DEVELOPMENTS IN PRIMATOLOGY: PROGRESS AND PROSPECTS
Series Editor: Russell H. Tuttle, University of Chicago, Chicago, IL

LEMURS

Ecology and Adaptation

EDITED BY

LISA GOULD AND MICHELLE L. SAUTHER

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This volume is dedicated to Mme. Berthe Rakotosamimanana
(Madame Berthe), who passed away in Antananarivo, Madagascar,
in 2005. Mme. Berthe's energy, wisdom, and leadership
contributed immensely to primatological research and to our
knowledge of the wonderful lemurs of Madagascar

PREFACE

When we first went to the Red Island to begin our respective studies of ring-tailed lemur ecology (nearly twenty years ago), we were both struck by the sheer wildness of Madagascar. A land of great contrasts, one could travel the major highway that bisects the continent, and go from devastated vistas directly linked to human-induced changes, to intact forests where one could encounter a fantastic array of organisms. At that time there were only a handful of researchers who had met the challenges of fieldwork there, but over the past fifteen years there has been a virtual renaissance of studies focusing on Madagascar's unique plants and animals (see volumes by Kappeler and Ganzhorn, 1993; Rakotosamimanana et al., 1999; Goodman and Benstead, 2003; Jolly et al., 2006).

The lemurs of Madagascar remain the primate ambassadors of adaptive radiation. True to Darwin, they exhibit a wonderful example of the interplay between geographic isolation and speciation. Having evolved in complete isolation from other primates—lemur evolution dates back to the Eocene epoch (55–37 million years ago) and possibly even earlier (Martin, 1972, 2000; Mittermeier et al., 1994; Yoder et al., 2003)—the amazing variety of lemurs that we know today arose from either one or several separate waves of migration (see Yoder et al., 2003; Tattersall, 2004; Karanth et al., 2005; Tattersall, this volume). Once they arrived on Madagascar, these ancestral forms spread geographically into numerous niches to become a remarkable array of lemur species. As of this writing (2006) there are between 49 and 63 extant lemur species, depending upon which taxonomic source is consulted (Groves, 2001; Jungers et al., 2002; Moreira, 2005; Mittermeier et al., 2006), but there are also at least 16 species of subfossil lemurs, most of which have only gone extinct within the last 2000 years (see, for example, Karanth et al., 2005; Godfrey et al., this volume). Furthermore, there are new lemur taxa still being discovered. Given such a wealth of species, both living and extinct, it is not surprising that Madagascar attracts researchers from all over the world.

Madagascar's lemurs are also enterprising primates. From both a climatic and a geographical perspective, Madagascar has provided numerous challenges to its inhabitants. Lemurs make a living in a variety of habitats, from exotic spiny forests to seasonal dry forests, diminishing rain forests, limestone forests, and even high-altitude terrain, eking out an existence in habitats with poor soils, low and very seasonal plant productivity, and often unpredictable and sometimes devastating climates (Wright, 1999). Like their fellow island hoppers in Australia, this has resulted in a diverse and unusual number of traits, including female dominance, sexual monomorphism, seasonal fat storage, and strict seasonal breeding (Jolly, 1984; Wright, 1999 and this volume; Curtis, this volume, Fietz and Dausmann, this volume).

With such a wealth of lemur research during the last fifteen years, the major purpose of this volume is to provide a single source for information from many of these new studies. This volume brings together information on newly studied taxa as well as summaries from long-term data on well-known lemur species from a number of sites. Information found in this volume provides us with answers to questions concerning life-history traits, adaptations to extreme seasonality, and natural disasters. It also brings up new information on the ecology and adaptations of the recently extinct subfossil lemurs, which has emerged from both new excavations and technological advances in primate paleontology. From these collected readings we hope to provide new insight into the study of lemur origins, and the ecology and adaptation of both extant and recently extinct species. In a larger context, the information contained in this book will expand our knowledge of primate ecology and allow us further insight into mammalian adaptations to unusual and often harsh environmental conditions that arise from both natural and anthropogenic factors.

We begin literally at the beginning, with Tattersall's (Chapter 1) overview of lemur evolution based on recent fossil, molecular, and ecological evidence. One of the biggest questions regarding lemur evolution is how did lemur ancestors arrive in Madagascar? Current evidence indicates that all of Madagascar's extant and extinct terrestrial mammalian species arrived via an overwater route that may have included ephemeral land bridges or "steppingstones" formed by geological forces in the seafloor. We move from prehistory to history in the chapter by Jolly and Sussman (Chapter 2), where we are introduced to the world of lemur studies in a lively recounting of the history of lemur research in Madagascar and a look at future prospects for conservation in Madagascar. Godfrey et al. (Chapter 3) then enliven the fossil record by using skeletal evidence from the extinct lemurs to suggest possible patterns of their social behavior, biology, and life history.

Given the unique phylogenetic status of the Malagasy lemurs, understanding their basic as well as unusual adaptations is key. Cuozzo and Yamashita (Chapter 4) provide an in-depth overview of what we currently understand regarding lemur dentition. Putting this discussion in a strongly ecological context, they discuss how the external environment leaves an imprint on lemur dentitions, either through adaptations to the physical requirements of specific environments or through environmental effects during the lifetime of the animal. Fietz and Dausmann (Chapter 5) discuss one of the most unusual primate adaptations to Madagascar's marked seasonal climate changes, that of hibernation in *Cheirogaleus medius*. The authors contrast the mechanisms of hibernation in this species, a tropical hibernator, with those of temperate climate hibernators in terms of physiological changes in body mass, internal temperature, and energy efficiency. They explain this unusual behavioral pattern as a response to low ambient temperature as well as food and water shortages during the cool, dry season in western Madagascar.

Freed (Chapter 6) notes that in most communities, different species of diurnal lemurs barely tolerate, displace, or chase one another; yet amicable polyspecific associations are common among members of crowned lemurs and Sanford's lemurs. He then explores these patterns and discusses why such an unusual association occurs.

Several lemur species have been described as cathemeral, and Curtis presents information on cueing mechanisms, adaptive significance, and the evolution of this unusual activity pattern in *Eulemur*, *Hapalemur*, and *Varecia* (Chapter 7). Hypotheses related to the development of cathemerality, which involve such variables as differences in canopy cover, predator avoidance, and offsetting food competition, are presented, as Curtis stresses that there is no single explanation for the evolution of cathemerality. Sterling and McCreless (Chapter 8) discuss the behavior and adaptations of Madagascar's most unusual-looking lemur, indeed one of the most unique primates, the aye-aye. The ecology and biology of this primate are likewise unique and in nearly every aspect, this species stands outside what is even the norm for lemurs.

During the past 15 years a wealth of new lemur studies have greatly enhanced our understanding of lemur taxonomy and ecology, making distinctive connections between ecological factors and patterns of social organization and behavior. Johnson (Chapter 9) presents an overview of the taxonomy and behavioral ecology of the brown lemur complex (*Eulemur fulvus* spp.), and explains recent taxonomic changes and genetic differences between species and subspecies. He clarifies the question of hybrids, subspecies, and species differentiation, and highlights ecological distinctions in this geographically widespread array of lemurs. Radespiel (Chapter 10) provides us with comparative information on both intra- and interspecific differences in mouse lemurs (*Microcebus*) covering ecological, physiological, reproductive, and social variables, some of these correlating with Madagascar's marked climatic seasonality. Radespiel also posits a model for ancestral mouse lemur social organization and sociality, which may in fact reflect the ancestral lemur, or even the ancestral primate condition. The way in which climate and environmental variables have likely shaped social organization and sociality are addressed in Overdorff and Tecot's chapter on red-bellied lemurs (Chapter 11). They discuss how ecological pressures in the habitat of *Eulemur rubriventer*, and resource defense by both sexes, may have led to the evolution of pair bonding in this species. Gould (Chapter 12) provides an in-depth update of what is currently known of the ring-tailed lemur's geographic distribution, variation in habitat and population density, diet and feeding ecology, and life-history variables, illustrating the remarkable adaptability of this species. Gould stresses that future research in non-gallery forest habitats is needed in order for us to fully comprehend this highly adaptable lemur. Vasey (Chapter 13) synthesizes both theoretical and empirical studies, and using her extensive fieldwork on wild *Varecia rubra*, the red ruffed lemur, she tests a number of hypotheses that link large body size to particular foraging and social patterns and reproductive costs.

Recent studies of the behavioral ecology of many lemur species have provided us with a much clearer picture of their diversity, and their behavioral and morphological adaptations. Irwin (Chapter 14) provides a summary of the ecology and behavior of the beautiful eastern sifakas. These species have only recently been studied in any depth, and Irwin summarizes what is currently known, revealing a striking level of variability in terms of home range, diet, and social structure. Thalmann (Chapter 15) provides important new information on aspects of behavior and ecology of two sympatric nocturnal lemurs, *Avahi occidentalis* and *Lepilemur edwardsi*. He notes striking differences in their feeding ecology, activity, and behavioral patterns, highlighting alternative solutions to similar ecological stresses experienced by the two lemur species. Powzyk and Mowry (Chapter 16) focus on ecological research on the indri (*Indri indri*) at three sites in different decades: Mantadia and Betampona in the 1990s and 2000, and Analamazaotra in the 1970s. They discuss distinctions between indri and other lemur species with respect to gut and dental anatomy, and point out intraspecific differences in diet between habitats and study sites. In light of *Indri indri* being the largest prosimian folivore, Powzyk and Mowry suggest that they be considered "energetic minimizers" and that their unique territorial calls may have evolved because calling requires less energy than scent-marking given their large home ranges. Tan (Chapter 17) presents an overview of *Hapalemur* ecology, with a focus on the unusual diet of this genus, the only primates to specialize on bamboo. She touches on new research focusing on physical properties of *Hapalemur* food items, and masticatory adaptations that have evolved in the genus to allow for the processing of bamboo. Tan also points out that we know little about the ability of *Hapalemur* to cope with and avoid cyanide in their bamboo intake, and she suggests directions for future research in this area.

Madagascar is a place of changes. We know that in many respects the particular patterns of Madagascar's climate play a critical role in understanding lemur adaptations. Anthropogenic change is also a part of Madagascar's landscape and lemurs have long faced additional stresses from human-induced changes. Many of the authors address how lemurs respond to such stressors. For example, a serious drought in 1991–1992 affected *Lemur catta* populations at both Berenty and Beza Mahafaly research sites, and Gould (Chapter 12) discusses how these populations recovered within a few years. Godfrey, Jungers, and Schwartz (Chapter 3) address how human impact through habitat destruction, introduction of domestic animals, and direct hunting led to the extinction of the giant lemurs, while Irwin (Chapter 14) highlights important conservation issues for the endangered eastern sifakas, for example, noting that in his own study on *Propithecus diadema*, fragmented habitats may alter diet composition in ways that may have both serious reproductive and social (i.e., competitive) effects. Cuozzo and Yamashita (Chapter 4) report that dental health may be compromised when lemurs begin to include foods of human origin.

Natural disasters and climate extremes are part of the climatic unpredictability of Madagascar, as discussed by Wright (Chapter 18). She notes that the Malagasy lemurs have a number of biological and behavioral responses to periods of food scarcity that may be responses to such unpredictability. Droughts and cyclones can seriously affect already fragile lemur populations, and likely have for thousands or millions of years. In this context Ratsimbazafy (Chapter 19) discusses the feeding and foraging strategies employed by a group of *Varecia variegata editorium* (black-and-white ruffed lemurs) at the Manombo rainforest site after a devastating cyclone hit southeastern Madagascar in 1997. Even though half of their preferred food trees were killed, many *Varecia* at this site survived and remained highly frugivorous, which Ratsimbazafy attributes to their use of two exotic plant species. He stresses that such diet flexibility prevented subsequent starvation in these lemurs after the cyclone hit. Monitoring health and understanding disease transmission in wild lemur populations is also critical with respect to future conservation efforts. Junge and Sauther (Chapter 20) explain how the relatively recent arrival of humans and domestic animals in Madagascar has had an important impact on pathogen transmission in lemur populations, and how introduced diseases can have serious detrimental effects on endemic lemur populations residing both in remote regions as well as in habitats undergoing rapid anthropogenic change.

Many populations of Madagascar's lemurs are threatened by anthropogenic and climatic factors, despite the fact that all lemur species are listed in the Convention on International Trade in Endangered Species (CITES). In just the past decade, several new species have been discovered (see for example Kappeler et al., 2005; Thalmann and Geissmann, 2005) bringing the number of extant species and subspecies to far more than previously thought.

The 2005 IUCN Red List assessment considers that 63% of today's lemur species are threatened with extinction, and 11 of these are considered Critically Endangered (Mittermeier et al., 2006). Anthropogenic effects such as habitat destruction (primarily for cattle grazing and crops), charcoal production, and hunting are still major threats to lemur population survival. A mere 3% of Madagascar's area is actually protected (Mittermeier et al., 2006), but Madagascar's president, Marc Ravalomanana, announced in 2003 that he plans to triple the amount of protected land in the next 5 years (Mittermeier et al., 2006; and see Jolly and Sussman, this volume, for a more detailed explanation). Hopefully this plan will be successful, and will allow for far greater protection for Madagascar's unique fauna and flora.

It is important that lemur conservation and scientific research go hand in hand, as one has a crucial influence on the other. New research conducted on well-known species as well as on newly discovered species, or species and populations for which little was previously known, can aid conservation strategies and programs, as such studies can clarify or contribute to diverse issues such as genetics, disease ecology, habitat change, hormone ecology, life-history and population ecology. Morphological and paleontological studies can also help us to understand the evolutionary history and adaptation of the lemurs, and give us greater perspective on past and present environments, and the multitude of ways that extinct and extant lemurs have coped with and adapted to the unique habitats found on the Red Island. In this volume, we present some of the recent and insightful research conducted on these topics, and at the same time, we look forward to an even further blossoming of future research on the remarkable lemurs of Madagascar.

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Lisa Gould and Michelle Sauther
Victoria, British Columbia and Boulder, Colorado, 2006

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SECTION ONE

Lemur Origins, History of Ecological Studies on Lemurs, and the Ecology of the Recently Extinct (Subfossil) Lemurs

CHAPTER ONE

Origin of the Malagasy Strepsirhine Primates

Ian Tattersall

The great island of Madagascar has a long insular history, having split from Africa some 120 million years (myr) ago and from India around 88 myr ago (see below). The length of its isolation has much to do with its extraordinary biotic uniqueness. Madagascar's endemic primates, the lemurs, are the most spectacularly diversified element of a highly unusual fauna that displays an adaptive variety surpassing that of any comparable primate group, especially if the recently extinct "subfossil" forms are taken into account. But although from a geographical perspective the strepsirhine primates of Madagascar represent a contained unit, there are many reasons why it is hardly possible, still less desirable, to discuss their origins separately from the larger biogeographic tapestry within which they are woven. This is particularly true given the current total lack in Madagascar of a terrestrial Tertiary fossil record that might give a direct indication of the ancestral stock(s) from which today's major groups of Malagasy strepsirhine primates emerged. At least for the Paleocene and Eocene, the fossil records of Africa and Asia are only marginally better, with the result that inferences about the primate colonization of Madagascar have largely to be made from indirect—even highly indirect—evidence. For these reasons I begin this survey well before the initial emergence of the strepsirhines, with a brief overview of Madagascar's geological and geographical histories.

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THE ISOLATION OF MADAGASCAR

Madagascar is separated from the southeastern African coast by the 350- to 750-mile-wide Mozambique Channel, and with a surface area of 230,000 square miles it is the world's largest oceanic island (Greenland, New Guinea, and Borneo are all larger, but are connected to the adjacent mainlands at times of lowered sea level). This isolation has evidently had a strong effect on the composition of Madagascar's fauna which, when compared to those of the continents and even to other very large islands, shows an unusual combination of low diversity at high taxonomic levels with high within-family diversity. Clearly the waters surrounding Madagascar have acted as a powerful faunal filter, albeit a slightly porous one.

The fragment of continental crust we know today as Madagascar once lay deep within the ancient supercontinent of Gondwana, with India to its east. But by the time that Gondwana began actively to fragment in the middle Jurassic, about 160 myr ago, the western edge of the island was already underwater and Madagascar, still attached to Antarctica in the south and to India in the east, began to move south-southeast away from Africa along a slip-strike fault, the modern remnant of which in the Mozambique Channel seafloor is called the Davie Fracture Zone (see review by Wells, 2003). This movement had ceased by the middle Cretaceous, about 125 myr ago, leaving Madagascar in roughly its present position vis-à-vis Africa (Coffin and Rabinowitz, 1988). It is not certain whether at this point Madagascar still retained a land connection to Africa and Antarctica via India (contrast Krause, 2003, with Smith et al., 1984). India parted company with Madagascar in the late Cretaceous, about 88 myr ago (Storey, 1995; Storey et al., 1997), definitively completing the island's isolation well before the beginning of the Age of Mammals at around 65 myr ago.

Although the current record of Cretaceous mammals in Madagascar consists of little more than a small handful of teeth, a remarkably wide range of taxa is represented. Among them are the world's oldest tribosphenic mammal, *Ambondro mahabo* (Flynn et al., 1999) from the middle Cretaceous, and the earliest marsupial, from the latest Cretaceous (Krause, 2001). The balance of late Cretaceous specimens includes a multituberculate and two gondwanatheres (Krause, 2000, 2003). But as impressive as this variety may be compared to the size of the collection, no modern placental groups are represented; and it is clear that none of Madagascar's modern mammalian groups (or any plausible precursor) is represented among Mesozoic fossils discovered so far, and that none can be shown to represent a Gondwanan remnant. Instead, it appears that all must be descended from ancestral forms that somehow contrived to cross a substantial water barrier (Krause et al., 1997). Terrestrial mammals are notoriously poor overwater dispersers (Lawlor, 1986), and the only even remotely plausible mechanism for getting them to Madagascar is by rafting on tangled mats of vegetation such as those that are swept out to sea by the floodwaters of African rivers.

Today's terrestrial Malagasy mammals belong to four orders: Primates, Lipotyphla (broadly, Insectivora), Carnivora, and Rodentia, all of which also occur on the African and Asian continents. A fifth order, the enigmatic and endemic Bibymalagasia (MacPhee, 1994), was also represented on Madagascar until recently, as was Artiodactyla in the form of pygmy hippopotamuses. However, large-bodied semiaquatic forms like the (probably quite recently arrived) hippopotamuses disperse by different rules from the strictly terrestrial forms, and the same is true for the volant Chiroptera. Among the strictly terrestrial groups, the ancestral primates (see below) and lipotyphlans probably arrived early in the Tertiary period, while the ancestral carnivores and rodents most plausibly reached Madagascar early in the Miocene epoch (see reviews by Tattersall, in press a and b). The general feeling at present is that the other Malagasy mammal groups are most likely monophyletic (see, for example, Goodman et al., 2003; Jansa and Carleton, 2003; Olson and Goodman, 2003; Yoder, 2003; Yoder and Flynn, 2003), and this is probably also true for the primates (e.g., Yoder and Yang, 2004, but see discussion below). If such is the case, then a minimum of five colonization events is still necessary to explain Madagascar's endemic terrestrial mammal diversity. Crossings were possibly concentrated into two periods of time, the early Tertiary and the early Miocene, which makes it necessary to look again at Madagascar's historical biogeography.

To say that Madagascar has been stable in its position relative to Africa since well before the beginning of the Age of Mammals is not to say that the geography of Madagascar and its surrounding crust has necessarily remained static throughout the Tertiary. Despite the fact that today most of the Mozambique Channel is of oceanic depth, it is possible that parts of its seafloor were raised in the past. Thus, McCall (1997) has argued that uplift along the Davie Fracture Zone in the period between about 45 and 26 myr ago resulted in its partial subaerial exposure, with subsequent tensional conditions returning the topographic highs. This scenario is based on core samples reported by Leclaire et al. (1989) and Bassias (1992) suggesting that subaerial sediments were deposited along the ancient fault line during late Eocene and Oligocene times. deWit and Masters (2004) have recently raised this possibility once more, and have also suggested a potential late Cretaceous or early Tertiary migration route along the set of fracture zones, known as the Antarctic–Africa Corridor, that lie between Antarctica and Africa/Madagascar. They have also proposed an alternative migration route from India, along the Deccan hotspot corridor to Madagascar's north and east. The latter suggestion evokes the notion of a potential Chagos/Laccadive filter connection between India and Madagascar that was recently mooted by Marivaux et al. (2001), echoing an earlier suggestion by Gingerich (1975).

The fact that Madagascar's modern mammalian fauna is so unlike Africa's (or Asia's) certainly suggests that the water barrier around the island has existed continuously throughout the Tertiary. Indeed, Krause (2003) has rejected the possibility of a landbridge at least partly because of the "extreme dissimilarity" of the African and Malagasy faunas This difference undeniably shows that crossings were rare, and therefore extremely difficult, but it is possible to read this evidence another way. As far as we know, no strictly terrestrial mammal has contrived to cross the water barrier surrounding Madagascar for at least the last 15–20 myr or so. In that case, it seems necessary at least to ask whether, under current geographical conditions, *any* crossing at all is possible for such inefficient overwater dispersers as placentals of this kind. And should this prove to be the case, the ephemeral existence of island-chain "steppingstones" at points during the Tertiary would clearly have been absolutely essential for the transfer to Madagascar of any terrestrial mammals at all. On the other hand, in the absence of a Tertiary terrestrial fossil record in Madagascar we have no way of knowing how many groups of mammals might have crossed the water barrier during this period without managing to establish themselves permanently on the island. If Madagascar's modern faunal composition is biased by selective extinction the implication is, again, that the barrier was more permeable in the past than it appears now, presumably also as a result of ephemeral land connections. It is because of such considerations that future clarification of the mode of primate colonization of Madagascar, and its source, is as likely to come from geological studies of the surrounding seafloor as it is from an enlarging fossil record, or from improved systematic knowledge of the island's endemic mammals and their closest continental relatives.

MADAGASCAR'S PRIMATES

By far the most renowned and diverse group of Madagascar's mammals is its primates, the lemurs. There is general agreement that the lemurs, including the recently extinct "subfossil" forms, should be classified into seven families: Cheirogaleidae, the dwarf lemurs, with five living genera; Lemuridae, the "true" lemurs and their close relatives, with five genera (one extinct); Lepilemuridae, with two genera (one extinct); Indriidae, with three living genera; Archaeolemuridae, with two genera (both extinct); Palaeopropithecidae, with four genera (all extinct); and Daubentoniidae, the aye-ayes, with a single living genus and species. Depending on whose classification one accepts, the living lemurs alone may embrace well over 40 species, and an astonishing total of up to (and possibly exceeding) 72 primate taxa if subspecies are included. Thus, even excluding the recently extinct lemurs from the count, Madagascar ranks third-highest on the list of high-primate-diversity countries worldwide, even though it is less than a tenth the size of the world leader, Brazil (Mittermeier et al., 1994).

This amazing diversity is potentially due to a combination of several factors (see Tattersall, 1982). First, while paling in comparison to the huge area of Brazil, Madagascar is nonetheless extremely large: at 1600 km long, and with a surface area of almost 600,000 km^2 it is the world's biggest oceanic island. When first colonized by humans, the island was largely if not entirely forested, providing primate-friendly habitats in virtually all but the most open areas and the most extreme montane environments. Second, due to both its geographical position and its varied topography, Madagascar offers a huge range of forest habitats. Lying almost entirely within the southern tropical zone, Madagascar lies in the path of the easterly trade winds. Its narrow eastern coastal plain is paralleled by a steep and rugged escarpment which captures the moisture borne by those winds, and as a result is naturally clothed by luxuriant rainforest. Madagascar's raised central plateau is deeply dissected, and offers a large range of microenvironments. Toward the west it gradually yields to drier and more seasonal coastal plains where forest cover varies from riverine gallery forests to dry brush and scrub habitats. Madagascar's northern and southern extremities are very dry indeed, the far south supporting the unique "spiny forest" where plant endemism is as high as 98% at the species level. Altogether, this unique island offers primates and other mammals a diversity of ecological settings that is unmatched in any comparable area elsewhere.

All of Madagascar's primate families are completely endemic to the island, and merely on the basis of systematic diversity it is clear that primate evolution there has taken an independent course for a very long time. But in the absence of a Tertiary fossil record, exactly how long is debatable. Because of the overall distinctiveness of the Malagasy primate fauna, it has generally been assumed that the lemurs form a monophyletic group. At the same time, the suborder Strepsirhini to which the Malagasy primates belong is not unique to Madagascar, since there is no question that it also contains the African galagos (Galagidae) and the Afro-Asian pottos and lorisis (Lorisidae). All living strepsirhines share a suite of features that includes the package of characteristics, primitively typical of macrosmatic mammals, that includes retention of a rhinarium and a fully functional vomeronasal organ. Additionally, all strepsirhines lack bony posterior closure of the less than fully frontated orbits, and share possession of an unfused mandibular symphysis, a relatively small brain-to-body size ratio, and extremities bearing divergent first digits. There are flat nails on all digits except the second pedal, which bears a "toilet" or "grooming" claw. The most prominent hard-tissue synapomorphy of the group is the presence of a procumbent toothcomb in the lower jaw. This unusual structure (unique in its morphological details if not in its existence) consists of four teeth in the indriids, archaeolemurids, and palaeopropithecids, and of six teeth in all the other lemurs except for the highly derived *Daubentonia*, in which it is autapomorphically replaced by a single pair of constantly growing anterior teeth.

Until recently, there was no ancient fossil record of toothcomb-bearing primates anywhere in the world before the African early Miocene, by which time a substantial fossil record has long shown that both modern Afro-Asian strepsirhine families were already well established (Simpson, 1967). Recently, however, an earlier strepsirhine record has begun to emerge, both in Asia (Marivaux et al., 2001) and in Africa (Seiffert et al., 2003; Martin, 2003).

THE TERTIARY FOSSIL RECORD OUTSIDE MADAGASCAR

The earliest fossil primate that undisputably bears a toothcomb is *Karanisia clarki*, described from a small sample of isolated teeth and jaw fragments by Seiffert et al. (2003). These specimens, which include a canine crown indicating the presence of a toothcomb, come from late middle Eocene (probably ca. 40 myr old) sediments of the Birket Qarun Formation, in the Egyptian Fayum. *Karanisia* is interpreted by its describers as dentally not only lorisiform but lorisid, possibly representing a sister genus to the living West African genus *Arctocebus.* Two teeth from the same stratigraphic were assigned to the galagid genus *Saharagalago misrensis.* Seiffert and his coauthors believe that these Fayum fossils establish the divergence of the two living non-Malagasy strepsirhine families by the mid-to-late Eocene.

Marivaux et al. (2001) allocated several isolated teeth from the Bugti Hills of Pakistan to the new species *Bugtilemur mathesoni*, in which a lower canine is said to confirm the presence of a toothcomb. Marivaux et al. assigned these very tiny early Oligocene (ca. 30 myr old) fossils to the Malagasy family Cheirogaleidae on the basis of cheektooth morphology, suggesting transfer via a putative sweepstakes/filter route involving a Chagos/Laccadive paleoridge system. Within Cheirogaleidae, Marivaux and colleagues most closely compared the molars of *Bugtilemur* to those of *Cheirogaleus*, and morphologically the resemblance is indeed remarkable. However, the living Malagasy genus is much larger in body size than the fossil one is, and it has a much longer and slenderer toothcomb than *Bugtilemur* apparently had.

The molar morphology of *Bugtilemur* is particularly interesting given that it has been argued that the cheirogaleid lemurs may in fact be more closely related to the Afro-Asian strepsirhines than to the other Malagasy lemurs (e.g., Szalay and Katz, 1973; Schwartz and Tattersall, 1985). In 1970 Charles-Dominique and Martin drew attention to the suite of behavioral similarities uniting the cheirogaleids and lorisoids. Charles-Dominique and Martin were content to regard these similarities as ancestral retentions; but Szalay and Katz (1973) proposed that many characters shared between lorisoids and cheirogaleids are in fact derived, and that in consequence the cheirogaleids and lorisoids are more closely related to each other than the cheirogaleids are to the other lemurs. Cartmill (1975) later added other features to the list of apparent cheirogaleid–lorisid synapomorphies. And a few years later Schwartz and Tattersall (1985) pointed to evidence from molar morphology that also supports this association. In addition, these authors found morphological justification for regarding the entire balance of the Malagasy primate fauna, including the aye-aye, as a monophyletic unit.

The paraphyly that these observations suggested had radical implications for lemur biogeography and origins. For if the cheirogaleids are in fact lorisoids, then there are only two biogeographical possibilities. The first of these is that the cheirogaleids are descended from an African (or conceivably Indian) ancestor that invaded Madagascar separately from the ancestor of the remaining lemur fauna (i.e., that there were two strepsirhine colonizations of Madagascar, the later one subsequent to the apparently Eocene or earlier divergence of the lorisiform and lemuriform groups in Africa). The second possibility is that, from a single African or Asian common ancestor, the lemurs diversified on Madagascar to the family level we now recognize and that today's Afro-Asian lorisoids are descended from a cheirogaleid ancestor that recolonized Africa (or conceivably India) from Madagascar, probably before the late Eocene. The pattern of ocean currents makes a Madagascar–Africa crossing considerably more probable than the reverse trip; but if the modern Afro-Asian families had already emerged by the late Eocene, as Seiffert et al. (2003) suggest, then the cheirogaleid back-crossing must have been an early one indeed. At the same time, however, a very early back-crossing of this kind might also be consonant with the presence of a cheirogaleid-like *Bugtilemur* in the early Oligocene of Pakistan, although Marivaux et al. (2001) prefer a dispersal event between Madagascar and Greater India.

A few years ago, before the finds in the Fayum and the Bugti Hills, any discussion of lemur origins would have begun with a look at the Eocene adapiform primates of Eurasia. This group formed part of the great Eocene radiation of early euprimates "primates of modern aspect," and produced a profusion of genera and species among which number some of the best-documented fossil primate species known. In the very vague sense of an evolutionary "grade" the adapiforms (possibly themselves paraphyletic in laxer definitions) seem generally to have resembled today's strepsirhine primates; and indeed, some recent primate classifications have included Adapiformes as an extinct infraorder of the suborder Strepsirhini (e.g., Delson et al., 2000). Within Adapiformes, signs of lemuriform ancestry have been particularly sought within the family Adapidae (first and still best known from Europe), despite the fact that all known adapiforms, including the adapids, primitively lack the principal strepsirhine synapomorphy, the toothcomb. Adapids also typically possess four premolars in each quadrant of the jaw as opposed to the three or two of lemurs, and show a fused mandibular symphysis. Intriguingly, though, a presumed adapid hindbody skeleton from Germany's middle Eocene Messel site does quite clearly show a grooming claw on the second digit of the foot (von Koenigswald, 1979); and adapids are well documented to have very lemurlike auditory bullae.

Impressed by these complex basicranial resemblances, Gregory (1920) argued that close molar similarities between the European Eocene adapid *Adapis* and the living Malagasy *Lepilemur* were of ancient derivation and provided a sort of evolutionary link between *Adapis* and the other modern strepsirhines. Gingerich (1975) later suggested that the closest molar resemblances were to be found between *Adapis* and *Hapalemur*, suggesting that *Adapis* had given rise to the other lemurs via a form that at least dentally resembled *Hapalemur*. Schwartz and Tattersall (1979) proposed the alternative notion that the dental morphologies of *Hapalemur*, *Lepilemur*, and *Adapis* were derived, thus indicating that the fossil taxon somehow nests *within* the strepsirhine clade, rather than lying at its origin. They later noted (Schwartz and Tattersall, 1985) that the indriid lemurs, in particular, shared a whole suite of dental and mandibular characters with adapids, whereas some of the dental characters of the cheirogaleid+lorisid+galagid group recalled those of some Eocene non-adapid adapiforms such as *Anchomomys* and *Periconodon*. However, Beard et al. (1988) observed that a wrist structure in which the os centrale overlaps the capitate to contact the hamate is unique to lemurs, to the exclusion of *Adapis*.

The paleontological argument over both the origin of the lemurs and the existence of potential lemur relatives in the Eocene is bedevilled by slender Paleocene and Eocene fossil records in the possible source areas of Africa and India. *Altiatlasius* from the early Eocene of Morocco is pretty indeterminate, while *Djebelemur* from the early Eocene of Tunisia is plausibly adapid but shows no particular affinity with any lemur. In the late Eocene of the Egyptian Fayum, the sketchily known genera *Aframonius* (Simons et al., 1995; Simons and Miller, 1997) and *Wadilemur* (Simons, 1997), plus an apparent representative of the European genus *Anchomomys* (Simons, 1997), show that adapiforms (though not adapids) may have survived there not only after the strepsirhines had originated, but also after the two modern lorisoid families had differentiated.

In Arabia, the poorly known *Omanodon* and *Shizarodon* from Oman indicate not much more than that adapiforms were present there in the early Oligocene. In the Indian region the two sivaladapid adapiforms *Indraloris* and *Sivaladapis* survived into the late Miocene, as recently as 8 myr ago (Gingerich and Sahni, 1984), and the possibly adapid genus *Panobius* has been described on the basis of a couple of teeth from early-to-middle Eocene deposits in Pakistan (Russell and Gingerich, 1987). However, *Sivaladapis* conspicuously lacks a toothcomb and otherwise bears no close resemblances to any lemur. Several other Asian fossil forms are also classified in the family Sivaladapidae, including the Eocene Chinese forms *Guanxilemur*, *Rencunius*, and *Hoanghonius.* The Eocene Chinese genus *Adapoides* may in contrast be a true adapid, as may *Wailekia* from Thailand. All in all, however, these various forms do little more at present than suggest that both adapids and other adapiforms were abundant in forests throughout the Old World tropics for much of both the Paleogene and the Neogene, at least back to about 55 myr ago. They do not shed any direct light on the origin of the Malagasy lemurs, and indeed the presence of *Aframonius* and the others in the Fayum, more or less contemporaneously with *Karanisia* and *Saharagalago*, implies that if the direct strepsirhine ancestor was an early member of the African adapid radiation it was very ancient, possibly even predating the early Eocene. This is in line with molecular phylogenies that suggest a much earlier initial diversification of the lemuriforms than of the lorisoids (see below).

