behaviours, including huddling, grooming, play and maternal behaviour were more frequent during the dry season (Figure 5.5a). Intergroup interactions, in contrast, were more peaceful during the wet season, and were rare during the dry season (Figure 5.5b). These were not statistically significant either for species effect or for season effect. Intergroup interactions were seen between both lemur species and with other lemur species such as Propithecus verreauxi and Hapalemur griseus.

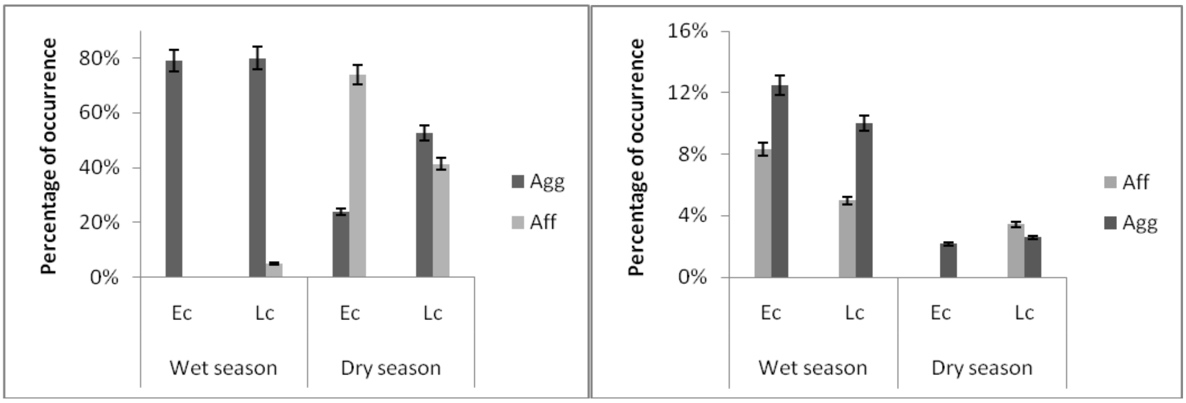


Figure 5.5a

Figure 5.5b

Figure 5.5: Frequences of intragroup (a) and intergroup (b) interactions in Lemur catta and Eulemur collaris
(Agg: aggression, Aff: Affiliation)

Table 5.4 Food plants and food items of Lemur catta and Eulemur collaris

			Lemur catta		Eulemur collaris	
Family	Species	Vernacular name	Parts consumed	No. of occas.	Parts consumed	No. of occas.
Anacardiaceae	Abrahamia sericea	Resonjo	Fr	1		
Aphloiceae	Aphloia theaeformis	Fandrama			ml, fr	3
Apocynaceae	Cabucala madagascariensis	Fekanala	Fr	1		
Arecaceae	Dypsis sp.	Sihara			Fr	1
Asphodelaceae	Aloe vahombe	Vahona			Ml	1
Burseraceae	Canarium sp.	Aramy			ml, fr	32
Cannabaceae	Trema orientalis	Anjarenjo			Ml	15
Dilleniaceae	Tetracera madagascariensis	Vaha	Ml	1		
Ebenaceae	Dioscorea sp	Forofoky	Fr	1	Fr	2
Erythroxylacea	Erythroxylum buxifolium	Taingalavo	ml, fr	11	Fr	1
Euphorbiaceae	Dalechampia sp.	Sariondro	Ml	7		
	Drypetes sp.	Hazofotsy	Fr	4	Fr	3
	Uapaca sp.	Voatapika	Ml	1		
Fabaceae	Cynometra dophinensis	Mapay			Nl	2
	Dialium sp.	Azofotsy	Fr	4	Fr	1
Faucheaceae	Faucherea sp.	Nato	Fr	1	Fr	10
Flagelliaraceae	Flagellaria indica	Vahimpiky	ml, fr	1		
Hippocrataceae	Hippomea sp.	Farivomanga	Ml	5	Ml	2
Hypericaceae	Harongana madagascariensis	Arongana	nl, ml, fl, fr	10	ml, fr	29
Icacinaceae	Pyrenacantha sp.	Vahikatepoka	nl, ml	2	nl, ml, fr	43
Lauraceae	Ocotea racemosa	Tefomoa			Fr	2
Liliaceae	Dracaena reflexa	Falinandro			bd, nl	5

Table 5.4-Contd

			Lemur catta		Eulemur collaris	
Family	Species name	Vernacular name	Parts consumed	No. of occas.	Parts consumed	No. of occas.
Linaceae	Hugonia sp.	Arisy	Ml	2		
	Hugonia sphaerocarpa	Kirisimor	ml, fr	15	Fr	1
	Hugonia littoralis	Vahipisoroka	ml, fr	13	Ml	1
Loranthaceae	Viscum ambongoenis	Velomihantona	Ml	3	Ml	1
Meliaceae	Melia azedarach	Vondelaka	nl, ml, fl, fr	197	nl, ml, fr	43
Moracea	Ficus lutea	Amonta	ml, fr	9	Fr	1
	Ficus sp.	Adabo	Fr		Fr	3
	Streblus dimepate	Arondela	ml, fr	12		
	Trilepisim madagascariensis	Andromena	Fr	1		
Musaceae	Muca paradisiaca	Akondro	Fr	2		
Myrtaceae	Eugenia sp.	Rojobo	Fr	2		
Pandanaceae	Pandanus sp.	Fandra			ml, fr	9
Rubiaceae	Bremerie cf. erectiloba	Andovosely	Fr	1		
	Canephra madagascariensis	Azogalala	ml, fr	6	ml, fr	9
	Coptosperma sp.	Valomangoro	ml, fr	37	ml, fr	7
	Peponidium sp.	Fasikaitra	Fr	13	Fr	6
	Breonia chinensis	Valotsy	Fr	3	Fr	3
	Psychotria Aff. subnubila	Pimakiro	ml, fr	6		
Rutaceae	Vepris araliodes	Ampoly	ml, fr	3	Fr	4
Salicaceae	Flacourtia ramontchi	Hily 1	Fr	23	Fr	11
	Slocopia madagascariensis	Lamoty	Fr	5	Fr	11
Sapindanaceae	Tina striata	Fandrinakanga 2			Fr	1
Sapotaceae	Chrysophyllum boiviniam	Malamasafo			Fl	1
Solanaceae	Solanum nigrum	Anamamy	nl, ml, fr	8		
Sterculiaceae	Nesogordonia sp.	Natoroboka			ml, fr	6

Table 5.4-Contd

Family	Species name	Vernacular name	Lemur catta		Eulemur collaris	
			Parts consumed	No. of occas.	Parts consumed	No. of occas.
Verbenaceae	Lantana camara	Radrika	ml, fl, fr	126	ml, fr	165
Violaceae	Rinorea angustifolia	Retsara			Fr	1
	Agelaca pentagina	Vahika	Ml	3		
	Chaetacne madagascariensis	Hily 2			Ml	17
	Saldina aegiolodes	Mangavoa	Fr	6		
	Unknown T1	Eimahavano	Ml	1		
	Unknown T3	Foto	Fr	6	Fr	7
	Unknown H2	Holatra	Ml	1		
	Unknown T4	Kisampotsy			Fl	1
	Unknown T5	Lendemo			Fr	3
	Unknown T6	Monky			Fr	1
	Unknown T7	Nonoka	ml, fr	8	Ml	3
	Unknown T8	Sarizaky			Fr	1
	Unknown T9	Sipotiky	Ml	1		
	Unknown T10	Trakavola	nl, ml	3		
	Unknown T11	Tsimahavanono	Ml	4		
	Unknown T12	Tsipotika	Fr	1		
	Unknown T13	Tsiriky	ml, fl	2		
	Unknown T14	Tsivonjavonja	Ml	2		
	Unknown L1	Vahikerotsy			Fr	7
	Unknown L2	Vahimbitsika	Ml	1		
	Unknown L4	Voanato			Fr	2
	Unknown L5	Voatavo	nl, ml	3		
	Unknown L6	Voavahy			nl, fr	11
	Unknown L7	Volombato	Ml	2	Ml	

5.4 Discussion

5.4.1 Feeding partitioning and adaptations

The unique cohabitation of ring-tailed and red collared brown lemurs in this transitional forest of Ambatotsirongorongo demonstrates different patterns from those seen at Antserananomby dry forest with ring-tailed and red fronted brown lemurs, thirty years ago (see Sussman, 1974). Both forests are different in terms of vegetation structure, soil composition and other abiotic parameters such as climate. In general, the overall diet of both lemur species is similar, with a resembling dietary diversity. Ring-tailed lemurs are more heterogeneous in the quantity of their diet's contents during the dry season, while the brown lemurs do so during the rainy season. Red collared brown lemurs exhibit high dietary uniformity particularly during dry season. They conserve their allopatric dietary pattern as frugivorous from season to season (see Bollen and Donati, 2005; Donati et al., 2007). Both lemur species exploit almost similar plant species but only differ it by eating different food items to ensure the feeding partitioning between them. The dietary partitioning is particularly quantitative rather than qualitative, as seen in the time spent on plant parts consumed. The use of habitats of both species is similar to what have been reported in previous studies on both species either in allopatric or in sympatric with other lemur species (Sauther, 1992; Sussman, 1999; Yamashita, 2002, Donati et al., 2007). Red collared brown lemurs are confined primarily to the upper regions of the forest especially during the dry season but occasionally forage on the ground. Lemur catta, in contrast, is found throughout the vertical range of the forest and exploits all forest sites. In terms of habitat use, the situation we found at Ambatotsirongorongo does not differ too much with that of Berenty reserve (see chapter 4; Donati et al., 2009). However, diet in both sites is different possibly because of differences between the two forests in terms of plant composition, food availability and nutrient contents. In Berenty, brown lemurs ate fruits for the large majority of their feeding time, while ring-tailed lemurs possess a diet of varied amount of fruits, flowers, mature leaves and new leaves when available, even though they feed on fruits up to 60% of their feeding time during the dry season (Rasamimanana and Rafidinarivo, 1993; Soma, 2006). Although, our sample sizes are quite small, it appears from our observations, that both lemur species at Ambatotsirongorongo are highly frugivorous due to the high quantity of fruits in their diet. It seems that each species adopts its own feeding behaviour that may reflect or not their natural habitat, in order to survive in this particular zone between dry and humid ecosystem. Ecological differences between both species were driven by their adaptation to their respective habitat type: humid littoral forest for red collared brown lemurs and dry deciduous forest for ring-tailed lemurs. This dietary separation reflects broader stratum preferences and a greater variety of habitats for ring-tailed lemurs. Ring-tailed and collared brown lemurs have more restricted diet of fruits but only differ in the use of forest: brown lemurs are more confined in the forest compared to ring-tailed lemurs (Donati et al., 2007; Ganzhorn, 1986). Various studies on niche partitioning of brown lemurs species with other lemur species show that they exhibit different ecological niches when occurring with other species to allow cohabitation (e.g., Overdorff, 1993; Overdorff, 1996; Vasey, 2000a; Vasey, 2004; chapter 3).

During the dry season when food is scarce, both lemur species reduce the number of intergroup aggression but increase intra-group affiliation. Intergroup encounters between both lemur species are more peaceful during the wet season though intra-group social interactions are more aggressive. This behaviour can be related to the ecology of the lemur species. During the harsh dry season, collared brown lemurs are more active during the nights (Donati et al., 2007), and feed mainly on fruits, two ways to increase nutritional intake, but decrease agonistic encounters with other lemur groups in order to conserve more energy. In contrast, ring-tailed lemurs feed more on qualitatively rich food such as fruits during the rainy season when they are more aggressive between each other and to other lemur groups in order to gain more energy and to maintain group cohesion and hierarchy (Ichino and Koyama, 2006; Jolly, 1966b; Kappeler, 1993; Rasamimanana, 1999; Sauther, 1993; Taylor, 1986). Reducing agonistic behaviour during the dry season can reflect an adaptation for reducing energy requirements for maintenance during a food-short season (Ganzhorn et al., 2003; Ross, 1992).

5.4.2 Niche partitioning at Ambatotsirongorongo

It has been reported that variation among sympatric species across the niche dimensions helps to reduce resource competition and facilitate coexistence in shared environments (Connell, 1980; Schoener, 1983). The specialization of ecological niche, in terms of food types, dietary diversity and habitat use, is considered as important in shaping ecological adaptations in primate communities across diverse habitats and taxonomic group (e.g., Chapman, 1988; Gautier-Hion, 1978; Gonzalez-Kirchner, 1996; Mittermeier and van Roosmalen, 1981; Norconk and Kinzey, 1994; Porter, 2001; Raemakers, 1979; Rodman, 1973; Struhsaker and Oates, 1975; Terborgh and Janson, 1986; Tomblin and Cranford, 1994; Tutin et al., 1997; Wright and Randrimanantena, 1989); and among Malagasy strepsirhines: (e.g., Freed, 1996; Ganzhorn, 1988; Overdorff, 1993; Overdorff, 1996; Powzyk, 1997; Sussman, 1977b; Tan, 1999; Vasey, 1997). The feeding ecology of various brown lemur species has been described from diverse localities in Madagascar (e.g., Donati et al., 2007; Donati et al., 1999; Johnson, 2002; Overdorff, 1993a; Rasmussen, 1999; Sussman, 1977a; Vasey, 2004; chapter 3). Brown lemurs have been characterised as highly flexible ecologically with relatively low dietary diversity (Tattersall and Sussman, 1998), which indicates a niche restriction that might be changed depending on the structure of community (Vasey, 2000a). As observed in this study, they are classified as primarily frugivorous (more than 50% of feeding time dedicated to fruits), but they also consume other food items such as flowers with a considerable quantity of leaves and other miscellaneous items (see Table 5.5 for comparison with other species of brown lemurs). From previous studies of brown lemurs with other lemur species (Lemur catta: Sussman, 1977b; Eulemur rubriventer: Overdorff 1991; E. coronatus: Freed, 1996; Varecia variegata rubra: Vasey 2000a; Vasey 2004; E. mongoz: Rasmussen 1999; Lemur catta: chapter 3), various mechanisms have been suggested to allow brown lemurs to share habitats with these potential competitors. These include, e.g. having greater dietary diversity (Vasey 2000a), utilizing higher (Sussman, 1974; Freed, 1996) or lower (Vasey, 2000a) vertical microhabitats, feeding in smaller patches (Vasey, 2000a), and/or consuming lower quality food items (leaves: Sussman, 1974; mature leaves, unripe fruit, and flowers: Overdorff, 1993; higher levels of toxic compounds: Ganzhorn, 1988); having a dietary uniformity and ranging in upper canopies and organizing their social interactions along with their energy requirements (chapter 3). In the present study, coexistence of red collared brown lemurs and ring-tailed lemurs is promoted by sharing feeding time on similar food items across seasons (E. collaris is more frugivorous during the dry season while Lemur catta during the wet season); and by exploiting higher level of vertical stratification for red collared brown lemurs during dry season compared to ring-tailed lemurs. These differences, even though relatively small, may contribute to niche separation of these sympatric competitors at Ambatotsirongorongo. Although ring-tailed lemurs reflect unclear generalist and opportunist behaviour in its diet compared to previous studies (e.g., Mertl-Millhollen et al., 2003; Rasamimanana and Rafidinarivo, 1993; Simmen et al., 2003; Soma, 2006b), both lemur species have similar dietary diversity, they are highly frugivorous. This is in contrast with the situation at Antserananomby, where red fronted brown lemurs have a highly monotonous, folivorous diet compared to sympatric ring-tailed lemurs, a more diverse frugivore (Sussman, 1977a). In littoral forest, south-eastern of Madagascar, collared brown lemurs, living in allopatry, do not shift its frugivorous diet (Donati et al., 2007). This latter observation is different from those seen in Mayotte with E. f. fulvus, where they have diverse diet, more generalist, in absence of any competitors (Tattersall, 1977).