MOLECULAR STUDIES

In recent years, approaches to lemur systematics have been dominated by molecular comparisons that have mostly yielded findings that support the monophyly of the entire lemur fauna. Anne Yoder and her colleagues (e.g., Yoder et al., 1996; Yoder, 2003; Yoder and Yang, 2004) have particularly vociferously rejected the notion that there is a special affinity between the cheirogaleids and the lorisoids. Most of this work has consisted of comparative studies of the mitochondrial cytochrome *b* gene, but lately certain nuclear elements have been added to the mix. Yoder and co-workers find that the basal split among the strepsirhine primates is between lorisiforms on the one hand, and lemuriforms including Cheirogaleidae on the other. Within Lemuriformes, they find that the basal split is between Daubentoniidae and all the rest.

Numerous lower-level problems of relationship among the species and genera of lemurs have been clarified by the molecular studies undertaken so far; but the rather fast-evolving mitochondrial genome is generally considered unreliable for assessing ancient splits, and DelPero et al. (2001) have found among the lemurs that while the 12S rRNA mitochondrial gene is useful for gauging within-family affinities, relationships among families separated by large genetic distances (<12% divergence) defy consistent resolution. This is most clearly the case among lorisids, galagids, daubentoniids and the apparent lemurid/indriid clade.

A recent study by Roos et al. (2004) that combined cytochrome *b* results with an analysis of nuclear short interspersed elements in a variety of strepsirhines situated the cheirogaleids within the lemuriform radiation, with a basal split between the aye-aye and all the others. This is another pointer toward the conclusion that the deeply entrenched notion of lemur monophyly may well be accurate—even though it suggests enormous levels of convergence and primitive retention respectively between and within the lorisoids and cheirogaleids. For the time being, definitive demonstration perhaps still awaits; but the evidence of historical biogeography, together with the fact that the other groups of Malagasy terrestrial mammals also appear most likely to be monophyletic, suggests that the external probabilities are on the side of lemur monophyly as well.

A further ramification of molecular studies is the estimation of divergence dates for the various higher taxa recognized (e.g., Yoder et al., 1996; Porter et al., 1997; Yoder and Yang, 2004). The most recent estimated date for the basal split among a monophyletic lemuriform group is 47 Ma (Porter et al., 1997), and Yoder has lately raised her estimate from >54 Ma (Yoder et al., 1996) to 62–65 Ma (Yoder and Yang, 2004), based on a variety of both mitochondrial and nuclear gene loci. Calibration was from the fossil record, with all the consequent uncertainties enumerated by Grauer and Martin (2004). Still, current molecular and morphological estimates of the divergence time seem to be in (very) approximate agreement. For if the lemurs are in fact monophyletic, the ancestral strepsirhine having given rise very early in the Tertiary (and most probably in Africa) to the ancestor of the Malagasy group on the one hand, and to the ancestor of the lorisids/galagids on the other; and if the lorisids and galagids had indeed differentiated by the mid-to-late Eocene (ca. 41–37 Ma) as *Karanisia* and *Saharagalago* seem to indicate, then some stretching of the molecular time scale would seem to be plausible. This is especially the case given the sheer scale of the diversification that has taken place among the lemurs subsequent to the time of their common ancestor, and it is supported by molecular comparisons that suggest that much of this diversification took place at an early stage—earlier than that of the living lorisoids (see, e.g., Yoder and Yang, 2004).

ECOLOGY

The lifeways (not to mention the identities) of the earliest primates have been much debated. But the fossil record has long shown that the basic package of prosimian/strepsirhine adaptations was in place by the early Eocene, about 55 myr ago; and if the earliest primate colonizers of Madagascar significantly predated this time, the strepsirhine bauplan would have been present substantially before. Early theories of euprimate origins (e.g., Jones, 1916; Smith, 1924) held that it was adoption of arboreality itself that was the key to the fixation of such primate features as grasping hands, binocular vision, and brain enlargement. However, since many other arboreal mammals do very well without such characteristics, this explanation is at the very least incomplete. Cartmill (e.g., 1972) added visual predation to the mix, with the implication that early primates had been at least mainly insectivorous. In contrast, Sussman and Raven (1978) noted that euprimate diversification followed closely on the heels of the radiation of flowering plants, and proposed that it was the "windfall" resources of abundant fruits and flowers that had provided early primates with the opportunity to radiate. Based on a field study of the "prosimian-like" neotropical marsupial *Caluromys*, Rasmussen (1990) integrated these two notions by concluding that the primate ancestor had been a visual predator that foraged in the fine terminal branches of the angiosperm canopy for a "combined windfall" of fruits and flowers and the insects attracted by them. Most authorities would currently accept this hypothesis.

Modern strepsirhine body sizes vary enormously, and within this large range *Bugtilemur* and the Fayum lorisoids vary from tiny to small. The majority of Eocene adapiform primates were larger than this, most of them also exceeding their omomyoid contemporaries in body size. Interestingly, this places the Fayum strepsirhines in the general size range of the modern lorisoids, while the adapiforms are more comparable to the midrange of Malagasy lemurs. As to locomotion, the Fayum lorisoids are known only from cranial material, but the adapiforms show a variety of locomotor types that apparently ranged from rather loris-like slow arboreal quadrupedalism in *Adapis* (Dagosto, 1983), to more active quadrupedalism in forms like *Pronyticebus* (Szalay and Dagosto, 1988) and thigh-powered leaping in *Smilodectes* (Covert, 1986). Smallish orbit sizes in almost all adapiforms point to diurnal activity, and molar form and wear suggest a preponderance of frugivory among many members of this group although some adapiforms, among them *Adapis* and *Leptadapis*, possess sharply crested molars that are suggestive of folivory (Covert, 1986).

It is, then, possible to view the radiation of adapiforms in the Eocene as a sort of early euprimate parallel of today's radiation of diurnal lemuriforms in Madagascar. If the modern lorisoid families had indeed diverged by the late Eocene, the Fayum genera (which derive from deposits that were laid down in moist lowland tropical forest conditions) were presumably fairly close ecological equivalents of their living counterparts. Interestingly, heterothermy, a potential facilitating factor in any rafting scenario, is absent in the few lorisoids so far studied (Mzilikazi et al., 2004), so that its presence in certain cheirogaleids seems most likely to be a specialization acquired in Madagascar rather than a dispersal advantage possessed by the original colonizers. The many adapiform genera are simply too diverse to suggest any ecological thread more precise than a preference for the canopies of tropical or semitropical forests. If the ancestral strepsirhine was a very early adapiform, it is thus difficult to surmise its exact ecological preferences; adapids were probably mostly frugivorous, but *Adapis*, the adapiform most frequently compared to lemurs, had the molar morphology of a folivore. On a comparative basis there is thus little to suggest the precise ecological niche or niches of Madagascar's founding primate. The problem is, of course, only exacerbated by the fact that *Daubentonia*, the probable outgroup of the diverse remaining Malagasy primate fauna, is so highly autapomorphic. And, in a fauna with such conspicuous diversity at low taxonomic levels, what may also be surprising is the typically rather eurytopic signal that emerges from field studies of living lemur species. Without doubt, this generalist tendency has been with euprimates from the very start, and we would do well to emphasize the role of geography/normal population variation above that of adaptation as determinant of the current genus- and species-level diversity of lemurs.

CONCLUSION

The lemur fauna of Madagascar is totally endemic at the family level, and it may well also be endemic at the infraordinal level, as moderately to strongly supported by recent molecular studies. These studies lean to the conclusion that that the lemurs are indeed monophyletic, derived from a single tropical forest canopy-dwelling common ancestor (whose precise ecological preferences are hard to determine, given the diversity of adaptations displayed by both its living descendants and its presumed fossil relatives) that somehow contrived to colonize Madagascar at some point very early in the Tertiary. Molecular estimates for the basal split among the Malagasy lemurs point to a Paleocene (even early Paleocene) age for this common ancestor (Yoder and Yang, 2004): an age consistent with the remarkably ancient late Cretaceous (ca. 77 myr) date for the origin of Primates derived from various molecular data sets by Springer et al. (2003). These dates are, however, so far unsupported (though not contradicted) by the scrappy fossil record, which is also unhelpful in determining the age of the basal strepsirhine. The presence of apparent lorisids and galagids in the Fayum at ca. 40 myr ago provides a minimum fossil date for the existence of Strepsirhini, but one that is presumably highly underestimated. At the same time, the discovery of more or less contemporaneous adapids and strepsirhines in the late Eocene of the Fayum has tended to marginalize the primarily Eocene adapids as a potential source of Strepsirhini. Further, the absence of toothcombed strepsirhines in the fairly abundant European (and the more limited Asian) Eocene fossil records may suggest that this group is of African derivation, and that it spread to Asia only a substantial time after its origin. It seems likely that only improvement in the currently lamentably restricted Paleocene and Eocene fossil records of Africa (and the discovery of any Tertiary primate record at all in Madagascar) will help shed direct light on the origin of the strepsirhine primates in general and the Malagasy lemurs in particular.

Madagascar has been isolated by a very substantial water barrier since even before the very ancient Springer et al. (2003) molecular date for primate origins. The inescapable conclusion is that the ancestors of the island's four endemic terrestrial mammal orders must have arrived there via an overwater sweepstakes route in spite of the very high probabilities against such a crossing. No terrestrial mammal (other than *Homo sapiens* and its dependents) has, as far as we know, contrived to make this crossing at any time in the last 15 myr or so. This raises the possibility that under current geographic conditions the barrier is absolutely impermeable to such notoriously poor dispersers. If such is the case, it is necessary to inquire whether in fact the geology and topography of the ocean floor surrounding Madagascar has indeed been stable back into the farthest reaches of the Tertiary. The assumption of stability has been called into question recently by a variety of authors (McCall, 1997; Marivaux et al., 2001; deWit and Masters, 2004), who between them have evoked potential "steppingstone" routes both toward and from Africa and India. Clearly, the ocean surrounding Madagascar has acted as a powerful filter to potential mammal invaders of the island; but equally evidently the barrier has not been a totally unbreachable one, at least at certain times during the Tertiary. And it is for this reason that fuller knowledge of the geology of the seafloor surrounding Madagascar will be necessary before we can properly test hypotheses about the mechanisms of Madagascar's colonization by terrestrial mammals, including primates.

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CHAPTER TWO

Notes on the History of Ecological Studies of Malagasy Lemurs

Alison Jolly and R.W. Sussman

INTRODUCTION

Ecological studies in Madagascar have been shaped by three underlying parameters. First is the geography of Madagascar—its 80-million-year isolation, and also the patchy distribution of forests around the island-continent. This geography has fostered baroque radiations of allopatric species. Madagascar's biodiversity is more like an archipelago than either an island or a continent. Each forest, whether wet eastern rainforest, dry western deciduous forest, or the semiarid spiny forest of the south, holds different lemurs, chameleons, butterflies, and other taxa from the next one, even within a similar climate. Combined with the perpetually perilous state of Madagascar's roads, the patchiness means that most scientists pick on a single part of the island in which to work. They tend to return to their intellectual "homes," deepening insight and infrastructure in a series of allopatric research sites.

Dedicated to the memory of Madame Berthe Rakotosamimanana, who has inspired so many primatologists to study lemurs.

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The second great influence is the changeable climate. Madagascar's forests have spread and shrunk over the scale of eons and millennia, in pluvials and interpluvials. The wealth of species evolved as the forest nuclei separated or rejoined. On the smaller timescale of a lemur's or a human's lifetime, Madagascar falls into the top quarter of the world's year-to-year erratic rainfall regimes. It swings from El Niño drought to cyclone-caused flooding. As study sites now persist over decades, ecologists are learning what Malagasy farmers have always known: survival has little to do with averages, everything to do with confronting harsh seasons and catastrophic years (Dewar and Wallis, 1999; Gould et al., 1999; Richard et al., 2002; Wright, 1999).

The third influence is the political history of Madagascar: coastal and highland people, elite and villagers, and the foreigners who have influenced the island-continent. It is at first tempting to write about ecological study as a chronicle of scientific ideas with each question blossoming solely from the ones which went before. However, that would be so narrow as to be actually false. Ecological studies have been inseparably intertwined with the economic possibilities open to people of different backgrounds, with the ideals of foreigners enchanted by the alternate world of Malagasy biodiversity, and with both Malagasy and foreign scientists' commitment to action for conservation. A mere history of scientific ideas would leave out most of the story.

This article is therefore divided into political periods. First, we make a few remarks about colonial and precolonial times. Modern lemur field studies date from 1955 to 1975, from just before Malagasy independence to the end of the First Republic. There was a hiatus at the start of the Second Republic, from 1975 to 1985, a period without research visas and with increasing national poverty. The period of reopening to the West and major foreign aid for biodiversity has lasted from 1985 to 2005. During this last 20 years, the separate research sites have become ongoing projects, and a table of scientists underlines geographic locality (Table 1). Finally, we conclude with a few remarks about changing prospects for the future.

Table 1. Scientists who have done field research on lemurs in Madagascar (PhDs and PhD candidates and above, or published authors, not MSc's and DEAs)

Site	Decade	Species
All areas		
Petter, Jean-Jacques	50s–80s	many
Petter-Rousseaux, Arlette	50s–80s	many
Nicoll, Martin	70s on	many
Goodman, Steven	80s on	many
Garbutt, Nick	80s on	many
Mittermeier, Russell	80s on	many
Lewis, Edward	90s on	many
Comoros		
Tattersall, Ian	70s	*Eulemur fulvus mayottensis, E. mongoz*
Dahl, Jeremy	70s	*E. mongoz*

Eastern domain		
Montagne d'Ambre		
Ratsirarson, Joelina	80s	*Lepilemur septentrionalis, L. mustelinus*
Freed, Benjamin	90s	*E. coronatus, E. fulvus sanfordi*
Darain		
Meyer, David	90s	*Propithecus tattersalli*
Mayor, Mireya	90s	*P. perrieri*
Marojejy		
Mayor, Mireya	90s	*P. candida*
Patel, E.	00s	*P. candida*
Anjanaharibé-Sud		
Mayor, Mireya	00s	*M. mittermeieri*
Schutze, O.	90s	*A. trichotis*
Sterling, Eleanor	90s	Inventory
Thalmann, Urs	90s	*Indri indri*
Nosy Mangabé		
Petter, Jean-Jacques	60s	*Daubentonia madagascariensis*
Peyrieras, André	60s	*D. madagascariensis*
Iwano,T.	80s	*D. madagascariensis*
Sterling, Eleanor	80s	*D. madagascariensis*
Morland, Hilary	80s	*Varecia variegata variegata*
Masoala		
Rigamonti, Marco M.	80s	*V. variegata rubra*
Vasey, Natalie	90s	*V. variegata rubra, E. fulvus albifrons*
Sterling, Eleanor	90s	Inventory
Mananara		
Albignac, Roland	80s	*D. madagascariensis*
Andriamasimanana, M.	80s	*D. madagascariensis*
Meier, Bernhard	80s	*Allocebus trichotis*
Tampolo		
Ratsirarson, Joelisoa	90s	Inventory
Betampona		
Andrianarisata, M.	90s	*V. variegata variegata*
Britt, Adam	90s	*V. variegata variegata*
Katz, Andrea	90s	Inventory
Welch, Charles	90s	Inventory
Lake Alaotra		
Mutschler, Thomas	90s	*Hapalemur griseus alaotrensis*
Feistner, Anna	90s	*H. griseus alaotrensis*
Mantadia, Andasibé		
Pollock, Jonathan	70s	*Indri indri*
Ganzhorn, Jörg	80s	*E. fulvus fulvus, A. laniger,* + 5 more
Wright, Patricia	80s	*H. griseus griseus*
Powzyk, Joyce	90s	*I. indri, P. diadema*
Rakotoarison, N.	90s	*A. trichotis*
Ranomafana		
Drague, C.	80s	*E. rubriventer*
Meier, Bernhard	80s	*H. aureus, E. rubriventer*
Overdorff, Deborah	80s on	*E. fulvus rufus, E. rubriventer*
Randriamanantenina, Martine	80s	*H. aureus, H. griseus, H. simus*
White, Frances	80s	*V. variegata variegata*

(*Continued*)

Table 1. Scientists who have done field research on lemurs in Madagascar (PhDs and PhD candidates and above, or published authors, not MSc's and DEAs)—Cont'd.

Site	Decade	Species
Wright, Patricia	80s on	*H. aureus, H. griseus, H. simus, P. edwardsi, C. major, Microcebus rufus*
Atsalis, S.	90s	*Microcebus rufus*
Balko, Elizabeth	90s	*V. variegata variegata*
Erhart, E.M.	90s	*P. edwardsi, E. fulvus rufus*
Grassi, C.	90s	*H. griseus*
Hemingway, Claire	90s	*P. edwardsi*
Karpanty, Sarah	90s	Raptor prey
Martin, L.B.	90s	*C. major, M. rufus*
Merenlender, Adina	90s	*E. fulvus rufus, E. rubriventer*
Tan, Chia	90s	*H. aureus, H. simus, H. griseus*
Yamashita, N.	90s	Many
Arigo-Nelson, S.	00s	*P. edwardsi*
Deppe, A.	00s	*Microcebus*
Morelli, T.L.	00s	*P. edwardsi*
Tecot, S.	00s	*Varecia* and *Eulemur*
Andringitra Massif		
Ratsirarson, Joelina	70s	*Lemur catta*
Rakotoarisoa, Soava	90s	*Lemur catta*
Sterling, Eleanor	90s	Inventory
Midongy		
Johnson, Steig E.	90s	*E. fulvus albocollaris, E. fulfus rufus*
Manombo		
Ratsimbazafy, Jonah	90s on	*V. variegatus variegatus*
Zaonarivelo, J.R.	90s	*V. variegatus variegatus*
Mandena, St. Luce		
Martin, Robert	70s	*M. murinus, M. rufus*
Ramananjato, Jean-Baptiste	90s on	Many
Ganzhorn, Jörg	90s on	Many
Dammhahn, Melanie	00s	*M. murinus*
Hapke, Andréas	00s	*M. murinus, M. griseorufus*
Donati, Giuseppe	00s	*E. fulvus collaris*
Norscia, Ivan	00s	*Avahi laniger*
Central domain		
Ambohitantely		
Ratsirarson, Joelisoa	90s	Inventory
South central		
Tsinjoarivo		
Irwin, M.	00s	*P. diadema*
Western domain		
Sambirano		
Andrews, Josephine	90s	*E. macaco*
Birkinshaw, Christopher	90s	*E. macaco*
Colquhoun, Ian	90s	*E. macaco*
Baly Bay		
Hawkins, Frank	1990s	Many

Ankarafantsika		
Albignac, Roland	60s–70s	*Avahi occidentalis, L. edwardsi*
Harrington, Jonathan	60s	*E. mongoz*
Richard, Alison	70s	*P. verreauxi coquereli*
Sussman, Robert W.	70s	*E. mongoz*
Tattersall, Ian	70s	*E. mongoz*
Andriatsarafara, R.	80s	*E. mongoz*
Barre, V.	80s	*Microcebus* sp.
Razanohoera, Marlène R.	80s	*L. edwardsi, A. occidentalis*
Boesching, C.	90s	*M. murinus*
Curtis, Deborah	90s	*E. mongoz*
Müller, A.E.	90s	*C. medius*
Radespiel, Ute	90s on	*M. murinus*
Rasoloharijaona, S.	90s	*L. edwardsi*
Thalmann, Urs	90s	*A. occidentalis, L. edwardsi*
Zaramody, A.	90s on	*E. mongoz*
Zimmerman, Elke	90s on	*M.murinus, M. ravelobensis*
Rasmussen, M. A.	90s	*E. mongoz*
Tsingy de Bemaraha		
Mutschler, Thomas	90s	
Rakotoarison, N.	90s	
Thalmann, Urs		
Rasoloarison, R.	90s	Inventory
Tsingy de Namoroka		
Thalmann, U.	90s	Inventory
Kirindy, Analabé		
Charles-Dominique, Pierre	70s	*Cheirogaleus medius, M. murinus, Mirza coquereli, Phaner furcifer, Lepilemur ruficaudatus*
Hladik, Marcel	70s	*C. medius, M. murinus, M. coquereli, P. furcifer, L. ruficaudatus*
Pages, Elisabette	70s	*M. coquereli*
Pariente, Georges	70s	*P. furcifer, L. ruficaudatus*
Petter, Jean-Jacques	70s	*C. medius, M. murinus, M. coquereli, P. furcifer, L. ruficaudatus*
Ganzhorn, Jörg	80s on	*C. medius, E. fulvus rufus, M. murinus*
Fietz, J.	90s	*C. medius*
Dausmann, K.H.	90s	*C. medius*
Donati, Giuseppe	90s	*E. fulvus rufus*
Gerson, J.S.	90s	*E. fulvus rufus*
Kappeler, Peter	90s on	*M. coquereli, E. f.rufus,* many
Ortmann, S.	90s	*M. murinus*
Ralisoamalala, R.C.	90s	*E. fulvus rufus, P. verreauxi*
Rasoloarison, R.M.	90s	Many
Schmidt, J.	90s	*M. murinus*
Schwab, D.	90s	*Microcebus berthae*
Rasoazanabary, E.	00s	*M. murinus*
Schulke, O.	00s	*P. furcifer*
Lewis, R.J.	00s	*P. verreauxi*
Tongobato		
Sussman, Robert	70s	*E. fulvus rufus*
Antseranomby		
Sussman, Robert	70s	*L. catta, E. fulvus rufus*

(*Continued*)

Table 1. Scientists who have done field research on lemurs in Madagascar (PhDs and PhD candidates and above, or published authors, not MSc's and DEAs)—Cont'd.

Site	Decade	Species
Isalo Massif		
Hawkins, Frank	90s	*L. catta, P. verreauxi*
Zombitse		
Ganzhorn, Jörg	90s	Inventory
Southern domain		
Beza Mahafaly		
Richard, Alison	70s on	*P. verreauxi verreauxi*
Sussman, Robert	70s on	*L. catta*
Rakotomanga, Pothin	80s–90s	*P. verreauxi verreauxi*
Sauther, Michelle	80s on	*L. catta*
Ratsirarson, Joelisoa	80s	*L. catta*
Gould, Lisa	90s on	*L. catta*
Brockman, Diane	90s on	*P. verreauxi verreauxi*
Kubzdela, Kashka	90s	*P. verreauxi verreauxi*
Nash, Leanne	90s	*Lepilemur leucopus*
Ranarivelo, N.A.	90s	*P. verreauxi verreauxi*
Yamashita, N.	90s	*L. catta, P. verreauxi verreauxi*
Rasoazanabary, E.	00s	*M. griseorufus and M. murinus*
Whitelaw, D.	00s	*L. catta*
Berenty		
Jolly, Alison	60s on	*L. catta, P. verreauxi*
Sussman, Robert	60s, 00s	*L. catta*
Klopfer, Peter	60s	*L. catta*
Charles-Dominique, Pierre	70s	*L. leucopus*
Hladik, M.	70s	*L. leucopus*
Budnitz, Norman	70s	*L. catta*
Dainis (Blumenfeld-Jones), Kathryn	70s on	*L. catta*
Russell, Jay	70s	*Lepilemur leucopus*
McGeorge (Durrell), Lee	70s	Many
Mertl-Millhollen, Anne	70s on	*L. catta*
Gould, Lisa	80s	*L. catta*
Koyama, Naoki	80s on	*L. catta*
O'Connor, Sheila M.	80s	*L. catta, P. verreauxi*
Rasamimanana, Hantanirina	80s on	*L. catta*
Hood, Laura C.	90s	*L. catta*
Ichino, Shinichiro	90s	*L. catta*
Oda, Ryo	90s	*L. catta, P. verreauxi*
Miyamoto, Naomi	90s	*L. catta*
Nakamichi, Masayuko	90s	*L. catta*
Pitts, Angela	90s	*L. catta*
Pride, R. Ethan	90s	*L. catta*
Saito, Chiemi	90s	*P. verreauxi*
Soma, Takayo	90s on	*L. catta*
Takahata, Y.	90s	*L. catta*
Hazofotsy, Andohahela		
Richard, Alison	70s	*P. verreauxi verreauxi*
Feistner, Anna	90s	Inventory

COLONIAL AND PRECOLONIAL TIMES

"May I announce to you that Madagascar is the naturalist's promised land?" wrote the botanist Philibert de Commerson in 1771. "Nature seems to have retreated there into a private sanctuary, where she could work on different models from any she has used elsewhere. There you meet bizarre and wondrous forms at every step . . . . What an admirable country, this Madagascar."

Of course it was the foreigner's eye, in an age of great scientific expeditions, which saw the lemurs and pitcher plants and travelers' palms as bizarre and wondrous. If Malagasy of the time traveled as far as Africa or Arabia they found the rest of the world equally peculiar, but their remarks have not survived.

The early recognition of lemurs as a group of primates which have evolved in parallel to monkeys and apes has been well chronicled, mainly by Ian Tattersall (Buettner-Janusch et al., 1975; Mittermeier et al., 1994; Tattersall, 1982, 1997; see also Andriamialisoa and Langrand, 2003). Though not the first, de Flacourt's (1658) is the best-known and most elaborate of the early descriptions of lemurs in Madagascar. It was not until the early eighteenth century that the first live lemurs reached Europe. Thereafter, the literature on lemurs grew as systematists described, illustrated, and named new lemur species (Tattersall, 1997). In the second half of the nineteenth century a growing discussion of the systematics and taxonomy of lemurs was developing. By then observations of lemurs in their natural habitats were being contributed by missionaries, European traders, professional collectors, and French scientists (Buettner-Janusch et al., 1975).

The most notable contribution of the late nineteenth century to the study of lemurs was that of Alfred Grandidier. Grandidier's 32-volume *History of Madagascar* celebrated the country's biodiversity even before French colonization in 1895 (Grandidier, 1875–1921). Milne-Edwards and Grandidier illustrated most of the diurnal lemurs known today, with some variants only recently rediscovered (Milne-Edwards and Grandidier, 1875) . Pioneering colonial French scientists wrote the many volumes of the *Faune de Madagascar* and *Flore de Madagascar*. They founded the Académie Malgache and the Botanical Garden of Parc Tsimbazaza in the capitol city, Antananarivo.

Above all, in 1927 they launched the creation of the first national parks and reserves in the African or Indian Ocean regions. Two National Parks were open to the public: the monumental rock formations of the Isalo and the waterfalls and crater lakes of the Montagne d'Ambre. The other seven "Reserves Intégrales" were conceived as reservoirs of natural habitat, diverse samples of Madagascar's biological riches officially open only to scientists armed with research permits issued in Antananarivo. These parks and reserves were located mainly in areas that were at the time considered to be relatively isolated geographically and with low human population densities. Most other forests were also deemed to belong to the government. They would be guarded for rational exploitation as "concessions" for timber or large-scale agriculture.

Sequestering the forests led to conflict between French power and local people. Conservation is always about access to land, resources, and manpower. To be fair, the French did not begin this. In the Code of 305 articles (1881), Merina rulers assigned all forest land to the state. It is relevant that most forests are on Madagascar's periphery, occupied by "coastal" people whom the Merina conquered and colonized. The French colonial government then perpetuated the same policy through an increasingly well-trained and effective forest service.

One ecological idea which became fundamental to both theory and practice was championed by botanist Henri Perrier de la Bathie. He chronicled plant endemicity: 80% of species endemic in the great rainforests of the east, 95% in the spiny forests of the south, but almost none in the grasslands which cover the central plateaus. He concluded that the grasslands are recent creations which result from clearance and fires set by Malagasy after their arrival less than 2000 years ago. The giant lemurs, elephant birds, tortoises, and pygmy hippos that left subfossil remains in the swamps of both plateau and coast had gone extinct from human hunting and forest destruction. Perrier de la Bathie himself attempted to restore the primeval nature of one region by sending cochineal beetles to the far south in order to eradicate introduced prickly pear. He succeeded, probably beyond his wildest dreams, precipitating one of the century's worst famines (Jolly, 2004; Middleton, 1999; Perrier de la Bathie, 1921).

Perrier de la Bathie's condemnation of Malagasy who cleared vast forests, killed off the megafauna, and threaten what remains, still resonates in Western writings. This is so in spite of Burney's (1997) pollen analyses which show that the plateau has always been a mosaic of grass and woodland swept by lightning-strike fires. Of course since human arrival grass is far more widespread and fire more frequent, from the impact of grazing by introduced cattle, sheep, and goats, and through fires set to improve pasturage (Burney, 1997; Dewar and Burney, 1994; Kull, 2004). Perrier de la Bathie, though, left a lasting legacy: the view that it is scientists, not local people, who should decide what Malagasy landscape ought to be. Now we know, however, that many of the forest patches that have existed from Perrier de la Bathie's day to the present are "sacred forests" protected by local beliefs and practices (Clark et al., 1998; Sussman et al., 2003).

1955–1975: INDEPENDENCE AND THE FIRST REPUBLIC

Despite the manifest interests of scientists, missionaries, and others in the behavior of lemurs in their natural habitat, our knowledge of lemur behavior and ecology remained strictly at the anecdotal level until the midtwentieth century (Tattersall, 1997). In fact, the study of the natural behavior and ecology of primates worldwide began in earnest during this time period (Sussman, 1997). Modern studies of wild lemurs began with Jean-Jacques Petter and Arlette Petter-Rousseaux. After World War II until the late 1960s, the Académie Malgache and the Institut de Recherche Scientifique de Madagascar (IRSM; later Office de la

Recherche Scientifique et Technique Outre-Mer, ORSTOM) supported frequent biological expeditions to Madagascar. The Petters' mission to study lemurs was sponsored by Jacques Millot, then director of IRSM (Andriamialisoa and Langrand, 2003). In 1956–1957 they visited most of the sites which later hosted long-term lemur studies. The Petters observed the variety of social groupings in lemurs, from the monogamous *Indri* to the small groups of *Propithecus*, larger groups of *Lemur* and *Eulemur*, and the apparently solitary foraging of most nocturnal forms. They studied *Lepilemur* in Ankarafantsika, finding that the home ranges clustered together, which suggested that even "solitary" nocturnal lemurs had some form of continuing social system. They watched subgroups of black lemurs (*Eulemur macaco*) on Nosy Komba which foraged apart during the daytime, but rejoined at night. Petter-Rousseaux focused on reproductive seasonality. She showed that almost all young lemurs are weaned around February–March, the richest time of year. Tiny mouselemurs gave birth in November, *Eulemur* in September, *Propithecus* in July, but all synchronize weaning (Petter, 1962; Petter and Albignac, 1977; Petter-Rousseaux, 1962, 1968).

Their work was both the end and the beginning: the last of the classic colonial faunal studies; the first of the modern era. Independence was 3 years away. In 1947–1949 Madagascar had its war of independence, or "insurrection." It was repressed amid torture of the leaders, tens of thousands of deaths, and in almost total blackout of news to the outside world. Petter-Rousseaux has remarked that it was only reading Jolly's history of southeastern Madagascar in 2004 that she had any idea of the horrors of that dark time (Jolly, personal communication, 2004). When the young Petters had toured the entire country less than 10 years after the "insurrection" they were hardly aware of resentment toward the French, greeted instead by Malagasy warmth, courtesy, and inclination to hide unpleasantness.

In 1960, the year of independence, David Attenborough made the first commercial film of wild lemurs, aided by ornithologist Georges Randrianasolo of the Institut de Recherche Scientifique de Madagascar. Attenborough introduced Malagasy fauna to a Western audience (Attenborough, 1961). His triumphant climax was finding that indri, intensely territorial animals, responded to a playback of their song by approaching within camera range—although they answered, not with song, but with an alarm call of "indignant trumpetings." Randrianasolo continued to assist Western biologists and primatologists for the next three decades.

Alison Jolly arrived in 1962, funded as a postdoc by NSF in the post-Sputnik phase of the Cold War. Jolly was a student of zoologist G. Evelyn Hutchinson at Yale University. She had completed her thesis work at Yale, working on captive prosimians which had been collected by John Buettner-Janusch, a biochemical geneticist then at Yale. Buettner-Janusch dedicated his life to the study of all aspects of prosimian biology and in the mid-1960s moved his prosimian collection to Duke University establishing the Duke University Primate Center. Buettner-Janusch encouraged Jolly to do research in Madagascar. Jolly was somewhat shocked to arrive in a supposedly independent country only to find a Frenchman behind every government door. However, security was good, roads passable, and hospitality from both French and Malagasy always forthcoming. She chose a study site at Berenty, a reserve on a sisal plantation founded by the de Heaulme family in 1936. They had created a private paradise, recognizing that the gallery forest of Berenty was too beautiful ever to cut down—ideal for intensive studies of lemur social behavior (Jolly, 1966, 2004).

She found that ring-tailed lemurs lived in multimale, multifemale troops of up to 25 animals. Females wholly dominated males. A few males ranged and fed in the center of the troop, while others trailed behind as the "Drones' Club." Mating in any one troop was compressed into only 2 weeks, each female in estrus for less than a day. It may be interesting to note what questions she did *not* ask. Female dominance seemed a quirk of lemurs, not a political statement. Dominance hierarchies were clear-cut but this did not translate into life history terms: intergenerational female bonding, male migration, dominance rise and fall with age or prowess. She recognized the evolution of intelligence in a social context, rather than as manipulative skill, but did not consider the intelligence needed to navigate between food trees. Sifaka troops confronted each other "like sets of opposing chessmen" (Jolly, 1966, p. 50). Jolly did not, however, put formalized territorial defense into the context of bounded populations in a forest fragment. All of these major ecological themes came later.

In 1970 the Malagasy government held their first international biological conference, with the theme "Malagasy Nature, World Heritage." It was organized by Jean-Jacques Petter and Monique Ramanantsoa Pariente, daughter of the General who would soon become Madagascar's interim President. The conference was held in the University, then called "Université Charles de Gaulle," on its high, clean hill with a long view of the smoke plumes of distant fires. The conference raised the urgency of conservation, but made almost no mention of economic development. Richard and Alison Jolly presented a paper entitled "Conservation: who benefits and who pays?" Charles Lindberg, President of WWF, and Sir Peter Scott, its founder, walked Alison around the flower-filled University garden. They instructed her that although it was obvious that poor people who lose their land pay most of the price of reserves, she should not say so. It would set back the cause of conservation to raise such issues. Then Perez Olindo of the Kenyan Game department, and David Wasawo, Vice Chancellor of the University of Dar es Salaam, walked her out around the garden again. "High time someone said that!" they declared. "Come and stay with our families in Kenya!"

Attending this conference were three young primatologists who were just beginning their research on the ecology and behavior of Malagasy lemurs and who have continued to work on lemurs to this day, Robert Martin, Alison Richard, and Robert Sussman. Robert Martin, a professor at University College, London, was assisted by J.-J. Petter and by P. Roederer, then director of ORSTOM. Martin reinforced the Petters' speculation that nocturnal lemurs have a social life: grey mouse lemurs shared sleeping nests in all combinations of sexes (Charles-Dominique and Martin, 1972). Martin has continued his interest in lemurs and directed the research of many students in Madagascar, first as head of the Wellcome Laboratories of Comparative Physiology at the Zoological Society of London, then as Professor and Director at the Anthropological Institute and Museum of the University of Zurich, Switzerland, and currently as President of Academic Affairs at the Field Museum in Chicago.

Alison Richard was a graduate student of John Napier at University College, London but was encouraged by Alison Jolly to do her thesis in Madagascar. She initially went off to do her Ph.D. thesis on the jaw mechanics of the indriids but changed her mind on the plane to Madagascar and decided to do a comparative study of the sifaka (Richard, personal communication, 2005). Richard studied white sifaka in two sites at opposite ends of Madagascar. Coquerel's sifaka (*Propithecus verreauxi coquereli*) in the northwestern deciduous forest of Ankarafantsika did not defend territory, rather, they simply avoided each other when they met in overlapping ranges. Verreaux's sifaka (*P. v. verreauxi*) in spiny forest scent-marked frontiers and confronted each other in ritualized combat. Richard's was among the early studies to emphasize the role of ecological differences rather than "species-typical" behavior (Richard, 1978). Alison Richard continued to advise students working in Madagascar as Professor of Anthropology and then as Provost of Yale University. She is now the Vice-Chancellor of Cambridge University.

Sussman had followed his professor, Jack Prost, from UCLA to Duke University, where Prost was taking on the position of Professor of Anthropology and Assistant Director of the Duke University Primate Center. The Duke University Primate Center was the main research site in the United States for the study of prosimians, primarily Malagasy lemurs. Buettner-Janusch as Director of the Center, Prost, and zoologist Peter Klopfer encouraged students to conduct research on this collection and supported Sussman's research in Madagascar. Sussman compared habitat use by brown lemurs, *Eulemur fulvus rufus*, and ringtails, *Lemur catta*, in the forest of Antseranomby, where both species coexist, at Tongobato with only browns, and at Berenty which then had only ringtails. He found that browns foraged high in the canopy of big tamarind trees, with a population density of up to 1000/ha. Ringtails slept in the big trees but ranged out daily to feed in the sunlit scrub, with a much more varied diet, and travel on the ground. Sussman confirmed Klopfer's observations that infant ringtails mature much more rapidly than browns. He made an extensive forest survey: ringtails seemed to need scrub as well as high trees; browns, only the high trees (Sussman, 1974). Sussman has continued to send students to work in Madagascar from Washington University, St. Louis.

Also, in the late 1960s and 1970s, the Petters' group studied a suite of nocturnal lemurs in the Menabé region, north of Morondava. In that western woodland most trees lost their leaves, not just flowers and fruit, during the 9 months without rain. Dwarf lemurs (*Cheirogaleus medius*) actually hibernated, mouse lemurs (*Microcebus murinus*) also retreated into sporadic torpor, forked lemurs ate tree gum, Coquerel's mouselemurs (*Mirza coquereli*) lived on insects and the sweet secretions of insect flower-mimics, while lepilemurs (*Lepilemur ruficaudatus*) chewed on remaining old leaves. Each lemur had a different strategy to confront the harsh dry winter (Charles-Dominique, 1977; Charles-Dominique et al., 1980).

In the early 1970s other non-French foreign scientists, mainly from London and the United States, began research on lemurs in Madagascar. Jonathan Pollock conducted his thesis research for University College, London on indri between 1972 and 1973. He found that indri, like ringtails, had absolute female dominance. Females fed higher in leafy branches, while the male waited his turn in a crotch below. Pollock speculated that in this monogamous species such female dominance was a form of parental investment by the male in the health of his own offspring. Pollock also pioneered analysis of ranging decisions, and found that a younger pair fed on fewer food trees than an older one (Pollock, 1977, 1979).

The Duke University Primate Center continued to sponsor research in Madagascar. Peter Klopfer of Duke University visited Berenty and then sent his graduate students. In 1972–1973, Norman Budnitz and Kathryn Dainis (now Blumenfeld-Jones) compared ranging patterns of ring-tailed lemurs in gallery forest and in scrub, noting the importance of succulent plants and the phenomenon of male migration. They censused and mapped a 1 km^2 study area at Berenty, still in use, both for lemurs and for plant community composition (Blumenfeld-Jones et al., 2006; Budnitz, 1978; Budnitz and Dainis, 1975; Jones, 1983). In 1974, Lee McGeorge (now Durrell) analyzed 24-hour time series of vocalizations of all the Berenty animals. She found vocal niche partitioning not unlike radio stations which broadcast either at different frequencies or at different times (McGeorge, 1978). Also, in 1974, Jay Russell, a student of Buettner-Janusch, was astounded by lepilemurs' (*Lepilemur leucopus*) ability to conserve energy, remaining motionless for long periods and leaping only as absolutely necessary. Charles Dominique and Hladik calculated that at the end of the dry season *Lepilemur* was at the extreme edge of energy balance, but Russell showed that the cold nights of July imposed even more strain on a small-bodied animal. Russell also foreshadowed later interest in ranging patterns by speculating that a lepilemur's brain may only be able to remember a few trees at a time, learning all it needs as a roving adolescent and staying put thereafter. This was not just the bile of a bored graduate student. Leanne Nash summed up in a later decade, "I have studied *Lepilemur* for a year, and the bottom line is that it eats what it sits on and sits on what it eats" (Charles-Dominique and Hladik, 1971; Nash, personal communication and 1998). In 1975, Anne Mertl-Milhollen showed that ringtails and white sifaka scent-mark territorial boundaries, not range boundaries. She noted that core areas of troops, and even some of the frontiers, remained the same from 1963 to 1979—now known to persist even to the present (Mertl-Millhollen, 1979, 1988, 2000; Mertl-Millhollen et al., 1979).

These studies of the early 1970s were the end of an age of innocence—or perhaps, of ignorance. Westerners could imagine themselves as pure scientists following untrammeled intellectual curiosity. They took for granted their privilege as the heirs of Rousseaux—and Commerson—in love with the romance of far-off wilderness, and boosted like multistage rockets by the funds of the Paris Museum or the NSF.

The First Malagasy Republic fell amid student riots in 1972. Students objected first of all to French domination of the University and high school systems, and second, to French domination of government jobs, leaving few places free for aspiring university graduates (Brown, 1995; Jolly, 2004). Xenophobia, a recurrent groundswell within Madagascar, now ran rampant. Left-wing ministers were appointed under the temporary presidency of General Ramanantsoa. When Anne Mertl-Millhollen arrived in early 1975 she had to travel via the Comoros to reach Antananarivo at all in order to apply for, and receive, an official research visa. By the time she left, Didier Ratsiraka was President of Madagascar.

1975–1985: THE SECOND REPUBLIC

"We know that Madagascar's biodiversity is a world heritage. We are not sure that the world knows it is our heritage." Joseph Andrianampianina of the School of Agronomy spoke these words in 1975, explaining his deep skepticism toward outside scientists (personal communication). The promises of funds made at the 1970 conference had vaporized when the government changed. One of the early acts of the Ratsiraka government was to cancel research visas for foreigners. This passed almost unnoticed amid the nationalization of banks, insurance companies, businesses, and cinemas. The U.S. Ambassador departed. Relations were opened with Russia, North Korea, and Mao's China. Ratsiraka's policy was "Tous Azimuts," all compass points, although France quietly remained the major outside donor. At that time Africa was yeasty with socialism, as led by the President of Tanzania, Julius Nyerere. Many in the West sympathized with the ideals of countries like Madagascar which attempted to lift themselves out of dependence, poverty and undereducation.

Meanwhile, it was clear that ecologists could no longer play at pure curiosity. What little influence we had should be turned to conservation. Foresters no longer resisted village pressure to occupy land. Madagascar's forest degradation visibly accelerated.

WWF International appointed Barthélémy Vaohita as WWF representative in Madagascar, with the backing of Luc Hoffmann and Jean-Jacques Petter. Vaohita was supposed to do everything—administer reserves, repair outboard motors for the boat to the island of Nosy Mangabé, and start conservation education, writing and launching a series of nature books for schools. He was somehow meant to convert the Government to backing conservation when that was the last thing on Ministers' minds.

Alison Richard and Robert Sussman thought that the best move instead would be local: a new reserve to demonstrate how research meshed with community welfare. Guy Ramanantsoa of the University's School of Agronomy identified a small forest in the southwest where the community actually wished to found a reserve. It was called Beza Mahafaly, lying beside the Sakamena River near the town of Betioky. Henri Rajaona, Dean of the Agronomy School, negotiated land rights and signed the papers. A cooperative project focused on research, conservation, and development was forged between the University of Madagascar (now University of Antananarivo), Washington University-St. Louis, and Yale University. It was an act of some courage to give foreign universities even limited rights over land. Beza became a research reserve where straight transects were cut and labeled, and lemurs were periodically captured and fitted with identifying collars and dog-tags. The reserve is now under the management of the University of Antananarivo and generations of university field trips and University of Antananarivo students came to Beza under the guidance of Pothin Rakotomanga (Sussman and Ratsirarson, 2006).

A third conservation strand was information and contacts. Césaire Rabenoro, President of the Académie Malgache, hosted a series of international meetings, including one on lemur biology in 1979. Among the participants were Gerald and Lee Durrell of Jersey Wildlife Preservation Trust. Tom Lovejoy and Russell Mittermeier of WWF-USA focused their attention on Madagascar, including commissioning Jolly's book *A World like our Own*, written as Ratsiraka came to power. She quoted Richard Jolly's advice "Tell the whole story—ecology with people, not just your animals." This sentiment was right in line with the changed spirit of the times (Jolly, 1980).

Within a few years, the socialist economy began to fall apart. Nationalization was not working. Agricultural production plummeted. The Mexican Debt Crisis of 1982 sent international finance into a panic. Madagascar was essentially bankrupt, in the receivership of the IMF. The IMF laid out a strict program of structural adjustment, debt repayment, and economic opening to the outside world.

The Durrells, at the request of the Malagasy Government, hosted a workshop on the island of Jersey, home of their famous Jersey Wildlife Trust (now the Durrell Wildlife Conservation Trust). Conservation NGO's and zoos attended. The Malagasy delegation was headed by Madame Berthe Rakotosamimanana, Permanent Secretary of the Ministry of Higher Education. Madame Berthe knew most of the participants—she had been in the awkward position of denying many of them visas. Now she negotiated a "Tripartite Commission" of the Ministries of Higher Education, Scientific Research, and Water and Forests to vet research requests. Foreign institutional programs must include Malagasy counterparts and provide equipment ranging from microscopes to 4 x 4 vehicles. When at last the agreement was hammered out, Madame Berthe was wreathed in smiles. No-one wanted collaboration more than she did.

Meanwhile, Barthélémy Vaohita of WWF toured government ministers' offices. Outboard motors were not his forté, but politics was. In 1984 he achieved the apparently impossible: a joint declaration signed by every single Minister in favor of Sustainable Development. This led directly to the WWF-funded International Conference on Environment and Sustainable Development held in Antananarivo in 1985.

The 1985 conference had a very different agenda from its predecessor in 1970. In 1985 scientific research was relegated to a 2-day preconference hosted by Madame Berthe and Russell Mittermeier. The main sessions took place at the Ministry of Foreign Affairs, not the disintegrating University campus. Five hundred civil servants from the provinces attended to learn the new government line. The Duke of Edinburgh, President of WWF, gave opening and closing addresses. Kim Jaycox, a Vice President of the World Bank, flew to Madagascar for an afternoon. He laid down the conditions for a possible World Bank Loan for conservation and sustainable development—and held out hope that such a loan could materialize. With the World Bank in the lead, other donors would fall into line. The conference achieved its aims.

1985–1998: PROGRAMMES D'ACTION ENVIRONNEMENTALES

Madagascar's timing could not have been better. In Washington, protestors hung bloody banners opposite the World Bank to declare "THE BANK MURDERS RAINFOREST." Madagascar seemed like a virgin country where foreign donors could promote environment sustainability, getting things right this time around. During the late 1980s the W. Alton Jones foundation gave WWF necessary seed money for the campaign. A meeting on St. Catherine's Island, and tour of U.S. and Jersey zoos, was headed by Joseph Randrianasolo, Minister of Water and Forests, and by Russell Mittermeier. In the end the Minister slapped Mittermeier's draft Environmental Action Plan down on a bed at midnight in front of his group, and told them to go home and persuade every ministry to adopt it. U.S. Aid became the major funder for biodiversity. The First Programme d'Action Environnemental, a $20M multidonor loan under World Bank auspices, was finally underway in 1991—just as the Ratsiraka government fell, to be replaced for 5 years by Albert Zafy's Forces Vives.

For the scientific community, the point was that political will and funding materialized to resume the study of lemur ecology.

A few of the new studies are islandwide in scope. Martin Nicoll and Olivier Langrand surveyed all the protected areas of Madagascar (Nicoll and Langrand, 1989), as has Conservation International's mapping projects. Peter Raven, who had attended the 1985 conference in Jersey and was the director of the Missouri Botanical Garden (MBG), sent Peter Lowry to Madagascar to develop a countrywide scheme for the classification of vegetation types. The MBG subsequently sponsored a large number of studies of the Madagascar flora, and continues to train Malagasy botanists. Wilson Lourenço and Steven Goodman organized conferences drawing together much current work (Lourenço, 1996; Lourenço and Goodman, 2000). Edward Lewis has toured the country with his blowgun, identifying a wealth of lemurs distinct at the species level. Above all, WWF and the Field Museum of Chicago have sponsored Steven Goodman's remarkable series of expeditions and rapid assessment teams to little-known forests, surveying lemurs as well as everything else. Goodman's work has culminated in the 1700-page edited volume, *The Natural History of Madagascar*, which summarizes current knowledge of Madagascar's biodiversity up to the day it went to press (Goodman and Benstead, 2003). Goodman's own fieldwork continues unabated.

In 1988, the Madagascar Fauna Group (MFG), an international consortium of zoos was formed after an international meeting attended by representatives of the Malagasy government, zoos, the IUCN Primate Specialist Group, and field biologists. It is now a consortium of about three dozen zoos and research institutes that collectively apply their resources and expertise to overcoming the biodiversity crisis in Madagascar (Durrell et al., in press). The MFG is currently committed to two major programs. One is the Parc Zoologique Ivoloina which is a zoo and outreach environmental education program. The second is focused on the protection and management of the Betampona Reserve, located in one of the few remaining lowland rainforests of eastern Madagascar. It is the location of the only successful release program of captive lemurs (black-and-white ruffed lemurs) into a natural habitat. After 15 years of leadership by the San Francisco Zoo and the Duke University Primate Center, in 2003, the headquarters of the MFG moved to the St. Louis Zoo with Jeffrey Bonner and Ingrid Porton as coordinators.

Major field sites have become research centers. Outstanding is Ranomafana, where Patricia Wright and Bernhard Meier discovered the golden bamboo lemur (*Hapalemur aureus*) in 1987. Wright began her work in Madagascar while a young professor at Duke University and continued her work there after moving to the State University of New York at Stony Brook. She has advised many students' research in Madagascar from these two universities. Wright's personal commitment has driven Ranomafana's gazetting as a national reserve (supported by Joseph Andrianampianina), then its designation as a national park. ValBio, the new research laboratory, overhangs the rapids of the Namorona river beside a waterfall that leaps down the escarpment. The research enterprise up to 2005 has produced 19 PhDs and 88 DEAs, and currently has 65 Malagasy in residence (Feistner, personal communication) They are proud that of 5 Malagasy who have earned doctorates in the USA, all have returned to Madagascar to work in conservation. One such is Jonah Ratsimbazafy of Durrell Wildlife who now heads his own research group on black-and-white ruffed lemurs in the coastal forest of Manombo.

Other centers of research and conservation are also firmly rooted: Ankarafantsika with Zimmermann, Kirindy with Kappeler, the littoral forest of Mandena with Ganzhorn, Berenty with Koyama, Jolly, Rasamimanana, and Simmen, and the Betampona Reserve supported by the MFG and Durrell Wildlife. At Beza Mahafaly Sussman, Richard, and Rakotomanga trained their students Brockman, Gould, Ratsirarson, and Sauther, who now send students of their own.

Perhaps the most symbolic change was the third international biodiversity conference of Antananarivo, the International Primatological Society's Congress in 1998.

Madame Berthe Rakotosamimanana, its president, persuaded the government to repair 25 years' neglect of the university, restoring lecture rooms, halls, gardens, and even toilets. Hantanirina Rasamimanana was scientific program chair. Students and lecturers volunteered. Suddenly, Madagascar demonstrated that it had enough primatologists to take its rightful place in its own country's research (Rakotosamimanana et al., 1999). The GERP, the Groupe d'Etudes et de Recherches des Primates, became one of the few developing country primatological societies to be a full member of the International Primatological Society. Madame Berthe was Secretary General of the GERP from its founding until her death in 2005, succeeded in 2006 by Jonah Ratsimbazafy.

Many of the results from the upsurge of studies over the last 20 years will be summarized in this volume. They will certainly reflect the changes in taxonomy: new species discovered or reidentified, making the wealth of the island-continent even more apparent. Community ecology has blossomed, as niche partitioning is deciphered not only between up to 13 living lemur species in the same forest, but with speculation concerning the missing niches filled by the extinct megafauna. Socioecology of lemurs makes them seem less and less like anthropoid monkeys, with the prevalence of pair-bonding, of female dominance or codominance between sexes, and with the lack of subtlety in reconciliation or tripartite interactions. Scent-marking as communication is slowly being understood. Long-term life history records, energy budgets, studies on ranging and population demography, and research using satellite imagery show how lemurs confront their environment of poor soils and challenging climate.

PROSPECTS FOR THE FUTURE

In the crisis year of 2002, Madagascar gained a new President, Marc Ravelomanana. As of this writing, the President is in charge of a business-friendly regime which welcomes foreigners and which is fixed on economic growth. It may be that rising oil prices and the structural weaknesses and poverty of Madagascar frustrate these goals, but for the present this is the country's trajectory.

In 2003 President Ravelomanana stunned the International Parks Congress in Durban, South Africa, by announcing that Madagascar plans to triple the amount of protected area from the present 2 million hectares of forest to a future 5 million hectares plus another million of marine reserves. It will take time for the "Durban Vision" to materialize on the ground. It envisages a whole new regime for forest management. The central government's rights over forests were promulgated in 1881 by the Merina Kingdom and have continued by every régime since then. The Durban Vision now plans to gradually transfer management of the new protected areas to local control, but with checks against felling and rewards for preservation. This would be a radical departure in policy. It is also a radical philosophical change, from Perrier de la Bathie's view of peasants as the executioners of the forest to seeing them as the only credible saviors of forest.

Ecological studies have for the most part focused on the remaining richest areas: indeed, within the great reserves first set aside in 1927 for their scientific treasures. The few surveys of forest fragments and degraded forests predictably find a much decreased species richness of lemurs. However, there will be great returns to ecologists who work on village-managed areas, and on forest corridors between the integral reserves. They will discover how many species can survive, in how much land—even, indeed gain insight into the future possibility for continued speciation in Madagascar.

A second new development is the involvement of big business, especially mining, in aiding conservation. This seems paradoxical, since mining in the past has been responsible for so much environmental degradation. It would be naive to expect a profit-making company to voluntarily diminish its own profits. However, a company that is vulnerable to public opinion worldwide, and which wishes to operate in a favorable environment in the local region, can see the profitability of environmental improvement. A case in point is the Rio Tinto subsidiary Quebec Madagascar Minerals. QMM has announced its investment decision in 2005 to open a titanium mine amid ancient littoral forests near Taolagnaro, in the far south. The actions of the company over the 20-year run-up to the decision have been a net gain for the biodiversity of the Anosy region as well as funding a great deal of fundamental research. It remains to be seen whether QMM fulfills the promises and hopes it has raised for the future, or in the end, simply destroys the mine site forests.

One very important difference from either government or external aid is the time horizon. A mine's lifetime and returns are calculated over 40–60 years. This is longer than the perspective of any democratically elected politician, and far longer than a 5-year aid program. As Jörg Ganzhorn points out, from the point of view of research scientists this opens the possibility of environmental protocols maintained over decades. Madagascar is now in the course of negotiations with other multinationals which may also prove to be long-sighted and lemur-friendly—or, of course, the opposite.

The final major prospect is global warming. Climate changes created the richness of Madagascar's biodiversity. Climate change will certainly impact the distribution of the remaining forests. Madagascar's abruptly adjacent climatic zones, like the "rainfall faultline" near Fort Dauphin or the mosaic of wet and dry forests around the Montagne d'Ambre, mean that a small global temperature change may drastically shift lemur habitats. The predicted increase in frequency and severity of tropical storms and El Niño droughts will test lemurs' physical adaptations to catastrophe—perhaps to the limit. For a pure scientist, what opportunities for research! But as global warming also tests the enduring resilience of Malagasy people, there will be ever less excuse for picturing lemur ecology only as a science of primeval creatures in ancient biological communities.

As Richard Jolly said long ago, "Tell the whole story: ecology with people, not just your lemurs."

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CHAPTER THREE

Ecology and Extinction of Madagascar's Subfossil Lemurs

Laurie R. Godfrey, William L. Jungers,
and Gary T. Schwartz

INTRODUCTION

Our goal in this chapter is to review recent research on the ecology of Madagascar's extinct lemurs, with particular attention to how strongly these species resembled their still-extant relatives. The literature on the ecology of lemurs is replete with proclamations regarding their special adaptations. These include hypometabolism (torpor in some), sperm competition or other forms of male–male competition for mates that involve relatively low agonism, small group size, seasonal breeding, cathemerality, territoriality, female dominance, fibrous diets (high folivory), and low encephalization. Extant lemurs, whether nocturnal, cathemeral, or diurnal, tend to exhibit low visual acuity (relatively high retinal summation). Some have extremely rapid dental development and are dentally precocious at birth and weaning. Lemurs are excellent climbers (although a few spend a fair amount of time on the ground). If these special adaptations are

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indeed phylogenetically constrained and therefore Malagasy lemur-specific, then one might predict that the giant lemurs were also characterized by many of these strategies and traits. If, on the other hand, body size is more important than phylogeny in influencing adaptations and lifestyles, then the extinct lemurs, especially the truly "giant" ones, should exhibit only limited similarities to their living relatives and converge instead on larger-bodied anthropoid primates.

There are two prevailing hypotheses that purport to explain the special adaptations of lemurs. The first, Wright's (1999) *energy frugality hypothesis*, builds on the energy conservation hypothesis of Jolly and others (Jolly, 1984; Richard and Nicoll, 1987; Young et al., 1990). According to this hypothesis, most lemur traits serve either to conserve energy (e.g., hypometabolism, relatively low agonism, seasonal breeding, small group size) or to maximize use of scarce resources (fibrous diets, cathemerality, territoriality, female dominance), thus enabling lemurs to survive in harsh, seasonal habitats with low productivity. Seasonal nutritional stress is prevalent among lemurs; it influences the timing of reproduction and weaning, and may be linked to female dominance and small group size. Early weaning may imply early acquisition of ecological (though not necessarily reproductive) "adulthood," with important implications for reduced maternal investment.

Van Schaik and Kappeler's (1996) *evolutionary disequilibrium hypothesis*, on the other hand, holds that extant lemurs are in the process of modifying their behavior and other niche characteristics in the wake of the extinction of major potential diurnal predators and possible competitors. Cathemerality, for example, is a step in the shift from nocturnality to diurnality. Small group size and female dominance are primitive retentions from more nocturnal, monogamous ancestors, and these adaptations are in the process of being replaced as the species become more diurnal and more gregarious, and thus more monkey-like.

If Wright's energy frugality hypothesis holds generally for Malagasy primates, then it should predict or explain the characteristics of extinct as well as extant species. If van Schaik and Kappeler's evolutionary disequilibrium hypothesis is correct, then the preextinction biota should differ from modern species in a fundamental manner. The larger-bodied, extinct lemurs should bear little resemblance to modern lemurs in terms of their salient ecological adaptations, but should rather resemble like-sized, diurnal anthropoids. The question is, to what extent can we draw behavioral/ecological inferences for extinct lemurs? What is registered in skeletons? How does what we *can* infer regarding extinct lemurs affect our perception of the ecospace occupied by the lemurs of Madagascar?

Space limitations prevent us from reviewing the entire literature on subfossil lemur paleoecology. Much research on subfossil lemur paleoecology and life histories has been done in the past two decades (Burney et al., 2004; Godfrey, 1988; Godfrey et al., 1993, 1997a,b, 1999, 2002, 2004a, 2005a,b, in press a,b; Godfrey and Jungers, 2003; Hamrick et al., 2000; Jungers et al., 1991, 1997, 2002, 2005a,b; King et al., 2001; Rafferty et al., 2002; Schwartz et al., 2002, 2005; Shapiro et al., 2005; Simons, 1994; Simons et al., 1992; Wunderlich et al., 1996), supplementing and expanding some excellent early work (see Godfrey and Jungers, 2002, and Tattersall, 1982, for historical reviews).

We focus here on questions of particular relevance to the focus of this book: the uniqueness of lemur behavioral ecology. Specifically, we ask: (1) Were extinct lemurs forest or woodland-limited? (2) Did extinct lemurs exhibit female dominance? (3) Were extinct lemurs energy conservers? (4) Did extinct lemurs exploit fibrous food sources? (5) Did extinct lemurs wean their offspring earlier than like-sized, diurnal anthropoids? (6) Did extinct lemurs exhibit low visual acuity? (7) Finally, if the process of extinction was not random, how can it be characterized? Table 1 provides a brief overview of the extinct lemurs (including the sloth, koala, and monkey lemurs) and their characteristics.

Table 1. Madagascar's extinct lemurs (modified from Burney et al., 2004; Godfrey, 2005)

Family and included genera	Characteristics
Palaeopropithecidae (sloth lemurs) *Palaeopropithecus* *Archaeoindris* *Mesopropithecus* *Babakotia*	This diverse family is entirely extinct. Called sloth lemurs because of similarities to arboreal sloths, these lemurs are most closely related to living indriids. The largest of all lemurs, *Archaeoindris*, belongs to this family. Sloth lemurs had long, curved digits, and most were specialized hangers. They fed on a combination of leaves, fruit, and seeds. Sloth lemurs survived the advent of humans to Madagascar by at least 1500 years. There is evidence of human butchery of sloth lemurs in southwest Madagascar more than 2000 years ago, shortly after humans first colonized the island.
Megaladapidae (koala lemurs) *Megaladapis* (*Megaladapis*) *Megaladapis* (*Peloriadapis*)	The koala lemurs are much larger than the sportive lemurs (Lepilemuridae) and the Lemuridae, both of which have been considered their sister clades. Koala lemurs resembled sportive lemurs in their dental morphology and diet of leaves. Slow climbers with huge, pincerlike feet, they were committed to life in the trees despite their large body size. The largest *Megaladapis* species was the size of a large male orangutan or female gorilla. *Megaladapis* was still alive when humans arrived on Madagascar, and well into the last millennium.
Archaeolemuridae (monkey lemurs) *Archaeolemur* *Hadropithecus*	These robust, baboon-sized lemurs may have been among the last giant lemurs to become extinct. Called monkey lemurs because of convergences to baboons and macaques, these were likely the most terrestrial of the giant lemurs. Archaeolemurids were able to break open hard objects (such as nuts) with their teeth; there is also direct evidence for omnivory in *Archaeolemur*.
Daubentoniidae (aye-ayes) *Daubentonia*	This family includes the living aye-aye and its giant extinct relative, *Daubentonia robusta*. The latter was still extant when humans arrived on Madagascar; its incisors were collected, drilled, and probably strung on necklaces. Aye-ayes are the largest nocturnal lemurs of Madagascar.
Lemuridae (ruffed lemurs, etc.) *Pachylemur*	This family of quadrupedal lemurs has one extinct member, the giant ruffed lemur, *Pachylemur* (three times the mass of the largest living member of this group, *Varecia*). Like *Varecia*, *Pachylemur* consumed fruit.

Were extinct lemurs forest or woodland-limited, as are extant lemurs?

The evidence strongly favors wooded-habitat preference for most, if not all, extinct lemurs. Both the postcranial anatomy (Jungers et al., 2002) and stable isotopes (Burney et al., 2004) bear testimony to such a habitat preference. Highly derived postcranial specializations suggest that leaping was rare (if ever practiced) by extinct lemurs, but that slow climbing and suspension were common (Jungers et al., 2002; Shapiro et al., 2005). Of course, due merely to their body size, the giant extinct lemurs would have had to spend a fair amount of time on the ground (if merely to cross from tree to tree), but ground locomotion would have been awkward, indeed ungainly, for some. Even the largest-bodied lemurs (i.e., the male-gorilla-sized *Archaeoindris*) have adaptations that suggest scansoriality (e.g., a femur with an extremely high collodiaphyseal angle and reduced greater trochanter). Terrestrial quadrupedalism may have been common in the archaeolemurids, but there is no evidence of cursoriality in either *Archaeolemur* or *Hadropithecus*. New discoveries of postcranial bones of *Hadropithecus* (Godfrey et al., 2005b, in press a) have confirmed the prior inferences of Godfrey et al. (1997a) that some of the earlier postcranial attributions for *Hadropithecus* (and conclusions based on them) were incorrect. The femora of *Hadropithecus* are robust, anteroposteriorly compressed, and far more like those of gorillas than baboons.

Stable carbon isotopes are now available for many extinct lemur taxa (Burney et al., 2004; Table 2). They corroborate consumption of C3 (generally closed forest) plants in all species except *Hadropithecus*, which had a mixed diet of C3 and C4 or CAM plants (or some combination of plants and animals, such as snails, consuming C4 plants). *Hadropithecus* is best represented in the arid south, including some more open habitats (e.g., Ambovombe) lacking other primates.

Did extinct lemurs exhibit female dominance?

For many species of living lemurs, females win the great majority of agonistic encounters with males—a phenomenon called "female dominance" (Digby and Kahlenberg, 2002; Genin, 2003; Jolly, 1984, 1998; Kubzdela et al., 1992; Overdorff et al., 2005; Pochron et al., 2003; Pollock, 1979; Radespiel and Zimmermann, 2001; Richard, 1987; Richard and Dewar, 1991; Richard et al., 2000; Sauther et al., 1999; Waeber and Hemelrijk, 2003). There is no simple way to determine whether extinct lemurs showed the same pattern of behavior. This is because female dominance in lemurs is not based on the physical superiority of females; therefore, variation in the degree and expression of female dominance is uncorrelated with variation in skeletal characteristics. It is possible that female dominance in lemurs depends on an *absence* of physical superiority of *males*; extant lemurs are notorious for their sexual monomorphism or low levels of sexual dimor-

Table 2. Stable carbon isotope determinations for giant lemurs (from Burney et al., 2004)[a]

Taxon	Site	Region	$\Delta^{13}C$
Archaeoindris fontoynontii	Ampasambazimba	C	–23.5
Archaeoindris fontoynontii	Ampasambazimba	C	–23.4
Palaeopropithecus ingens	Ampoza	SW	–20.6
Palaeopropithecus ingens	Ankazoabo Cave	SW	–19.0
Palaeopropithecus ingens	Belo-sur-Mer	W	–21.0
Palaeopropithecus ingens	Taolambiby	W	–20.2
Mesopropithecus pithecoides	Ampasambazimba	C	–22.1
Mesopropithecus globiceps	Ankazoabo Cave	SW	–15.8
Mesopropithecus globiceps	Belo-sur-Mer	W	–20.3
Mesopropithecus globiceps	Tsiandroina	SW	–19.3
Pachylemur insignis	Belo-sur-Mer	W	–20.2
Pachylemur insignis	Belo-sur-Mer	W	–20.6
Pachylemur insignis	Belo-sur-Mer	W	–20.2
Daubentonia robusta	Beloha Anavoha	SW	–16.3
Megaladapis edwardsi	Beloha Anavoha	SW	–20.4
Megaladapis sp. infant femur	Andrahomana Cave	SE	–20.1
Megaladapis madagascariensis	Belo-sur-Mer	W	–22.4
Megaladapis madagascariensis	Taolambiby	SW	–18.9
Archaeolemur cf. edwardsi	Anjohibe	NW	–27.5
Archaeolemur majori	Belo-sur-Mer	W	–19.9
Archaeolemur sp.	Belo-sur-Mer	W	–20.5
Archaeolemur majori	Belo-sur-Mer	W	–18.3
Archaeolemur majori	Belo-sur-Mer	W	–19.9
Hadropithecus stenognathus	Andrahomana	SE	–9.1
Hadropithecus stenognathus	Tsirave	SW	–13.2
Hadropithecus stenognathus	Belo-sur-Mer	W	–8.4

[a] Note that $\Delta^{13}C$ determinations for *Hadropithecus stenognathus* (–8.4 to –13.2) suggest a diet richer in C4 and/or CAM plants (or in animals consuming these plants) than in any other subfossil lemur. For comparative purposes (see Peters and Vogel, 2005), we note that $\Delta^{13}C$ values for specialized grazers, including *Theropithecus*, generally range from ~ +1 to –4. *Paranthropus robustus* and *Australopithecus africanus* have stable carbon isotope values ranging from ~ –6 to –11 (thus overlapping *Hadropithecus*).

phism (Jenkins and Albrecht, 1991; Kappeler, 1991, 1996). Nevertheless, low sexual dimorphism, by itself, does not generate female dominance.