Table 5.5 Fruit consumption of Eulemur sp. at different sites

Study site	**Lemur species**	**Dietary - % Fruits consumed**		**Authors**
Ranomafana National Park	E. fulvus rufus	Primarily frugivorous	66.80%	Overdorff 1993, 1996
Kirindy forest	E. f. rufus		91.50%	Donati et al. 1999
Montagne d'Ambre	E. f.sanfordi		89%	Freed 1996
Andranobe	E. f. albifrons		69%	Vasey 1997, 2000
Mayotte	E. f. mayottensis		67.40%*	Tattersall 1977
Berenty Reserve	E. rufus x E. collaris		65%	Donati et al. 2009, this study
Mandena/Sainte Luce	E. collaris		74%	Donati et al. 2007
Ambatotsirongorongo	E. collaris		73%	This study
Antserananomby/Tongobato	E. f. rufus	Folivorous	42/7%**	Sussman 1977

*Wet season
**Wet/Dry season

In summary, the sympatric association between ring-tailed and red collared brown lemurs is conditioned by seasonality. It can be related either to the season (wet or dry), or to the energy requirements for each season, or to the seasonal shifts in resource availability. Our prediction is partly confirmed as ring-tailed lemurs have conserved part of their ancestral behavioural ecology as generalist in terms of food quantity and quality by feeding on flowers during the high energetic cost period (lactation during the rainy season), ranging in lower levels, on the ground or in bushes. Red collared brown lemurs adopt its behaviour as in allopatry and are peaceful with ring-tailed lemurs particularly when food is scarce and life in group is much harder. It appears that ring-tailed lemurs adopt a more specialized frugivorous diet by imitating parts of the collared brown lemur's ecology which is not far from their natural habitat distribution (littoral forest). This might be due to the fact that the leaves in littoral/wet forest are nutritionally poor and it might not be an option to shift to a more folivorous diet to them in order to meet their energy demands (Donati et al., 2007). Niche partitioning between both species has been well reflected in habitat utilization. The cathemeral activity of the collared brown lemurs compared to the diurnal ring-tailed lemurs, also reflects the dichotomy of the ecological niche of both lemur species (Donati et al. 2007).

Although both lemur species occur without difficulties in this fragmented forest, it has been documented that they are vulnerable to habitat loss (Irwin et al., 2005; Sussman et al., 2006b). The combination of fragmentation and geographic barriers has affected the distribution patterns of lemurs and has exerted pressure on the remaining forest (Godfrey et al., 1999; Wilmé et al., 2006). Although niche separation exists between both lemur species in this small fragment of forest, a long-term study of the effects of fragmentation and food availability on their cohabitation is necessary in order to set up efficient conservation management plan for this unique ecosystems and its lemur population.

6. Behavioural ecology of ring-tailed lemurs at Bealoka forest, south-eastern Madagascar: population density, diet, habitat use and social interactions

Abstract

I examine the behavioural ecology (population density, feeding behaviour and habitat use) of the isolated and little-studied population of ring-tailed lemurs (Lemur catta) in Bealoka gallery forest, southeastern of Madagascar. The findings presented here reflected 311 hours of study, 120 and 191 of which were allotted for observation during dry and wet season respectively. One troop of 18 ring-tailed lemurs was followed during 11-12 hours per day follow. In 80s, the ring-tailed population density in Bealoka was very low. A translocation of 12 animals in 1993, added significantly to the population. Between 1993 and 2008, the population of ring-tailed lemurs at Bealoka increased substantially, reaching the density of 193 individuals per km^2, though it decreased into 167 individuals per km^2 in 2009. The diet of the ring-tailed lemurs in Bealoka was more frugivorous, particularly during the dry season. Smaller feeding patches were exploited mainly during the wet season and bigger patches were used during the dry season. Ring-tailed lemurs made use of all forest levels but they were more arboreal than terrestrial. When they exploited the upper levels of forest, they took advantage of the tree crown. Intragroup interactions were more frequent during the dry season when food is scarce, while intergroup interactions were more peaceful both during wet and dry seasons. Lemur catta in Bealoka adopted a monotonous diet, were less territorial and cryptic, exploited larger home range compared to other population of ring-tailed lemurs in other sites. These adaptations may elucidate behavioural mechanisms employed by ring-tailed lemurs to cope with small isolated forest where human pressure and hunting were pervasive.

6.1 Introduction

Madagascar's native biodiversity is highly threatened by the degradation and loss of natural habitat (Mittermeier, 1988; Wilmé et al., 2006). The habitat of the ring-tailed lemurs, Lemur catta, the island's flagship species, is threatened due to conversion of forest for charcoal production, extensive grazing by cattle and goats, fires, and slash-and-burn agriculture (Ralison, 2006; Sussman et al., 2003). The south of Madagascar is of special concern for conservation efforts because of its underrepresentation in the amount of its protected areas. Habitat destruction is the main threat to the lemurs of southern Madagascar and studies have shown that lemur diversity in the south is the lowest in Madagascar (Goodman et al., 2006). Ring-tailed lemurs is one of the lemurs suffering from habitat loss and hunting in Madagascar (Mittermeier et al., 2010). This species has been classified as Near Threatened (NT) according to the IUCN Red List assessment (IUCN, 2010). Many studies have been conducted on ring-tailed lemurs in terms of behavioural ecology, social behaviour, distribution patterns in Madagascar (Jolly, 2004; Jolly and Pride, 1999; Sauther et al., 1999). One study discussing the effect of human impact on vegetation and its consequences to ring-tailed lemurs was conducted in Bealoka forest during the two consecutive years of 1983-1984, when a very small population of this species lived there (O'Connor, 1987). A short survey of the ring-tailed lemur population there, was performed by Crowley in 1992-1993 when she worked as the reserve manager of Berenty estate. The present research reports the evolution of the behavioural ecology of the isolated ring-tailed lemur population in Bealoka forest, in terms of population density, feeding behaviour, social behaviour and habitat use. In this paper, I report data from a short control study, conducted in each season, on ring-tailed lemurs at Bealoka forest, where Propithecus verreauxi is the only diurnal sympatric lemur species occuring with them.

6.1.1 Background on *Lemur catta*

Among all prosimians, ring-tailed lemurs have been the species most extensively studied (Gould, 2006; Jolly et al., 2006a). They are diurnal primates, described as both terrestrial and arboreal and are social animals that live in multi-male, multi-female troops numbering roughly six to twenty-four individuals (At Berenty, 4-33) (Anderson, 2008). Territories are well-defined and fiercely protected (Jolly and Pride, 1999; Jolly et al., 2006c; Mertl-Millhollen, 2000). Although rigid intra-troop hierarchies dictate social interactions between members of each gender, males are unwaveringly subordinate to females (Jolly, 1998; Nakamichi and Koyama, 1997; Rasamimanana et al., 2006; Sauther, 1993). The population of ring-tailed lemurs plummets when their habitats have been degraded and, in some regions, completely decimated by human activity (Ganzhorn et al., 1997). The majority of their natural range, strectching across southern and southwestern Madagascar, is dominated by spiny bush, however, the distribution also extends into corridors of dry deciduous forest in the western lowlands and a few montane habitats in the central highlands (Goodman et al., 2006). Ring-tailed feeding behaviour is largely “unselective and opportunistic” (Simmen et al., 2006a). They consume fruits, leaves, stems, flowers, seeds, dirt, and decaying organic matter. Occasional dietary supplements include invertebrates and vertebrates as well (Sauther, 1992; Simmen et al., 2003; Soma, 2006; Sussman, 1977a; Yamashita, 2002). Tamarindus indica is the only food source exploited throughout the year in sizable quantities and constitutes the keystone resource of Lemur catta in southern gallery forest (Mertl-Millhollen et al., 2006; Rasamimanana and Rafidinarivo, 1993; Simmen et al., 2006b; Soma, 2006a).

6.2 Methods

6.2.1 Study site: Bealoka private reserve

Jolly (1966) reported that in 1963 the gallery forest made a narrow strip almost 80 km long on the lower Mandrare River wherever there was alluvial soil. Thirty years later, it appears that only two remnant patches remain intact in this same region of southern Madagascar: Bealoka forest and the well-known Berenty reserve (Jolly et al., 2006a). Both forests were interconnected 50 years ago, but due to the large scale removal of forest for the production of sisal, the two forests were separated by 7km, becoming isolated to each other (O'Connor, 1987). Both forests are similar and have approximately the same complement of flora and fauna (see chapter 2 for detailed description of vegetation), hunting was banned in both, although more recently in Bealoka (around 1970s). Bealoka has an area of 100 ha and is completely isolated from other riverine forest by sisal fields and the river. Ring-tailed and sifaka lemurs constitute the diurnal lemur species occuring natively in the forest. O’Connor (1987) suggested that the Bealoka population of ring-tailed lemurs was not viable breeding population. The population density was below what is to be expected for a gallery forest and is very low when compared to Berenty reserve. However a group of 12 animals translocated from Berenty to Bealoka in early 1993 adds significantly to the population (Crowley, 1995).

6.2.2 Population density study

Population censuses of ring-taile lemurs were undertaken during the birth season, October and November, in 2008 and during August in 2009, to accurately define the total number of groups in Bealoka forests. Census records also provided information on the total number of lemurs in the forest as well as their group composition, sex ratio and births. Group locations were mapped with GPS and group composition and size were collected frequently and supported by systematic sampling. Groups were spotted from trails and contact was maintained until all members were counted and described (see Jolly et al., 2002; Jolly et al., 2006c; chapter 3). Animals off trails were also censused to reduce the probability of certain groups evading detection. Although sexual dimorphism or dichromatism is absent in ring-tailed lemurs, identification of individuals were possible through facial features, pelage patterns and ear notches. Nevertheless, location and group size often facilitated identification.

6.2.3 Behavioural observations

The findings presented here reflect 311 hours of study, 120 and 191 of which were allotted for observation during dry and wet season respectively. The duration of observation spanned eleven days during the dry season, in May and July 2009; and sixteen days during the rainy season, from October 2009 to January 2010. One troop of ring-tailed lemurs was followed during 11-12 hours per day follow. The group was composed of 16 individuals including 6 aldult males, 8 adult females, 2 juvenile females and 2 peripheral males. Scan group sampling every five minutes (Altmann, 1974) was the primary method for quantifying activity budget, feeding behavior, height and forest site utilization. When an animal was observed to be feeding, the food source, the plant part fed on and the canopy diameter of the feeding patches were recorded. In addition to employing the scan survey method, social behaviors such as intra and intergroup aggression and affiliation were noted ad libitum. Agonistic behaviour such as presenting, chasing and cuffing; as well as affiliative behaviour including approach and cuddling were recorded by onset of the interactions.

6.2.4 Data analysis

For analysis of the scan survey data, the number of scan records of plant parts, forest height, forest site and canopy diameter for feeding patches were added daily. These sums were then expressed as a percentage of total scan survey counts. Daily proportions of diet, substrate and height were tested statistically using non-parametric tests (Dytham, 2007; Field, 2005). Wilcoxon signed ranks test was used to test differences between the pairs of data of the diet, forest substrate, forest height and social behaviors from dry and wet season.

6.3 Results

6.3.1 Ring-tailed population density at Bealoka

The population number of ring-tailed lemurs in Bealoka forest is represented in Table 6.1. The population density in Bealoka in 1983 was below what is to be expected for a gallery forest. Since 1985, the population has increased but still seems to be low. Between 1993 and 2008, the population of ring-tailed lemurs at Bealoka increased substantially, reaching the density of 193 individuals per km^2, though it decreased into 167 individuals per km^2 in 2009. Few females and some males censused in 2008 were missing during 2009. The infant survival reached 63% of the total newborn in 2008.

Table 6.1 Troop size and population number of ring-tailed lemurs in Bealoka forest

Year	Troops counted	Adult females	Adult males	Juveniles	Infants	Average Troop size	Total population number	Sources
1983	1				1	±12	12+	O'Connor 1987
1985	2	6	5	5	5	±10	21	
1992	3					±12	35+	Crowley 1995
1993	4					±12	47*	
...								
2008	13	78	100	15	52	14.8	193***	this study
2009	13	68	66	33	**	12.8	167	

*12 animals were translocated from Malaza Berenty to Bealoka in early 1993
**Observation was conducted at the end of dry season, no birth records
***The number of newborn infants is excluded from the total number

6.3.2 Diet and feeding patches

During the dry season, when the availability of food species is relatively low, ring-tailed lemurs at Bealoka forest focalized their feeding time on fruits (80% of their feeding time) and mature leaves (15%). During the rainy season, the presence of leaf buds and new leaves added to the actual food consumed (Wilcoxon Signed Ranks Test, Z = -1.89, P = 0.05). New leaves and mature leaves accounted for 15% of their feeding time compared to 69% for fruits (Figure 6.1a). The diet of the ring-tailed lemurs in Bealoka was predominantly frugivorous, particularly during the dry season. The use of feeding patches varied accross season, smaller feeding patches (canopy diameter between 1-5 m) were exploited mainly during the wet season and bigger patches (with canopy diameter greater than 15 m) were used during the dry season (Figure 6.1b) but these were not statistically verified.

6.3.3 Forest level and substrate

Ring-tailed lemurs made use of all forest levels but they are more arboreal than terrestrial. Lower height (between 1 to 5 m) were used the most during the dry season (Wilcoxon Signed Ranks Test, Z = -1.93, P = 0.05) (Figure 6.2a). Upper forest strata were exploited during the wet season (Wilcoxon Signed Ranks Test, Z = -2.7, P < 0.01). When ring-tailed lemurs ranged in lower level, they made the best use of major branches and partly the canopy crown (Wilcoxon Signed Ranks Test, Z = -2.66, P < 0.01) (Figure 6.2b). In the upper levels of forest, they mainly used the tree crown. Ring-tailed lemurs also spent 21% of their time on the ground in the forest during the wet season (Wilcoxon Signed Ranks Test, Z = -2.20, P < 0.05). It was only during this season, when ring-tailed lemurs at Bealoka forest made excursions on the ground outside of the forest.

6.3.4 Social interactions in ring-tailed lemurs at Bealoka forest

Of the total interaction events observed (106), 57% occured within the study group and 43% intergroup or interspecific (Figure 6.3). Intragroup interactions, involving agonistic events such as chasing, biting and cuffing, were more frequent during the dry season when food was scarce. There was also an appreciable presence of agonisitc behaviour during the wet season within the study group. Intergroup interactions were mainly peaceful during both wet and dry seasons, though it was much more considerable during the wet season.

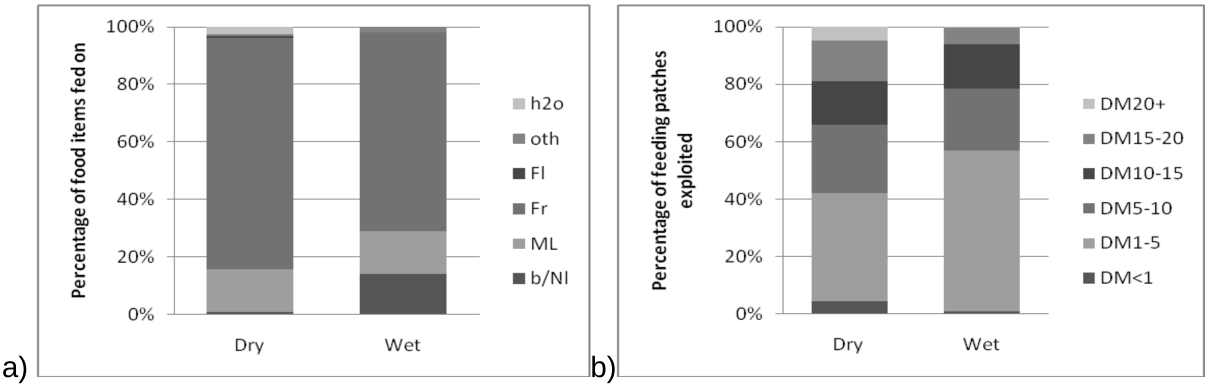


Figure 6.1: Percentage of a) plant parts fed on and b) canopy diameter of feeding patches exploited during the dry and wet seasons.

H20: water, Oth: other (includes soil, dirt, cicada, spiders), Fl: Flowers, Fr: ripe and unripe fruits; ML: Mature leaves, b/Nl: Leaf buds and new leaves. DM: canopy diameter measured in meters.

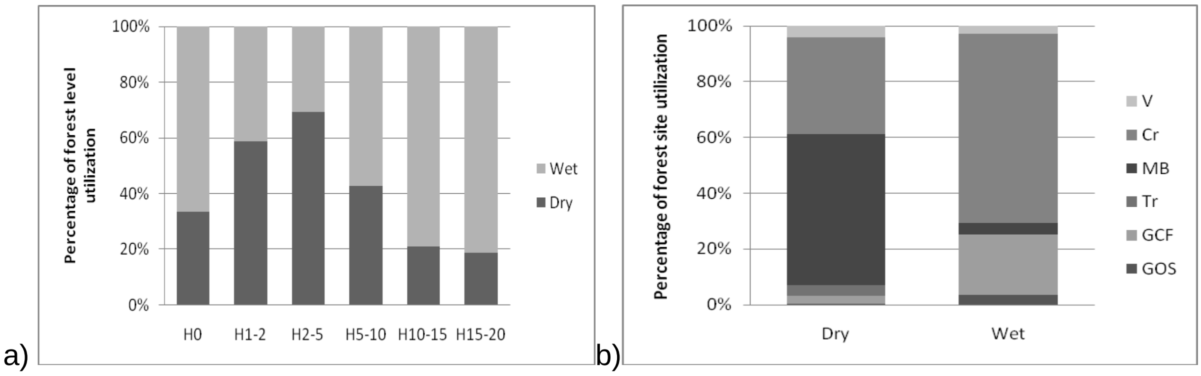


Figure 6.2: Frequencies of height utilization (a) and different forest sites (b) during dry and wet seasons.

V: Vine, Cr: tree crown, MB: Major branches, Tr: Trunk, GCF: ground in the closed canopy forest, GOS: ground outside of the forest. H: Height measured in meter.

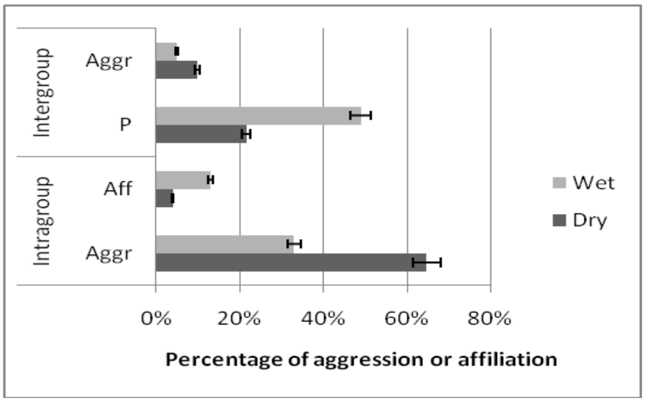


Figure 6.3: Inter and intragroup interactions in ring-tailed lemurs during wet and dry seasons.
Aggr: aggression, P: peaceful, Aff: affiliation

6.4 Discussions

The low population of ring-tailed lemurs living in Bealoka was considered as not a viable breeding population in 1985 (O’Connor, 1987). This is undoubltedly a result of former hunting pressure during the sisal production around the area. However, this population has increased but still seems to be low afterwards. The group translocated to Bealoka forest added significantly to the population (Crowley, 1995). In comparison with earlier studies, the density estimate of ring-tailed lemurs in Bealoka forest around the 1980s was markedly lower than reported of any other population of this species studied in different localities (Budnitz, 1978; Budnitz and Dainis, 1975; Jolly, 1972; Jolly et al., 1982b; Mertl-Millhollen et al., 1979; Sussman, 1977b). Apart from the translocation of 12 animals from Berenty reserve, the population increase may be due to a few individuals (hand reared or market bought) that have been released into the forest as well as natural increase. Furthermore, other small populations are known to have survived, or there are species which increased their population size, regadless of the levels of genetic variability (see Anderson, 1982; O'Brien et al., 2004). The present level approaches that which Jolly (1966) suggested as the density at Berenty in the richest part of Berenty gallery forest, that is, 250/ha, and which was confirmed by subsequent researchers (Mertl-Millhollen et al., 1979). Given the uncertainties of extrapolation from 10 ha of the richest area, the gallery forest of Bealoka may be near carrying capacity.

The decrease of the population from 2008 to 2009 may be explained by the failure of juvenile recruitment from 2008 to 2009 due to the drought year in 2008. It has been reported that post-drought years increase dramatically adult/juvenile mortality and reproductive failure, as seen in other gallery forests such as Beza Mahafaly and Berenty reserve (Godfrey et al., 2003; Gould et al., 1999; Jolly et al., 2002). The high density of ring-tailed population at Berenty reserve was explained by food availability and access to the water (Jolly et al., 2002; Jolly et al., 2006c; chapter 2). The availability of food sources all year round in Berenty due to the presence of introduced plant species affects the increase of the ring-tailed lemur population there. However in Bealoka, introduced plant species are almost absent, except in the botanical garden area where one group of ring-tailed lemurs occurs. Moreover, water provisioning in Bealoka was only implemented in different parts of the forest since

2000. Alterations in resource availability can result in changes in primate populations and behavioural ecology (Fleagle, 1988; Johns, 1986). Thus, these factors may explain the light decrease of the population there. The actual ring-tailed lemur population density in Bealoka is more than the half of the density in Berenty reserve before the arrival of brown lemurs (167 individuals/km^2 in Bealoka compared to 250 individuals/km^2 in Berenty, Jolly, 1966). Since Bealoka forest is virtually all gallery forest (see chapter 2 for vegetation description), the current density of ring-tailed lemurs cannot be compared with that of Berenty reserve with a density of 229 individuals/km^2, which averages rich gallery forest and scrub habitats.

The dietary patterns of ring-tailed lemurs at Bealoka forest is slightly different compared to the pattern in adjacent Berenty gallery forest. Ring-tailed lemurs at Berenty reserve have a diet of varied amount of fruits, flowers, mature leaves and new leaves when available and feed substantially in relatively small food patches particularly during the rainy season (see chapter 3). In comparison with Bealoka forest, ring-tailed lemurs in Bealoka adopt a monotonous diet composed of fruits from different plant species during both rainy and dry seasons. Soma (2006) reports that ring-tailed lemurs at Berenty reserve spend 40% of their feeding time on fruits for all over the year, and this proportion may differ among seasons from year to year: ring-tailed lemurs spend 60% of their feeding time on fruits during the birth and lactation periods (data from 1987 – 1989; Rasamimanana and Rafidinarivo, 1993); ring-tailed lemurs spend 31% of their feeding time during the rainy season in 2001-2002 (Soma, 2006). But in general, ring-tailed lemurs in Berenty are considered as generalist opportunistic when they have diet flexibility depending on seasons and years (Rasamimanana and Rafidinarivo, 1993; Simmen et al., 2003; Soma, 2006). At Bealoka forest, only 25% of the ring-tailed lemur feeding time was spent on other food items apart from fruits. It seems that they optimize their chances of survival by maintaining a preference for a highly nutritious food resource or items. In short, the ring-tailed lemur diet at Bealoka resembles Berenty's brown lemur diet, while at Berenty they have been displaced from some of the richer fruiting trees. Although ring-tailed lemurs in Bealoka adopt a different feeding strategy compared to nearby Berenty forest, the use of small feeding patches is similar for both population.

Habitat utilization also differs markedly between both sites. Ring-tailed lemurs are considered the most terrestrial of the lemurs (Sussman, 1974; Mittermeier et al., 2010). This behaviour can also be modified given the lack of brown lemur competition for the canopy crowns: they choose upper canopy trees for 88% of their activity time. This may also relate to defensibility where hunters and dogs cannot climb. Bealoka had permitted hunting until the 1970s, and is still further from effective patrol so may have continued hunting pressure. The population in Bealoka forest ranges rarely on the ground, particularly outside of the forest. These trends in feeding and habitat use may also relate to more subtle habitat differences between Berenty and Bealoka forests (see chapter 2).

As seen in other studies in Beza Mahafaly and in Berenty reserve, ring-tailed lemurs in Bealoka forest are highly aggressive within their group, particularly during the dry harsh season (Chapter 3; Pereira, 2006a; Sauther, 1993), and ring-tailed lemurs are highly territorial (Jolly et al., 2006c; Jolly and Pride 1999; Mertl-Millhollen, 2000). However, in Bealoka, intergroup encounters were more peaceful rather than aggressive. Agonistic intergroup encounters represent 7% only of the records during the observations. This suggests that ring-tailed lemurs in Bealoka are less territorial that may be due to the problem of defensibility and may consequently have saved energy. In this case, home range size was increased. This can be also explained by the fact that just as ecotones determine global ring-tailed lemur range (Goodman et al., 2006), density and variety of food influence ring-tailed lemur distribution range on a local scale, thus, with decreasing food density, home range size must increase to meet demands of minimum food intake. The alteration of feeding regime have affected energy budget, thus the behavioural ecology of the species. This behaviour may have been a consequence of low population density and have reduced intraspecific competition. A further indication of low competition was the low rates of long distance calls (Razafindramanana, pers. obs.). Hence, competition was altered with respect to territoriality.

Ring-tailed lemurs in Berenty were considered as non vulnerable in the early 1980's, (O'Connor, 1987) (because of the high population) and were highly territorial, whereas lemurs in Bealoka were vulnerable. In 2008-2009, although ring-tailed lemurs at Bealoka forest have achieved a good number of population, they may be still considered as threatened due to the changes of their behavioural ecology such as adopting a monotonous diet item but higher quality, becoming less territorial and more cryptic, exploiting larger home range. These behavioural changes may also reflect ecological flexibility of this species when living in allopatry. Some primates species with specialized diets, sometimes monotonous ones (e.g., Clutton-Brock, 1977; Sussman, 1977a; Sussman, 1999), often live on the edge of their tolerance levels and could be the first to suffer if the tree species they need were to be harvested, damaged or destroyed (O'Connor, 1987). But this is not the case of the ring-tailed lemurs in Bealoka as they concentrate on their preferred foods. These adaptations may elucidate behavioural mechanisms employed by ring-tailed lemurs to cope with small isolated forest where human pressure and hunting were pervasive by specializing in their diet, adopting larger home range size and by becoming more affiliative to each other.

A conservation management plan should be implemented in Bealoka forest in order to save the population of lemurs and its forest in this reserve. The management should include interventions such as a control of the invasive vine Cissus quandrangularis, an implementation of a forest regeneration study so that forest management can be monitored, a regular demography survey of the lemur population, and above all, prohibition and control of the entry of dogs and livestock into the forests.