In displaying low levels of sexual dimorphism and widespread female dominance, extant lemurs differ from anthropoids. Among anthropoids, polygyny is common, and the degree of canine and body size dimorphism is correlated largely with the degree of contest competition among males for mates (Plavcan, 2001). Except in cases where females form coalitions capable of challenging males, anthropoids generally display male social dominance coupled with moderate to high levels of sexual dimorphism. In short, anthropoids conform to the basic predictions of sexual selection theory—polygynous species tend to exhibit greater degrees of sexual dimorphism in canine height and in body size, and males dominate females in agonistic encounters. Relative canine size is also correlated with agonism.

The lack of dimorphism in extant lemurs has been related to selective forces affecting male and female reproductive strategies (e.g., Fietz, 1999 a,b; Kappeler, 1991; Kraus et al., 1999; Lawler et al., 2005). Monogamy is common among lemurs (especially among nocturnal species), but others exhibit promiscuity with scramble competition, suppression of sexual function in subordinate individuals, or forms of male–male contest competition that avoid direct combat. Levels of social agonism appear to be correlated with relative canine height (the relationship of canine height to other measures of size, such as molar length) (Godfrey et al., 2002; Plavcan et al., 1995). In some species (e.g., *Lemur catta*), both males and females have long, trenchant upper canines (and both sexes tend to exhibit high agonism), whereas in others (e.g., *Indri indri*), both sexes have low-crowned canines (and tend to exhibit low agonism).

Extinct lemurs resemble extant lemurs in showing little or no skull length or canine height dimorphism and in showing tremendous interspecific variation in the height of the canine relative to measures of body size (Godfrey et al., 1993, 2002). The virtual absence of canine or skull length dimorphism among giant lemurs confirms a lack of convergence to the size-correlated anthropoid pattern (Smith and Cheverud, 2002). Male social dominance, with strong intrasexual combat competition for mates, seems unlikely. Nothing contravenes the possibility of female dominance in giant lemurs. Furthermore, if agonism for both sexes is correlated with relative maxillary canine height, then certain extinct lemurs (especially *Megaladapis*) likely exhibited agonism on a par with diurnal lemurs such as *L. catta* and other lemurids, while others had lower levels of agonism (Table 3). It is noteworthy that the canines of extinct lemurs are generally not nearly as long and daggerlike as those of male cercopithecines.

Were extinct lemurs energy conservers?

Several lines of evidence suggest that the answer is affirmative, especially for some of the largest subfossil species. All extant strepsirhines studied to date, including Malagasy cheirogaleids, lepilemurids, lemurids, and indriids, have basal or resting metabolic rates (BMRs) well below Kleiber's line and reduced in comparison to most size-matched anthropoid primates (Genoud, 2002; Ross, 1992; Schmid and Ganzhorn, 1996). Based on this phylogenetic effect alone, we suspect that the giant lemurs were also comparatively hypometabolic, and it seems reasonable to extend this inference from BMR to FMR (field metabolic rate; Nagy, 1987) and MMR (maximal metabolic rate; Weibel et al., 2004). Although daily torpor adds to the energy conservation of very small lemurs during the cooler dry season (Schmid et al., 2000), we doubt that this extreme metabolic strategy was practiced by the large extinct species. Nevertheless, long periods of inactivity

Table 3. Relative maxillary canine height index values for extinct lemurs and other species[a]

Family	Genus and species	Relative maxillary canine height index (maxillary canine height divided by M1 mesiodistal length) for pooled-sex or separate-sex samples	
Cercopithecidae	*Trachypithecus obscurus*	♂2.08	♀1.33
	Semnopithecus entellus	♂2.42	♀1.25
	Colobus guereza	♂2.54	♀1.94
	Papio cynocephalus	♂2.43	♀0.83
	Cercopithecus mitis	♂2.85	♀1.55
	Macaca fascicularis	♂3.22	♀1.58
	Mandrillus leucophaeus	♂3.13	♀0.96
Indriidae	*Propithecus verreauxi*	1.18	
	Propithecus diadema	1.27	
	Propithecus tattersalli	1.21	
	Indri indri	0.88	
	Avahi laniger	0.76	
Lemuridae	*Lemur catta*	2.25	
	Eulemur fulvus	2.00	
	Varecia variegata	1.78	
Archaeolemuridae	*Archaeolemur majori*	1.44	
	Archaeolemur edwardsi	1.43	
	Hadropithecus stenognathus	0.82	
Palaeopropithecidae	*Palaeopropithecus maximus*	1.21	
	Palaeopropithecus sp. nov.	1.26	
	Palaeopropithecus ingens	1.11	
	Babakotia radofilai	1.35	
	Mesopropithecus globiceps	1.49	
	Mesopropithecus pithecoides	1.48	
	Mesopropithecus dolichobrachion	1.59	
Megaladapidae	*Megaladapis edwardsi*	2.00	

[a] Data from Godfrey et al. (2002:136) revised to include additional species. Data for sexes displaying insignificant differences in mean canine height ($p > 0.05$) were pooled. Due to the dearth of skulls of *Megaladapis* with associated canines, the index value for this genus was estimated on the basis of unassociated teeth.

and resting between feeding bouts would serve further to reduce the energy budgets of giant lemurs (not unlike *Indri indri* in the wild; Powzyk, 1997; WLJ, personal observations). If all or most of them were diurnal (Jungers et al., 2002), they may well have followed the example of many of their living relatives in Madagascar, and indulged in sun-basking to rev up their relatively sluggish metabolisms.

Reconstructed positional behaviors of the giant lemurs are largely consistent with slow movement and an inference of overall energy conservation. All of the extinct species have relatively very short and robust limbs when adjusted for their estimated body masses (Jungers et al., 2002; see Figure 1). It follows biomechanically that

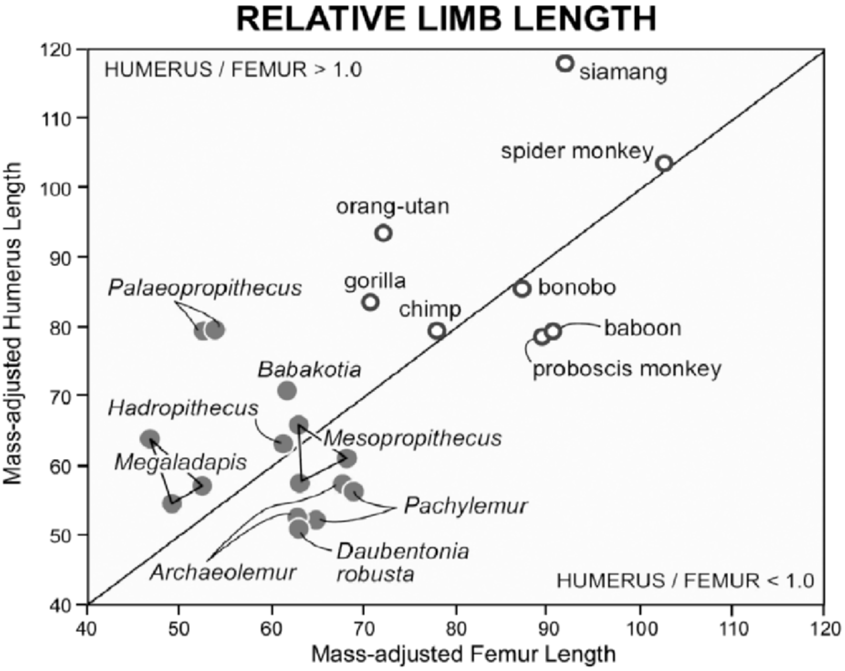

Figure 1. When limb lengths (humerus and femur) are adjusted for body size (i.e., length divided by the cube root of body mass), it is apparent that large-bodied subfossils have a fundamentally different Bauplan than large-bodied anthropoid primates. The subfossils possess relatively very short (and very robust) limbs regardless of locomotor adaptations. Even the most suspensory species (e.g., *Palaeopropithecus*) have relatively much shorter limbs than antipronograde anthropoids. The most terrestrial of the subfossils, the archaeolemurids, are also clearly distinct from baboons in this regard.

none of the subfossils is designed for speed of locomotion, including those belonging to the most terrestrial clade, the archaeolemurids (Jungers et al., 2005a). To be fair, however, dramatic adaptations to speed (cursoriality) are quite rare among mammals, and most animals optimize their anatomy instead for reducing locomotor costs (Christiansen, 2002). The palaeopropithecids (sloth lemurs) evolved extreme suspensory adaptations that converged on true sloths of South America, a mammalian group not well known for either speed of movement or energetic profligacy! Huge grasping feet (and hands) on relatively short limbs of the large-bodied (but primarily arboreal) *Megaladapis* imply slow climbing in the trees and awkward and deliberate movements when these large folivores ventured to the ground to travel (Wunderlich et al., 1996). Very large body size (similar to male gorillas) and the (admittedly few known) skeletal remains of *Archaeoindris* are also consistent with a slow-moving form of locomotion, whether it occurred in the trees or on the ground.

Recent work on the comparative sizes of the semicircular canals in giant lemurs largely corroborates these reconstructions (Walker et al., 2004). Relatively large canals are found in quick-moving, "jerky" taxa like leapers, whereas cautious, slow-moving lorisines tend to have relatively small canals (see Spoor, 1993). *Megaladapis* and the sloth lemurs also possessed relatively small canals, and this implies slothful locomotor repertoires. The size of the canals of *Archaeolemur*, however, is well predicted by the scaling relationship seen in other primates, and this could translate into a more active lifestyle and faster locomotion than seen among the more arboreal extinct taxa.

Perhaps giant lemurs economized their energetic needs by living in small groups with spatially limited resources, thereby reducing travel costs. If sociality is indeed correlated positively with encephalization (Dunbar, 1992, 1995), the relatively small brains of giant lemurs (Jungers, 1999) might suggest they lived in rather small groups, especially the largest taxa. This inference is complicated by the observation that their brain-size/body-size scaling is remarkably similar to that documented for social carnivores (Gittleman, 1986). Regardless, giant lemurs faced the extreme seasonality of resources experienced by all Malagasy primates (Wright, 1999), and it seems reasonable to conclude that they were also were forced to evolve energy-conserving lifestyles and anatomies.

Did extinct lemurs exploit fibrous food sources?

Evidence for folivory in many of the extinct lemurs also supports the inference of energy-conserving lifestyles. In general, herbivores consuming low-calorie, fiber-rich foods have lower basal and field metabolic rates than those consuming higher "quality" foods, and certainly than carnivorous or omnivorous species (Anderson and Jetz, 2005; Calder and Dawson, 1978; Cruz-Neto and Bozinovic, 2004; McNab, 1974, 1983, 1986). This applies to large as well as small-bodied animals (e.g., Christiansen, 2004). Among extant lemurs, folivorous species have very low total energy budgets (Nash, 1998; Warren and Crompton, 1997, 1998). It is likely that the same applied to the large-bodied, folivorous subfossil lemurs.

Trophic adaptations are registered in the teeth as well as aspects of cranial architecture of extinct species. The second molar shearing quotients and ratios, calculated on the basis of shearing crest and molar lengths for *Megaladapis* spp., *Palaeopropithecus* spp., and *Babakotia radofilai*, are all extremely high, suggesting strong folivory (Jungers et al., 2002; see also Kay, 1984). The sharp edges formed as the molars wear bear further testimony to folivory (Figure 2). Microwear data also support folivory in many species—particularly the largest of the subfossil lemurs, *Archaeoindris fontoynontii* and all members of the genus *Megaladapis* (Godfrey et al., 2004a; Rafferty et al., 2002).

The most speciose family to have succumbed to extinction was the Palaeopropithecidae (sloth lemurs: *Palaeopropithecus* spp., *Archaeoindris*, *Babakotia*, and *Mesopropithecus* spp.)—the sister clade to the extant Indriidae.

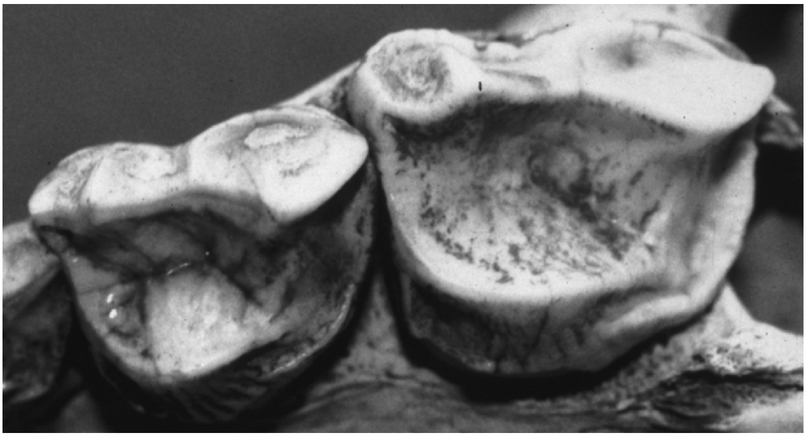

Figure 2. Maxillary first and second molars of a young *Megaladapis edwardsi*. This individual has unreplaced deciduous premolars and its third molar is in its crypt. The M^2 is not quite in occlusion. Note the long shearing crests, which form sharp edges as they begin to wear (e.g., M^1).

About 40% of all known extinct lemur species are sloth lemurs. Not merely do their teeth bear long shearing crests but their microwear signatures are very like those of indriids (Godfrey et al., 2004a). *Palaeopropithecus* is known to have shared with indriids a highly unusual dental developmental trajectory signalling early acquisition of ecological adulthood (Schwartz et al., 2002; see below). Indeed, the entire suite of digestive specializations that distinguish indriids from lemurids and other extant lemurs may have been present in the common ancestor of the Indriidae and Palaeopropithecidae. Like all lemurids (except the highly derived bamboo lemurs), indriids consume varying amounts of fruit and foliage, but they differ from the former in their lower dependence on ripe fruit, higher dependence on seeds, and adaptations for processing and digesting fiber-rich foods (Campbell et al., 2000, 2004; Hemingway, 1996; Meyers and Wright, 1993; Overdorff and Strait, 1998; Yamashita, 2003). In effect, the indriids are (and most probably, the palaeopropithecids were) physiological folivores, adapted to maximize the potential utilization of resources rich in structural carbohydrates.

Not all of the extinct lemurs were folivorous. There is compelling evidence (in the form of macrowear signalling heavy chemical erosion, presumably due to the consumption of highly acidic foods, as well as microwear) that *Pachylemur*, the sole extinct member of the family Lemuridae, preferred fruit (Godfrey et al., 2004a; Vasey et al., 2005). The Archaeolemuridae appear to have had extremely coarse and probably diverse diets most similar to those of tufted capuchins, pitheciins, and aye-ayes (Godfrey et al., 2004a, 2005a). Indeed, not merely is the microwear signature of *Archaeolemur* remarkably like that of *Cebus apella* (omnivore, seed predator, hard-object processor; Anapol and Lee, 1994; Peres, 1994;

Phillips et al., 2004; Port-Carvahlo et al., 2004; Sampaio and Ferrari, 2005; Simmen and Sabatier, 1996), but fecal pellets found associated with a young individual in a cave in northwest Madagascar demonstrate that *Archaeolemur* consumed small vertebrates and gastropods as well as plants (Burney et al., 1997). The occlusal relief characteristics of the molars of *Archaeolemur* are also more similar to *C. apella* than to papionins (King et al., 2005). Cranial architecture and molar microstructure (heavy enamel prism decussation, extraordinarily thick enamel; Godfrey et al., 2005a) also support hard-object processing in *Archaeolemur. Hadropithecus* may have included some C4 grasses in its diet (see the discussion above of its stable isotope signature) but its coarse microwear and cranial architecture suggest some hard-object processing (Godfrey et al., 2004a, 2005a). A diverse, omnivorous diet somewhat similar to that inferred here for *Archaeolemur* as well as to that attributed to *Paranthropus robustus* or *Australopithecus africanus* (Peters and Vogel, 2005) is also consistent with its stable isotope signature. There are no known molars of the giant aye-aye (*Daubentonia robusta*), but postcranial adaptations (an elongate, filiform third digit of the hand) confirm a pattern of exploitation of structurally-defended resources very like that of its much smaller congener, *D. madagascariensis* (Simons, 1994). Fruits, seeds, and animal matter were likely staples for the Archaeolemuridae as well as the giant extinct aye-aye.

In summary, leaves were likely staples or important fallback foods in the diets of most subfossil lemurs (certainly the sloth and koala lemurs), but alternative special diets (e.g., exploitation of hard or structurally-defended resources) characterized other clades (the Archaeolemuridae and Daubentoniidae). *Pachylemur* was highly frugivorous.

Did extinct lemurs wean their offspring earlier than like-sized, diurnal anthropoids?

Teeth contain an internal chronometer of their own growth in the form of short-term (i.e., daily) and long-term incremental lines. By making thin sections through the crowns and roots and by counting daily incremental lines throughout all of crown and root formation, one can determine prenatal and postnatal crown formation time as well as root extension rates. These can be used to study the pace of dental development within the context of other aspects of cranial and skeletal growth and development. Using this technique, we have been able to infer not merely overall molar crown formation time but dental precocity at birth, age at molar crown completion, and likely age at M1 gingival eruption for three extinct lemurs: *Megaladapis edwardsi*, *Palaeopropithecus ingens*, and *Archaeolemur majori* (Godfrey et al., 2005a, in press b; Schwartz et al., 2002, 2005). Table 4 documents these data alongside data for like-sized anthropoids and much smaller-bodied extant lemurs. *Megaladapis* and *Palaeopropithecus* have short crown formation times, early initiation of molar crowns (well before birth),

Table 4. Reconstructing extinct lemur life-history parameters[a]

A. Crown Formation Time (CFT) and inferred M1 eruption in extinct lemurs

Taxon	M1 CFT	Prenatal CFT	Age at M1 crown completion	Likely age at M1 gingival emergence
Palaeopropithecus ingens	221 days	187 days	34 days (1.1 mo)	~ 0.2–0.5 year
Megaladapis edwardsi	380 days	132 days	248 days (8.3 mo)	~0.75–1.1 year
Archaeolemur majori	522 days	85 days	437 days (14.6 mo)	~1.25–1.6 year

B. Crown Formation Time (CFT) and observed M1 eruption in extant lemurs and other primates

Taxon	M1 CFT	Prenatal CFT	Age at M1 crown completion	Age at M1 gingival emergence
Propithecus verreauxi	191 days	94 days	97 days	~0.25–0.33 year
Lemur catta	195 days	67 days	128 days	~0.4–0.5 year
Varecia variegata	220 days	55 days	165 days	~0.5–0.6 year
Pongo pygmaeus	993 days	24 days	969 days	~4.6 years
Gorilla gorilla	1237 days	25 days	1212 days	~3.5 years
Papio hamadyras	529 days	36 days	493 days	~1.7 years

[a] Data on extinct and extant lemurs are taken from Schwartz et al. (2002, 2005, in press) and Godfrey et al. (2005a, in press b). Data on *Pongo* are taken from Kelley and Schwartz (2005), on *Gorilla* from Willoughby (1978) and D. Reid (unpublished), and on *Papio* from Dirks (2003), Dirks et al. (2002), and Smith et al. (1994). We assume that weaning occurred in giant lemurs at around the age of M1 gingival emergence. Some living lemurs wean their offspring before the first molar erupts, while others wean them shortly thereafter.

and rapid root extension rates (and thus short root formation times). Likely behavioral correlates of this accelerated pace of dental development and eruption include early processing of fibrous foods. In contrast, crown formation begins and finishes later (relative to birth) in the smaller-bodied *Archaeolemur*.

Our projected ages at weaning are much earlier in *Palaeopropithecus* and *Megaladapis* than in like-sized anthropoids (*Pongo* and *Gorilla*), and slightly earlier in *Archaeolemur* than in baboons (*Papio*). In light of our data on dental development, we believe that weaning occurred at a very young age (probably before 6 months) in *Palaeopropithecus*, at around 1 year in *Megaladapis*, and later yet in *Archaeolemur*. By studying microwear across an ontogenetic series, Flanagan (2004) found evidence of a juvenile foraging phase—i.e., prolonged acquisition of foraging skills—in *Archaeolemur*, similar to that exhibited by *Macaca fascicularis* (a full adult foraging microwear signal is not manifested until after the emergence of the second molar; Godfrey et al., 2005a). Preliminary data suggest very prolonged molar crown formation time and late weaning in *Hadropithecus*; unfortunately, our data here are limited to the second molar (Godfrey et al., 2005a, in press a). Preliminary microwear data across ontogenetic series also suggest early acquisition of full-adult foraging skills in *Palaeopropithecus* and *Megaladapis* (Godfrey et al., in press b).

Did extinct lemurs exhibit low visual acuity?

On the basis of the relatively small size of their orbits, giant extinct lemurs have been reconstructed as having diurnal activity cycles (Gingerich and Martin, 1981; Jungers et al., 2002; Martin, 1990; Walker, 1967). No orbits are preserved for the giant aye-aye, *Daubentonia robusta*, but one might infer nocturnality based on its detailed similarity to the nocturnal living aye-aye (Godfrey et al., 1997b). Because there are no large-bodied, nocturnal anthropoids to which we can make direct comparisons, the accuracy of such inferences remains unknown. The largest extinct lemur, *Archaeoindris fontoynontii*, has an orbit area within the range of gorillas, whereas most other subfossil lemurs have orbits considerably smaller than size-matched diurnal anthropoids (Table 5). *Archaeolemur*, *Pachylemur*, *Babakotia*, *Mesopropithecus,* and *Palaeopropithecus* have orbits roughly the absolute size of much smaller, diurnal living lemurs. If we accept the conventional wisdom that virtually all the extinct lemurs were indeed diurnal, that does not imply that their visual acuity was also comparable to living, size-matched anthropoids (Kirk et al., 2002). It also seems highly unlikely that, as a group, they possessed trichromatic color vision.

Kay and Kirk (2000) offer osteological metrics that are correlated with the degree of retinal summation and inferred visual acuity. These indices are based on the relative size of the optic foramen or optic canal. If orbit size is used as a surrogate for eyeball size, and since eyeball size is proportional to retinal area, one can construct a ratio of optic foramen area to orbit area as an "index of summation," the Optic Foramen Index (OFI); lower indices imply higher retinal summation. Nocturnal primates tend to sacrifice visual acuity in order to maximize sensitivity, and they are characterized by low indices. When compared to diurnal anthropoids, strepsirhines as a clade have low indices and reduced acuity regardless of their activity cycle. The nearly ubiquitous strepsirhine tapetum (only *Eulemur macaco macaco* is reported to have lost it; Pariente, 1979), a light-reflecting membrane within the eye, is consistent with this reduced visual acuity. Kay and Kirk (2000) also noted a confounding allometric trend within each major clade of primates such that the OFI also decreases with increasing body/skull size. We have employed a slightly modified version of their OFI. We measure area of the optic foramen or canal directly by digitizing cross sections of molds (Coltene President Plus Jet); we use the smaller of the vertical or horizontal diameter of the orbit to calculate area as a circle. The ratio of the two areas is multiplied by 100 to create our version of the OFI (Table 5).

The aforementioned allometric trend is evident within strepsirhines when the large subfossils are compared to living lemurs. Large-bodied taxa such as *Archaeoindris* (~160 kg), *Hadropithecus* (~35 kg), and *Megaladapis* (~ 45–90 kg) have the lowest OFIs. Within clades of extinct lemurs, the pattern is striking: among sloth lemurs (family Palaeopropithecidae), *Palaeopropithecus* (~ 40–45 kg) and especially *Archaeoindris* have values lower than *Mesopropithecus* (~10–15 kg) and *Babakotia* (~20 kg). Among monkey lemurs (family Archaeolemuridae), *Hadropithecus* has values lower than *Archaeolemur* (~18–25 kg). Among koala

Table 5. Orbit size and the Optic Foramen Index—an osteological estimate of retinal summation in giant lemurs and selected living primates

	Optic Foramen Index[a]			Orbit area (mm²)	
Species	*N*	Mean	SD	Mean	SD
Subfossil lemurs					
Archaeolemur majori	13	1.23	0.14	408	30
A. edwardsi	14	1.47	0.33	417	27
Hadropithecus stenognathus	1	0.98	—	503	—
Pachylemur insignis	12	1.85	0.36	259	17
P. jullyi	5	1.76	0.51	252	30
Megaladapis madagascariensis	4	1.00	0.21	481	57
M. grandidieri	1	1.02	—	697	—
M. edwardsi	15	0.91	0.18	762	78
Palaeopropithecus maximus	6	1.29	0.42	411	76
Archaeoindris fontoynontii	1	0.61	—	946	—
Babakotia radofilai	1	1.96	—	260	—
Mesopropithecus globiceps	2	1.86	—	185	—
M. pithecoides	1	1.41	—	298	—
Living lemurs					
Diurnal					
Indri indri	5	1.23	0.23	408	35
Propithecus diadema	5	1.47	0.14	349	22
P. verreauxi	10	1.80	0.34	277	23
Varecia variegata	3	1.48	0.22	321	28
Lemur catta	3	1.91	0.24	223	9
Cathemeral					
Eulemur fulvus rufus	3	1.52	0.08	256	6
Nocturnal					
Daubentonia madagascariensis	3	1.06	0.13	291	8
Avahi laniger	10	1.10	0.22	213	19
Lepilemur species	7	1.52	0.31	173	15
Living anthropoids					
Hominoids					
Gorilla gorilla	8	1.35	0.32	1131	179
Pan troglodytes	9	1.91	0.35	834	96
Pan paniscus	10	2.09	0.51	758	179
Pongo pygmaeus	4	1.97	0.39	903	83
Cercopithecoids					
Theropithecus gelada	4	3.58	0.23	330	37
Cercocebus torquatus	6	2.96	0.52	423	30
Miopithecus talapoin	3	3.77	0.14	225	6

[a] 100 x (optic foramen area/orbital area); SD, standard deviation.

lemurs (family Megaladapidae), *Megaladapis* (*Peloriadapis*) *edwardsi* (~ 90 kg) displays values lower than *Megaladapis* (*Megaladapis*) *grandidieri* (~75 kg) and *M. madagascariensis* (~ 45 kg). The largest-bodied species actually resemble living nocturnal lemurs in estimated degree of summation more so than their diurnal or cathemeral counterparts.

Overall, however, and despite their much larger body sizes, most extinct lemurs have indices well within the observed ranges of extant diurnal lemurs. In size-matched comparisons, *all* subfossil lemurs have OFIs lower than diurnal anthropoids (e.g., compare *Archaeoindris* to gorilla or *Megaladapis* to orangutans), and it seems reasonable to conclude that their visual acuity was also correspondingly lower, even if they were predominantly diurnal in their activity cycles. In other words, despite their large, "anthropoidlike" body sizes, the giant lemurs appear to be typical strepsirrhines in terms of their lower visual acuity. This conclusion needs to be qualified somewhat by the well-known observation that absolutely larger eyes, such as those of giant lemurs, may improve acuity to some unknown degree. This follows because photoreceptor cell size is more or less constant across animals of all body sizes (Land and Nilsson, 2002); a larger eye can therefore pack in an absolutely greater number of photoreceptors.

Was extinction selective, and if so, how so?

Our knowledge of the environments in which the extinct species lived and of the chronology of extinction events derives largely from sediment cores but also directly from the fossils and associated evidence of human occupation. Burney et al. (2004) provide a review of the chronology of late prehistoric Madagascar, and of hypotheses regarding the extinction process (see also Burney, 1999). A few observations are worth repeating here. First, most if not all of the extinct lemurs (as well as giant ratites, pygmy hippos, and giant tortoises) were living on Madagascar when humans first colonized the island over 2000 years ago. Second, there was a major insult to these taxa shortly after humans arrived, as evidenced by a precipitous decline (in sediment cores) in the spores of the coprophilous fungus, *Sporormiella* (Burney et al., 2003). This fungus is an excellent proxy for megafaunal biomass because it cannot complete its life cycle in the absence of dung of large animals. That decline, possibly due to megafaunal hunting by humans, did not lead to their immediate extinction, as many survived into the last millennium, and some were still alive only a few hundred years ago if not later (Burney et al., 2004). A peak in charcoal microparticles (signalling an increase in the number and intensity of fires) occurs *after* the initial megafaunal decline. Ultimately, many factors (including natural aridification, hunting, fires, and habitat disturbance) contributed to megafaunal extinction. There is direct evidence in the form of butchery marks that giant lemurs were hunted and eaten by humans in Madagascar (Perez et al., 2005), but we do not know the relative contribution of hunting (as opposed to habitat disturbance, etc.) to their disappearance.

Most relevant for our purposes is the selectivity of the extinction process. The extinctions were not limited to particular regions or habitat types, although some regions, such as the central highlands, lost more primate species (possibly because they lost more wooded habitat) than others. There are still some lemurs living in central Madagascar, but they persist only in isolated forest patches. Still-extant taxa were far more widespread in the past than they are today, and they coexisted with now-extinct taxa in regions that are today entirely devoid of lemurs (Godfrey et al., 1999). There is no reason to believe Madagascar's extinction "event" is over. The very factors that apparently killed the giant lemurs continue to threaten their smaller-bodied relatives.

Clearly and without exception, large body size increased the risk of extermination. There are a number of reasons why large-bodied taxa may be most vulnerable to extinction. Certainly, they are easy targets of human hunting. Second, larger-bodied species often require more suitable habitat area to maintain minimum viable populations, and are therefore more vulnerable to habitat loss and fragmentation. Finally, large-bodied indriids are surprisingly slow reproducers (despite their rapid dental development; see Godfrey et al., 2004b; Richard et al., 2002) and we suspect that the same was true of many of the subfossil species.

DISCUSSION AND CONCLUSIONS

This chapter summarizes some of our inferences to date regarding the behavior and ecology of extinct lemurs. We now ask how those inferences affect our perception of the ecospace occupied by past and present lemur communities? Do they offer support for either of the competing explanations of unusual living-lemur traits?

First, we know that the hard-object processing guild was larger in the past than it is today. The only remaining member of this guild is *Daubentonia madagascariensis*, whereas in the past it was occupied by several widespread archaeolemurid species as well as at least two species of *Daubentonia*. Looking particularly at *Archaeolemur* spp., we see postcranial adaptations reminiscent of cercopithecines, signalling greater commitment to ground locomotion than in other lemurs. We now know that these species also displayed: (1) molars with thick enamel and unusually heavy enamel prism decussation; (2) relatively high encephalization; (3) relatively slow dental development, with delayed weaning and a protracted period for acquisition of adult foraging skills; (4) a diverse diet, probably including difficult-to-extract food resources; and (5) a relatively high total energy budget (inferred from enlarged semicircular canals). Interestingly, *Daubentonia madagascariensis* also exhibits, in addition to anatomical adaptations for omnivory and hard-object processing: (1) molars with unusually thick enamel; (2) relatively high encephalization; (3) a protracted period for acquisition of adult foraging skills, with weaning at ~ 2 years; (4) the ability to exploit a wide range of difficult-to-extract food resources; and (5) relatively high activity levels, with long nightly range lengths and large home ranges (Erikson, 1995; Feistner and Ashbourne, 1994; Krakauer and van Schaik, 2005; Sterling, 1993, 1994). Note that we are *not* suggesting a close relationship of the Archaeolemuridae to the Daubentoniidae, but rather strong anatomical and developmental convergence with ecological underpinnings. We might speculate that *Archaeolemur*, like *Daubentonia* and *Hapalemur* (Mutschler, 2002; Sterling, 1993; Tan, 1999), targeted resources that are available year round (to species able to extract and process them), and therefore exhibited little or no reproductive synchrony. *Archaeolemur* may have done in the daytime what *Daubentonia* does at night.

Most of the subfossil lemurs were decidedly unlike *Archaeolemur*, however. The koala lemurs (three species, family Megaladapidae) were large-bodied, slow-climbing, small-brained folivores with rapidly developing dentitions, and, most probably, early weaning. The sloth lemurs (family Palaeopropithecidae) were very slow-moving climbers and hangers with extreme dental developmental precocity; they were also likely folivore/frugivores with adaptations to exploit seeds and other tough, fibrous foods. Among subfossil lemurs, only *Pachylemur* (a lemurid) appears to have been committed to frugivory (perhaps like *Varecia*, its close relative), but it too was a small-brained, slow climber (Jungers et al., 2002; Shapiro et al., 2005). In effect, most of the giant lemurs appear to have been energy conservers, quite like most extant lemurs.

It is important not to exaggerate the terrestrial monkey-likenesses of *Archaeolemur*. Although *Archaeolemur* was certainly more like large, semiterrestrial cercopithecoids than other lemurs, many features distinguish these groups. For example, there is no evidence that *Archaeolemur*, with its broad pelvis, short and wide scapula, short, robust limbs, and exceptionally short digital rays, was cursorial. Its microwear is far closer to that of *C. apella* and other hard-object processors than to that of terrestrial cercopithecoids. While its brain was large in comparison to those of other lemurs, it was much smaller than those of like-sized baboons. And while dental development was certainly slow in *Archaeolemur* in comparison to other lemurs, it was not nearly as slow as that of baboons. Unlike the latter, also, *Archaeolemur* was apparently monomorphic, with only moderately tall canines.

In conclusion, we maintain that the ecological profiles of primate communities in Madagascar were different in the past than in the present, mainly in the prevalence of large-bodied, diurnal forms, but also in the relatively higher representation of omnivorous, hard-object processors. Nevertheless, Wright's (1999) energy frugality hypothesis appears to account for features exhibited by most extinct as well as extant lemurs in Madagascar far better than does the evolutionary disequilibrium hypothesis. We draw this inference largely on the basis of what we believe is increasingly strong evidence (especially postcranial but also dietary and developmental) of energy-conserving lifestyles. Extinct lemurs resembled extant lemurs in displaying relatively low encephalization, little (or no) sexual dimorphism, high folivory, accelerated dental development (with early initiation of molar crown formation, early age at crown completion, and early weaning), and low visual acuity (even if none were nocturnal or cathemeral). Early weaning and rapid dental development probably signals relatively low postnatal maternal investment and social dynamics very unlike those of like-sized anthropoids. It is tempting also to infer that most lived in small groups with limited home ranges, and that female dominance was prevalent among them. One might imagine, for example, that the combination of long canines and little or no sexual dimorphism in *Megaladapis* signalled small groups occupying small territories defended by both sexes. Perhaps the strongest argument in favor of small groups, limited ranges, and widespread female dominance among extinct lemurs is that they, like many of their extant counterparts, were not merely small-brained and sexually monomorphic, but also probably hypometabolic. We caution that skeletal correlates of group size, range size, and female dominance are tenuous, and such inferences must be regarded as speculative. We can assert with confidence, however, on the basis of our reconstructions of the locomotor, trophic, and, especially, developmental characteristics of these remarkable species, that the giant lemurs had lifestyles very different from those of like-sized, diurnal anthropoids. Lemurs—both extant and extinct—are indeed unique among members of the order Primates.

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SECTION TWO

The Evolution of Lemur Traits, Basic and Unusual Patterns

CHAPTER FOUR

Impact of Ecology on the Teeth of Extant Lemurs:

A Review of Dental Adaptations, Function, and Life History

Frank P. Cuozzo and Nayuta Yamashita

INTRODUCTION

Lemur dental morphology has been characterized by a number of workers (e.g., Godfrey et al., 2004a; Kay et al., 1978; Milton, 1978; Sauther et al., 2001; Schwartz and Tattersall, 1985; Seligsohn, 1977; e.g., Seligsohn and Szalay, 1974, 1978; Strait, 1993; Tattersall, 1982; Yamashita, 1998a,b) who have investigated these teeth from descriptive, functional, developmental, and ecological perspectives. In this chapter, we discuss how the external environment leaves an imprint on lemur dentitions, either through adaptations to the physical requirements of specific environments or through environmental effects during the lifetime of the animal. We also discuss the patterns of intraspecific dental variation in selected lemurs, and comment on the role of this variability in lemur taxonomy.

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In addition, we briefly review the relationship between dental microstructure, growth and development, and ecology.

The chapter begins with an introductory section describing the major issues that concern us from functional and ecological perspectives, including a brief review of dental development and microstructure. We then discuss anterior and posterior teeth in separate sections, each describing basic morphology, functional morphology, and indicators of dental health. Throughout this chapter, we refer to examples from the lemur community at the Beza Mahafaly Special Reserve, southern Madagascar (see Sussman and Rakotozafy, 1994, for a description of the reserve at Beza Mahafaly), a location at which each of us has conducted long-term research.

Diet and Tooth Morphology

Primates, like most mammals, possess heterodont dentitions, with virtually all taxa having incisors, canines, premolars, and molars (see reviews in Martin, 1990; Swindler, 2002; Tattersall, 1982). Living lemurs also share the derived toothcomb with other members of the Strepsirhini (the aye-aye [*Daubentonia madagascariensis*] is the one exception [e.g., Martin, 1990; Swindler, 2002; Tattersall, 1982]). Despite sharing a common heritage likely resulting from a single ancestral colonization of Madagascar (e.g., Karanth et al., 2005; Yoder, 1994), the Malagasy lemurs display considerable variation in dental morphology across their radiation. In addition to expected differences in gross morphology and topography of the teeth, there are differences in tooth formulae. As seen in Table 1, the maximum primate dental formula of $I^2_2\ C^1_1\ P^3_3\ M^3_3$, a derivation of the ancestral placental mammal condition, is present in most lemurs, with secondary reductions in the indriids, *Lepilemur*, and *Daubentonia* (Martin, 1990).

In any discussion of functional relationships between diet and tooth form, the physical properties of foods play an important role. The primary function of teeth is to reduce food particle size for further digestion in the gut. This physical interaction occurs between foods of varying compositions and teeth that have designs suitable for efficiently breaking down those foods. Relationships between tooth morphology and the physical parameters of foods in primates have been well documented (Happel, 1988; Hiiemae and Crompton, 1985; e.g., Hylander, 1975; Kay, 1975, 1977, 1978; Kinzey and Norconk, 1990; Lucas, 1979, 2004; Maier, 1984; Rosenberger and Kinzey, 1976; Seligsohn, 1977; Strait, 1993; Wright, 2003; Yamashita, 1998b).

How a food fragments depends on its composition. Physical properties of foods include external properties, such as size and shape, and internal properties that are related to material composition (see Lucas, 2004, and Strait, 1997, for extended discussions). Fragmentation depends on the ability of the consumer to initiate and continue runaway crack formation in foods with particular mechanical properties. Tough foods are able to deform considerably before failing and

Table 1. Dental formulae for extant lemurs

Taxon	Dental formula[a]	Total number of teeth
Lemuridae		
Eulemur	$I^2\ C^1\ P^3\ M^3/I_2\ C_1\ P_3\ M_3$	36
Lemur	$I^2\ C^1\ P^3\ M^3/I_2\ C_1\ P_3\ M_3$	36
Hapalemur	$I^2\ C^1\ P^3\ M^3/I_2\ C_1\ P_3\ M_3$	36
Varecia	$I^2\ C^1\ P^3\ M^3/I_2\ C_1\ P_3\ M_3$	36
Cheirogaleidae		
Cheirogaleus	$I^2\ C^1\ P^3\ M^3/I_2\ C_1\ P_3\ M_3$	36
Microcebus	$I^2\ C^1\ P^3\ M^3/I_2\ C_1\ P_3\ M_3$	36
Phaner	$I^2\ C^1\ P^3\ M^3/I_2\ C_1\ P_3\ M_3$	36
Lepilemuridae		
Lepilemur	$I^0\ C^1\ P^3\ M^3/I_2\ C_1\ P_3\ M_3$	32
Indriidae		
Propithecus	$I^2\ C^1\ P^2\ M^3/I_2\ C_0\ P_2\ M_3$	30
Indri	$I^2\ C^1\ P^2\ M^3/I_2\ C_0\ P_2\ M_3$	30
Avahi	$I^2\ C^1\ P^2\ M^3/I_2\ C_0\ P_2\ M_3$	30
Daubentonidae		
Daubentonia	$I^1\ C^0\ P^1\ M^3/I_1\ C_0\ P_0\ M_3$	18

[a] Data compiled from Martin (1990), Swindler (2002), Tattersall (1982).

are good at arresting cracks once they start. Brittle foods are the opposite; they propagate cracks readily once they are initiated. Elastic modulus is a measure of stiffness or resistance to bending. Hardness is resistance to indentation. The relationship between toughness (R) and elastic modulus (E) describes how plants mount mechanical defenses against herbivory (Agrawal et al., 1998; Lucas, 2004; Lucas et al., 2000). Stress-limited foods ($\sqrt{ER}$) are brittle and shatter when sufficient stress levels are reached. A plant that invests in this type of defense relies on herbivores being unable to generate the required force to fragment it. Displacement-limited defenses ($\sqrt{R/E}$) depend on predators being unable to strain the plant part to failure (Agrawal et al., 1998). Thin materials, such as leaves, tend to rely solely on toughness as a defense.

In order for herbivores to overcome physical plant defenses, it would be advantageous for them to possess morphologies that are suitable for fragmenting plant parts with distinct mechanical properties. Tough foods should require bladed features to initiate and guide crack formation since they do not easily propagate cracks. The carnassial teeth of carnivores represent a bladed system for fracturing soft, tough foods. Flat, tough foods such as leaves also require crests, though in a configuration that resembles a "milling machine" (Hiiemae and Crompton, 1985). Hard/brittle foods are best fractured with blunt cusps that can tolerate the high stresses involved in overcoming stress-limited defenses. In addition, fine reduction of hard foods would be made easier with a loose occlusal fit between a cusp and basin to locate weak areas in the food (Lucas, 1979). In this chapter, we examine this relationship between tooth form and diet in the varied dentition of lemurs.

Dental Development and Microstructure

In addition to variation in tooth form and function, lemurs display a wide variety of dental developmental patterns. In fact, lemur dental development often does not "play by the rules" with the quickest pace of tooth formation and eruption sometimes occurring among the largest forms, a pattern which contrasts with the general pattern seen in anthropoid primates (e.g., Godfrey et al., 2005, this volume; Schwartz and Godfrey, 2003; Schwartz et al., 2002). Of note, patterns of dental development appear linked to phylogeny, with extinct, large-bodied relatives of smaller living forms (e.g., *Propithecus* and *Palaeopropithecus*) sharing similar patterns of development, despite significant differences in body size (e.g., Godfrey et al., this volume; Schwartz and Godfrey, 2003; Schwartz et al., 2002). Dental development also corresponds to diet and feeding ecology, with noticeable differences between sympatric folivorous and more frugivorous and/or omnivorous lemurs, for example *Propithecus v. verreauxi* and *Lemur catta*, in terms of the pace of dental eruption (e.g., Eaglen, 1985; Godfrey et al., 2001, 2004a). In fact, specialized folivores such as *Propithecus* display early and rapid dental eruption, often possessing a number of erupted deciduous teeth at birth (Eaglen, 1985; Godfrey et al., 2001, 2004a; Schwartz et al., 2002, 2005).

As with morphology and dental development, dental microstructure reflects the feeding ecology of extant (and fossil) lemurs. When compared to anthropoids, lemurs (and extant prosimians in general) possess relatively thin dental enamel (e.g., Godfrey et al., 2005; Martin et al., 2003; Shellis et al., 1998). Because enamel thickness generally corresponds to diet among primates (although not a perfect relationship [e.g., Maas and Dumont, 1999; Martin et al., 2003]), Shellis et al. (1998) argued that, given their thicker enamel, the diet of anthropoids likely consists of a higher proportion of tough foods than does that of prosimians. As seen in Table 2, only highly derived forms such as extant *Daubentonia* and the large, subfossil *Archaeolemur*, both of which are quite specialized in their dietary adaptations, possess thick enamel, comparable to well-known hard-object feeders, for example the extant New World capuchins (*Cebus*) (e.g., Godfrey et al., 2005) and the fossil hominid *Paranthropus* (e.g., Teaford and Ungar, 2000). Maas (1994) suggested that thin enamel is the primitive condition for lemurs. The rarity of thick-enameled lemurs supports this suggestion.

In addition to enamel thickness, the structure and organization of enamel also reflects dietary adaptations. Along with their thin enamel, extant lemurids exhibit significant enamel decussation (i.e., differentially oriented enamel prisms [Janis and Fortelius, 1988]), with up to 90% of the enamel in *Varecia*, *L. catta*, and *Eulemur macacao* consisting of these prisms (Maas, 1994). Enamel decussation is thought to provide resistance to crack propagation, and often correlates with diets dominated by hard foods (Godfrey et al., 2005; Maas and Dumont, 1999; Martin et al., 2003). Despite the dietary variability exhibited by extant lemurids, the presence of noticeable decussation in this group suggests an adaptation to hard foods

Table 2. Relative enamel thickness (R.E.T.) of extant lemurs compared with other primates

Taxon[a]	Mean R.E.T.[b,c]
Varecia variegata†	5.7
Lemur catta†	7.3
Gorilla gorilla	10.0
Pan troglodytes	10.1
Propithecus verreauxi†	10.7
Hylobates lar	11.0
Paleopropithecus ingens† (extinct)	11.3
Propithecus diadema†	13.0
Hadropithecus stenognathus† (extinct)	14.4
Papio cynocephalus	15.4
Theropithecus gelada	15.6
Pongo pygmaeus	15.9
Cebus apella	19.2
Daubentonia madagascariensis†	21.7
Homo sapiens	22.4
Archaeolemur majori† (extinct)	28.3

[a] † = Malagasy lemurs.
[b] Data from Godfrey et al. (2005).
[c] See Godfrey et al. (2005) for a review of calculating R.E.T.

(at least some time in the past), as seen in its extreme condition in extinct archaeolemurids (e.g., Godfrey et al., 2005, this volume).

Dental Health, Feeding Ecology, and Behavior

Mammalian teeth, in addition to providing a record of both growth and development and evolutionary relationships (e.g., Schwartz and Dean, 2000), also reflect an individual's life experience or life story (e.g., Morbeck, 1997). Even among humans, diet and behavior leave a record of life on the teeth (e.g., Molnar, 1971). Despite the hardness of dental enamel (e.g., Maas and Dumont, 1999) and its assumed resistance to damage and crack propagation, tooth wear is common across the mammalian radiation (e.g., Hillson, 1986, 2005). Tooth damage, including severe wear, breakage, and pathology, is also common throughout the primate order (e.g., Schultz, 1935). However, to date data on patterns of dental health in lemurs are limited when compared to anthropoid primates, especially hominoids (e.g., Kilgore, 1989; Lovell, 1990). Patterns of dental damage often correlate with behavior in anthropoids, for example the high frequency of tooth loss resulting from breakage among male howler monkeys, which is often a result of intermale aggression (Smith et al., 1977). A similar pattern likely exists in

African apes (Lovell, 1990). Among ring-tailed lemurs, tooth damage most often occurs in the anterior teeth, which likely results from their use in both grooming and feeding, as well as aggression, especially among males (e.g., Cuozzo and Sauther, 2006; Sauther et al., 2002).

ANTERIOR TEETH: INCISORS AND CANINES

Lemur anterior teeth function to aid the cheek teeth in reducing food particle size, but are also involved in food procurement. In addition, the mandibular toothcomb is often used for grooming. With the exception of the mandibular toothcomb, the anterior teeth are relatively little studied.

Basic Morphology

Maxillary incisors range within and among Malagasy lemurs from entirely absent (*Lepilemur*) or reduced (lemurids, *Avahi*) to relatively prominent (cheirogaleids, indriids) (see Table 1) (Martin, 1972; Tattersall, 1982). Maxillary canine size varies considerably among lemurs, with some taxa exhibiting very large (i.e., high) canines, relative to first molar size (see Table 3 in Godfrey et al., this volume). *Daubentonia* has no permanent canines (Swindler, 2002; Tattersall, 1982). In *Hapalemur*, the maxillary canine is comparatively short and robust, especially so in *H. simus* (Milton, 1978). In contrast, *Lemur catta* displays large, prominent maxillary canines (Figure 1). Although Malagasy strepsirhines are generally viewed as dentally monomorphic (e.g., Kappeler, 1996), a view supported in numerous studies (e.g., Lawler et al., 2005), some taxa do exhibit significant sexual dimorphism in favor of either males or females (e.g., Kappeler, 1996). For example, a recent study of brown lemurs (*Eulemur*) (Johnson et al., 2005) indicates a contrast in maxillary canine height between *E. albocollaris* and *E. fulvus rufus*, with *E. albocollaris* displaying significant male-biased canine height dimorphism. However, the patterns of sexual dimorphism seen among lemurs are not consistent with those in anthropoid primates, as to date, hypotheses concerning intermale competition, female dominance, and mating system do not display a clear correspondence among lemurs (Kappeler, 1996). In addition to their large, projecting canines, ring-tailed lemurs exhibit a high degree of metric variability in both canine length (e.g., Cuozzo and Sauther, 2004a; Sauther et al., 2001) and height (e.g., Kappeler, 1996). Metric variability in anterior teeth (when compared to the postcanine dentition) can indicate sexual dimorphism in primates, including fossil forms (e.g., Gingerich, 1995). Given the large canines and intense intermale aggression seen in ring-tailed lemurs, significant (anthropoid-like) canine dimorphism would not be unexpected, as suggested by Kappeler's (1996) work. Preliminary data from the ring-tailed lemurs at Beza Mahafaly indicate

Figure 1. Projecting maxillary canine (white arrow) in a male *Lemur catta* (Black 240) from Beza Mahafaly (photo courtesy of Michelle Sauther).

significant male-biased canine height dimorphism (Sauther and Cuozzo, unpublished data).

The mandibular anterior teeth of lemurs are elaborated into a toothcomb, which represents a diagnostic character for all strepsirrhines. As such, there are few departures from the basic structure across Malagasy lemur families. The basic morphology involves integration of the two incisors plus the canine from each side to form a procumbent six-tooth comb (Figure 2). There is a loss of one tooth per side in the indriids, which leaves a comb comprised of an incisor and a canine (Schwartz, 1974, 1978) or two incisors (Gingerich, 1977) (Figure 3). In *Daubentonia*, the toothcomb, as well as the maxillary anterior tooth, has been further reduced to a single, continuously growing (hypselodont) tooth that has been identified as an incisor (Swindler, 2002) or a canine (Tattersall, 1982) (Figure 4). The anterior premolar among lemurs is often caniniform (Figure 2) (Swindler, 2002; Tattersall, 1982).

Origin and Function of the Toothcomb

The original function of the toothcomb has been a matter of some debate for many years (e.g., Avis, 1961; Stein, 1936). Depending on the study, the toothcomb

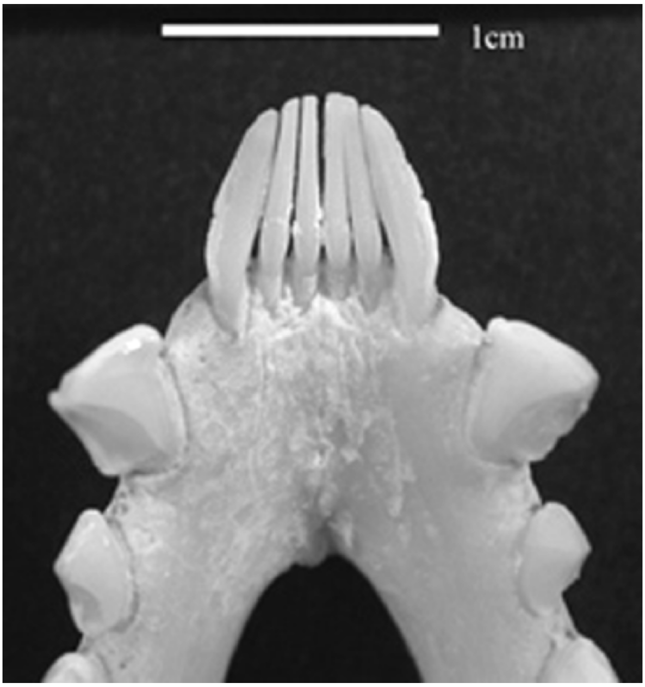

Figure 2. Six-toothed mandibular toothcomb in *Lemur catta* (USNM 395517) (photo by Frank Cuozzo).

originally functioned as a grooming tool (Rosenberger and Strasser, 1985; Szalay and Seligsohn, 1977), for food procurement (Martin, 1972), or one or both of these scenarios, though there is insufficient evidence to support either hypothesis unequivocally (Asher, 1998; Rose et al., 1981). Martin (1972) argues that the grooming function of the toothcomb is secondary to its tooth-scraping role. The addition of the canine demonstrates that the scraping role of the structure took precedence over the normal piercing role of the canine. In contrast, Szalay and Seligsohn (1977) posit that the inclusion of the canine in the six-toothed comb does not increase the cutting surface of the comb, forming instead an additional interdental space. The resulting comb was used for fur grooming. The more transversely compressed comb of the exudate-feeding *Phaner* and the robust four-toothed indriid structure (Figure 3) are interpreted as derived. Rosenberger and Strasser (1985) suggest that the toothcomb is part of an olfactory complex that follows the reduction of the upper incisors away from a feeding function, which allows a connection of the philtrum with the vomeronasal organ through the resulting interincisal diastema. The toothcomb functions to stimulate and distribute

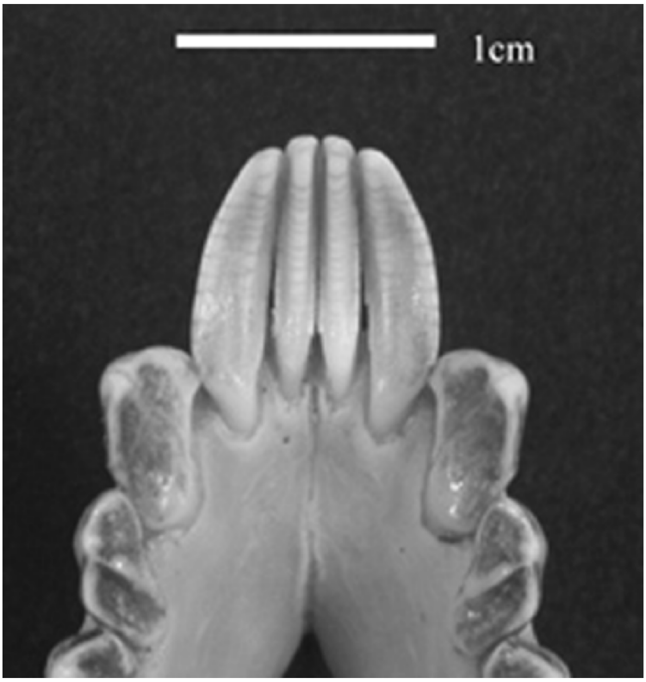

Figure 3. Four-toothed mandibular toothcomb in *Propithecus diadema* (USNM 63349) (photo by Frank Cuozzo).

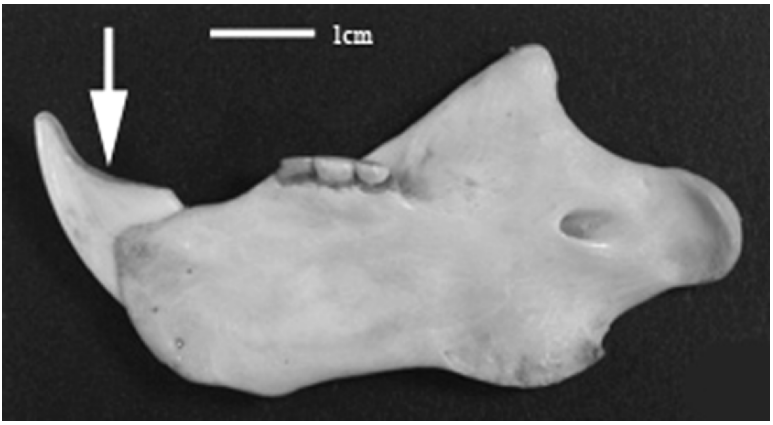

Figure 4. Lingual view of the single anterior tooth (white arrow) in *Daubentonia madagascariensis* (USNM 199694) (photo by Frank Cuozzo).

olfactory secretions throughout the body and brings secretions up to the vomeronasal organ. Whatever its original function, the incisiform canine represents an unusual addition to the toothcomb, especially since the anterior premolar subsequently became caniniform in many taxa (Martin, 1972; Swindler, 2002; Tattersall, 1982).

Among extant lemurs, the toothcomb is used as both a grooming and a feeding tool (e.g., Richard, 1978; Sauther et al., 2002). In addition to numerous field accounts of such usage, Rose et al. (1981) demonstrated via SEM that the interstitial facet of the central incisor had grooves and scratches consistent with hair grooming, and Asher (1998) found that the interincisal gap is wider in gregarious taxa, which presumably groom socially. In indriids, *Daubentonia*, and *Phaner*, the toothcomb has a more derived adult morphology, which is probably related to its use in food procurement in these taxa. Food ingestion in *L. catta* and *P. v. verreauxi* takes place both anteriorly in the mouth and on the postcanines, depending on the size of the fruit or leaf (Yamashita, 2003). Initial food placement is related to food size more than to a material property such as toughness, as seen in the processing of large tamarind fruit (*Tamarindus indica*) by *L. catta* (Cuozzo and Sauther, 2006, in press).

Functional Morphology of Anterior Teeth

Few fruits with peels occur in Madagascar forests, so the correlation between incisor morphology and fruit preparation in anthropoids observed by Hylander (1975) is not found to the same extent in lemurs. Though some folivorous lemurs have reduced upper incisors, the largest incisors are found in exudate feeders, not frugivores.

The upper incisors are reduced or absent in folivorous lemurs (with the exception of the indriids) to form a complex with the mandibular toothcomb that resembles an ungulatelike browsing pad (Avis, 1961). In *Phaner* and *Allocebus* the incisors are enlarged, presumably to work in concert with the toothcomb for exudate feeding (Martin, 1972). This condition is further elaborated in *Daubentonia*, where the upper and lower anterior teeth have been reduced to a single tooth on each side (Figure 4). Aye-ayes use these teeth to scrape off resistant fruit pulp and gouge dead wood in their search for insect larvae (Erickson, 1994; Iwano and Iwakawa, 1988; Kitko et al., 1996).

In the *Hapalemur* species, the canine is shorter and more robust than in other lemurids. This, coupled with the short P^2, is probably related to the stereotypical harvesting behavior that these species employ when feeding on bamboo shoots, in which a shoot is pulled across the mouth behind the canines to liberate it from its sheath (Milton, 1978). *H. simus* also uses its stout upper canine to puncture bamboo culm preparatory to stripping it (Yamashita et al., 2004). This tooth is often worn in older individuals (NY, personal observation).

Indicators of Dental Health

Data on primate dental health primarily come from anthropoids (e.g., Lovell, 1990; Schultz, 1935; Smith et al., 1977), and only recently have data been published for lemurs. Lemur dental health (e.g., wear, pathology, and antemortem tooth loss) reflects many variables, including age, diet, habitat, life history, and even human impact (e.g., Cuozzo and Sauther, 2004a, 2006, in press; Sauther et al., 2006). *L. catta* at Beza Mahafaly often display excessive damage to the toothcomb, with a number of individuals having toothcombs worn more than 50% (Figure 5) (Cuozzo and Sauther, 2006; Cuozzo et al., unpublished data; Sauther et al., 2002).

In addition, the teeth of ring-tailed lemur toothcombs are often broken, chipped, and even missing (Cuozzo and Sauther, 2004a, in press; Sauther et al., 2002), with the majority of dental damage in *L. catta* occurring in the anterior teeth (e.g., Cuozzo & Sauther, 2006; Cuozzo et al., 2004; Sauther et al., 2002). It is likely that the excessive damage seen in ring-tailed lemur anterior teeth results from the use of the toothcomb in both feeding and grooming (e.g., Sauther et al., 2002; Yamashita, 2003). The frequency of severe wear and antemortem loss of the maxillary incisors in ring-tailed lemurs is also a result of the dual function of anterior tooth use (e.g., Cuozzo and Sauther, 2006, in press). It is important to note that individuals can and do survive for a number of years with anterior tooth

Figure 5. Severe toothcomb wear in an adult ring-tailed lemur (Yellow 195) from Beza Mahafaly: compare with the unworn toothcomb in Figure 2. Also note the severe wear on right P_2 (white arrow) (photo courtesy of Michelle Sauther).

damage, and even missing teeth in the toothcomb (e.g., Cuozzo and Sauther, 2004a, in press; Sauther et al., 2002). Also among ring-tailed lemurs, abscessed maxillary canines, which present as open wounds on the muzzle in living individuals, are a regular occurrence at Beza Mahafaly (Cuozzo et al., 2004; Sauther et al., 2006). Their presence corresponds to areas of human impact, and may reflect an increased consumption of nonnative foods in these areas (Cuozzo et al., 2004; Sauther et al., 2006). Decayed and possibly abscessed canines have also been noted among ring-tailed lemurs at Berenty Reserve in southeastern Madagascar (Crawford, personal communication; see Cuozzo and Sauther, in press), an area also impacted by human activity.

POSTCANINES: PREMOLARS AND MOLARS

The cheek teeth are the primary chewing teeth, and as such, are more subject to selection by the physical properties of the foods they masticate. Molar tooth form approximates designs that are best suited for inducing and continuing fragmentation in the foods they contact, especially in more specialized forms such as folivorous *Propithecus* or insectivorous *Daubentonia*. However, in more generalized taxa, especially those with a wide geographic range that inhabit a variety of environments (e.g., *L. catta*), the relationship between tooth morphology and diet becomes less distinct. In this section, we review the basic morphology of postcanine teeth and then discuss correlates between individual tooth features and the mechanical properties of the diets the lemurs eat. Finally, we discuss patterns of postcanine dental health with respect to their ecological and environmental contexts.

Basic Morphology

Indriids have reduced the number of premolars from the standard number of three to two (Table 1), and *Daubentonia* has a single, peglike upper premolar. The upper premolars vary among the families. In cheirogaleids the first two premolars are bladelike. Among the lemurids and cheirogaleids, P^4 has a well-developed protocone, though it is not molariform except in *Hapalemur* (and *Lepilemur*; Tattersall, 1982). This tooth in *L. catta* is also broad and molarlike, although with some individual variation, for example the presence of accessory cusps (FC, personal observation). The two indriid premolars are not molariform. The lower anterior premolar is caniniform in all lemurs (Swindler, 2002; Tatersall, 1982). In *Hapalemur*, P_4 is molariform and possesses two distinct basins (Tattersall, 1982).

The mammalian tribosphenic molar pattern has not been greatly modified in the primates as a whole. In the Malagasy lemurs, the lemurids retain the original pattern of three cusps (paracone, metacone, protocone) that surround the trigon basin in the first two maxillary molars (Figure 6). A lingual cingulum is variably present with an anterior protostyle. M^3 is reduced but less so in *Hapalemur*

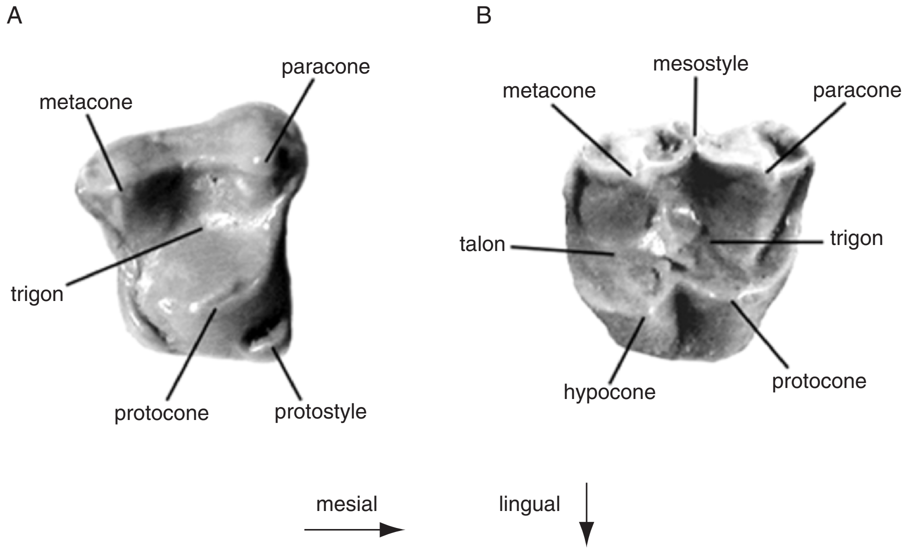

Figure 6. Occlusal features from casts of upper second molars of (A) *Eulemur rubriventer* (RMNH d) and (B) *Propithecus diadema edwardsi* (RMNH b). Not to scale (photos by Ny Yamashita).

(Tattersall, 1982). The indriids developed a characteristic quadritubercular maxillary molar that extends to their subfossil members (Martin, 1990). A mesostyle is present on the first two molars. A fourth cusp, the hypocone, and its crests surround a second basin, the talon. The hypocone occludes with the trigonid basin (Figure 6). Other families either completely lack the hypocone or it is variably developed, as in the cheirogaleids (Martin, 1990) and *Hapalemur* (Tan, 2000). In *Daubentonia*, the molars are square in outline, though the cusps are not well-defined (Tattersall, 1982).

Generally, lemurids have a more varied molar morphology than indriids (Yamashita, 1998b). In the lower molars, the lemurids have lost the paraconid and lack a hypoconulid. The anterior basin, the trigonid, is tilted mesially and at an angle to the cervical plane of the talonid (Figure 7). The trigonid does not have an occluding cusp. *L. catta* has a lingual notch and a distinct entoconid on the M_2 that are lacking in the other lemurids (except for *Hapalemur*) that interrupts the continuous crest on the postero-lingual aspect of the tooth. *Hapalemur simus* has crenulated enamel on both upper and lower molars (Schwartz and Tattersall, 1985).