7. General summary and conclusions: implications for sympatric ecological niches of ring-tailed and brown lemurs.

In the preceding chapters, I have investigated the ecology and population structure of ring-tailed lemurs (Lemur catta) and brown lemurs (Eulemur collaris and E. rufus x collaris hybrids) in three forest fragments of semi-arid southeastern Madagascar, both to understand the development of primate niche separation and to provide conservation recommendations as support for management of the forests and species threatened with extinction (Ganzhorn, 1989; Ganzhorn and 2000, 2007; Pinkus, 2004; Sussman, 1977b; Sussman, 1999; Sussman et al., 2006). One of the largest protected populations of the ring-tailed lemur lives in fragmented gallery forest at Berenty Reserve, a 400 ha riverine forest (Jolly et al., 2006b). About eight brown lemurs were introduced into Berenty in 1974, followed by a similar number of collared lemurs (E. collaris) (O'Connor, 1987). The gallery forest at Berenty Reserve is declining in terms of resource productivity (J. De Heaulme, pers. comm.; Sussman et al., 2006; Blumenfeld-Jones et al., 2006), accompanied by a simultaneous near-exponential increase in the population of introduced brown lemur hybrids (Jekielek, 2004; this study) and a shift in range and population distribution of the ring-tailed lemurs (this study). The questions were: 1) Do ecological and behavioural factors permit ring-tailed and hybrid brown lemur populations at Berenty reserve to coexist viably? 2) What are the effects of the introduced hybrid population of brown lemurs on the behaviour and distribution of native ring-tailed lemurs at Berenty reserve? Is feeding competition with brown lemurs among the reasons for forest decline and changes of ring-tailed behaviour? To be able to analyse the effects of the introduced lemur' species at Berenty, I chose two other forests fragments: Bealoka and Ambatotsirongorongo, as controls. Bealoka Forest Reserve is similar to Berenty, but does not contain brown lemurs (Jolly et al., 2006a) and this forest seems to be the original situation of Berenty Reserve before brown lemurs were introduced. It is used as a control for the forest changes and habitat parameters within both forests where the species are sympatric. Ambatotsirongorongo Forest, some 30 km to the southeast of Berenty, lies in the transition zone between wet and semi-arid habitats

(Andrianarimisa et al., 2005). Its forests are isolated and threatened by local village use. This is now the only known site where the endangered collared lemurs live in natural sympatry with ring-tailed lemurs (Ramanamanjato et al., 2002). This site is assumed to represent the natural situation where both lemur species live together; hence it will be the control for ecological interactions between both species in natural sympatry. The hypothesis were trees in the gallery forest at Berenty are being over-grazed (Mert-Millhollen et al., 2006) causing ring-tailed lemurs to shift from dense, territorial spacing in the gallery forest to ranges that are larger and undefended, in adjacent open forest and scrub areas that contain alternative food sources, but with a reduction population density (Soma, 2006).

As reported in chapter 2, although Bealoka and Berenty forests are similar in terms of tree density and microhabitat types (each site has a part of gallery closed canopy forest, a part of transitional forest and scrub habitat); the differences rely on tree structure, floristic diversity, and forest regeneration. Tree diameter and canopy width are significantly greater in Bealoka. Forest regeneration and survival in Malaza is poorer than in Bealoka. On the other hand, Malaza has higher species diversity which made this forest richer than other gallery forests. These results may be due to the greater degree of disturbance in Malaza from flooding, human influences by introducing exotic plant species and lemur population. We could not discern appreciable differences in plant communities between habitat types, which suggest an overlap of tree species in the different types. Although, Bealoka is more diverse in structure, our study suggests that it suffers from isolation compared to Berenty reserve. In summary, both forests resemble but only differ from some habitat parameters that might be resulted from anthropogenic influences and climate variation. These differences although small may have affected the behavioural ecology of the lemur population in each site.

From the population density and distribution study at Berenty reserve (chapter 3), it seems that the dynamic of the native ring-tailed lemur population was conditioned by food availability and habitat quality. The factor “water provisioning” does not affect markedly the population density, except the decrease of the population in the gallery closed canopy forest when access to water was abolished. Apart from food abundance and adaptation to exploit abundant and uniformly distributed resources during the food scarcity period, the brown lemur growth and distribution also appears to be affected by the water availability. The removal of water provisioning in Malaza forest resulted in a decrease of the brown lemur population, particularly in the scrub dry habitat. At Berenty, brown lemurs have colonised all parts of the reserve, even the edge habitat normally monopolised by ring-tailed lemurs. This situation changed once the water provisioning was stopped in 2007, leading to a shift of ring-tailed lemurs range to the marginal habitat and brown lemurs to the closed-canopy forest. Ring-tailed lemurs make use of both closed-canopy forest and edge habitat regularly, while brown lemurs are confined in the forest. This scenario confirms that brown's ecological niche is included within that of the ring-tailed lemurs (Hutchinson, 1978; May and MacArthur, 1972), making them a good competitor with a restricted niche compared to the broader niche of ring-tailed lemurs who are the lesser competitor. Although, a trend toward similar ecology to that in natural sympatry has been seen at Berenty reserve in terms of population structure, this might be in doubt because of the high density of both lemur species in the reserve. Food competition of ring-tailed lemurs with brown lemurs, particularly in scrub, may reduce the high recruitment needed for ring-tailed to recover from post-drought food shortages. Ring-tailed lemurs are adapted to rebound rapidly from population declines (Gould et al., 1999), but their diet and use of edge habitat suggest they may be less able to do so while competing for food with brown lemurs.

The study of the ecological niche interactions between native ring-tailed and introduced brown lemurs at Berenty (chapter 4), reflects the increasing spatial separation between brown and ring-tailed troops, as brown lemurs take the centre of the forest and ring-tailed the periphery. Ring-tailed and brown lemurs partition the environment in other ways including foraging and feeding within different sized patches for some seasons. Ring-tailed lemurs adopt a diet of varied amount of fruits, flowers, mature leaves and new leaves when available and feed substantially in relatively small food patches particularly during the rainy season; whereas brown lemurs have a more homogeneous diet consisting mainly of fruits and a bit of mature leaves or new leaves depending on the season. They partition food and microhabitat use effectively by feeding or being active in different portions of the tree or with different timing even though they may exploit the same food patches of keystone resources. It seems that individual energy demands for various activity rhythms play a big role in brown lemurs' ecology; however, food availability, hierarchy and territory are the main niche dimensions that shape ring-tailed lemurs' ecology. Brown lemurs, considered as specialists, concentrate on taking the best food from the environment to meet their ultimate energy demands. This defines them as superior competitors which prevent the ring-tailed lemurs from occupying some part of their fundamental niche. The inferior competitors, the ring-tailed lemurs, previously inhabited the closed canopy gallery forest at Berenty. For the case of Berenty, ring-tailed lemurs adopt a bimodal niche which includes a realized niche the forest edges and the open area and their fundamental niche, the gallery closed canopy forest. This study shows that both lemur species have now reached a possible competitive equilibrium of reduced niche overlap and interspecific competition, unless ring-tailed lemurs cannot recover from extreme food shortages, as suggested above.

In comparison the situation in Berenty reserve, niche partitioning between native population of ring-tailed lemurs and red collared brown lemurs at Ambatotsirongorongo forest is very narrow (chapter 5). The dichotomy relies mainly on habitat use where ring-tailed lemurs range in lower levels, on the ground, in bushes, and particularly in marginal habitat, while collared brown lemurs exploit higher level of vertical stratification in compensation with tree crown and lianas. Cohabitation of red collared brown lemurs and ring-tailed lemurs is possible by the fact that they share their feeding time on similar food items across seasons: Although, collared brown lemurs are more frugivorous during the dry season while ring-tailed lemurs during the wet season; both lemur species are considered as frugivorous. It seems that in this harsh fragmented habitat, collared brown lemurs adopt similar behaviour as in allopatry and is peaceful with ring-tailed lemurs. However, it appears that ring-tailed lemurs imitate part of the brown lemur's ecology which might be due to the poor nutrient contents in the leaves of wet forest that may not allow shifting to a generalist diet. The sympatric association between both lemur species is conditioned by seasonality that might be related either to the season, or to the energy requirements for each season, or to the seasonal shifts in resource availability.

Feeding ecology of the native allopatric ring-tailed lemurs in Bealoka forest is quite similar to that of ring-tailed lemurs in Ambatotsirongorongo forest: diet dominated by fruits (chapter 6). However, their habitat utilization in Bealoka differs markedly from both Berenty reserve and Ambatotsirongorongo forest. The population in Bealoka forest ranges rarely on the ground, particularly outside of the forest. This behaviour might be adopted because of former hunting and because of poor defensibility: they choose upper canopy trees for 88% of their activity time where hunters cannot climb. It seems that ring-tailed lemurs in Bealoka optimize their chances of survival by maintaining a preference for a particular food resource or item. They are more peaceful compared to the ones in Berenty and Ambatotsirongorongo forests, which suggest that ring-tailed lemurs in Bealoka are less territorial due to the problem of defensibility and may consequently have saved energy. These behavioural adaptations clarify behavioural mechanisms employed by ring-tailed lemurs to cope with a small isolated forest where anthropogenic pressure and hunting were formerly pervasive.

In summary, back to the research questions, changes in ring-tailed lemurs' behaviour and distribution at Berenty reserve are partly due to the competition with the introduced brown lemurs occurring with them in the reserve. However this situation has now brought to a niche partitioning between both species by creating a bimodal niche for ring-tailed lemurs. We found that brown lemurs' niche is conditioned by energy demands while food availability, hierarchy and territory shape ring-tailed lemurs' ecology. The broader question, whether the high total population of brown and ring-tailed lemurs is having a negative effect remains unanswered as more data on population survey are needed. However, preliminary analysis shows that juvenile recruitment of brown lemurs declined as combined population density increased. The comparisons with ecological mechanisms and evolution of Bealoka and Ambatotsirongorongo forests show that Berenty has shifted from a situation more like Bealoka's to a situation more like natural sympatry. The population of ring-tailed lemurs has not decreased significantly since the rise in brown lemur population. This suggests that niche separation in Berenty may allow both species lemurs to co-exist in the long term, although censuses should continue, particularly during and after the harshest years The drying trend of Berenty began prior to the high present brown lemur population. Therefore, while continuing to monitor the brown and ring-tailed lemur populations, the next stage of research should also focus on water table and tree history, as well as on the lemurs. Apart from the diurnal dichotomy of the ecological niches of brown and ring-tailed lemurs, reported in this study, cathemeral behaviour of Eulemur ssp. also contributes towards niche separation between both species.

The results of this comparison of the lemur adaptations in different circumstances and ecosystems will help further implementation of conservation management plan for each site, and will serve as basis for further ecological survey of the evolution of the sympatric association between brown and ring-tailed lemurs. Conservation action should focus of reforestation in each site, particularly in Bealoka and Ambatotsirongorongo fragmented forests. Environmetal education are urgently needed for the local people Ambatotsirongorongo in order to encourage them to protect this unique habitat with high level of biodiversity endemism. A pilot study of birth control of the hybrid population of brown lemurs at Berenty reserve might be needed in order to stabilize this population to prevent further negative impacts on the native lemur species and its forest.

References

Alley, T. R. (1982). Competition theory, evolution, and the concept of an ecological niche. Acta Biotheoritica 31 (3), pp.165-179.

Altmann, J. (1974). Observational study of behavior: sampling methods. Behaviour 49 (3), pp.227-267.

Anderson, D. J. (1982). Baboon movement: exploring models of random movement. Ph.D dissertation. University of Washington.

Anderson, R. (2008). Lemur catta. Animal Diversity Web (online). [Online].

Andrews, J. R., Birkinshaw, C.R. (1998). A comparison between the daytime and night-time diet, activity and feeding height of the black lemur, Eulemur macaco (Primates: Lemuridae), in Lokobe Forest, Madagascar. Folia Primatologica 69 (suppl 1), pp.175–182.

Andrianarimisa, A., Andrianjakarivelo, V., Rakotomalala, Z. and Anjeriniaina, M. (2005). Communautés faunistiques Ambatotsirongorongo: futur site de conservation dans la région de Fort-Dauphin. Wildlife Conservation Society Antananarivo Madagascar

Atsalis, S. (2000). Spatial distribution and population composition of the brown mouse lemur (Microcebus rufus) in Ranomafana National Park, Madagascar, and its implications for social organization. American Journal of Primatology 51 (1), pp.61-78.

Austin, M. P. (1999). A silent clash of paradigms: some inconsistencies in community ecology. Oikos 86 (1), pp.170-178.

Bagchi, S., Goyal, S. P. and Sankar, K. (2003). Niche relationships of an ungulate assemblage in a dry tropical forest. Journal of Mammalogy 84 (3), pp.981-988.

Blumenfeld-Jones, K. C., Randriamboavonjy, T. M., Williams, G., Mertl-Millhollen, A. S., Pinkus, S. and Rasamimanana, H. (2006). Tamarind recruitment and long-term stability in the gallery forest at Berenty, Madagascar. In: Jolly, A., Sussman, R. W., Koyama, N. and Rasamimanana, H. (eds.) Ringtailed Lemur Biology. New York: Springer.

Boinski, S., Sughrue, K., Selvaggi, L., Quatrone, R., Henry, M. and Cropp, S. (2002). An expanded test of the ecological model of primate social evolution: competitive regimes and female bonding in three species of squirrel monkeys (Saimiri oerstedii, S. boliviensis, and S. sciureus). Behaviour 139, pp.227-261.

Boinski, S., Treves, A. and Chapman, C. (2000). A critical evaluation of the influence of predators on primates: effects on group travel. In: Boinski, S. and Garber. P. (eds.) On the Move: How and Why Animals Travel in Groups. Chicago: University of Chicago Press, pp.43-72.

Bollen, A. and Donati, G. (2005). Phenology of the littoral forests of Sainte Luce, Southeastern Madagascar. Biotropica 37 (1), pp.32-43.

Bollen, A. and Donati, G. (2006). Conservation status of the littoral forest of south-eastern Madagascar: a review. Oryx 40 (1), pp.1-10.

Boucher, D. H. (1985). The Biology of Mutualism. London: Croom Helm.

Bradshaw, W. E., Zani, P. A. and Holzapfel, C. M. (2004). Adaptation to temperate climates. Evolution 58 (8), pp.1748-1762.

Budnitz, N. (1978). Feeding behavior of Lemur catta in different habitats. In: Bateson, P. P. G. and Klopfer, P. H. (eds.) Perspectives in Ethology. Vol. 3. New York: Plenum, pp.85-108.

Budnitz, N. and Dainis, K. (1975). Lemur catta: ecology and behavior. In: Tattersall, I. and Sussman, R. W. (eds.) Lemur Biology. New York: Plenum, pp.219-235.

Burton, F. and Chan, L. (1996). Behavior of mixed species groups of macaques. In: Fa, J. and Lindburg, D. (eds.) Evolution and Ecology of Macaque Societies. Cambridge: Cambridge University Press, pp.389-412.

Butynski, T. (1982). Vertebrate predation by primates: a review of hunting patterns and prey. Journal of Human Evolution 11, pp.421-430.

Chapman, C. (1987). Flexibility in diets of three species of Costa Rican primates. Folia Primatologica 49, pp.90–105.

Chapman, C. (1988). Patterns of foraging and range use by three species of neotropical primates. Primates 29, pp.177-194.

Chapman, C. A. et al. (1992). Estimators of fruit abundance of tropical trees. Biotropica 24, pp.527-531.

Charles-Dominique, P. (1975). Nocturnality and diurnality: an ecological interpretation of these two modes of life by an analysis of the higher vertebrate fauna in tropical forest ecosystems. In Luckett, W.P. and Szalay, F. S. (eds.) Phylogeny of the Primates: An Interdisciplinary Approach. New York: Plenum Press, pp 69–88.

Charles-Dominique, P. (1977). Ecology and Behavior of Nocturnal Primates. New York: Columbia Press.

Cheney, D. and Wrangham, R. (1987). Predation. In: Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. and Struhsaker, T. T. (eds.) Primate Societies. Chicago: University of Chicago Press, pp.227- 239.