Lepilemur also possesses a distinct entoconid and pronounced crests radiating obliquely anteriorly and posteriorly from the hypoconid (Schwartz and Tattersall, 1985). In the cheirogaleids, the molars are variable, with all except

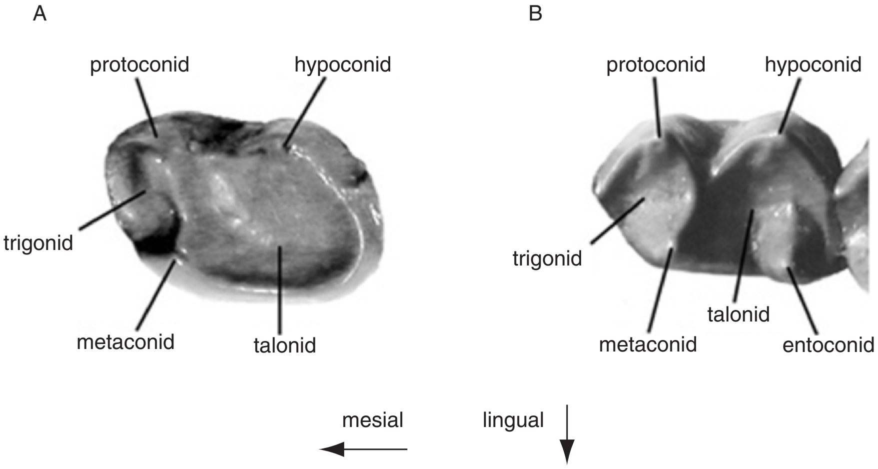

Figure 7. Occlusal features from casts of lower second molars of (A) *Eulemur rubriventer* (RMNH m) and (B) *Propithecus diadema edwardsi* (RMNH b). Not to scale. Note: no distinct entoconid on *E. rubriventer* specimen (photos by Ny Yamashita).

Phaner possessing a hypoconulid on M_3 and exceptionally low, rounded cusps in *Cheirogaleus* (Tattersall, 1982). Cuozzo (2000) has reported a great deal of morphological variation in the dentition of a large sample (n=126) of mouse lemurs (*Microcebus* c.f. *murinus*) housed at the American Museum of Natural History (Buettner-Janusch and Tattersall, 1985). For example, approximately 7% of the individuals in this sample exhibit a distinct, variably developed lingual cusp, originating from the cingulum disto-lingual to the hypocone on the first maxillary molar (Cuozzo, 2000). In addition, at least one individual in the sample displays this trait on M^2 (Cuozzo, 2000). Even the presence of an M_3 hypoconulid, a trait viewed as diagnostic of the cheirogaleids (e.g., Tattersall, 1982), varies in this sample (Cuozzo, 2000). Indriids have retained the paraconid and have a hypoconulid on the third molar only. The indriid trigonid is on the same occlusal plane as the talonid (Schwartz and Tattersall, 1985). Strong transverse crests connect the anterior and posterior cusps to approach a bilophodont condition that is fully realized in *Indri*.

For many years the focus of morphological study of lemur teeth has emphasized interspecific differences and lemur taxonomy (e.g., Schwartz and Tattersall, 1985; Swindler, 2002; Tattersall, 1982). More recently, work on a limited number of large samples of extant lemurs has allowed for a better understanding of dental variation, which has implications for addressing a variety of questions in primate paleontology and lemur taxonomy (e.g., Cuozzo, 2000; Cuozzo et al., 2004; Sauther et al., 2001). In the set of 23 dental traits used by Tattersall and Schwartz (1991) and Tattersall (1993) in their analyses of extant lemur taxonomy (critiqued by Groves and Trueman, 1995), 9 show a distinction between *L. catta* and the other lemurids (e.g., *Eulemur*, *Varecia*). In a pair of studies examining dental variation in the ring-tailed lemurs at Beza Mahafaly (Cuozzo et al., 2004; Sauther et al., 2001), two of these traits do not show a distinction. This includes the presence of several individuals that display distinct protostyles on the lingual cingula of the maxillary molars (Cuozzo et al., 2004), and roughly half of the population exhibiting distinct metaconids on P_4 (Cuozzo et al., 2004; Sauther et al., 2001). The maxillary molar protostyles seen in some individuals at Beza Mahafaly (compare Figures 8 and 9) are exactly what one would expect in other lemurids, such as *Eulemur fulvus* (e.g., Swindler, 2002; Tattersall, 1982, 1993).

In contrast to molecular data, in which *L. catta* is most closely allied with *Hapalemur* (e.g., Karanth et al., 2005; Poux et al., 2005), these dental data suggest that *L. catta* and the other lemurids are more similar dentally than has generally been recognized (Cuozzo et al., 2004). This example, along with our discussion of dental variation in mouse lemurs, emphasizes the need for large samples when considering traits used in systematic and phylogenetic analyses, and indicates that morphological variation, even within single populations, is pronounced in extant lemurs. Understanding the degree of dental variation in extant lemur species therefore has a number of implications for interpreting variation in fossil assemblages and identifying species in the primate fossil record (Cuozzo, 2000, 2002; Cuozzo et al., 2004; Sauther et al., 2001).

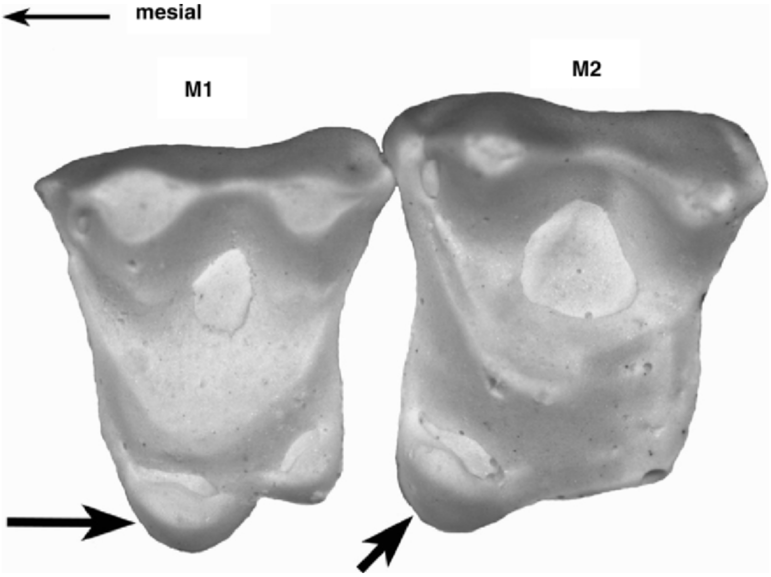

Figure 8. Lingual molar morphology as shown in a cast of an adult ring-tailed lemur from Beza Mahafaly (Hot Pink II 199) with distinct protostyles (black arrows) common to species of *Eulemur* (photo by Frank Cuozzo).

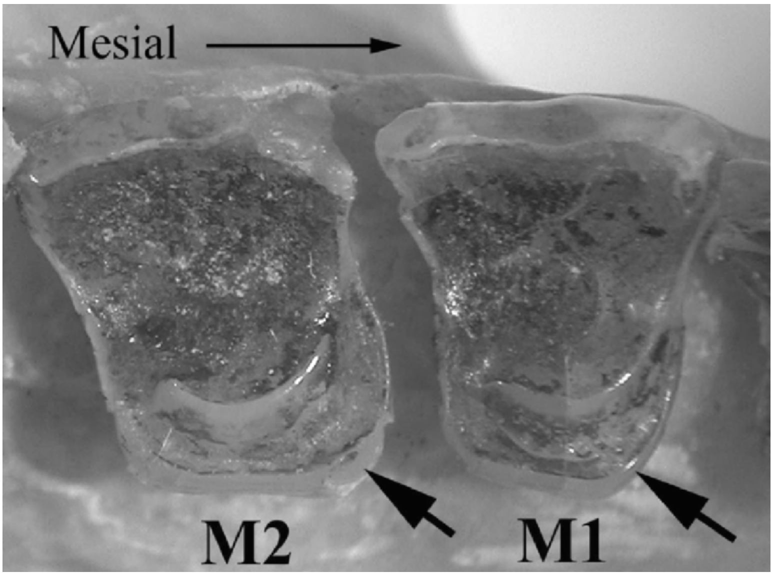

Figure 9. Lingual molar morphology in *Lemur catta* (AMNH 170740), showing the common presence of a thick cingulum (black arrows) without the distinct cusps (protostyles) common to species of *Eulemur* (photo by Frank Cuozzo).

Functional Morphology: Relationships between Tooth Form and Diet

Most Frequently Eaten versus Most Stressful Foods

As discussed above, tooth form is primarily related to the material components of the foods encountered. The heterogeneity found in the cheek teeth among lemur families is directly related to the mechanical variety of the foods they chew. The close relationship between tooth form and food properties increases efficiency, which is here defined as maximizing reduction of food particles with a minimum of time and energy. Molar efficiency has been investigated through analyses of strepsirhine (Kay and Sheine, 1979; Sheine and Kay, 1977) and marsupial (Moore and Sanson, 1995) fecal particles and cercopithecine stomach contents (Walker and Murray, 1975) that related finer size reduction to the presence of specific molar morphologies.

Diets, however, are usually mechanically quite variable, though they may be dominated by foods of a single property. Whether the properties of the most frequently eaten or the most mechanically stressful foods have the highest correlations with molar morphology is a matter of some debate (Kay, 1975; Kinzey, 1978; Rosenberger and Kinzey, 1976). The question has been framed to take into account seasonal differences in diets and food availability. Either the foods that are eaten during peak abundance are most related to the morphology, or those eaten during periods of scarcity, when animals are supposedly eating less preferred and more mechanically challenging foods ("fallback foods"), are more significant. An estimated 45% has been suggested as the minimum amount that an animal must eat of a food category in order for its mechanical properties to have an impact on tooth form (Kay, 1975). Rosenberger and Kinzey (1976) and Kinzey (1978) emphasize the importance of "critical" secondary dietary items that are eaten at times of resource scarcity. Tooth features that enable an animal to process foods during marginal periods are presumably under strong selection (Lambert et al., 2004). Yamashita (1998a) found that the most stressful foods were more highly correlated with molar features than the most frequently eaten foods, though the result was not applicable to all tooth features (e.g., crest lengths).

Correlates between Tooth Morphology and Physical Properties

An increasing number of studies are investigating food properties in the field (e.g., Happel, 1988; Kinzey and Norconk, 1990, 1993; Kitko et al., 1996; Lucas et al., 1991, 1995; Strait and Overdorff, 1996; Wright, 2004; Yamashita, 1996, 2002), though for the most part primate diets have not been characterized mechanically. Among the Malagasy lemurs, few studies on physical food properties have been conducted to date.

Yamashita (2002) carried out extensive work on mechanical dietary properties of two sympatric lemurs. The diets of sympatric groups of *L. catta* and *P. v. verreauxi* were tested throughout the year at Beza Mahafaly, a deciduous dry forest in southwestern Madagascar. Though the pooled species dietary toughness values were not significantly different, individual sifaka groups often had tougher diets than those of ring-tailed lemurs, while the converse never occurred. The two species overlapped significantly in the hardness of foods consumed (Yamashita, 2000). However, sifakas had a higher hardness threshold. Sifaka groups were uniform in toughness values regardless of location within the microhabitat gradient of this particular site, whereas toughness of ring-tailed lemur diets differed by group. This is consistent with, on a lower taxonomic level, the larger pattern of greater overall similarity in indriid teeth compared to those of lemurid taxa.

Crests. Long molar crests are frequently associated with a folivorous or insectivorous diet (Kay, 1975, 1978; Kay and Hylander, 1978; Kay et al., 1978; Kinzey, 1978; Rosenberger and Kinzey, 1976; Seligsohn, 1977; Seligsohn and Szalay, 1978). Although dietary categories themselves are usually not sufficient to classify foods mechanically ("frugivory" for example encompasses an array of foods with a variety of physical properties ranging from seeds to fleshy mesocarp), these particular foods are similar in either shape or consistency.

Leaves have a uniform geometry and composition that contribute to toughness when mature. Though the lamina comprises most of the volume of leaf tissue, toughness is conferred by sclerenchyma fibers that sheathe the midrib and veins (Lucas et al., 1991; Vincent, 1982). Leaves are notch insensitive (Vincent, 1983), that is, local cracks do not weaken the leaf. The veins blunt cracks or divert crack energy without fragmenting the leaf tissue. As a result, strain energy must be continuously fed into a crack to propagate it. A tooth design that encourages and directs continued crack propagation would be the most efficient for producing leaf failure.

Folivorous primates have reciprocal crests on occluding molars that slide past one another along their lengths. These well-developed crests appear to be functionally analogous to the elaborate lophed patterns found in herbivorous browsers and grazers for dividing tough, fibrous foods (Hiiemae and Crompton, 1985; Janis and Fortelius, 1988; Lumsden and Osborn, 1977). Insectivore molars also emphasize the development of crests. However, as Strait (1997) has demonstrated, there is a distinction between fragmenting hard-bodied as opposed to soft-bodied insects. The former are strong, brittle, and stiff (stress-limited), requiring a shorter crest that concentrates stresses along its length, and the latter are soft and tough (displacement-limited) and are best fractured with a crest with a longer contact area.

Among the lemurs, crest length and degrees of folivory have been linked in *Lepilemur mustelinus* (Seligsohn and Szalay, 1978), the indriids (Seligsohn, 1977; Yamashita, 1998b), and *L. catta* (Seligsohn, 1977; Yamashita, 1998b). Seligsohn (1977) also associated insectivory with crest development. The inclusion of *L. catta* in this list may be surprising; however, Kay et al. (1978) earlier grouped it with folivorous taxa based on crest length. Although often viewed as a mixed-fruit eater (e.g., Godfrey et al., 2004b), *L. catta* is best viewed as an opportunistic omnivore (e.g., Sauther et al., 1999). In southwestern Madagascar, *L. catta* spent equal amounts of time on fruits and leaves (Yamashita, in preparation) and were more folivorous than rainforest confamilials (Yamashita, 1996). Furthermore, the toughness of their diets was not significantly different from that of sympatric groups of the indriid *Propithecus v. verreauxi* (Yamashita, 2002). *L. catta* and *Indri* had relatively the longest crests within their respective families (Yamashita, 1998a).

Indriids possess molars dominated by crests (Seligsohn, 1977; Yamashita, 1998b). Though the degree of folivory in indriids differs by population, season, and location, all indriids are folivorous to some extent (Powzyk and Mowry, 2003; Richard, 1978; Yamashita, 1996, 1998b), and they possess additional specializations of the gastrointestinal tract to facilitate leaf eating (Campbell et al., 2000, 2004).

Yamashita (1998b), however, did not find a relationship between crest length and food shear strength in comparisons of five lemurid and indriid species, though there was a positive correlation between total crest length and percent folivory. Crest sharpness, and not just crest length, may be an important and heretofore largely unquantified feature that is relevant for understanding tooth–food interactions (Lucas, 2004). For example, a recent study of longitudinal tooth wear on *Propithecus diadema edwardsi* at Ranomafana (King et al., 2005) suggested that with continued wear, second molar crests continually "readjust" themselves, remaining secondarily sharp, in order to maintain functional occlusion. Only with excessive age and wear do these teeth experience declining function, which corresponds to a decline in reproductive success among females in this population (King et al., 2005).

Bilophodonty in Indriids. The bilophodont (or cross-lophed) crests of *Indri* have been compared to those of cercopithecids (the crests of other indriids approach the bilophodont condition). A puzzling aspect of the diets of the indriids is the occurrence of seed predation in addition to folivory (Hemingway, 1996; Powzyk and Mowry, 2003; Yamashita, 1998b). These two food types would seem to require different morphologies. However, Lucas and Teaford (1994) describe how bilophodont colobine crests combine wedges with blades. The blunter wedges split apart tough seeds and the sharp crests fracture leaf material. In cercopithecines, the central basin of the lower molars, formed by the anterior and posterior bilophs, presumably holds seeds in place while the occluding molar shatters them (Happel, 1988). Bilophodonty in indriids converges on a similar morphology to that described for Old World monkeys, which combines two different crest types for fracturing leaf material and seeds.

Cusps and Basins. Blunt cusps have been linked to frugivorous diets that include seeds, nuts, and insects in *Cebus* and soft fruits in *Pithecia* (Kinzey, 1978; Rosenberger and Kinzey, 1976). Hard/brittle foods, such as seeds, are stiff (high E) and require high stresses to initiate crack formation since stress increases with stiffness. Blunt cusps should be better able to tolerate high stresses than acute cusps, and their greater surface area would more efficiently fracture brittle foods that readily propagate cracks once they start. Furthermore, though a tight fit of a cusp to its occluding basin can produce high forces, reducing hard foods to fine particles can be achieved by unrestricted movement of the cusp in the basin to find weak points in the foods as they are being fragmented.

Frugivorous and gummivorous strepsirhines had low, blunt cusps, short crests, and shallow basins (Seligsohn, 1977). However, as noted earlier, fruits are a mechanically diverse dietary category. Presumably the mechanical properties of these foods were responsible for the association. The Malagasy taxa identified with this morphology were *Microcebus, Phaner*, and *Cheirogaleus. Microcebus rufus* has a diet that consists primarily of small fruits and insects (Atsalis, 1999). The hardness values of the ripe and unripe fruits eaten are comparable to the average hardness values found for three sympatric lemur species (Yamashita, 1996). *Cheirogaleus medius* and *C. major* appear to have a similar diet, consisting primarily of small fruits and berries (Fietz, 2003; Hladik et al., 1980). The exceptionally rounded molar cusps of *Cheirogaleus* suggest a hard fruit diet. The majority of the *Phaner* diet consists of plant exudates with secondary contributions from insects and flowers (Schülke, 2003). Its molar morphology may be more indicative of secondary dietary items, though the molars are bunodont.

The expected positive association between blunt cusps and food hardness was not clear-cut in Yamashita (1998b) since the relationship was positive for upper molars only. However, the harder diet of *Eulemur rubriventer* was reflected in blunter cusps and deeper basins than the sympatric *E. fulvus rufus.* Seligsohn (1977) found that crest length was negatively correlated with cusp acuity. *E. rubriventer* shared this pattern, while the features had mixed positive and negative correlations in *L. catta* and *E. fulvus rufus.*

The featureless molars of *Daubentonia* are probably related to its diet of insect larvae and seeds, which would not require much more than crushing platforms since the anterior dentition perform the hard work of extraction. Hard food items were correlated with short cusps, a tight occlusal fit of the protocone to the talonid, small trigon and large talonid areas, and deep, acute basins in a study of five lemur species (Yamashita, 1998a,b). Unrestricted basins were correlated with shear strength (mostly of leaf material) and not with food hardness. The larger basin area increased the excursion of the crest, a finding also noted by Kay (1975).

Indicators of Dental Health

The postcanine dentition is central for food processing, therefore, the patterns of dental pathology in premolars and molars are most often related to diet and the breakdown of food. This contrasts with patterns seen in the anterior teeth across primates, in which dental damage (often leading to disease) results from social behaviors, for example interindividual aggression (Lovell, 1990; Smith et al., 1977) or, in the case of ring-tailed lemurs at Beza Mahafaly, the possible impact of human activity and introduced foods (Sauther et al., 2006). As noted earlier, to date there is a paucity of information on lemur dental pathology, including patterns of wear (see Cuozzo and Sauther, 2004a,b, 2005, 2006, in press; Cuozzo et al., 2004; King et al., 2005; Sauther et al., 2002). Classic studies, such as the seminal work of Schultz (1935), and Miles and Grigson's (1990) revision of Colyer's work, present few if any examples of lemur dental health.

The lemur community at Beza Mahafaly, because of its long-term study (including the collection of skeletal remains from the reserve (Cuozzo and Sauther, 2004a, 2006, in press), allows for an initial understanding of dental health in wild lemurs, and provides important data for recognizing the role of ecology and the environment in dental pathology and tooth wear. Both ring-tailed lemurs and Verreaux's sifakas have been the focus of long-term dental study at Beza Mahafaly (e.g., Cuozzo and Sauther, 2004a,b, 2005, 2006, in press; Cuozzo et al., 2004; Lawler et al., 2005; Sauther et al., 2001, 2002, 2006; Yamashita, 1996, 1998a,b, 2000, 2002, 2003). Despite their sympatry, these taxa display quite different patterns of dental health and tooth wear. For example, while *L. catta* at Beza Mahafaly exhibits a high frequency of severe postcanine wear and antemortem tooth loss (Cuozzo and Sauther, 2004a,b, 2005, 2006, in press; Sauther et al., 2002), *P. v. verreauxi* does not (Cuozzo and Sauther, in press). In fact, in comparison to ring-tailed lemurs, in which 27% of the living individuals studied displayed antemortem tooth loss, most of which have been lost due to excessive wear (Cuozzo and Sauther, 2004a, 2006, in press), only 6% of the sifaka skeletal specimens at the reserve exhibit tooth loss (Cuozzo and Sauther, in press; Cuozzo, unpublished data). Among sifaka, most tooth loss results from dental pathology, not excessive wear (Cuozzo and Sauther, in press; Cuozzo, in preparation). In addition, the degree of tooth wear in the sifaka sample, while sometimes pronounced in older individuals relative to others in the sample (including the anterior dentition [Cuozzo and Sauther, in press; Cuozzo, unpublished data]), is far exceeded by ring-tailed lemurs, in which many teeth are worn down to the roots, and often completely lost, a condition seen in both living individuals and skeletal specimens (e.g., Cuozzo and Sauther, 2004a, 2005, 2006, in press; Sauther et al., 2002). A recent study of tooth wear in *Propithecus edwardsi* at Ranomafana National Park (King et al., 2005) illustrates that, although sifaka experience noticeable wear, even at advanced ages the degree of tooth wear is far less than that displayed by ring-tailed lemurs at Beza Mahafaly (Cuozzo and Sauther, in press).

The patterns of wear in this population of ring-tailed lemurs are clearly related to ecology, diet, and tooth use. In *L. catta*, the most frequently worn and missing teeth (P3, P4, and M1) are those used in the initial processing of tamarind fruit (Cuozzo and Sauther, 2004a, 2006, in press). This fruit (*Tamarindus indica*) is both hard and tough when ripe (Yamashita, 2000), and dominates the diet of ring-tailed lemurs living in gallery forest (Sauther, 1998; Simmen et al., in press), despite their opportunistic omnivory (e.g., Sauther et al., 1999). In contrast, *P. v. verreauxi* displays more excessive wear on P3, P4, and M3 (sifakas have only two premolars in each quadrant, see Table 1 [e.g., Swindler, 2002; Tattersall, 1982]), with M1 and M2 often retaining much of the original crown structure (Cuozzo and Sauther, in press; Cuozzo, unpublished data). The more limited wear and lower frequency of tooth loss in *P. v. verreauxi* at Beza Mahafaly when compared to *L. catta* likely reflects differences in diet, as well as tooth form. Although both taxa have relatively thin dental enamel (Table 2) (e.g., Godfrey et al., 2005), sifakas have very large molars relative to skull size (Godfrey et al., 2002), in addition to a specialized folivorous morphology (see comparisons of the molar morphologies of the lemurid *Eulemur* and indriid *Propithecus* in Figures 7 and 8) (Tattersall, 1982; Yamashita, 1998a,b). Sifakas at Beza Mahafaly do consume tamarind fruit, but most often eat the less tough, unripe fruits (e.g., Yamashita, 2002). As such, sifaka teeth are apparently a “better match” for their diet than seen in ring-tailed lemurs, which appear to represent an ecological “mismatch” between tooth structure and diet (Cuozzo and Sauther, 2005, in press). Understanding this relationship between ecology and dental health in living lemurs, in addition to aiding in our knowledge of lemur biology, provides an important context in which to understand lemur paleobiology and evolution (Cuozzo and Sauther, 2004b, in press), as seen in recent work on the subfossil lemurid *Pachylemur*, which displays noticeable tooth wear (Godfrey et al., this volume; Vasey et al., 2005).

CONCLUSIONS

In this chapter, we have presented lemur tooth morphologies as having specific designs related to the material properties of the foods they consume. Of course, this relationship is not perfect, seen for example in the patterns of severe tooth wear in some taxa (e.g., *L. catta*) living in specific habitats and utilizing diets dominated by specific food sources. The simple model for optimal designs used here does not take into account phylogenetic history and physical heterogeneity of food items that appear in individual diets, or in various habitats used by members of the same species. The relative importance of specific food parts to tooth form is still a matter of some debate, and perhaps, can never be completely resolved given variation in diets between seasons and regional differences in food availability, even within a single subspecies or widely dispersed specific populations. What animals ultimately eat involves a dialogue between what they can eat (dictated by their morphology, in a broad sense) and what is available (determined by the environment), a dialogue also influenced by socioecology (e.g., female dominance, social rank).

Further research on food properties is clearly needed in many Malagasy lemur taxa, especially for those with wide geographic ranges (e.g., *L. catta*), and the nocturnal members of the radiation that are barely represented in this review. As seen in our discussion of ecology and dental health (i.e., tooth wear and loss), much of the data for the better-known forms (e.g., *L. catta*, *P. v. verreauxi*) come from long-term studies at a limited number of locations (e.g., Beza Mahafaly). Therefore, comprehensive research on food properties and feeding from a wide range of habitats is imperative. Further quantification of lemur tooth morphology is also required, especially for the smaller-bodied, nocturnal forms.

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CHAPTER FIVE

Big Is Beautiful—Fat Storage and Hibernation as a Strategy to Cope with Marked Seasonality in the Fat-Tailed Dwarf Lemur (Cheirogaleus medius)

Joanna Fietz and K. H. Dausmann

TROPICAL AND SEASONAL: THE CLIMATE OF THE MALAGASY WEST COAST

Organisms of the ecosystems of the dry forests along the Malagasy west coast show distinct adaptations to the marked seasonality of this region. All plants and animals occurring here need to cope with the long and relatively cold dry season during the austral winter, with virtually no precipitation and no open water available from April through October (Figure 1). The dry season alternates with the rainy season, which lasts from mid-November to mid-March, with most rain

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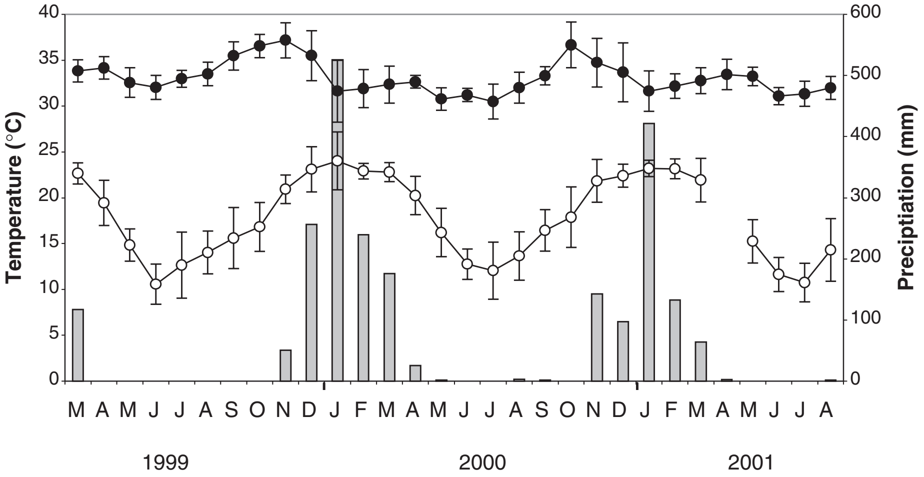

Figure 1. Climate of the Kirindy forest. Shown are data from March 1999 to August 2001, taken at a standard location in the field camp. Temperature is given as monthly mean ± standard deviation. For precipitation cumulative data per month are shown. (●) Daily maximum temperature; (○) daily minimum temperature. Data on daily minimum temperature are not available for April 2001. Note the interannual variation in climate, especially in the timing and amount of precipitation.

falling during the hottest months between December and February. Mean annual precipitation is 800 mm (range 390 – 1511 mm; Ganzhorn and Sorg, 1996).

While average daily maximum temperature is comparable between dry and rainy season (around 32°C; Table 1), average daily minimum temperature differs dramatically between the two seasons, with ambient temperature dropping to about 13°C at night during the dry season, but only to about 23°C during the rainy season. The average amplitude of daily temperature fluctuations is therefore about twice as great during the dry season (about 19°C) than during the rainy season (about 10°C; Table 1). The coldest months are June and July, with ambient temperature dropping below 10°C at night (Figure 1).

Concomitant with these climatic changes, variations in the availability of food resources like fruits and insects occur. Even though fruits are produced throughout the year, the percentage of fleshy fruits decreases dramatically during the dry season (Bollen et al., 2005). Insect abundance is positively correlated with rainfall and leafing of the trees, and therefore insects are also less abundant during the dry season (Hladik et al., 1980).

The austral winter in the dry deciduous forest of western Madagascar thus represents a bottleneck of energy and water supply, combined with energetically disadvantageous low ambient temperature. However, the occurrence of this period of scarcity is very predictable, giving organisms inhabiting these ecosystems the opportunity to take measures to master these challenges.

Table 1. Climate of the Kirindy forest

		T_{max} (°C)	T_{min} (°C)	Daily amplitude (°C)	N	Precipitation (mm)	First heavy rain	Last heavy rain
Rainy	1998/99					803.3	15.02.99	09.03.99
Dry	1999	32.8 ± 1.4	13.0 ± 3.0	19.8 ± 3.0	118			
Rainy	1999/00	33.5 ± 3.4	22.8 ± 1.8	10.6 ± 4.1	109	1274.4	08.12.99	06.03.00
Dry	2000	31.1 ± 1.5	13.6 ± 3.0	17.5 ± 3.5	112			
Rainy	2000/01	32.6 ± 2.5	23.1 ± 1.5	10.0 ± 2.9	72	915.9	21.11.00	31.01.01
Dry	2001	31.8 ± 1.4	12.5 ± 2.9	19.3 ± 2.7	88			

Dry season (*Dry*): May – August. Rainy season (*Rainy*): mid-November – mid-March. *Precipitation*: total rainy season. *N* gives the number of days within the respective season included in the analysis. T_{max}: maximum daily temperature; T_{min}: minimum daily temperature. *Heavy rain* is defined as > 50 mm precipitation. Temperature data are not available for the rainy season 1998/1999.

The fat-tailed dwarf lemur (*Cheirogaleus medius*) occurs throughout the western dry-deciduous forest and has adapted to this marked seasonality and resource limitation in a particularly intriguing manner. During the unfavorable dry season these lemurs suspend their activities and hibernate for up to 7 months (Petter, 1978; Dausmann et al., 2004, 2005).

In the following section we will give insight into the ecological, behavioral, and physiological adaptations of *C. medius* to the described climatic challenges and resource restrictions, that we have gained during a long-term (1995–2005) field study on this species conducted in the Kirindy forest, western Madagascar. Demographic data were achieved by capture-recapture and individual marking (Fietz, 1999a). Behavioral and nutritional data were recorded during nightly follows of radio-collared individuals (Fietz and Ganzhorn, 1999; Fietz et al., 2000). Physiological measurements were performed with the help of temperature-sensitive collar transmitters (Dausmann et al., 2004, 2005), portable gas analyzers (Dausmann et al., 2000, submitted), and fat biopsies (Fietz et al., 2003).

CHEIROGALEUS MEDIUS—A PRIMATE WITH AN EXCEPTIONAL LIFE HISTORY

C. medius are small-bodied (130 g; Fietz, 1999a) nocturnal lemurs that live in small family groups consisting of the reproducing male–female pair and the offspring from one or more breeding seasons (Fietz, 1999a; Müller, 1999). Males and females live in lifelong pair bonds and usually separate only when one partner dies. Even though yearlings or older offspring may remain in their family group when new offspring is born, they do not help raising their kin. Members of one family inhabit a common territory of 1–2 ha, and use the same tree holes as sleeping sites (Fietz, 1999a; Fietz et al., 2000). Territories are defended and olfactorily marked by the adult male–female pair, especially along the territory borders (Müller, 1998; Fietz, 1999a,b; Wiedemann, unpublished data). Depending on climatic conditions, adults mate during November or December (Hladik et al., 1980; Fietz, 1999a) and females give birth to one or two infants after a gestation period of 61–64 days (Figure 2). Remarkably, both sexes take extensive care of their offspring (Fietz, 1999a; Fietz et al., 2000). During the first 2 weeks after birth, infants remain in the nest holes, and parents take turns caring for them. As soon as infants start to leave their nest holes, either the male or the female accompanies them on their excursions (Fietz, 1999a). The participation of males seems to be crucial for the survival of the newborns, as females without paternal help were not able to raise their offspring successfully and infants died shortly after birth. Surprisingly, especially in view of the high investment of infant care by males in this species, genetic parentage analyses revealed an extraordinarily high incidence (44%) of extra-pair young (Fietz et al., 2000).

BODY MASS ALMOST DOUBLES BEFORE HIBERNATION

During hibernation *C. medius* do not feed and rely entirely on their endogenous fat reserves. Typical for a hibernating species, they exhibit remarkable prehibernation fattening during the period of food abundance from March until May (Figure 3) and adults may double their body mass during this time (from about 130 g to over 250 g; Fietz and Ganzhorn, 1999; Fietz et al., 2003). Part of the fat is stored within the tail, which swells from 10 ml to approximately 50 ml in volume, giving the fat-tailed dwarf lemur its name (Petter et al., 1977; Hladik et al., 1980).

In order to accumulate these fat deposits, different strategies are feasible, by which either energy intake is maximized, or energy expenditure minimized. *C. medius* seem to employ both methods. They feed generally on flowers, nectar, fruits, gum, seeds, insects, and spiders. The proportion of animal prey varies seasonally, depending on availability, and comprises about one-fifth of the diet. During the period of extreme fat accumulation before the onset of hibernation,

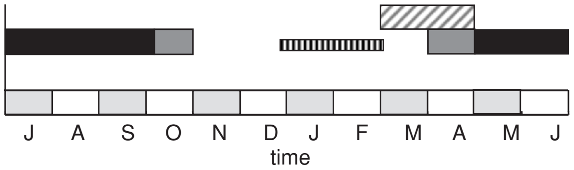

Figure 2. Seasonal temporal patterns in adult *Cheirogaleus medius* in Kirindy forest. *Black bars*: time of hibernation; *dark gray bars*: variability of immergence and emergence, and occurrence of daily torpor; *hatched bar*: prehibernation fattening period; *striped bar*: time of birth (variability between years).