Clutton-Brock, T. H. (1973). Feeding levels and feeding sights of red colobus monkeys in the Gombe National Park. Folia Primatologica 19, pp.368–379.

Clutton-Brock, T. H. (1977). Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In: Clutton-Brock, T. H. (ed.) Primate ecology. New York: Academic Press, pp.539–556.

Colquhoun, I. C. (1998). Cathemeral behaviour of Eulemur macaco macaco at Ambato Massif, Madagascar. Folia Primatologica 69, pp.2–34.

Connell, J. (1980). Diversity and the coevolution of competitors, or the ghosts of competition past. Oikos 35, pp.131-138.

Cowlishaw, G. and Dunbar, R. (2000). Primate Conservation Biology. Chicago: University of Chicgo Press.

Crawley, M. J. (1992). Natural Enemies. Predators, Parasites and Diseases. Oxford: Blackwell.

Crockett, C. M. and Wilson, W. L. (1980). The ecological separation of M. fasicularis in Sumatra. In: Lindburg, D. (ed.) The Macaques, Studies In Ecology, Behaviour, and Evolution. New York: Van Nostrand Rheinhold, pp.148-181.

Crook, J. H. and Aldrich-Blake, P. (1968). Ecological and behavioral contrasts between sympatric ground dwelling primates in Ethiopia. Folia Primatologica 8, pp.192–227.

Crowley, H. (1995). Berenty Reserve management plan. Berenty reserve, Fort-Dauphin Madagascar.

Curtin, S. H. (1976). Niche separation in sympatric Malaysian leaf-monkeys (Presbytis obscura and Presbytis melalophos). Yearbook of Physical Anthropology 20, pp.421-439.

Curtis, D. J. and Rasmussen, M. A. (2002). Cathemerality in lemurs. Evolutionary Anthropology Suppl 1, pp.83-89.

Curtis, D. J. and Rasmussen, M. A. (2006). The evolution of cathemerality in primates and other mammals: A comparative and chronoecological approach. Folia Primatologica 77, pp.178–193.

Curtis, D.J., Zaramody, A. and Martin, R.D. (1999). Cathemerality in the mongoose lemur, Eulemur mongoz . American Journal of Primatology 47, pp. 279–298.

De Ruiter, J. (1986). The influence of group size on predator scanning and foraging behavior of wedgecapped capuchin monkeys (Cebus olivaceus). Behavior 98, pp.240-258.

Demment, M. W. (1983). Feeding ecology and the evolution of body size of baboons. African Journal of Ecology 21, pp.219–233.

Dirzo, R. and Sussman, R. W. (2002). Human impact and species extinction. In: Chazdon, R. L. and Whitmore, T. C. (eds.) Foundations of Tropical Forest Biology: Classic Papers with Commentaries. Chicago: University of Chicago Press, pp.703-711.

Donati, D., Baldi, N. Moreli, V., Ganzhorn, J. U. and Borgognini-Tarli, S. M. (2009). Proximate and ultimate determinants of cathemeral activity in brown lemurs. Animal Behaviour 77, pp.317–325.

Donati, G., Bollen, A., Borgognini-Tarli, S. M. and Ganzhorn, J. U. (2007). Feeding over the 24-h cycle: dietary flexibility of cathemerak collared lemurs (Eulemur collaris). Behavioral Ecology and Sociobiology 10.

Donati, G. and Borgognini-Tarli, S. M. (2006). Influence of abiotic factors on cathemeral activity: the case of Eulemur fulvus collaris in the littoral forest of Madagascar. Folia Primatologica 77, pp.104 – 122.

Donati, G., Lunardini, A. and Kappeler, P. (1999). Cathemeral activity of red-fronted brown lemurs (Eulemur fulvus rufus) in the Kirindy Forest/CFPF. In: Rakotosamimanana, B., Rasamimanana, H., Ganzhorn, J. U. and Goodman, S. M. (eds.) New Directions in Lemur Studies. New York: Kluwer Acad/Plenum, pp.119-137.

Donati, G., Lunardini, A., Kappeler, P. M. and Borgognini-Tarli, S. M. (2001). Nocturnal activity in the cathemeral redfronted lemur (Eulemur fulvus rufus) , with observations during a lunar eclipse. American Journal of Primatology 53, pp.69–78.

Dunbar, R. I. and Dunbar, E. P. (1979). Ecological relations and niche separation between sympatric terrestrial primates in Ethiopia. In: Sussman, R.W. (ed.) Primate Ecology: Problem-oriented Field Studies. New York: John Wiley and Sons, pp.187-209.

Dytham, C. (2007). Choosing and using statistics, A biologist’s guide. 2nd ed. Blackwell publishing.

Eisenberg, J., Muckenhirn, N. and Rudran, R. (1972). The relation between ecology and social structure in primates. Science 176 (4037), pp.863-874.

Erhart, E. M. and Overdorff, D. J. (2008). Population demography and social structure changes in Eulemur fulvus rufus from 1988 to 2003. American Journal of Physical Anthropology 136, pp.183-193.

Feldhamer, G. A., Drickamer, L. C., Vessey, S. H. and Merritt, J. F. (1999). Mammalogy: Adaptation, Diversity, and Ecology. Boston: McGraw-Hill.

Fernandez-Duque, E. (2003). Influences of moonlight, ambient temperature, and food availability on the diurnal and nocturnal activity of owl monkeys (Aotus azarai). Behavioral Ecology and Sociobiology 54, pp.431–440.

Field, A. (2005). Discovering statistics using SPSS. 2nd ed. London: Sage.

Fleagle, J. G. (1988). Primate Adaptation and Evolution. New York: Academic Press.

Fleagle, J. G. (1999). Primate Adaptation and Evolution. 2nd ed. New York: Academic Press.

Fleming, T. (1982). Foraging strategies of plant-visiting bats. In: Kunz, T.H. (ed.) Ecology of Bats. New York: Plenum Press, pp.287-325.

Foibe Tao-tsarin-tanin'i Madagasikara (1979). Ranopiso, feuille M-62. Antananarivo, Madagascar: Institut National de Geodesie et Cartographie.

Fowler, J., Cohen, L. and Jarvis, P. (1998). Practical Statistics for Field Biology. New York: John Wiley and sons Ltd.

Freed, B. (1996). Co-occurrence among crowned lemurs (Lemur coronatus) and Sanford’s lemurs (Lemur fulvus sanfordi) of Madagascar. PhD Dissertation. Washington University.

Ganzhorn, J. U. (1985). Habitat separation of semifree-ranging Lemur catta and Lemur fulvus. Folia Primatologica 45, pp.76–88.

Ganzhorn, J. U. (1986). Feeding behavior of Lemur catta and Lemur fulvus. International Journal of Primatology 7, pp.17-30.

Ganzhorn, J. (1988). Food partitioning among Malagasy primates. Oecologia 74, pp.436- 450.

Ganzhorn, J. U. (1989). Niche separation of seven lemur species in the eastern rainforest of Madagascar. Oecologia 79, pp.279-286.

Ganzhorn, J. U. (1995). Low-Level forest disturbance effects on primary production, leaf chemistry, and lemur populations. Ecology 76 (7), pp.2084-2096.

Ganzhorn, J. (2003). Habitat description and phenology. In: Setchell, J.M. and Curtis, D.J. (eds.) Field and Laboratory Methods in Primatology. A Practical Giude. Cambridge: Cambridge Univ Press, pp.40-56.

Ganzhorn, J. U., Goodman, S. M., Ramanamanjato, J. B., Ralison, J., Rakotondravony, D. and Rakotosamimanana, B. (2000). Effects of fragmentation and assessing minimum viable populations of lemurs in Madagascar. In: Rheinwald, G. (ed.) Isolated Vertebrate Communities in the Tropics. Germany: Proceedings of the 4th International Symposium, Bonn, pp.265–272.

Ganzhorn, J. U. and Kappeler, P. M. (1996). Lemurs of the Kirindy forest. In: Ganzhorn, J. U. and Sorg, J.-P. (eds.) Ecology and Economy of A Tropical Dry Forest, Primate report.

Ganzhorn, J. U., Klaus, S., Ortmann, S. and Schmid, J. (2003). Adaptation to seasonality: some primate and non-primates examples. In: Kappeler, P. M. and Pereira, M. E. (eds.) Primate Life Histories and Socioecology. Chicago: University of Chicago Press, pp.132–148.

Ganzhorn, J. U., Malcomber, S., Andrianantoanina, O. and Goodman, S. M. (1997). Habitat characteristics and lemur species richness in Madagascar. Biotropica 29 (3), pp.331-343.

Ganzhorn, J. U., Wright, P. C. and Ratsimbazafy, J. (1999). Primate communities: Madagascar. In: Fleagle, J. G., Janson, C. H. and Reed, K. E. (eds.) Primate Communities. Cambridge: Cambridge University Press, pp.75-89.

Gause, G. F. (1934). The struggle for Existence. Williams and Wilkins, Baltimore, MD, USA.

Gautier-Hion, A. (1978). Food niches and coexistence in sympatric primates in Gabon. In: Chivers, D. H. J. (ed.) Recent Advances in Primatology. Vol. 1. Academic Press, pp.269-286.

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

Gautier-Hion, A., Emmons, L. H. and Dubost, G. (1980). A comparison of the diets of three major groups of primary consumers of Gabon. Oecologia 45, pp.182–189.

Gentry, A. H. (1988). Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden 75, pp.1-35.

Gentry, A. H. (1993). Diversity and floristic composition of lowland tropical forest in Africa and South America. In: Goldblatt, P. (ed.) Biological Relationships Between Africa and South America. New Haven: Yale University, pp.500-547.

Gilbert, B. and Lechowicz, M. J. (2004). Neutrality, niches, and dispersal in a temperate forest understory. Proceedings of the National Academy of Sciences of the United States of America 101 (20), pp.7651-7656.

Gittens, G. P. and Raemaekers, J. J. (1984). Siamang, lar and agile gibbons. In: Chivers, D. J. (ed.) Malayan Forest Primates. New York: Plenum Press, pp.63–105.

Glander, K. E., Fedigan, L. M. and Chapman, C. A. (1991). Field methods for capture and measurement of three monkey species in Costa Rica. Folia Primatologica 57, pp.70-82.

Glander, K. E., Wright, P. C., Daniels, P. S. and Merenlender, A. M. (1992). Morphometrics and testicle size of rain forest lemur species from southeastern Madagascar. Journal of Human Evolution 22, pp.1–17

Glander, K. E., Wright, P. C., Seigler, D. S., Randrianasolo, V. and Randrianasolo, B. (1989). Consumption of cyanogenic bamboo by a newly discovered species of bamboo lemur. American Journal of Primatology 18, pp.1-7.

Godfrey, L. R., Jungers, W. L., Simons, E. L., Chatrath, P. S. and Rakotosamimanana, B. (1999). Past and present distributions of lemurs in Madagascar. In: Rakotosamimanana, B., Rasamimanana, H., Ganzhorn, J. U. and Goodman, S. M. (eds.) New Directions in Lemur Studies. New York: Kluwer Academic /Plenum Publishers, pp.19-53.

Godfrey, L. R., Samonds, K. E., Jungers, W. L., Sutherland, M. R. and Irwin, M. T. (2004). Ontogenic correlates of diet in Malagasy lemurs. American Journal of Physical Anthropology 123, pp.250–276.

Godfrey, L. R., Samonds, K. E., Junges, W. L. and Sutherlet, M. R. (2003). Dental development and Primate life histories. In: Kappeler, P. M. and Periera, M. E. (eds.) Primate Life Histories and Socioecology. Chicago: University of Chicago Press.

Gonzalez-Kirchner, J. (1996). Habitat preference of two lowland sympatric guenons on Bioko Island, Equatorial Guinea. Folia Zoologica 45, pp.201-208.

Gonzalez-Solis, J. et al. (2001). Population density of primates in a large fragment of the Brazilian Atlantic rainforest. Biodiversity and Conservation 10, pp.1267-1282.

Goodman, S. M. and Ganzhorn, J. U. (2004). Biogeography of lemurs in the humid forests of Madagascar: the role of elevational distribution and rivers. Journal of Biogeography 31, pp.47–55.

Goodman, S. M. and Langrand, O. (1996). A high mountain population of the ring-tailed lemur Lemur catta on the Andringitra Massif, Madagascar. Oryx 30, pp.259-268.

Goodman, S. M. et al. (1997). The birds of southeastern Madagascar. Fieldiana: Zoology (new series) 87.

Goodman, S. M., Rakotoarisoa, S. V. and Wilmé, L. (2006). The distribution and biogeography of the ring-tailed lemur (Lemur catta) in Madagascar. In: Jolly, A., Sussman,R. W., Koyama, N. and Rasamimanana, H. (eds.) Ring-tailed Lemur Biology Lemur catta in Madagascar. New York: Springer.

Gould, L. (2006). Lemur catta ecology: what we know and what we need to know. In: Gould, L. and Sauther, M. L. (eds.) Lemurs: Ecology and Adaptation. New York: Springer, pp.255-274.

Gould, L., Sussman, A. R. W. and Sauther, A. M. L. (1999). Natural disasters and primate populations: The effects of a 2-year drought on a naturally occuring population of ring-tailed lemurs (Lemur catta) in Southwestern Madagascar. International Journal of Primatology 20 (1), pp.69-83.

Gould, L., Sussman, A. R. W. and Sauther, A. M. L. (2003). Demographic and life-history patterns in a population of ring-tailed lemurs (Lemur catta) at Beza Mahafaly Reserve, Madagascar: a 15-year Perspective. American Journal of Physical Anthropology 120, pp.182-194.

Gould, L. and Sussman, R. (2001). Analysis of a 13-year demographic study on ringtailed lemurs at the Beza-Mahafaly Reserve, Madagascar. American Journal of Physical Anthropology (Suppl 32), p.72.

Green, K. M. and Sussman, R. W. (1990). Deforestation history of the eastern rain forests of Madagascar from satellite images. Science 248, pp.212-215.

Grinnell, J. (1904). The origin and distribution of the chestnut-backed chickadee. In: Whittaker, R.H. and Levin, S.A. (eds.) Niche Theory and Application. Stroudsberg: Dowden, Hutchison, and Ross,. Vol. 21. Auk, pp.375-377.

Halle, S. and Stensteth, N. C. (2000). Chronoecology: new light through old windows – a conclusion. In Halle, S. and Stensteth, N.C. (eds.) Activity Patterns in Small Mammals: An Ecological Approach. Berlin: Springer, pp.275–284.

Hanley, M. E. et al. (2007). Plant structural traits and their role in anti-herbivore defence. Perspectives in Plant Ecology, Evolution and Systematics 8, pp.157-178.

Harcourt, C. S. and Thornback, J. (1990). Lemurs of Madagascar: The IUCN Red data Book. Switzerland and Cambridge, U. K.

Harrington, J. (1975). Field observations of social behavior of Lemur fulvus fulvus. In: Tattersall, I. and Sussman, R. W. (eds.) Lemur biology. New York: Plenum Press, pp.259-279.

Harrington, J. E. (1978). Diurnal behavior of Lemur mongoz at Ampijoroa. Folia Primatologica 29, pp.291–306.

Harrison, S., Thomas, C. D. and Lewinshon, T. M. (1995). Testing a metapopulation model of coexistence in the insect community on ragwort (Senecio jacobaea). The American Naturalist 145 (4), pp.546-562.

Hashimoto, T. (1999). Modeling categorization dynamics through conversation by constructive approach. In: Floreano, D., Nicoud, J.-D. and Mondada, F. (eds.). Advances in Artificial Life. Proceedings of the Fifth European Conference, Lecture Notes in Computer Science, Vol. 1674. New York: Springer, pp.730 - 734.

Hawkins, A. F. (1999). The primates of Isalo National Park, Madagascar. Lemur News 4, pp.10–14.

Heymann, E. W. (2000). The number of adult males in callitrichine groups and its implications for callitrichine social evolution. In: Kappeler, P. M. (ed.) Primate Males: Causes and Consequences of Variation in Group Composition. Cambridge: Cambridge University Press, pp.64–71.

Hill, R. A. (2006). Why be diurnal? Or, why not be cathemeral? Folia Primatologica 77, pp.72-86.

Hirzel, A. H. and Le Lay, G. (2008). Habitat suitability modelling and niche theory. Journal of Applied Ecology 45, pp.1372-1381.

Hladik, C. (1981). Diet and the evolution of feeding strategies among forest primates. In: Harding, R. and Teleko, G. (eds.) Omnivorous Primates. New York: Columbia University Press.

Hladik, C. M. (1977). A comparative study of the feeding strategies of two sympatric species of leaf monkeys: Presbytis senex and Presbytis entellus. In: Clutton-Brock, T. H. (ed.) Primate Ecology: Studies of Feeding and Ranging behaviour in Lemurs, Monkeys and Apes. London, New York: Academic press, pp.323-353.

Hladik, C. M., Charles-Dominique, P. and Petter, J. J. (1980). Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar. In: Charles-Dominique, P. (eds.) Nocturnal Malagasy primates. New York: Academic press, pp.41-73.

Holt, R. (2003). On The Evolutionary Ecology of species' ranges. Evolutionary Ecology Research 5, pp.159-178.

Hughes, F. M. R. (1988). The ecology of African floodplain forests: A review. Biogeogr. 15, pp.127-140.

Hutchinson, G. (1957). Concluding Remarks. Cold Spring Harbor Smposium on Quantitative Biology 22, pp.415-427.

Hutchinson, G. E. (1978). An Introduction to Population Ecology. New Haven: Yale University Press.

Ichino, S. and Koyama, N. (2006). Social changes in a wild population of ringtailed lemurs (Lemur catta) at Berenty, Madagascar. In: Jolly, A., Sussman, R. W., Koyama, N. and Rasamimanana, H. (eds.) Ring-tailed Lemur Ecology: Lemur catta in Madagascar. New York: Springer, pp.234-244.

Irwin, M. T., Johnson, S. E. and Wright, P. C. (2005). The state of lemur conservation in south-eastern Madagascar: population and habitat assessments for diurnal and cathemeral lemurs using surveys, satellite imagery and GIS. Oryx 39 (2), pp.204-218.

IUCN (2010). IUCN Red list of threatened species. [Online]

Janson, C. H. (1988). Intra-specific food competition and primate social structure: A synthesis. Behaviour 105, pp.1-17.

Janzen, D. H. (1988). Tropical dry forests. The most endangered major tropical ecosystem. In: Wilson, E. O. (ed.) Biodiversity. Washington D.C.: National Academy Press, pp.130-137.

Jekielek, J. (2004). Hybridization of brown lemurs at Berenty Reserve, Madagascar. Masters Abstracts (42(2)), p.526.

Johns, A. D. (1986). Notes on the ecology and current status of the buffy saki, Pithecia albicans. Primate Conservation 7, pp.26-29.

Johnson, S. E. (2002). Ecology and Speciation in Brown Lemurs: White-collared Lemurs (Eulemur albocollaris) and Hybrids (Eulemur albocollaris X Eulemur fulvus rufus) in Southeastern Madagascar. PhD dissertation. University of Texas.

Jolly, A. (1966a). Lemur Behavior. Chicago: University of Chicago Press.

Jolly, A. (1966b). Lemur social behavior and primate intelligence. Science 153, pp.501-506.

Jolly, A. (1972). Troop continuity and troop spacing in Propithecus verreauxi and Lemur catta at Berenty (Madagascar). Folia Primatologica 17, pp.335-363.

Jolly, A. (1984). The puzzle of female feeding priority. In: Small, M. F. (ed.) Female Primates: Studies by Women Primatologists. New York: Alan R. Liss, pp.197–215.

Jolly, A. (1998). Pair-bonding, female aggression, and the evolution of lemur societies. Folia Primatologica (Suppl. 1) 69, pp.1-13.

Jolly, A. (2004). Lords and Lemurs: Mad Scientists, Kings with Spears, and the Survival of Diversity in Madagascar. Boston: Houghton Mifflin.

Jolly, A. (2006a). Ringtailed lemur biology : Lemur catta in Madagascar. Developments in primatology : progress and prospects. New York: Springer.

Jolly, A., Dobson, A., Rasamimanana, H., Walker, J., O'Connor, S., Solberg, M. E. and Perel, V. (2002). Demography of Lemur catta at Berenty Reserve, Madagascar: effects of troop size, habitat and rainfall. International Journal of Primatology 23, pp.327-353.

Jolly, A., Gustafson, H. L., Oliver, W. L. R. and O'Connor, S. (1982a). Propithecus verreauxi population and ranging at Berenty, Madagascar, 1975 and 1980. Folia Primatologica 39, pp.124-144.

Jolly, A., Koyama, N., Rasamimanana, H. Crowley, H. M. and Williams, G. (2006b). Berenty reserve: a research site in southern Madagascar. In: Jolly, A., Sussman, R. W., Koyama, N. and Rasamimana, H. (eds.) Ringtailed Lemur Biology. New York: Springer.

Jolly, A., Oliver, W. L. R. and O'Connor, S. M. (1982b). Population and troop ranges of Lemur catta and Lemur fulvus at Berenty, Madagascar: 1980 census. Folia Primatologica 39, pp.115-123.

Jolly, A. and Pride, E. (1999). Troop histories and range inertia of Lemur catta at Berenty, Madagascar: a 33-year perspective. International Journal of Primatology 20, pp.359-373.

Jolly, A., Rasamimanana, H., Braun, M., Dubovick, T., Mills, C. and Williams, G. (2006c). Territory as bet-hedging: Lemur catta in a rich forest and an erratic climate. In: Jolly, A., Sussman, R. W., Koyama, N. and Rasamimanana, H. (eds.) Ring-tailed Lemur Biology Lemur catta in Madagascar. New York: Springer.

Jongman, R. H. G., Ter Braak, C. J. F. and Van Tongeren, O. F. R. (1995). Data Analysis in Community and Landscape Ecology. Cambridge: Cambridge University Press.

Kappeler, P. M. (1990). The evolution of sexual size dimorphism in prosimian primates. American Journal of Primatology 21, pp.201-214.

Kappeler, P. M. (1993). Sexual selection and lemur social systems. In: Kappeler, P. M. and Ganzhorn, J. U. (eds.) Lemur Social Systems and their Ecological Basis. New York: Plenum Press, pp.225-242.

Kappeler, P. M. (1995). Life history variation among nocturnal prosimians. In: Alterman, L.; Doyle, G. A. and Izard, M. K. (eds.) Creatures of the Dark: the Nocturnal Prosimians. New York: Plenum Press, pp.75-92.

Keddy, P. A. (1989). Competition. London: Chapman & Hall.

Kent, M. and Coker, P. (1992). Vegetation Description and Analysis: A Practical Approach. Chichester, England: John Wiley & Sons.

Klopfer, P. H. and Boskoff, K. (1979). Maternal behavior in prosimians. In: Doyle, G. A. and Martin, R. D. (eds.) The Study of Prosimians. New York: Academic Press, pp.123-157.

Klopfer, P. H. and Jolly, A. (1970). The stability of territorial boundaries in a lemur troop. Folia Primatologica 12, pp.199-208.

Koenig, A., Borries, C., Doan-Sheehy, D. M. and Janson, C. H. (2006). How important are affiliation and cooperation? A reply to Sussman et al. American Journal of Physical Anthropology 131, pp.522–524.

Koyama, N. (1991). Troop division and inter-troop relationships of ringtailed lemurs (Lemur catta) at Berenty, Madagascar. In: Ehara, A., Kimura, T., Takenaka, O. and Iwamoto, M. (eds.) Primatology Today. Amsterdam: Elsevier, pp.173–176.

Koyama, N., Soma, T., Ichino, S. and Takahata, Y. (2006). Home ranges of ring-tailed lemur troops and the density of large trees at Berenty Reserve, Madagascar. In: Jolly, A., Sussman, R. W., Koyama, N. and Rasamimanana, H. (eds.) Ringtailed Lemur Biology: Lemur catta in Madagascar. New York: Springer, pp.86-101.

Krebs, C. J. (1999). Ecological Methodology. 2nd ed. Don Mills, Ontario: Addison-Wesley Educational Publishers, Inc.

Krebs, C. J. (1994). Ecology: The Experimental Analysis of Distribution and Abundance. 4th ed. New York: Harper Collins College Publishers.

Kronfeld-Schor, N., Shargala, E., Haimb, A., Dayana, T. Zisapelc, N. and Heldmaierd, G. (2001). Temporal partitioning among diurnally and nocturnally active desert spiny mice: energy and water turnover costs. Journal of Thermal Biology 26, pp.139-142.

Lambert, J. (1998). Primate digestion: interactions among anatomy, physiology, and feeding ecology. Evolutionary Anthropology: Issues, News, and Reviews 7, pp.8-20.

Laughlin, D. C., Abella, S. R., Covington, W. W. and Grace, J. B. (2007). Species richness and soil properties in Pinus ponderosa forests: A structural equation modeling analysis. Journal of Vegetation Science 18, pp.231-242.

Lehman, M. S., Rajaonson, A. and Day, S. (2006). Edge effects and their influence on lemur density and distribution in Southeast Madagascar. American Journal of Physical Anthropology 129, pp.282-241.

MacArthur, R. and Levins, R. (1964). Competition, habitat selection, and character displacement in a patchy environment. Proceedings of the National Academy of Sciences 51, pp.1207-1210.

MacNally, R. (1995). Ecological Versatility and Community Ecology. Cambridge: Cambridge University Press.

Marcelli, M., Fusillo, R. and Boitani, L. (2003). Sexual segregation in the activity patterns of European polecats (Mustela putorius). Journal of Zoology 261, pp.249–255.

Marshall, A., Ancrenaz, M., Fredriksson, G, Ghaffar, N., Leighton, M., McConkey, K. R., Morrogh-Bernard, H., van Schaik, C. P., Yeager, C. P., Wich, S. A., Proctor, J. and Bearley, F. (2006). The effects of habitat quality, phenology, and floristics on populations of Bornean and Sumatran orangutans: are Sumatran forests more productive than Bornean forests? International Journal of Primatology (27(Suppl 1)), p.Abst #381.

Martin, P. and Bateson, P. (2007). Measuring Behaviour an Introductory Guide. 3rd ed. New York: Cambridge university press.

May, R. M. and MacArthur, R. H. (1972). Niche overlap as a function of environmental variability. Proc. Nat. Acad. Sci. 69 (5), pp.1109-1113.

McGarigal, K., Cushman, S. and Stafford, S. (2000). Multivariate Statistics for Wildlife and Ecology Research. New York: Springer.

Mertl-Millhollen, A. (2000). Components of scent marking behavior by male ringtailed lemurs (Lemur catta) at Berenty Reserve, Madagascar. American Journal of Primatology (51(Suppl 1)), p.74.

Mertl-Millhollen, A. S., Moret, E. S., Felantsoa, D., Rasamimanana, H. Blumenfeld-Jones, K. C. and Jolly, A. (2003). Ring-tailed lemur home ranges correlate with food abundance and nutritional content at a time of environemental stress. International Journal of Primatology 24, pp.969-985.

Mertl-Millhollen, A. S., Rambeloarivony, H., Miles, W., Kaiser, V. A., Gray, L., Dorn, L. T., Williams, G. and Rasamimanana, H. (2006). The influence of tamarind tree quality and quantity on Lemur catta behaviour. In: Jolly, A., Sussman, R. W., Koyama, N. and Rasamimanana, H. (eds.) Ringtailed Lemur Biology. New York: Springer.

Mertl-Millhollen, S. A., Gustafson, H. L., Budnitz, N., Dainis, K. and Jolly, A. (1979). Population and Territory stability of Lemur catta at Berenty, Madagascar. Folia Primatologica 31, pp.106-122.

Mittermeier, R. and van Roosmalen, M. (1981). Preliminary observations on habitat utilization and diet in eight Surinam monkeys. Folia Primatologica 36, pp.1-39.

Mittermeier, R. A. (1988). Primate diversity and the tropical forest: case studies from Brazil and Madagascar and the importance of the megadiversity countries. In: Wilson, E. O. and Peters, F. M. (eds.) Biodiversity. Washington DC: National Academy Press, pp.145-154.

Mittermeier, R. A., Louis, E. E., Richardson, M., Schwitzer, C., Langrand, O., Rylands, A. B., Hawkins, F., Rajaobelina, S., Ratsimbazafy, J., Rasoloarison, R., Roos, C., Kappeler, P. M. and Mackinnon, J. (2010). Lemurs of Madagascar. 3rd ed. Tropical Field Guide Series. Conservation International.

Mortelliti, A., Amori, G. and Boitani, L. (2010). The role of habitat quality in fragmented landscape: a conceptual overview and prospectus for future research. Oecologia 163 (2), pp.535-547.

Mueller-Dombois, D. and Ellenberg, H. (1974). Aims and Methods of Vegetation Ecology. Blackburn Press.

Mutschler, T. W. (1998). The Alaotran Gentle Lemur (Hapalemur griseus alaotrensis) : A Study in Behavioural Ecology . PhD thesis, Zurich, University of Zurich.