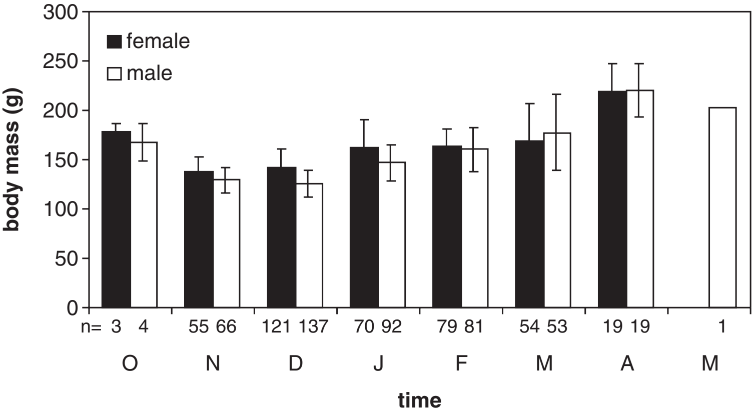

Figure 3. Seasonal variations of body mass in adult male and female *Cheirogaleus medius* of Kirindy forest. Given are mean and SD; data are pooled over the whole study period; body mass of each individual was included maximally once per month of a certain year.

berries with high sugar content are the staple food, and seem to be preferred to fruit items with low sugar content (Petter, 1978; Hladik et al., 1980; Petter-Rousseaux and Hladik, 1980; Fietz and Ganzhorn, 1999). In addition to seasonal variations in diet, the fat-tailed dwarf lemur also shows seasonal changes in locomotor activity. After emergence from hibernation in November, nightly travel distances increase until February. Between February and April, which is shortly before the onset of hibernation (Figure 2), locomotor activity is extremely reduced and nightly travel distances are halved (Fietz and Ganzhorn, 1999). Thus, during the prehibernation fattening *C. medius* accumulate fat stores for winter by eating high-energy, sugary fruits, as well as by drastically reducing their locomotor activity.

In hibernating species, the quantity of fat stored before the onset of hibernation is believed to influence winter mortality, as only individuals with sufficient energy stores are able to survive (Geiser and Kenagy, 1993; Florant, 1998). Furthermore, body condition at emergence, which again is dependent on levels of prehibernation fat storage, was shown to critically influence fecundity and reproductive success in the following reproductive period in several hibernating species (Barnes, 1984; Kenagy, 1985; Kenagy and Barnes, 1988; Hackländer and Arnold, 1999; Millesi et al., 1999). In mammals, females generally incur higher reproductive costs than males, due to pregnancy and lactation (Clutton-Brock and Harvey, 1978; Clutton-Brock et al., 1989). Nevertheless, in species exhibiting male parental care, high reproductive costs should be anticipated for both sexes. This is the case for *C. medius.* Here not only do females incur considerable energetic costs through reproduction, but also males through infant care, resulting in reduced fat stores and body condition in both sexes in comparison to nonreproducing individuals before the onset of hibernation (Fietz and Dausmann, 2003). The effects of such energy expenditure on winter survival and future fecundity are so far unknown. Nevertheless, in Kirindy forest *C. medius* exhibit a biannual fluctuation of reproduction, which is synchronized within the population (Fietz, 1999b). Factors causing such fluctuations remain speculative, but resource depletion during one reproductive year might reduce reproductive activity in the following year. This assumption fails to explain why nonreproductive years are synchronized on a population level, but higher survival rates of offspring due to density-dependent advantages are conceivable.

ECTOTHERMIC PATTERN OF BODY TEMPERATURE REGULATION DURING HIBERNATION

Besides reproduction another important energy expenditure in endotherms is the maintenance of their relatively high body temperature, especially when ambient temperature is low. Hibernation is the most powerful means for endotherms to reduce this cost (Heldmaier et al., 2004) and is therefore seen as an important adaptation to survive predictably unfavorable periods. It is usually defined by a controlled reduction of metabolic rate down to a fraction of the euthermic level, and a substantial decrease of body temperature down to the level of ambient temperature (Lyman et al., 1982; Heldmaier, 1989; Geiser and Ruf, 1995). Temperate animals, however, cannot enjoy several months of continuous hibernation, but must awaken regularly to experience phases of euthermic body temperature for one to several days. The function of these so-called arousals remains an unsolved mystery, but they are presumably necessary for the maintenance of vital body functions during hibernation with otherwise permanently low body temperature.

The tropical *C. medius* show a fascinatingly different thermal behavior during hibernation compared to that of their temperate counterparts. The hibernation phase of *C. medius* can be divided into 5 months of deep hibernation (May – September) and 2 months of transition (April and October; Figure 2). Before the entrance into deep hibernation, lemurs leave their tree holes occasionally, and therefore do not yet have to rely exclusively on their endogenous fat reserves during this time. During the coldest hours of the night, they employ short bouts of torpor, which means that their body temperature drops to almost ambient values for some hours during the early morning, but reaches euthermic levels again the next night (Dausmann et al., 2005). Combined with their decreased locomotor activity, this allows them additional fat storage during the last weeks before hibernation. From May onward, the adult animals retreat into tree holes and engage in continuous hibernation. Juveniles remain active for a few more weeks, but also suspend their activities by the end of May (Figure 2).

The pattern of body temperature and metabolic rate during hibernation in *C. medius* is astonishingly flexible for a mammal, and depends on the insulation capacities of the tree hole used during hibernation (hibernaculum). The lemurs adjust their body temperature to the prevailing ambient temperature in the tree holes, and their thermal behavior resembles an ectothermic pattern, as observed in reptiles (Figure 4; Dausmann et al. 2004, 2005).

Whenever a tree hole has relatively thin walls or the sleeping chamber is very close to the entrance, the sleeping chamber is then poorly insulated against the strong daily fluctuations of ambient temperature. *C. medius* using these kinds of tree holes passively heat and cool during hibernation, closely tracking the daily fluctuations of ambient temperature with its diurnal increase and nocturnal fall. This results in strong daily fluctuations of body temperature of up to 20°C

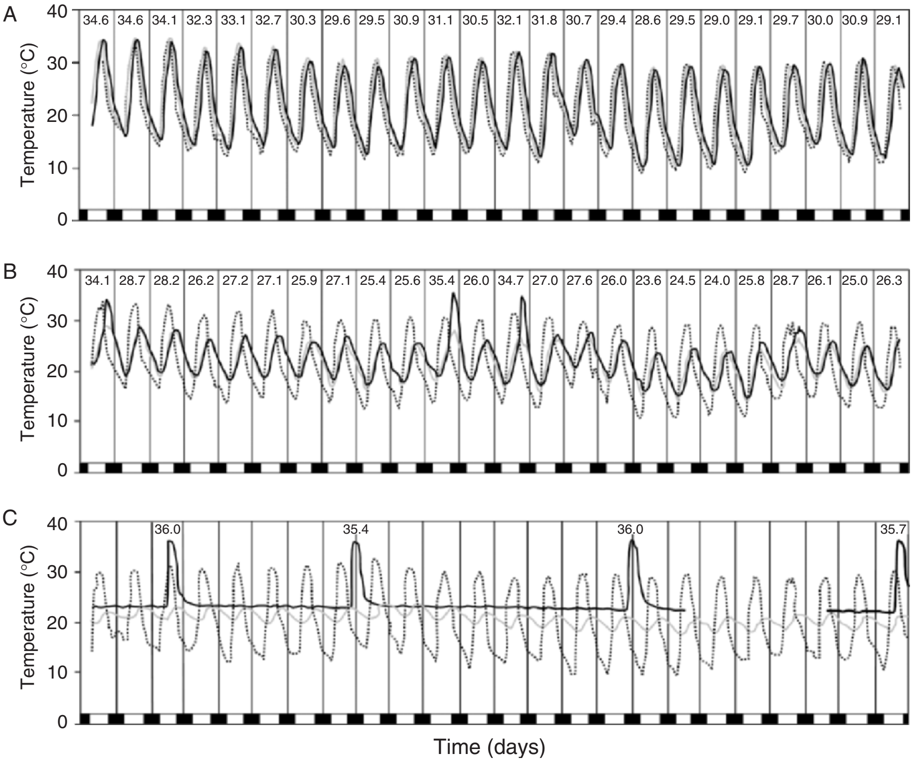

Figure 4. Patterns of body temperature during hibernation in *Cheirogaleus medius* (A) in a poorly insulated tree hole. Body temperature passively follows tree hole temperature in amplitude and slope and the lemur does not show arousals. (B) In a moderately insulated tree hole. Body temperature fluctuates with tree hole temperature, but is sometimes actively increased to euthermic levels. (C) In a well-insulated tree hole. Body temperature fluctuates little and the lemur shows regular arousals with euthermic body temperature. *Inserted numbers* give the daily maximum of body temperature (A, B) and the maximum body temperature during arousals (C). *Vertical lines* indicate midnight. *Black horizontal bars* show the dark phase. *Black line*: body temperature; *gray line*: tree hole temperature; *dotted line*: ambient temperature. Modified from Dausmann et al. (2004, 2005).

between about 10°C and 30°C (Figure 4A). Lemurs using these kinds of tree holes as hibernaculum do not interrupt hibernation by spontaneous arousals, as temperate hibernators have to, but show this pattern of passively fluctuating body temperature over many weeks or even months. However, the observations of predator attacks and other disturbances have proven that, contrary to reptiles, the ability for thermoregulation persists during hibernation. The lemurs are therefore at all times able to actuate the endogenous regulation of body temperature whenever they need to.

Some lemurs hibernate in large trees with thick walls, which provide better thermal insulation. Their body temperature fluctuates only by a few degrees (around 25°C), but contrary to the body temperature profile described above they exhibit regular arousals, similar to temperate hibernators (Figure 4C).

All transitions between completely passively fluctuating body temperature with high daily amplitude, and barely fluctuating body temperature with regular wake-up phases can occur during hibernation of *C. medius* (Figure 4B; Dausmann et al., 2004, 2005). Considering how meticulously body temperature is usually adjusted within a narrow range in mammals and birds, it is truly astounding how *C. medius* tolerate high daily fluctuations of body temperature and various patterns of thermoregulation, that can be changed from one day to the next.

ENERGY SAVINGS DURING TROPICAL HIBERNATION AMOUNTS TO 70%

The pattern of metabolic rate follows the pattern of body temperature. Therefore, as is the case for body temperature, the pattern of metabolic rate and the extent of its daily fluctuations are exogenously determined by the pattern of hibernaculum temperature and thus the properties of the tree hole used as hibernaculum. However, in lemurs that hibernate in well-insulated tree holes, the high costs of increased metabolic rate during the regular arousals seem to be balanced-out by an otherwise steady, relatively low metabolic rate. Surprisingly, therefore, the choice of hibernaculum seems to be of relatively little energetic relevance, despite the great implications with respect to the pattern of thermoregulation for the lemurs.

Due to the overall higher levels of body temperature in the tropical hibernator *C. medius*, mass specific metabolic rate is about tenfold higher than that of temperate hibernators, which hibernate at body temperature close to the freezing point. This corresponds to the finding that overall energetic savings of tropical hibernation do not reach the high levels of temperate hibernation (over 90%), but rather lie within the range of temperate daily torpor. Nevertheless, overall energetic savings of tropical hibernation in *C. medius* amounts to about 70% (Dausmann et al., submitted).

Temperate hibernators increase their body weight by about 40–50% before hibernation (Humphries et al., 2003), compared to about 90% in *C. medius* (Fietz and Ganzhorn, 1999). Based on the measurement of metabolic rates, 0.77 g body lipids are consumed by *C. medius* on average per day during the hibernation period. Given 5 months of deep hibernation (à 30 days), this means that they should have at least 115.5 g lipid at their disposal during hibernation. This corresponds to the observed increase in body mass before hibernation of about 120 g. However, it also shows that the energy supply of *C. medius* is fairly limited, clearly restricting the extension of the hibernation phase (Dausmann et al., submitted).

Besides the amount of fat accumulated before hibernation, the composition of the fatty acids seems to be equally important to the hibernation ability and quality in temperate hibernators (Frank, 1991; Geiser, 1993). During the prehibernation fattening period, temperate hibernators selectively store polyunsaturated, essential fatty acids in their white adipose tissue (Armitage, 1979; Geiser and Kenagy, 1987). This is thought to represent an adaptation to low body temperature during hibernation (Frank, 1991; Geiser, 1993). Considering the relatively high and diurnally fluctuating body temperature of *C. medius* during tropical hibernation, polyunsaturated fatty acids would not be expected to play a key role under these conditions. Indeed, *C. medius* have an unusually low content (<3%) of essential fatty acids in their white adipose tissue compared to 35–45% found in temperate hibernators (Geiser and Kenagy, 1987) before the onset of hibernation (Fietz et al., 2003).

The changes in thermoregulation and energy expenditure compared to the activity period show that tropical hibernation in *C. medius* is an important, well-regulated adaptive response to survive the unfavorable dry season.

IS TROPICAL HIBERNATION AN ADAPTATION TO WATER SHORTAGE?

In temperate hibernators the occurrence of hibernation is interpreted as an adaptation to the combination of low ambient temperature and food scarcity. Accordingly, temperate hibernators show physiological and behavioral adaptations to low ambient and consequently low body temperature during hibernation like the fatty acid pattern of the fatty tissue or the location of their hibernacula. Due to climatic differences between temperate zones and the tropics, the intriguing question remains, which are the driving factors for the evolution of hibernation in a tropical species like *C. medius*? Is the occurrence of hibernation in *C. medius* ultimately an adaptation to food scarcity, or to water shortage? Water is definitely a scarce resource during the long dry season. It is therefore conceivable that *C. medius* does not only need its fat stores for energy reserves, but additionally for the extraction of metabolic water, especially as it does not hibernate in water-saturated burrows as do its temperate counterparts, but in tree holes with comparatively low humidity (Dausmann et al., 2005). This hypothesis is supported by the finding that the closely related mouse lemur (*Microcebus murinus*) saves notable amounts of water by entering daily torpor (Schmid and Speakman, 2000).

Therefore, tropical hibernation could possibly also be considered as a measure to cope with water shortage.

Ultimately, hibernation in *C. medius* is a successful adaptation to both food scarcity and water shortage, taking energetic advantage of the cool nighttime temperatures of the dry season.

HOW ARE BIOLOGICAL RHYTHMS INDUCED?

In many hibernators circannual cycles of reproductivity, body mass, and hibernation are known to be generated by an endogenous program either independently or synchronized by environmental cues such as photoperiod or ambient temperature (*Spermophilus lateralis*: Kenagy, 1980; *Eutamias* ssp.: Kenagy, 1981; *Marmota*: Davis and Finnie, 1975). Least chipmunks (*Eutamias minimus*), for example, have strong internal programming and emerge from hibernation with year-to-year precision, irrespective of environmental conditions (Kenagy, 1981). In other species, emergence dates correlate with changes in temperature of the air or soil, and snow cover (Michener, 1977; Bronson, 1980; Murie and Harris, 1982; Kenagy, 1985; French and Forand, 2000). In the tropical mouse lemurs (*Microcebus murinus*), the prehibernation fattening phase was found to be dependent on photoperiod (Genin and Perret, 2000). The occurrence of daily torpor, on the other hand, seems to be a rapid response to food restriction, whatever the photoperiod, but enhanced by short photoperiod and low ambient temperature (Genin and Perret, 2003).

In *C. medius*, circannual cycles of reproduction, body mass, and body temperature depend on the variations of the photoperiod (Pages and Petter-Rousseaux, 1980; Petter-Rousseaux, 1980). Day length is a very reliable cue for such predictable seasonal changes as occurring in Kirindy forest. Indeed, the mean dates of entrance into hibernation do not change greatly between the years, despite differences in the progression of the vegetation period and thus the availability of food resources, due to differences in amount and timing of precipitation during the rainy season (Table 1, Figure 1). Taking the last change of tree hole before hibernation as an indicator of when hibernation starts, the mean date varied only little more than a week between the years 1999 and 2001. Within one year, however, the range is much greater, with the first animals occupying their hibernation tree holes at the end of March, and the last at the end of May (Figure 2). The opposite pattern is true for birth dates. The population is highly synchronized within one year, with all females giving birth within a tight time frame of about 2 weeks. Between the years, however, variation is high, and birth may occur any time between December and February (Figure 2). The cause for such flexibility remains unknown, but climatic conditions or food availability after the emergence from hibernation when mating takes place seem plausible. Thus, these seasonal patterns seem to be flexible up to a certain degree within the individual, as well as on the population level.

OTHER CHEIROGALEIDS IN KIRINDY FOREST

Although hibernation and daily torpor occur in nearly all mammalian orders and all over the world (Lyman et al., 1982; Carey et al., 2003; Heldmaier et al., 2004), among primates the occurrence of torpid states is so far only known in cheirogaleids. It is interesting to see how the different Cheirogaleidae species of the Kirindy forest have evolved different ways to cope with the marked seasonality of their habitat. As shown above, *C. medius* is capable of prolonged hibernation over many months. *Microcebus berthae*, at 30 g the smallest known primate (Schmid and Kappeler, 1994), shows short bouts of metabolic depression over a few hours (daily torpor) during the cold nights of the dry season (Schmid et al., 2000). Presumably this species is too small to undergo prolonged hibernation, as body size limits the amount of body fat that can be accumulated to fuel hibernation. *Microcebus murinus* (60 g), the second species of the *Microcebus* genera in Kirindy forest, seems to show a mixed strategy of staying active, showing daily torpor or going into hibernation for several days, depending on ambient temperature, body weight, and sex (Schmid and Kappeler, 1998; Schmid, 1999). No physiological parameters are yet known of *Mirza coquereli* (300 g). But as this lemur is found curled up and cold to the touch in traps after cold nights of the dry season, there is no doubt that it is capable of showing torpid stages at least occasionally. *Phaner furcifer* (330 g), the last of the Cheirogaleidae family in the Kirindy forest, is found active throughout the night until dawn all year long (Hladik et al., 1980; Schülke and Kappeler, 2003); it is not assumed to show stages of hypometabolism. Indeed, this lemur has a very specialized diet, feeding mainly on tree exudates that are self-maintained, and is therefore largely independent of seasonal environmental changes.

All lemur species occurring sympatrically with *C. medius* on the west coast have to cope with the strong seasonality of their habitat. Even though hibernation seems to be a very elegant method to survive this period of scarcity, only *C. medius* exhibits obligate hibernation. Life history parameters such as body size and feeding ecology, as well as phylogenetic constraints, may explain the occurrence or absence of hibernation and daily torpor of the lemurs living in the dry deciduous forest of western Madagascar.

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CHAPTER SIX

Polyspecific Associations of Crowned Lemurs and Sanford's Lemurs in Madagascar

Benjamin Z. Freed

INTRODUCTION

In polyspecific associations, groups of more than one species stay close, communicate, and coordinate activities together over a prolonged period. Biologists have observed such interspecific coordination of activities in a variety of fish, reptiles, birds, and mammals (Terborgh, 1990; Au, 1991; Ohtsuka et al., 1995; Stensland et al., 2003; Lee et al., 2005). One might predict that the potential for increased resource competition results in few polyspecific associations among closely related species. Primatologists have observed many of these associations among closely related anthropoid species (e.g., Gautier and Gautier-Hion, 1969; Waser, 1980; Struhsaker, 1981; Terborgh, 1983; Yoneda, 1984; Garber, 1988; Cords, 1990; Norconk, 1990; Oates and Whitesides, 1990; Podolsky, 1990; Burton and Chan, 1996; Holenweg et al., 1996; Leonard and Bennett, 1996; Nickle and Heymann, 1996). As in the nonprimate literature, the purported benefits of these primate associations include: more efficient feeding, foraging, and insect predation; better predator protection, detection, and vigilance; and enhanced social and mating opportunities (Gautier-Hion et al., 1983, 1997; Mitani, 1991; Buchanan-Smith,

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1990, 1999; Manohar and Mathur, 1992; Peres, 1992; Höner et al., 1997; Noë and Bshary, 1997; Wachter et al., 1997; Chapman and Chapman, 2000; McGraw and Bshary, 2001; Bicca-Marques and Garber, 2003; Korstjens and Noë, 2004). One species may gain the benefit of having more eyes and more ears against predators without any increase in food competition that might otherwise occur with larger groups of the same species (Eckardt and Zuberbuhler, 2004). In other cases, primates may parasitize or confer little benefit to their associates (Porter, 2001). Finally, primate associations may simply result from chance occurrences (Waser, 1982, 1984; Buchanan-Smith et al., 2000).

Yet polyspecific associations have not been readily observed in most daylight-active prosimian communities. Typically when closely related species of lemurs share a habitat, they rarely coordinate their activities. In Antserananomby ring-tailed lemurs (*Lemur catta*) and rufous lemurs (*Eulemur fulvus rufus*) rarely meet (Sussman, 1972). In Ranomafana rufous lemurs displace red-bellied lemurs (*Eulemur rubriventer*), ruffed lemurs (*Varecia variegata*) chase rufous lemurs, and diademed sifakas (*Propithecus diadema*) rarely meet lemurs (Overdorff, Balko, and Hemingway, personal communication). In Beza Mahafaly sifakas (*Propithecus verreauxi*) and smaller troops of ring-tailed lemurs form polyspecific associations that may be an antipredator strategy during important reproductive periods (Sauther, 2002). Indri (*Indri indri*) and diademed sifakas in Mantadia meet every 2 or 3 days; they feed together, but never travel, forage, or rest with one another (Powzyk, 1997). In northern Madagascar, only Arbelot-Tracqui (1983) and Wilson et al., (1989) have found a pair of sympatric, congeneric lemurs that seemed to tolerate one another readily, crowned lemurs (*Eulemur coronatus*) and Sanford's lemurs (*Eulemur fulvus sanfordi*). By 1989, many of the details as to the frequency and context under which associations potentially formed were still unstudied.

In 1989 I began an etho-ecological study of co-occurrence among crowned lemurs and Sanford's lemurs (Freed, 1996). The primary focus of this study was to understand how these two morphologically similar, congeneric species shared the same habitat. Although both species shared highly overlapping home ranges, significant year-round and seasonal differences occurred in habitat use. Crowned lemurs selected understory resources, ranged farther, lived in slightly larger groups, and formed foraging subgroups to disperse themselves within their home range. Sanford's lemurs selected more middle story resources, ranged less, and lived in slightly smaller, more spatially cohesive groups. During seasons when resources (especially fruit from *Leea spinea*) were superabundant, both species tolerated each other, and generally consumed these widely available resources in somewhat different proportions. When resources became less available, both species foraged more often. It was during this season that both species sought each other, and associated regularly.

The purpose of this article is to examine why crowned lemurs and Sanford's lemurs readily interact and form polyspecific associations in northern Madagascar. Results are from two studies I conducted: a quantitative behavioral study from

1989 to 1991 in Mt. d'Ambre National Park (Freed, 1996); and 2004 surveys of both species west of Mt. d'Ambre and north in the Cap d'Ambre. I address to what extent both species associate with one another; the context under which both species associate; activity, foraging, and feeding preferences within associations; and whether associations of these species are limited to Mt. d'Ambre. Finally, I discuss the benefits of association between these species.

MATERIALS AND METHODS

Study Sites

Quantitative behavioral data were collected at Ampamelonabe, along the western edge of the protected forest of Mt. d'Ambre National Park (12°32′ 3.2″S latitude., 49° 7′55″ E longitude., elevation 875 m) (Figure 1). The site includes 83 hectares of humid forest near the origin of the Antserasera, Bevoay, and Sandrampiana rivers. Local people use a footpath through the site to transport produce between the nearby western savannah and Joffre-Ville, a farming town on the eastern edge of Mt. d'Ambre. Disturbance at the site is largely limited to this path; people have used it daily for over 60 years. Neither hunting nor logging has occurred at the site. The site receives 1959 mm of rain annually. The wet season occurs December through April, during which rain falls nearly every day (83% of the annual rainfall), temperatures are warm, and the wind is calm (except for tropical storms). It is during this season when the food species responsible for nearly 25% of both lemurs' diets, *Leea spinea*, bears no fruit. Dry season, the coolest season (low 14.4°C), occurs May through August. A trace of rain falls on one-third of the days. The season is typified by daily strong 80 km/hr seasonal winds known as the *varatraza*. Hot season, September through November, is the warmest season (high 29.4°C), receives 14% of the annual rainfall, and lacks the *varatraza*. The common fruit, *Leea spinea*, is readily available during the dry season and hot season.

Ampamelonabe is mostly evergreen, humid forest with five distinct strata. The forest floor includes herbaceous growth, dominated by *Piper umbellatum*. An understory below 9 m contained bushes (*Lantana camara* and *Solanum indicum*), saplings, and treelets (e.g., *Malleastrum* sp., *Erythroxylum ferrugineum*, *Tarenna* sp., and *Bakerella* sp.). A middle story occurs from 9 to 17 m, and is dominated by *Leea spinea* and *Chrysophyllum boivinianum*, for which the site is named locally. The canopy (17–25 m) is mostly continuous, and includes *Cryptocarya* sp., *Chrysophyllum* sp., and *Harungana madagascariensis*. An emergent layer above the canopy is also present, and typically includes trees such as *Canarium madagascariensis*.

The only daylight-active primates are the study species. Nocturnal primates include *Microcebus rufus*, *Cheirogaleus major*, *Phaner furcifer*, *Lepilemur septentrionalis*, and *Daubentonia madagascariensis*. Potential predators include mammals

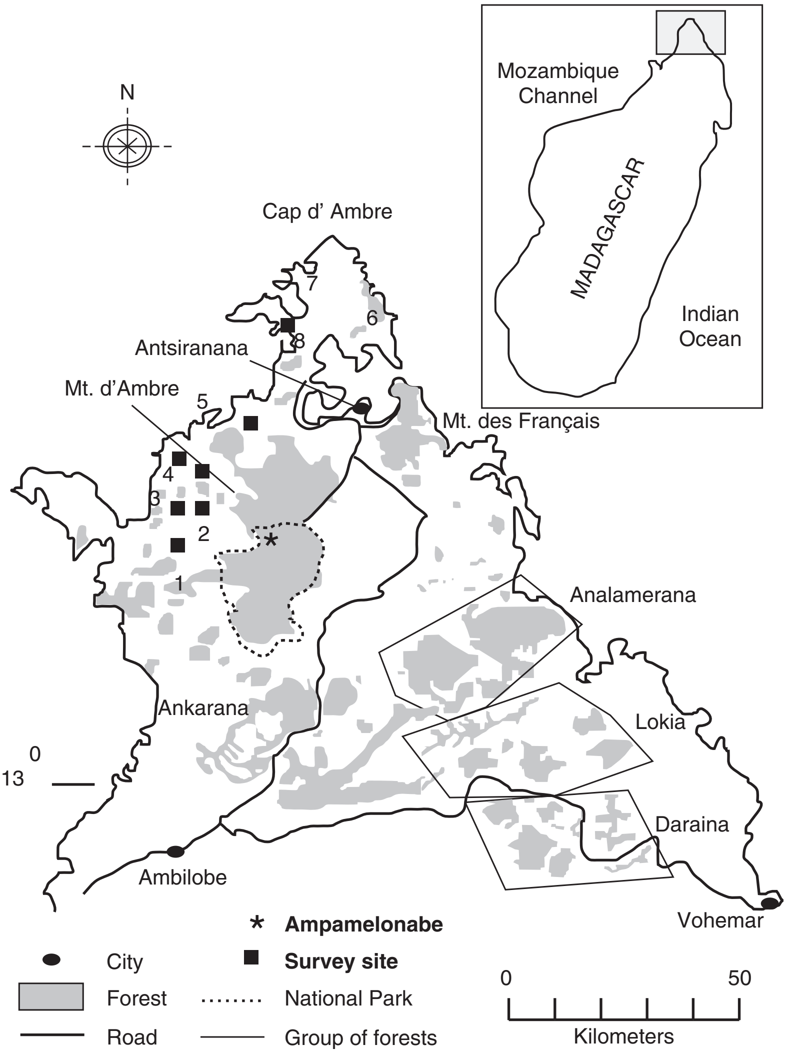

Figure 1. Survey sites in northern Madagascar. Numbers refer to survey sites discussed in the article.

(*Viverricula indica*, and fossa, *Cryptoprocta ferox*) and birds (*Accipiter madagascariensis*, *Buteo brachypterus*). Large Madagascar crested ibis (*Lophotibis cristata*), however, were present throughout the forest. On at least five different mornings, I found their feathers and bones on the forest floor in what was likely predation from a fossa. Owls and fish eagles are present (*Tyto soumagnei*, *Tyus* sp., *Haliaeetus vociferoides*), but neither lemur made distinct vocalizations for these potential predators. The only potential reptilian predator is a terrestrial constrictor, *Acrantophis* sp. Lemurs sometimes grunted loudly upon seeing this snake, but no attacks were ever witnessed. No hunting was ever observed at Ampamelonabe. I found no evidence of hunting at any survey sites.

Broad surveys took place in smaller forests in two regions much different from Ampamelonabe (Figure 1). I examined 12 forests that extend west of Mt. d'Ambre to the Mozambique Channel, and five forests north of Mt. d'Ambre in the very dry Cap d'Ambre. All of these forests are highly disturbed, and have been subjected to extensive regional deforestation. Strong local Antankarana and Sakalava traditions have translated to a lack of local hunting, but sportsmen and nonnative inhabitants hunt, especially in the Cap d'Ambre. Although three seasons exist in this region, annual rainfall is less than one-fourth that of Ampamelonabe, rain is strictly limited to the wet season, and temperatures are much warmer than in Mt. d'Ambre. Although many rivers flow throughout the year west of Mt. d'Ambre, no rivers flow throughout the year in the Cap d'Ambre.

Forest patches in both regions are too small to depict on most maps. Most of the area is dominated by savannah grass and small bushes. Forest is often no wider than 15–100 m, and is limited to rivers and ancient lava flows from Mt. d'Ambre. Two food trees, *Tamarindus indica* and *Mangifera indica*, often dominate the existing forests. Dense *Lantana camara* and *Mucuna* sp. border the forests west of Mt. d'Ambre; these plants are more sparse in Cap d'Ambre. Overall, forest patches seem to connect with one another and with potential seasonal food resources for lemurs, including small farming communities and continuous deciduous forest. The only other lemurs I have seen in these forests are nocturnal *Microcebus*; few mammalian, avian, and reptilian predators live here.

Methodology

During October 1989 to September 1990, Ampamelonabe was located, trails and botanical transects were established, lemur groups were censussed, reconnaissance observations were collected, and study groups were habituated. Quantitative behavioral data and biweekly botanical phenological data were collected from October 1990 to October 1991. A total of 2080 hours of data were collected. To identify individual and group patterns in resource use and social behavior I used a combination of instantaneous focal animal and scan sampling strategies every 5 minutes from dawn until dusk. The ethogram, specific variables, and details of data analysis have been described elsewhere (Freed, 1996).

Individuals within four study groups were easily recognized on the basis of physical features. Reproductive state and other critical individual descriptions were assessed easily, as all individuals were habituated quickly to the presence of humans, and both species generally spent most of their time beneath the forest canopy. Breeding occurred for both species at the end of May, near the beginning of the dry season. Offspring were born nearly 120 days later in early October, during the hot season. The last possible bout of nursing I observed occurred in the wet season, at the end of January.

Groups were small. Each group had small, distinct home ranges. Throughout the field site both species lived in highly overlapping groups that were comprised typically of 2–5 adult females, a nearly equal number of adult males, and subadults ($n = 14$ crowned groups; $n = 13$ Sanford's groups). During the study two crowned lemur groups ranged in size between 5 and 7 individuals (northern group) and 7 and 13 individuals (southern group). Sanford's lemur study groups were between 4 and 7 individuals (northern group) and 3 and 5 individuals (southern group). Home ranges of the Sanford's study groups overlapped remarkably with those of their crowned lemur counterparts. The northern groups had home ranges of 8.89 ha (Sanford's) and 15.50 ha (crowned), but the area of overlap was 8.66 ha, 97% of the Sanford's lemur group. The southern Sanford's group's home range was 7.11 ha, and the crowned lemur counterpart was 9.18 ha. The area of overlap was 6.51 ha, or 92% of the Sanford's home range. Each study group shared parts of its home range with at least six groups each of crowned lemurs and Sanford's lemurs.

Statistically significant differences in species mean values were calculated using a randomized version of a paired-comparisons *t*-test. The actual differences in mean percentages between crowned lemurs and Sanford's lemurs are expressed by "Δ0." In randomization, an estimate of statistical significance is made by having software proceed through 1000 reshufflings of the data. After each reshuffle the statistic is recalculated, and compared with the actual statistic. Results were considered statistically significant when $p < 0.05$ (i.e., when fewer than 50 out of 1000 iterations were greater than the actual value). To guard against Type II errors, another 5000 iterations were made when results were nearly significant (see Edgington, 1980, and Manly, 1991).

Polyspecific associations occurred when groups of both species: stayed within 20 m of one another for more than 20 minutes; and when they routinely communicated and conducted activities with one another as if one group. Each time a group approached the focal group, I recorded the most frequent behavior and forest level of the approaching group. Quantitative data on intergroup interactions were also collected every 5 minutes. For each group (other than the focal animal's group) within 20 m of the focal animal, the name of the group and its distance from the focal animal were recorded. If a member of another group was within 10 m of the focal animal, the name and the activity of that individual were recorded. A subjective scale was used to describe the relative distance between the focal animal and the closest member of another group. All occurrences of agonism involving the focal animal were recorded. The duration of each intergroup interaction was the difference between the first and final 5-minute observation intervals in which the two groups associated.

Dry forest surveys were conducted in the dry season, June 2004 to August 2004. During the first 2 weeks, surveys were conducted as part of a larger interdisciplinary team investigating deforestation in northern Madagascar. The purpose of these surveys was to identify lemur populations and biogeography of this largely unexplored region. Local guides who had received training through Madagascar's regional ANGAP bureau served as translators with local people. Observations were made of all primates within 25 m of survey paths. Surveys were conducted silently at a pace of 1 km/hr. The following data were collected whenever primates were found: descriptions of the habitat; an estimate of visibility; the number of individuals of different sexes and age classes; the forest level, height, and activity of each individual; and the individual's reaction to the presence of humans. Each group was observed for 10 minutes to ensure that most group members were found, and to evaluate their reaction to the presence of humans. Dominant plant species in each forest level were recorded for each forest edge, midpoint in the forest, and each location in which lemurs were found.