Nakamichi, M. and Koyama, N. (1997). Social relationships among ring-tailed lemurs (Lemur catta) in two free-ranging troops at Berenty Reserve, Madagascar. International Journal of Primatology 18, pp.73–93.

Newton, P. N. (1989). Associations between langur monkeys (Presbytis entellus) and chital deer (Axis axis): chance encounters or mutualism? Ethology 83, pp.89-120.

Nicoll, M. E. and Langrand (1989). Madagascar: Revue de la Conservation et des Aires Protégées. W E Gland.

Norconk, M. and Kinzey, W. (1994). Challenge of neotropical frugivory: Travel patterns of spider monkeys and bearded sakis. American Journal of Primatology 34, pp.171-183.

O'Brien, T. G., Kinnaird, M. F., Nurcahyo, A., Iqbal, M. and Rusmanto, M. (2004). Abundance and distribution of sympatric gibbons in a threatened Sumatran Rain Forest. International Journal of Primatology 25 (2), pp.267-284.

O'Connor, S. M. (1987). The effect of human impact on vegetation and the consequences to primates in two riverine forests, southern Madagascar. PhD thesis. cambridge university.

Odling-Smee, F., Laland, K. and Feldman, M. (2003). Niche Construction: the Neglected Process in Evolution. Princeton: Princeton University Press.

Opler, P. A., Baker, H. G. and Frankie, G. W. (1980). Plant reproductive characteristics during secondary succession in Neotropical lowland forest ecosystems. Biotropica 12 (Suppl. 1), pp.24–39.

Ostner, J. and Kappeler, P. M. (1999). Central males instead of multiple pairs in redfronted lemurs, Eulemur fulvus rufus (Primates, Lemuridae)? Animal Behaviour 58, pp.1069-1078.

Ostner, J. and Kappeler, P. M. (2004). Male life history and the unusual adult sex ratios of redfronted lemur, Eulemur fulvus rufus, groups. Animal Behaviour 67 (2), pp.249-259.

Overdorff, D. J. (1988). Preliminary report on the activity cycle and diet of the red-bellied lemur (Lemur rubriventer) in Madagascar. American Journal of Primatology 16, pp.143–153.

Overdorff, D. J. (1991). Ecological correlates to social structure in two prosimian primates: Eulemur fulvus rufus and Eulemur rubriventer in Madagascar. PhD Dissertation. Duke University.

Overdorff, D. J. (1993). Similarities, differences, and seasonal patterns in the diets of Eulemur rubriventer and Eulemur fulvus rufus in the Ranomafana National Park, Madagascar. International Journal of Primatology 14 (5), pp.721-754.

Overdorff, D. J. (1996). Ecological correlates to activity and habitat use of two prosimian primates: Eulemur fulvus rufus and Eulemur rubriventer in Madagascar. American Journal of Primatology 40, pp.327-342.

Økland, R. H. (1990). Vegetation ecology: theory, methods and applications with reference to Fennoscandia. Sommerfeltia 4, pp.1-233.

Patterson, B. D., Willig, M. R. and Stevens, R. D. (2003). Trophic strategies, niche partitioning, and patterns of ecological organization. In: Kunz, T. H. and

Fenton, M. B. (eds.) Bat Ecology. Chicago: University of Chicago Press, pp.536-579.

Pearson, R. G. and Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12 (5), pp.361-371.

Pereira, M. E. (1993). Seasonal adjustments of growth rate and adult body weight in ringtailed lemurs. In: Kappeler, P. M. and Ganzhorn, J. U. (eds.) Lemur Social Systems and Their Ecological Basis. New York: Plenum.

Pereira, M. E. (2006). Obsession with agonistic power. In: Jolly, A., Sussman, R. W., Koyama, N. and Rasamimanana, H. (eds.) Ring-tailed Lemur Biology Lemur catta in Madagascar. New York: Springer.

Pereira, M. E. and Kappeler, P. M. (1997). Divergent systems of agonistic relationship in Lemurid primates. Behaviour 134, pp.225-274.

Pereira, M. E and McGlynn, C. A. (1997). Special relationships instead of female dominance for redfronted lemurs, Eulemur fulvus rufus. American Journal of Primatology 44, pp.239-258.

Pereira, M. E., Strohecker, R., Cavigelli, S. A., Hughes, C. and Pearson, D. (1999). Metabolic strategy and social behavior in lemuridae. In: Rakotosaminanana, B., Rasamimanana, H., Ganzhorn, J. U. and Goodman, S. (eds.) New Directions in Lemur Studies. New York: Plenum/Kluwer, pp.93-118.

Peres, C. and Dolman, P. (2000). Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. Oecologia 122, pp.175-189.

Petrik, P., Pergl, J. and Wild, J. (2010). Recording effort biases the species richness cited in plant distrivution atlases. Perspectives in Plant Ecology, Evolution and Systematics 12 (57-65).

Pianka, E. (1994). Evolutionary ecology. 5th ed. New York: Harper Collins.

Pielou, E. C. (1984). Interpretation of Ecological Data. New York: John Wiley and Sons.

Pinkus, S. (2004). Impact of an introduced population of Eulemur fulvus on a native population of Lemur catta at Berenty reserve, Madagascar. Msc. Thesis. University of British Columbia.

Pinkus, S., Smith, J. N. M. and Jolly, A. (2006). Feeding competition between Introduced Eulemur fulvus and native Lemur catta during the birth season at Berenty Reserve, Southern Madagascar. In: Jolly, A., Sussman, R. W., Koyama, N. and Rasamimanana, H. (eds.) Ringtailed Lemur biology. New York: Springer.

Porter, L. M. (2001). Dietary differences among sympatric Callithrichinae in northern Bolivia: Callimico goeldii, Saguinus fuscicollis and S. labiatus. International Journal of Primatology 22, pp.961-992.

Powzyk, J. (1997). The socio-ecology of two sympatric indriids: Propithecus diadema diadema and Indri indri, a comparison of feeding strategies and their possible repercussions on species-specific behaviors. PhD Dissertation. Duke University.

Pride, R. E., Felantsoa, D., Randriamboavonjy, T. and Randriambelona. (2006). Resource defense in Lemur catta: the importance of group size. In: Jolly, A., Sussman, R. W., Koyama, N. and Rasamimanana, N. (eds.) Ringtailed Lemur Biology: Lemur catta in Madagascar. New York: Springer, pp.208-232.

Putz, F. E. and Milton, K. (1982). Tree mortality rates on Barro Colorado Island. In: Leigh, R. and Windsor (eds.) The Ecology of A Tropical Forest : Seasonal Rhythms and Long-term Changes. Washington DC: Smithonian Institution Press, pp.95-100.

Raemaekers, J. J. (1978). The sharing of food sources between two gibbon species in the wild. Malaysian Nature Journal 31, pp.181-188.

Raemakers, J. J. (1979). Ecology of sympatric gibbons. Folia Primatologica 31, pp.227-245.

Ralison, J. (2006). Rapid assessment of lemurs in southern and south western Madagascar. Lemur News 11, pp.39-40.

Ramanamanjato, J. B., Mcintyre, P. B. and Nussbaum, R. A. (2002). Reptile, amphibiens and lemur diversity of the Malahelo forest, a biogeographical transition zone in southeastern Madagascar. Biodiversity and Conservation 00, pp.1-10.

Rambeloarivony, H. (2009). Feeding flexibility of Lemur catta in Berenty reserve: Benefits and Costs. MSc thesis. Oxford Brookes University.

Randriamboavonjy, T. M. (2003). Etude des besoins en eau de Lemur catta (Linné 1758), pendant la saison sèche, dans la Réserve Privée de Berenty, au Sud de Madagascar. Mémoire CAPEN. Ecole Normale Supérieure.

Rasamimanana, H. (1999). Influence of social organization patterns on food intake of Lemur catta in the Berenty Reserve. In: Rakotosamimananana, B., Rasamimanana, H., Ganzhorn, J. U. and Goodman, S. (eds.) New Directions in Lemur Studies. New York: Kluwer Academic, pp.173-188.

Rasamimanana, H. (2004). La dominance des femelles makis (Lemur catta) Madagascar? PhD Thesis. Museum National de l'Histoire Naturelle Paris France.

Rasamimanana, H., Andrianome, V. N., Rambeloarivony, H. and Pasquet, P. (2006). Male and female ringtailed lemurs? energetic strategy does not explain female dominance. In: Jolly, A., Sussman, R. W., Koyama, N. and Rasamimanana, H. (eds.) Ring-tailed Lemur Ecology: Lemur catta in Madagascar. New York: Springer, pp.271-295.

Rasamimanana, H. and Rafidinarivo, E. (1993). Feeding behavior of Lemur catta females in relation to their physiological state. In: Kappeler, P. M. and Ganzhorn, J. U. (eds.) Lemur Social Systems and Their Ecological Basis. New York: Plenum press.

Rasamimanana, H., Razafindramanana, J., Mertl-Millhollen, A., Blumenfeld-Jones, K., Raharison, S. M., Tsaramanana, D. R., Razoliharisoa, V. and Tarnaud, T. (on press). Berenty Reserve: Interactions between the diurnal lemur species and their gallery forest. In: Masters, J. C. (ed.) Leaping Ahead: Advances in Prosimian Biology.

Rasmussen, M. (1999). Ecological influences on activity cycle in two cathemeral primates, the mongoose lemur (Eulemur mongoz) and the common brown lemur (Eulemur fulvus fulvus). PhD Dissertation. Duke University.

Rasmussen, M. A. (2005). Seasonality and predation risk: varying activity periods in lemurs and other primates. In: Brockman, D. K. and van Schaik, C. P. (eds.) Seasonality in Primates: Implications for Human Evolution. Cambridge: Cambridge University Press, pp.105–128.

Raven, P. H. and Johnson, G. B. (1999). Biology. 5th ed. Boston: McGraw-Hill.

Razafindramanana, J. (2005). Impact de l'introduction des lémurs bruns hybrides dans la reserve de Berenty - sud de Madagascar. Mémoire CAPEN. Ecole Normale superieure.

Razafindramanana, J. (2007). Distribution et densité de la population de Lemurs bruns (Eulemur rufus x Eulemur collaris) dans la Reserve de Berenty. Mémoire D.E.A. E.S.S.A.

Reed, K. E. and Fleagle, J. G. (1995). Geographic and climatic control of primate diversity. Proc. Natl. Acad. Sci. USA 72, pp.7874–7876.

Richard, A. F., Dewar, R. E., Schwartz, M. and Ratsirarson, J. (2000). Mass change, environmental variability and female fertility in wild Propithecus verreauxi. Journal of Human Evolution 39, pp.381–391.

Rodman, P. (1973). Synecology of Bornean primates I. A test for interspecific interactions in spatial distribution of five species. American Journal of Physical Anthropology 38, pp.655-660.

Ross, C. (1992). Basal metabolic rate, body weight and diet in pimates: an evaluation of the evidence. Folia Primatologica 58, pp.7-23.

Sauther, M. L. (1991). Reproductive behavior of free-ranging Lemur catta at Beza Mahafaly Special Reserve, Madagascar. American Journal of Physical Anthropology 84, pp.463-477.

Sauther, M. L. (1992). The Effect of Reproductive State, Social Rank and Group Size on Resource Use Among Free-Ranging Ringtailed Lemurs (Lemur catta) of Madagascar. Ph.D. thesis. Washington University.

Sauther, M. L. (1993). Resource competition in wild populations of ring-tailed lemurs (Lemur catta): Implications for female dominance. In: Kappeler, P. M. and Ganzhorn, J. U. (eds.) Lemur Social Systems and Their Ecological Basis. New York: Plenum Press, pp.135-152.

Sauther, M. L. (1994). Wild plant use by pregrant and lactating ring-tailed lemurs, with implications for early hominid foraging. In: Etkin, N. L. (ed.) Eating on The Wild Side: The Pharmacologic, Ecologic, and Social Implications of Using Noncultigens. Tucson: University of Arizona Press, pp.240–256.

Sauther, M. L. (1998). Interplay of phenology and reproduction in ring-tailed lemurs: implications for ring-tailed lemur conservation. Folia Primatologica 69, pp.309-320.

Sauther, M. L., Sussman, R. W. and Gould, L. (1999). The socioecology of the ringtailed lemur: Thirty-five years of research. Evolutionary Anthropology 8, pp.120-132.

Schnell, R. (1971). Introduction à la Phytogéographie Comparée des Pays Tropicaux. C.N.R.S. Paris France.

Schoener, T. (1983). Field experiments on interspecific competition. American Naturalist 122, pp.240-285.

Schoener, T. W. (1974). Resource partitioning in ecological communities. Science 185, pp.27-39.

Scholz, F. and Kappeler, M. P. (2004). Effects of seasonal water scarcity on ranging behaviour of Eulemur fulvus rufus. International Journal of Primatology 25 (3), pp.599-613.

Setchell, J. M. and Curtis, D. J. (2003). Field and laboratory methods in Primatology, a practical guide.

Simmen, B., Bayart, F., Rasamimanana, H., Zahariev, A., Blanc, S. and Pasquet, P. (2010). Total energy expenditure and body composition in two free-living sympatric lemurs. PLoS ONE 5 (3).

Simmen, B., Hladik, A. and Ramasiarisoa, P. (2003). Food intake and dietary in Native Lemur catta and Propithecus verreauxi and introduced Eulemur fulvus at Berenty, Southern Madagascar. International Journal of Primatology 24 (5), pp.949-996.

Simmen, B., Peronny, S., Jeanson, M., Hladik, A. and Marez, A. (2006a). Diet quality and taste perception of plant secondary metabolites by Lemur catta. In: Jolly, A., Sussman, R. W., Koyama, N. and Rasamimanana, H. (eds.) Ring-tailed Lemur Biology Lemur catta in Madagascar. New York: Springer.

Simmen, B., Sauther, L. M., Soma, T., Rasamimanana, H., Sussman, R. W., Jolly, A., Tarnaud, L. and Hladik, A. (2006b). Plant species fed on by Lemur catta in gallery forests of the southern domain of Madagascar. In: Jolly, A., Sussman, R. W., Koyama, N. and Rasamimanana, H. (eds.) Ring-tailed Lemur Biology Lemur catta in Madagascar. New York: Springer.

Simmen, B., Tarnaud, L., Bayart, F., Hladik, A., Thiberge, A. L., Jaspart, S., Jeanson, M. and Marez, A. (2005). Richesse en métabolites secondaires des forêts de Mayotte et de Madagascar et incidence sur la consommation de feuillage chez deux espèces de lémurs (Eulemur spp.). Rev. Ecol. (Terre Vie) 60, pp.297–324.

Smith, A. P. (1997). Deforestation, fragmentation and reserve design in western Madagascar. In: Laurance, W. F. and Bierregaard, R. O., (eds.) Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. Chicago: University of Chicago Press.

Sokal, R. R. and Rohlf, F. J. (1981). Biometry. San francisco: W.H. Freeman.

Soma, T. (2006). Tradition and novelty: Lemur catta feeding strategy on introduced tree species at Berenty Reserve. In: Jolly, A., Sussman, R. W., Koyama, N. and Rasamimanana, H. (eds.) Ring-tailed Lemur Biology: Lemur catta in Madagascar. New York: Springer.

Sterling, E. (1993). Patterns of range use and social organization in aye-ayes (Daubentonia madagascariensis) on Nosy Mangabe. In: Kappeler, P. M. and Ganzhorn, J. U. (eds.) Lemur Social Systems and Their Ecological Basis. New York: Plenum Press, pp.1-10.

Stiling, P. D. (2001). Ecology: Theories and Applications.

Strier, K. B. (2007). Primate Behavioral Ecology. 3rd ed. Boston: Allyn and Bacon.

Strong, D., Szyska, L. and Simberloff, D. (1979). Tests of community-wide character displacement against null hypotheses. Evolution 33, pp.897-913.

Struhsaker, T. T. (1981). Polyspecific associations among tropical rain-forest primates. Zeitschrift fur Tierpsychologie, pp.268-304.

Struhsaker, T. T. and Oates, J. (1975). Comparison of the behavior and ecology of red colobus and black-and-white colobus monkeys in Uganda: A summary. In: Tuttle, R. H. (ed.) Socioecology and Psychology of Primates. The Hague: Mouton, pp.103-124.

Stuart, S. N., Adams, R. J. and Jenkins, M. D. (1990). Biodiversity in sub-saharan Africa and its islands: conservation, management, and sustainable use. Occasional papers of the IUCN Species Survival Commission 6, p.242.

Sussman, R. W. (1972). An ecological study of two Madagascar primates: Lemur fulvus (Audebert) and Lemur catta (Linnaeus). PhD dissertation. Duke University.

Sussman, R. W. (1974). Ecological distinctions in sympatric species of Lemurs. In: Martin, R. D., Doyle, G. A. and Walker, A. C. (eds.) Prosimian Biology. London: Duckworth, pp.75-108.

Sussman, R. W. (1977a). Feeding behavior of Lemur catta and Lemur fulvus. In: Clutton-brock, T.H. (ed.) Primate Ecology: Studies of Feeding and Ranging in Lemurs, Monkeys and Apes. New York: Academic Press, pp.1-36.

Sussman, R. W. (1977b). Socialization, social structure, and ecology of two sympatric species of Lemur. In: Chevalier-Skolnikoff, S. and Poirier, F. E. (eds.) Primate Bio-social Development. New York and London: Garland publications, pp.515-528.

Sussman, R. W. (1999). Primate Ecology and Social Structure. Needham Heights: Pearson Custom Publishing.

Sussman, R. W. and Rakotozafy, A. (1994). Plant diversity and structural analysis of a tropical dry forest in southwestern Madagascar. Biotropica 26 (3), pp.241-254.

Sussman, R. W., Garber, P. A. and Cheverud, J. M. (2005). Importance of cooperation and affiliation in the evolution of primate sociality. American Journal of Physical Anthropology 128, pp.84–97.

Sussman, R. W., Green, G. M., Porton, I., Andrianasolondraibe, O. L. and Ratsirarson, J. (2003). A survey of the habitat of Lemur catta in southwestern and southern Madagascar. Primate Conservation 19, pp.32-57.

Sussman, R. W., Sweeney, S., Green, G. M., Porton, I., Andrianasolondraibe, O. L. and Ratsirarson, J. (2006). A preliminary estimate of Lemur catta population density using satellite imagery. In: Jolly, A., Sussman, R. W., Koyama, N. and Rasamimanana, H. (eds.) Ringtailed Lemur Biology. New York: Springer.

Tallmon, D. A. and Mills, S. C. (2004). Edge effects and isolation: red backed voles revisited. Conservation Biology 18 (6), pp.1658-1664.

Tan, C. (1999). Group composition, home range size, and diet of three sympatric bamboo lemur species (genus Hapalemur) in Ranomafana National Park, Madagascar. International Journal of Primatology 20, pp.547-566.

Tanaka, M. (2007). Habitat use and social structure of a brown lemur hybrid population in the Berenty Reserve, Madagascar. American Journal of Primatology 69, pp.1189–1194.

Tarnaud, L. (2006). Cathemerality in the Mayotte brown lemur (Eulemur fulvus): Seasonality and food quality. Folia Primatologica 77, pp.166–177.

Tattersall, I. (1977). Ecology and behavior of Lemur fulvus mayottensis (Primates: Lemuriformes). Anthropol. Pap. Am. Mus. Nat. Hist. 54, pp.422-481.

Tattersall, I. (1982). The primates of Madagascar. New York: Columbia University Press.

Tattersall, I. (1987). Cathemeral activity in primates: a definition. Folia Primatologica 49, pp.200–202.

Tattersall, I. and Sussman, R. W. (1998). "Little Brown Lemurs" of northern Madagascar. Phylogeny and ecological role in resource partitioning. Folia Primatologica 69 (Suppl 1), pp.379-388.

Taylor, L. L. (1986). Kinship, dominance and social organization in a semi-free-ranging group of ringtailed lemurs (Lemur catta). PhD Dissertation. Washington University.

Terborgh, J. (1983). Five New World Primates. Princeton: Princeton University Press.

Terborgh, J. and Janson, C. (1986). Socioecology of primate groups. Annual Review of Ecology and Systematics 17, pp.111-135.

Tomblin, D. and Cranford, J. (1994). Ecological niche differences between Alouatta palliata and Cebus capucinus comparing feeding modes, branch use, and diet. Primates 35, pp.265-274.

Tomimatsu, H. and Ohara, M. (2010). Demographic response of plant populations to habitat fragmentation and temporal environmental variability. Oecologia 162, pp.903-911.

Tutin, C., Ham, R. M., White, L. J. T. and Harrison, M. J. S. (1997). The primate community of the Lope Reserve, Gabon: Diets, responses to fruit scarcity, and effects on biomass. American Journal of Primatology 42, pp.1-24.

van Schaik, C. (1996). Phenology: forest seasonality in an everwet environment. In: van Schaik, C. and Supriatna, J. (eds.) Leuser: A Sumatran Sanctuary. Depok, Indonesia: Yayasan Bina Sains Hayati Indonesia, pp.120-131.

van Schaik, C. and Griffiths, M. (1996). Activity periods of Indonesian rain forest mammals. Biotropica 28, pp.105–112.

Vasey, N. (1997). Community ecology and behavior of Varecia variegata rubra and Lemur fulvus albifrons, on the Masoala Peninsula, Madagascar. PhD Dissertation. Washington University.

Vasey, N. (2000a). Niche separation in Varecia variegata rubra and Eulemur fulvus albifrons: Interspecific patterns. American Journal of Physical Anthropology 112, pp.411-431.

Vasey, N. (2000b). Plant species composition of diet in two sympatric lemurs: Varecia variegata rubra and Eulemur fulvus albifrons. American Journal of Physical Anthropology [suppl] 30, pp.309-310.

Vasey, N. (2002). Niche separation in Varecia variegata rubra and Eulemur fulvus albifrons: II. Intraspecific patterns. American Journal of Physical Anthropology 118, pp.169-183.

Vasey, N. (2004). Circadian rhythms in diet and habitat use in red ruffed lemurs (Varecia rubra) and white-fronted brown lemurs (Eulemur fulvus albifrons). American Journal of Physical Anthropology (124(4)), pp.353-363.

Waser, P. (1987). Interactions among primate species. In: Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. and Struhsaker, T. T. (eds.) Primate Societies. Chicago: University of Chicago Press, pp.210-226.

Waser, P. M. and Case, T. J. (1981). Monkeys and matrices: coexistence of “omnivorous” forest primates. Oecologia 49, pp.102–108.

WCS (2005). Etude de Faisabilité de la C*réation de l’Aire Protégée d’Ambatotsirongorongo.* Antananarivo, Madagascar.

Webb, C. O. and Peart, D. R. (2000). Habitat associations of treesand seedlings in a Bornean rain forest. Journal of Ecology 88, pp.464–478.

Weiher, E. (2003). Species richness along multiple gradients: testing a general multivariate model in oak savannas. Oikos 101, pp.311-316.

White, L. and Edwards, A. (2000). Conservation Research in the African Rain Forests: A Technical Handbook. New York, USA: Wildlife Conservation Society.

Wilmé, L., Goodman, S. M. and Ganzhorn, J. U. (2006). Biogeographic evolution of Madagascar`s microendemic biota. Science 312, pp.1063-1065.

Wilson, J. M., Stewart, P. D., Ramangason, G. S., Denning, A. M. and Hutchings, M. S. (1989). Ecology and conservation of the crowned lemur, Lemur coronatus, at Ankarana, N. Madagascar, with notes on Sanford's lemur, other sympatrics and subfossil lemurs. Folia Primatologica 52, pp.1–26.

Wrangham, R. W., Conklin-Brittain, N. L. and Hunt, K. D. (1998). Dietary responses of chimpanzees and Cercopithecines to seasonal variation in fruit abundance. I. Anti-feedants. International Journal of Primatology 19 (6), pp.949-969.

Wright, P. C. (1989). The nocturnal primate niche in the New World. Journal of Human Evolution 18, pp.635–658.

Wright, P. C. (1999). Lemur traits and Madagasar ecology: Coping with an island environment. Yearbook of Physical Anthropology 42, pp.31–72.

Wright, P. C. and Randrimanantena, M. (1989). Comparative ecology of three sympatric bamboo lemurs in Madagascar. American Journal of Physical Anthropology 78, p.327.

Wroe, S. et al. (2007). Computer simulation of feeding behaviour in the thylacine and dingo as a novel test for convergence and niche overlap. Proceedings of the Royal Society B 274, pp. 1-10.

Wroe, S., Field, J. and Grayson, D. K. (2006). Megafaunal extinction: climate, humans and assumptions. Trends in Ecology and Evolution 21, pp.61-62.

Yamashita, N. (2002). Diet of two lemur species in different microhabitats in Beza Mahafaly Special Reserve, Madagascar. International Journal of Primatology 23 (5), pp.1025-1051.

Zanne, A. E. and Chapman, C. A. (2005). Diversity of woody species in forest, treefall gaps, and edge in Kibale National Park, Uganda. Plant Ecology 178, pp.121-139.

Ziv, Y. and Smallwood, J. A. (2000). Gerbils and heteromyids – interspecific competition and the spatio-temporal niche. In Halle, S. and Stensteth, N. C. (eds.) Activity Patterns in Small Mammals: An Ecological Approach. Berlin: Springer, pp.159–176.

Appendices

Appendice 1. Plant species recorded from transects in Malaza Berenty and Bealoka forests

Identified Plant species

Plant family	Scientific names	Life Form	Malaza	Bealoka
Apocynaceae	Hazonta modesta	Tree	+	+
Aristolochiaceae	Aristolochia acuminata	Liana	-	+
Ascepiadaceae	Secamone sp.	Liana	+	+
	Secamone uncinata	Liana	+	+
	Leptaderia sylvestre	Liana	+	-
	Pentopetia androsaemifolia	Liana	-	+
	Secamone capitata	Liana	+	+
Bignoniaceae	Fernandoa madagascariensis	Tree	+	-
	Phylloctenium decaryanum	Liana	+	-
Boraginaceae	Cordia caffra	Tree	+	+
Burseraceae	Commiphora trifolii	Tree	+	+
Cactaceae	Opuntia vulgaris	Tree	+	-
Capparaceae	Crateva Excelsa	Tree	+	+
	Capparis sepiaria	Liana	+	+
	Cadaba virgata	Tree	+	-
Ceasalpinoideae	Tamarindus indica	Tree	+	+
Celastraceae	Maytenus fasciculata	Tree	+	-
	Loeseneriella rubiginosa	Liana	+	-
	Loeseneriella urceolus	Liana	+	-
Combretaceae	Combretum albiflorum	Liana	+	+
Combretaceae	Combretum subumbellatum	Liana	+	-
Crassulaceae	Kalanchoe sp.	Liana	+	-
Cucurbutaceae	Xerosycios perrier	Liana	-	+
Didieraceae	Alluaudia procera	Tree	+	-
Euphorbiaceae	Croton meridionalis	Tree	+	-
	Euphorbia leucodendron	Tree	+	+
	Euphorbia encoclada	Tree	-	+
	Euphorbia stenoclada	Tree	+	-
	Euphorbia sp.	Liana	+	+
Hippocrateaceae	Hippocratea sp.	Liana	-	+
liliaceae	Asparagus aymoninorum	Liana	-	+
Loganiaceae	Strichnos madagascariensis	Tree	+	+
Lythraceae	Lawsonia sp.	Tree	-	+
Malpighiaceae	Microsteira blesomatensis	Liana	+	-
	Microsteria sp.	Liana	+	+
Meliaceae	Azadirachta indica	Tree	+	-
	Quisiviante papinea	Tree	+	+

Menispermaceae	Anisocyclea grandidieri	Liana	+	+
	Cissampelos pariera	Liana	+	-
Mimosoideae	Acacia rovumea	Tree	+	+
	Albizzia polyphilla	Tree	+	+
	Pithecelobium dulce	Tree	+	-
	Acacia sp.	Liana	+	+
Olacaceae	Ximenia perrieri	Tree	+	-
Portulaceae	Talinella grevei	Tree	+	-
Rubiaceae	Enterospermum sp	Tree	+	+
Salicaceae	Flacourtia ramantalu	Tree	-	+
Salvadoraceae	Azima tetracantha	Tree	+	+
	Salvadora angustifolia	Tree	+	+
Sapendaceae	Neotina isoneura	Tree	+	+
	Tina sp.	Tree	+	-
Sterculiaceae	Byttmeria sp.	Liana	+	-
Tiliaceae	Grewia sp.	Tree	+	-
Ulmaceae	Celtis bifida	Tree	+	-
	Celtis phillippensis	Tree	+	+
Urticaceae	Urera sp.	Tree	+	-
Violaceae	Rinorea greveana	Tree	+	+
Vitaceae	Cissus quadrangularis	Liana	+	+

Unidentified plant species

Vernacular name	Scientific names	Life Form	Malaza	Bealoka
	Unidentified 1	Tree	+	-
Entenente	Unidentified 4	Liana	-	+
Kita	Unidentified 3	Liana	-	+
	Unidentified 2	Liana	+	-
	Unidentified 5	Liana	+	-
Sakavirondambo	Unidentified 5	Liana	-	+
teloravina	Unidentified 6	Liana	+	-
Takasy	Unidentified 7	Liana	-	+

+ Presence, - Absence