Data also were collected on lemurs that were heard, but unseen. As both species routinely give distinct vocalizations shortly before dusk, 90-minute listening sessions occurred at each site. Crowned lemurs exchanged a series of piercing, shrill "WAE" calls that were often followed by distinct, loud grunts. Sanford's lemurs offered loud grunts as well, but also gave very loud, raspy sustained calls. During these sessions three people listened and recorded the location from which vocalizations originated. Groups were said to be present when all three individuals heard the same vocalizations from the same locations. Locations of nocturnal vocalizations were also recorded. Data of unseen, but otherwise located groups were recorded when these groups could not have been found where groups had been previously identified.

RESULTS

To What Extent Do Both Species Associate with One Another?

Overall, crowned lemur and Sanford's lemur groups met each other nearly twice daily for nearly 90 minutes. Each study group met at least three groups of the other species per season. Of the 353 encounters throughout the study, 237 were scored as associations, in which activities were coordinated among members of both species (Table 1). On average, associations lasted more than 70 minutes in most seasons. Unlike encounters between groups of the same species, those between different species usually lacked alarm vocalizations (alarm calls, trill-grunts, and raspy calls). Most vocalizations upon meeting groups of other species included contact grunts that group members offered each other during routine feeding and foraging.

Associations seemed to vary seasonally in frequency, average length, and maximum length (Table 1). Wet season values were typically longer than those for other seasons. During the wet season both species associated with one another in 20–30% of daily observations. Crowned lemurs associated significantly more of their typical wet season day than did Sanford's lemurs ($\Delta\bar{x} = 9.80$, $p < 0.05$). The

Table 1. Frequency of polyspecific encounters and associations among crowned lemurs and Sanford's lemurs at Ampamelonabe

	Polyspecific encounters	Association time while observing crowned lemurs	Association time while observing Sanford's lemurs
Wet season	3.50/day $n=140$	214.55 minutes/day $n=65$ 29.80% observations 68.60 minutes/association	143.40 minutes/day $n=47$ 19.92% observations 62.45 minutes/association
Dry season	1.69/day $n=105$	71.12 minutes/day $n=30$ 9.88% observations 73.81 minutes/association	83.21 minutes/day $n=33$ 11.56% observations 77.14 minutes/association
Hot season	1.92/day $n=108$	70.08 minutes/day $n=39$ 9.73% observations 51.97 minutes/association	38.43 minutes/day $n=23$ 5.34% observations 48.61 minutes/association

two lemurs formed associations in 75% or more of their wet season encounters. In other seasons both lemurs associated in only 5–12% of daily observations, and neither species associated more than did the other. Associations formed in most encounters. For most of the study associations lasted an average of 62–77 minutes, but hot season associations were typically shorter ($\Delta\overline{x}=48.61$–51.97 minutes). Maximum association length varied seasonally as well. The maximum wet season association lasted 305 minutes; the maximum association length was shorter in other seasons (110–288 minutes).

What Is the Context under Which Both Species Associate?

Study groups seemed to have preferred associate groups throughout the year. Each study group usually associated with the group whose home range most overlapped its own. For example, the two southern study groups associated with one another in 43–77% of all polyspecific associations. Likewise, 90% or more of the associations that the northern crowned lemur study group formed usually included the northern Sanford's group. More than half those associations that the Sanford's group formed included the crowned lemur group. Only in the hot season did the crowned lemur group associate with another group nearly as much as it did with the Sanford's group.

Neither species seemed to initiate associations more than did the other (Freed, 1996). Each species initiated associations during similar activities (Figure 2). During the wet season lemurs initiated two-thirds or more associations during feeding and foraging. Otherwise, feeding and foraging accounted for only slightly more of the associate's behavior than did resting and grooming. The initiation of associations seemed to differ seasonally in at least one aspect, the forest level of the initiators. Throughout most of the year, initiators generally began associations from within their own preferred vertical strata. Crowned lemurs initiated associations

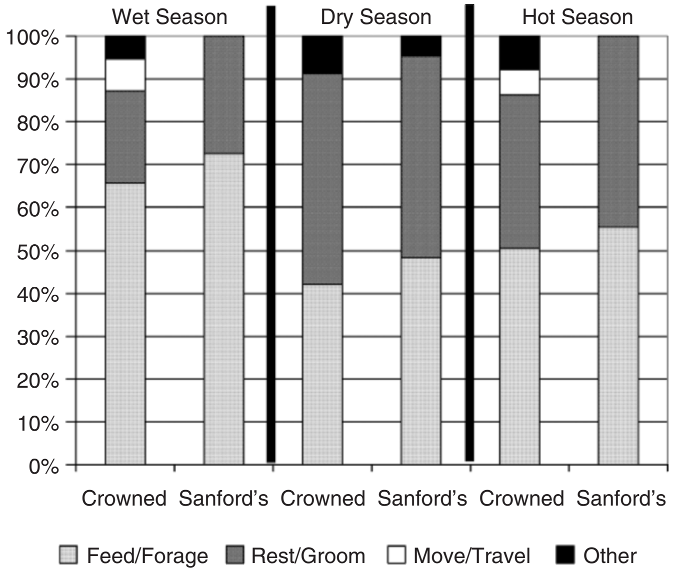

Figure 2. Activities of recipient associates when polyspecific associations were initiated.

from the understory 92.5% and 65.1% of the time during the dry season and the hot season, respectively; Sanford's lemurs initiated associations from the middle story 59.5% and 56.6% during the dry season and the hot season. In the wet season, however, association initiators left their preferred forest levels, and sought out their associates elsewhere below the forest canopy. Crowned lemurs initiated associations 56% of the time in the wet season from the middle story. Sanford's lemurs initiated 58.4% of their wet season associations from the understory.

Although both species participated in frequent agonistic displays (i.e., face-offs, fights, and charges) upon meeting conspecific groups, both species displayed little agonism upon meeting one another and associating. Interspecific agonism occurred in 20–25% of encounters in any season. Only 14% (wet season) to 22% (hot season) of encounters ended due to this agonism. Although both lemurs usually tolerated one another, Sanford's lemurs initiated more than 75% of interspecific agonism in any season. Most agonism occurred when both species fed or foraged together. Less than 38% of the agonism took place when Sanford's lemurs chased crowned lemurs from large fruit trees (e.g., *Ficus brachyclada*, *Diospyros* sp., and *Canarium madagascariensis*). In nearly two-thirds of agonistic interactions, crowned lemurs responded by withdrawing from Sanford's lemurs. Although Sanford's lemurs sometimes chased crowned lemurs from large fruit trees, crowned lemurs usually consumed these resources anyway. Crowned lemurs either waited for Sanford's lemurs to finish eating, or returned to the food source when no other groups were present.

Table 2. Average daily percent age of focal observations in which the focal animal was within a polyspecific association[a]

	Average distance between focal animals and associates			Closest distance between focal animals and associates		
Season	10–20 m	<10 m	Total	10–20 m	<10 m	Bouts
Wet	39.13%	60.87%	1404	8.61%	91.39%	112
Dry	58.16%	41.84%	906	19.42%	80.58%	63
Hot	54.18%	45.82%	758	19.70%	80.30%	62

[a] "Total" equals the total number of focal observations in which the focal animal associated with another species. "Bouts" equals the number of polyspecific associations.

Focal animals and associates readily approached one another, especially in the wet season. *Associates* refer to individuals with whom a focal animal associated; they do not include the focal animal's conspecifics. Both lemurs usually associated 10–20 m apart, but during the wet season they usually associated *within* 10 m (Table 2). When associations occurred within 10 m, associates were closer to the focal animal than was at least one of the focal animal's group. Associates were a focal animal's nearest neighbor in 30–43% of the time that associates and focal animals were within 10 m of each other.

Within associations, both lemurs responded to one another's vocalizations. For example, lemurs usually stopped their activities in response to one another's alarm calls or barks, especially if other vocalizations did not precede the alarms. Both species exchanged at least five forms of vocalizations. Much as they did within their own groups, lemurs responded with movements (e.g., head-turns) or similar vocalizations. Neither species reacted to three types of vocalizations that occurred within associations: those offered when conspecific groups met; vocalizations associated with intragroup agonism; and "echo" or lost calls.

Both species responded to one another's alarm vocalizations both within and outside association. Alarm vocalizations were so loud that lemurs more than 500 m away responded with their own alarm vocalizations. Eight or more groups of lemurs that shared parts of the same home range responded quickly to alarm vocalizations. Such widespread reactions occurred after lemurs detected either a raptor or a fossa (*Cryptoprocta ferox*). In one nocturnal observation, the lemurs in the middle story spotted a terrestrial fossa and vocalized before I could spot it no more than 30 m from me.

Activity, Foraging, and Feeding Preferences within Associations

Crowned lemurs and Sanford's lemurs conducted a variety of activities while associating (Figure 3). The only behaviors they never conducted together were resting, grooming, and mating. The two species never huddled together or groomed

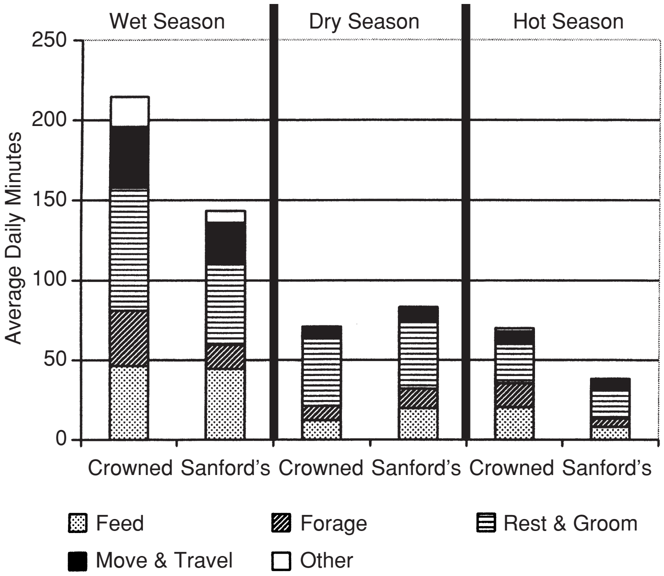

Figure 3. Average daily minutes spent in each activity within polyspecific associations.

each other. Otherwise, most behaviors were well-coordinated with one another. For example, during the wet season play comprised most "other" behavior. Juveniles and other subadults of both species wrestled, played tag, or jump-played with one another, while adults conducted other activities.

Within associations, both species spent nearly equal time conducting similar activities. Both lemurs foraged and fed slightly more than they rested; they rested more during dry season associations. Average hourly distance traveled did not differ much within and outside associations, except during the wet season. Within wet season associations, crowned lemurs traveled significantly less distance than they did alone ($\Delta\bar{x} = 30.97$, $p < 0.05$). Neither species appeared to follow the other within polyspecific associations.

Although less than one third of a species' wet season feeding time occurred within associations, the presence of associations had little effect on food item preferences (Table 3). In the wet season, lemurs within associations primarily fed on ripe fruit, much as they did outside of associations. No statistically significant differences between or within species occurred during this season. Crowned lemurs fed slightly more on midsized trees than they did outside of associations; Sanford's lemurs consumed slightly more treelets than they did outside of associations (Table 4). Again, lemurs selected similar food sources within and outside associations. No statistically significant differences occurred. During the rest of the year lemurs fed too infrequently within associations for statistical analysis.

Table 3. Average daily percentage of items consumed within associations and alone during the wet season[a]

	Unripe fruit	Ripe fruit	Flowers	Leaves	Other	Total
Crowned within associations	17.28	74.32	2.88	2.29	3.23	1016
Crowned alone	16.33	73.04	4.87	3.43	2.32	2303
Sanford's within associations	12.16	87.60	0.00	0.24	0.00	511
Sanford's alone	11.00	83.92	1.14	2.05	1.89	1561

[a] "Total" refers to the number of scan records during which individuals consumed items. Too few bouts of feeding occurred within associations during the dry season and hot season.

Table 4. Average daily percentage of resources consumed within associations and alone during the wet season[a]

	Nontree	Treelet	Midsize tree	Tall tree	Total
Crowned within associations	16.01	30.68	25.25	27.86	1030
Crowned alone	16.75	35.70	17.62	29.65	2303
Sanford's within associations	8.99	45.68	15.02	30.31	511
Sanford's alone	6.46	50.71	7.46	34.41	1561

[a] "Total" refers to the number of scan records during which individuals consumed items. Too few bouts of feeding occurred within associations during the dry season and hot season.

Food species selection within and outside associations varied only slightly throughout the study. Generally, both lemurs ate similar food species within associations, and they consumed different food species outside of associations. The greatest exception occurred in the wet season when crowned lemurs ate the same food species within and outside associations (Table 5).

Table 5. Average daily percentage of each lemur's feeding IARs made up of food species that are eaten exclusively, in slightly different proportions, and similarly[a]

		Wet crowned	Wet Sanford's	Dry crowned	Dry Sanford's	Hot crowned	Hot Sanford's
Within associations	Exc	14.29	20.22	13.38	14.84	27.76	13.92
	Dif	27.94	22.50	25.75	15.71	27.43	35.85
	Sim	57.76	57.28	60.88	69.46	44.81	50.23
Alone	Exc	9.20	12.94	1.33	8.03	1.07	2.79
	Dif	58.53	53.43	53.95	36.62	74.89	71.61
	Sim	32.27	33.63	44.72	55.36	24.04	25.60

[a] Exc: a food species eaten exclusively by one of the two lemur species. Dif: both lemurs ate the species, and either lemur ate the species one-third more than did the other lemur. Sim: both lemurs ate the same species, and neither lemur ate the food species at least one-third more than did the other lemur.

Do Polyspecific Associations Exist outside of Mt. d'Ambre?

Prior to 2004, few researchers had identified populations of Sanford's lemurs outside of the continuous canopy forests of Mt. d'Ambre, Ankarana, and Analamerana. Wilson et al. (1989) suspected that the two species associated in Ankarana. Freed (1996) found no populations outside of these three reserved forests. One might have inferred that the two species associated, given an overabundance of resources.

In 2004, populations of Sanford's lemurs were found west of Mt. d'Ambre in at least four forests that stretch west and north of Mt. d'Ambre to the Mozambique Channel (Figure 1). In most previously studied regions Sanford's lemurs are known locally as *ankombabe*, or "big lemurs." West of Mt. d'Ambre in traditional Sakalava/Antankarana language, they are known as *barivaokao*, or "bearded ones." By surveying at early morning, dusk, and by listening for nocturnal vocalizations, populations of both crowned lemurs (*ankomba fieky*) and Sanford's lemurs were found within 100 m of one another in isolated forests near Bobakilandy (Figure 1, #1: 12°37′ 0.3″ S lat., 49°2′ 44.1″ E long., elevation 304 m), Bemanevikakely (Figure 1, #2: 12°32′ 27″ S lat., 49°3′ 43″ E long., elevation 455 m), Befotaka (Figure 1, #3: 12°29′ 14.3″ S lat., 48°56′ 42.8″ E long., elevation 3 m), Ambatomitangolo (Figure 1, #4: 12°29′ 41.2″ S lat., 48°56′ 54.3″ E long., elevation 16 m), and Baie d'Antalaha (Figure 1, #5: 12°18′ 2.0″ S lat., 49°2′ 50″ E long., elevation 0 m). All but one other site had crowned lemurs living in them. In Bemanevikakely one group of each species was observed for 45 minutes foraging, feeding, and traveling with one another in *Lantana camara* and *Bombax* sp. on successive days, on the edge of a rice field. The observed groups exchanged calls at dusk with neighboring groups of both species. Local people reported populations of both species that live together. Neighboring groups were also found traveling beside a rice field near Bobakilandy.

Associations of crowned lemurs and Sanford's lemurs may also occur in the Cap d'Ambre peninsula. The east coast of Cap d'Ambre (e.g., Anjiabe, Figure 1, #6) has crowned lemurs throughout its forests. These forests are almost identical to those of Mt. des Français, a limestone-based set of forests that contain only crowned lemurs, found east and southeast of the city of Antsiranana. I found no evidence of Sanford's lemurs along these forests. In contrast, forest structure along the Cap d'Ambre center and west coast is not unlike that of the northernmost forests of Mt. d'Ambre. This region includes primary deciduous forests connected by small forests (less than 25 m wide) that line seasonal riverbeds. Beside the Antsahabe River (Figure 1, #7: 12°05′ 43.2″ S lat., 49°13′ 25.5″ E long., elevation 27 m) I found five groups of crowned lemurs and one group of Sanford's lemurs traveling together and exchanging vocalizations. The groups did not appear to be afraid of humans. Local guides also report populations of both species nearby (Figure 1, #8: 12°14′ 10″ S lat., 49°10′ 2″ E long., elevation 191 m), but this could not be verified.

Far from being limited to forests that have continuous canopy, Sanford's lemurs are now known from a number of forests that are structurally much different from the protected areas of Mt. d'Ambre, Ankarana, and Analamerana. These forests are extremely different from those that have been investigated, but polyspecific associations most likely occur throughout this region.

DISCUSSION

No matter the season or location, crowned lemurs and Sanford's lemurs associate daily. Neither species routinely led or followed the other. When associating both species were often their nearest neighbors. Short of grooming, resting, and mating with each other, both species treated each other as members of the same group. Both responded to each other's group vocalizations; neither species was the recipient of agonistic vocalizations targeted at neighboring conspecific groups. The level of association among these species is unlike most other populations of sympatric, congeneric daylight-active lemurs. In most other communities lemurs barely tolerate, displace, or chase one another. When compared with other primate associations, especially those of tamarins and guenons, the lemur associations did not occur as often, they were not permanent, and neither species routinely dominated the other (Gautier-Hion et al., 1983; Buchanan-Smith, 1999; Bicca-Marques and Garber, 2003). As in Porter (2001), associations varied seasonally in frequency; critical aspects of the lemurs' behaviors within associations did not change.

In northern Madagascar, lemurs receive at least three benefits by forming polyspecific associations. First, during the wet season, when resources are least available, both species in Ampamelonabe perhaps gain increased foraging efficiency by forming associations. Specifically, both species partition their habitat, and continue to forage throughout their home range. When resources are nearly exhausted in the middle story, the Sanford's lemurs' preferred forest level, these lemurs actively seek crowned lemurs in the understory while the latter are feeding or foraging there. This may come at some cost to crowned lemurs. They wind up losing some of their food. Yet the Sanford's lemurs never deplete the crowned lemurs' resources, so the extent to which this poses a cost to the crowned lemurs is unclear. Likewise, when resources deplete in the lower story, crowned lemurs seek Sanford's lemurs that are feeding or foraging in the middle story. Although the Sanford's lemurs may displace the crowned lemurs from certain trees, the crowned lemurs eventually get fruit from these resources simply by waiting their turn. Crowned lemurs often returned to feed on these larger, middle-story resources (e.g., *Neotina isoneura* and *Celtis gomphophylla*) when Sanford's lemurs were not present. By doing so, crowned lemurs took advantage of the limited time that tall trees bore fruit. Cords (1990) reported a similar relationship between red-tailed guenons and blue guenons. Blue guenons displaced the smaller red-tailed guenons from food trees, but the latter species fed in the food trees when the former species was not in them. For the most part, the lemurs, as do the guenons, readily consume similar food species while associating, without much interspecific agonism. In terms of costs to the Sanford's lemurs, the crowned lemurs never truly depleted the Sanford's resources. By following this pattern, both crowned lemurs and Sanford's lemurs waste little time and energy foraging for food, while not depleting their associates' resources. They continue to devote their energy to monitoring food availability throughout their range, even when resources are not readily available. In this sense, both species gain a measure of feeding and foraging efficiency by forming polyspecific associations during periods of resource scarcity.

One question that arises is whether forest productivity accurately predicts the frequency of polyspecific associations among these lemurs. For example, in Guyana Lehmann (2000) showed that plant productivity was directly related to the frequency of polyspecific associations. Among these lemurs plant productivity does not seem to predict reliably the incidence of polyspecific associations. Associations were found in both humid, highly productive forests (e.g., Ampamelonabe) and drier, smaller, much less productive forests west of Mt. d'Ambre. Temporally, the frequency of associations was inversely related to the availability of resources within the same forest. Further investigation would be needed to address this question.

Researchers have suggested that species associate to improve food acquisition. White-fronted capuchins (*Cebus albifrons*) and squirrel monkeys (*Saimiri sciureus*) may have associated with brown capuchins (*Cebus apella*) to find available resources (Terborgh, 1983). Whereas the first two species had large home ranges, brown capuchins had small ranges and were probably more aware of available resources. Blue guenons (*Cercopithecus mitis*) and gray mangabeys (*Cercocebus albigena*), species with large home ranges, initiated associations with smaller-ranged, red-tailed guenons (*Cercopithecus ascanius*) (Struhsaker, 1981). Blue guenons and gray mangabeys probably benefited from the red-tailed guenons' familiarity with resources. Red-tailed guenons probably also benefited, as gray mangabeys made available food that was otherwise too large or hard for the red-tailed guenons. Unlike these cases, the crowned lemurs and Sanford's lemurs have small, highly overlapping home ranges. Neither species has a more detailed knowledge and familiarity with the horizontal range. On the other hand, given the lemurs' year-round differences and resource partitioning, the lemurs, as do other primates, probably have different familiarity of resources in each forest level. Buchanan-Smith (1999) suggested that such vertical segregation may make more stable associations, and may increase an associate species' likelihood of finding new resources.

Both lemur species probably receive some year-round benefit as well by being able to respond to antipredator vocalizations of associates. Fossa predation of lemurs has been suspected or observed at other sites in Madagascar (Wright et al., 1997; Britt et al., 2004). At Ampamelonabe, however, all groups, whether within or outside associations, benefit from the alarm calls of other lemur groups. As soon as one group in the forest gives an alarm vocalization, the warning spreads quickly throughout the forest, within and outside associations, among both species. I observed similar alarm responses in the small forest patches west of

Mt. d'Ambre, where populations of both lemur species often exchange vocalizations at dusk and when potential predators are spotted.

As in other primate polyspecific associations, some antipredator benefit is likely obtained by associating. Unlike other primate associations, potential predators are few. The exact scope of predation pressure in Ampamelonabe is hard to determine, as predator densities are largely unknown, but is suspected to be low. In terms of predator behavior and food preferences, most potential mammalian predators of lemurs are nocturnal and were likely preying on large crested ibis. Avian predators are rare. During the day, the lemurs are rarely exposed to predators as they feed, forage, and travel, as most of these activities occur in dense cover away from any potential predator. Daylight resting perhaps exposes Sanford's lemurs somewhat more to predators, as these lemurs tended to sleep on larger main branches. They did not sleep as often as did crowned lemurs on smaller, more terminal branches. As in Bicca-Marques and Garber (2003), increased exposure to potential predators may have occurred more often during one of the lemur associates' behaviors, but too few predators were observed during the day. Potential predator protection may be a benefit, but it may not be as useful in predicting the occurrence of polyspecific associations among these lemurs. Treves (1999), for example, readily questioned the usefulness of predation as an explanatory tool to predict social systems in arboreal primates.

Both lemur species benefit socially from associations in at least two ways. First, subadults often form playgroups while adults associate during feeding or resting time. In both 1989 and 1990 groups of subadult lemurs played low in the forest for over 45 minutes, while adults rested or fed in upper forest levels. By forming associations, small groups found additional play partners, and more individuals could detect potential predators of young lemurs. Although Burton and Chan (1996) saw cross-species infant care across macaque associates, none of the lemurs ever exhibited such social behavior. A second social benefit may arise rarely when an individual leaves its group. In 1990 one adult female Sanford's lemur was spotted associating with a group of crowned lemurs for two full days after it left its original Sanford's group, and before it rejoined that group. In this case, the individual was neither dominant nor subordinate to its crowned lemur associates, nor did there seem to be any agonism directed to or from the individual.

Another hypothesis is that the groups form associations by chance alone. Given that the two species have highly overlapping home ranges, one might expect that the groups would run into each other and associate at such high levels. Waser (1982, 1984) and Whitesides (1989) derived a formula to predict the expected encounter frequencies and duration of associations. Assuming knowledge of group velocities, group radii, and densities, Whitesides (1989) calculated that Tiwai forest Diana monkeys associated less than would be expected by chance alone. Using the same formulas, Holenweg et al. (1996) found that the same species and red colobus associated more than expected by chance in Taï forest. Yet in Ampamelonabe, the Waser/Whitesides formula was inappropriate for several reasons: groups of crowned lemurs were variably spatially cohesive and often subgrouped; the breadth or spread of each crowned lemur group could not be determined reliably; and each study group associated with more than one group. I also did not monitor the precise overlap in home ranges with nonstudy groups. Each study group had a home range that overlapped with home ranges of at least seven groups of the other species. Assessments of these groups' home ranges were simply not feasible.

To some extent many of the associations may form by chance alone. In Ampamelonabe, dry season and hot season polyspecific associations seem to differ from those of the wet season in frequency. The dry season and hot season associations seem to be initiated not while lemurs are feeding, and initiators rarely leave their preferred forest level to start these associations. During these seasons, resources are much more superabundant, as *Leea spinea* is readily available throughout the forest. Perhaps resource abundance reduces the potential benefit of association. Gautier-Hion et al. (1997), for example, observed that seasonal reduction in fruit availability probably contributed to an increase in the number of polyspecific associations in black colobus monkeys.

In contrast, seasonal variation in the incidence and form of association make chance less likely an explanation for wet season associations. During this time the two lemurs associated nearly twice as often and three times as long as in other seasons. Both lemurs formed associations more readily upon meeting one another. Lemurs initiated associations from outside their preferred forest levels, and most often while associates fed or foraged. Within associations, the two lemurs were usually less than 10 m apart. Finally, groups had clear preferences as to the specific groups with which they readily associated.

Sauther (2002) suggested that polyspecific associations may have substantial benefits for species that face severe energetic demands posed by pregnancy and lactation, especially in habitats where food availability changes greatly with seasons. I was unable to test this hypothesis on crowned lemurs and Sanford's lemurs. During periods of pregnancy (the dry season) and for most of lactation (hot season), polyspecific associations formed at a fairly low rate. During these periods food was superabundant, especially the widely available *Leea spinea*. As the food became less available, both species increased the frequency of associations. Shortly afterwards females ceased lactating. For nearly the next 4 months, prior to the demands of pregnancy, foraging and feeding times increased. I saw little evidence of body size increases at this time. Yet daily path length and time spent traveling also rose during this season. Thus, energy expenditure for all individuals increased during this period.

In conclusion, a combination of these benefits likely helps explain the incidence of polyspecific associations among crowned lemurs and Sanford's lemurs in northern Madagascar. In a highly seasonal habitat, associations seem to confer better foraging and feeding efficiency during periods of resource scarcity, and may provide some subtle advantage in predator protection during certain activities. Occasionally, social benefits occur, perhaps in the formation of play-groups and also when individuals have no same-species group membership. Some associations may occur by chance alone, particularly during periods of resource superabundance. Overall, the evolutionary benefit of these associations is that both primate species flourish in habitats throughout the far northern tip of Madagascar. These habitats include forests that vary in disturbance, resource availability, and structure. By forming these associations, both lemurs can survive temporary shortages of resources, increases in potential predation and hunting, and threats from the islanding of local forests.

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CHAPTER SEVEN

Cathemerality in Lemurs

Deborah J. Curtis

INTRODUCTION AND HISTORY

The primate order has traditionally been subdivided into diurnal and nocturnal species, a dichotomy that is broadly reflected in their taxonomic division into haplorhines and strepsirhines. The former are predominantly day-active, while the latter are predominantly night-active, with notable exceptions found in both groups. The focus of this chapter will be on the strepsirhine true lemurs (Lemuridae), the majority of which are neither diurnal nor nocturnal, but exhibit a mixture of daytime and nighttime activity.

In the 1960s, Petter (1962) first noted that the activity cycles of some lemurids (*Varecia, Hapalemur, Eulemur*) were neither diurnal nor nocturnal and preferred the use of the term "crepuscular." Studies conducted both in the field and in captivity during the 1970s revealed that this activity cycle was characterized by substantial nocturnal activity, in addition to peaks of activity around dawn and dusk, and bouts of diurnal activity (Table 1). The first rigorous, longer-term observations throughout the 24-hr period were conducted on *Eulemur fulvus* ssp. by Conley (1975) in captivity and by Tattersall (1979) on Mayotte, Comoros Islands.

Tattersall did much to stimulate further research, also proposing a new term, "cathemerality" (meaning "through the day"), to describe this activity rhythm (Tattersall, 1987): "The activity of an organism may 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 traveling, occur within both the light and the dark portions of that cycle." More reports on cathemerality in lemurs appeared in the 1980s, marking the start of a plethora of studies since the 1990s (Table 1). Most notably, recent developments in technology

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Table 1. Summary of studies reporting on cathemerality in the Lemuridae in the 1970s, 1980s, and 1990s to present

Species	Reference(s)
1970s	
E. fulvus rufus	Sussman, 1975
E. f. fulvus	Harrington, 1975; Tattersall and Sussman, 1975
E. f. albifrons	Conley, 1975
Eulemur mongoz	Tattersall and Sussman, 1975; Tattersall, 1976; Sussman and Tattersall, 1976; Harrington, 1978
E. f. mayottensis	Tattersall, 1977, 1979
1980s	
Hapalemur aureus	Meier et al., 1987
E. f. rufus	Meyers, 1988
E. rubriventer	Overdorff, 1988
E. f. fulvus	Andriatsarafara, 1988
E. mongoz	Andriatsarafara, 1988
E. f. sanfordi	Wilson et al., 1989
E.coronatus	Wilson et al., 1989
E. f. albifrons	Erkert, 1989
1990s to present	
E. f. rufus	Overdorff and Rasmussen, 1995; Donati et al., 1999, 2001; Gerson, 2000; Kappeler and Erkert, 2003
E. f. fulvus	Rasmussen, 1999; Ratsirarson and Ranaivonasy, 2002
E. f. albifrons	Erkert and Cramer, 2006; Traber and Müller, 2006
E. f. mayottensis	Tarnaud, 2006
E. f. sanfordi	Freed, 1996
E. f. collaris	Donati and Borgognini-Tarli, 2006
E. f. albocollaris	Johnson, 2002
E. mongoz	Curtis, 1999; Rasmussen, 1999
E.coronatus	Freed, 1996
E. rubriventer	Overdorff and Rasmussen, 1995
E.macaco macaco	Colquhoun, 1993, 1998; Andrews and Birkinshaw, 1998
L. catta	Traina, 2001
H. griseus griseus	Santini-Palka, 1994; Ratsirarson and Ranaivonasy, 2002
H. griseus alaotrensis	Mutschler, 1998; Olivieri, 2002
H. simus	Santini-Palka, 1994; Tan in Wright, 1999
Varecia variegata variegata	Morland in Hoffmann et al., 1992; Balko in Wright, 1999

have seen dedicated long-term and continuous 24-hr recording of cathemeral activity using accelerometer/data logger devices in the field (Kappeler and Erkert, 2003; Fernandez-Duque and Erkert, 2006).

Most data on cathemerality have been collected within the framework of behavioral and ecological studies, with little research into its physiological and morphological bases. Recent research into the evolution of primate activity patterns and visual morphological adaptations gives us an insight into how lemurs cope with the different challenges posed by night and day. Visual morphologies vary between diurnal and nocturnal primates (Martin, 1990; Kay and Kirk, 2000; Heesy and Ross, 2001; Kirk, 2006). Nocturnal primates generally possess a *tapetum lucidum*, large relative orbit size, high degrees of retinal summation (large numbers of photoreceptor cells per ganglion), large curved corneas, and a high proportion of rods relative to cones, all of which increase sensitivity. Diurnal primates generally possess an *area centralis* (strepsirhines) or a *fovea* (haplorhines), small relative orbit size, low degrees of summation, small flattened corneas, and an increased proportion of cones to rods, all of which increase acuity. Cathemeral primates appear ambiguous as they exhibit a mixture of these characteristics (*tapetum* generally absent or reduced; *area centralis* present or absent; high, low, or intermediate retinal summation; intermediate cornea size/shape; intermediate rod/cone ratios). It is precisely this intermediate visual morphology that permits these primates to cope with the different demands posed by night and day (Kirk, 2006).

Cathemerality is one of a number of lemur behavioral traits found in few, if any, other primates (Wright, 1999). The only other primate that exhibits regular day–night activity is *Aotus azarai* in seasonal habitats in the New World (Wright, 1989; Fernandez-Duque, 2003; Fernandez-Duque and Erkert, 2006). In this chapter, I will investigate the following questions: What are the proximate cueing mechanisms underlying cathemerality? What is its adaptive value? How and when might cathemerality have evolved in lemurs and why did it evolve?

THE CATHEMERAL ACTIVITY CYCLE

In 1999, Rasmussen proposed a model splitting cathemerality into three modes A, B, and C (Rasmussen, 1999). All three modes exhibit peaks of activity at dawn and dusk and involve some form of mixture of diurnal and nocturnal activity across the year. Curtis and Rasmussen (2002) linked these modes to habitat types, in the light of apparent associations of modes A and B with seasonal habitats in Madagascar and mode C occurring in rainforest habitat and lake-side reed beds. However, data have recently been published which call into question any strict connection between habitat types and cathemeral modes of activity (Donati and Borgognini-Tarli, 2006).

The approach I take here describes the different modes on the basis of annual photoperiodic changes. Periods of long daylengths (austral summer) and short daylengths (austral winter) coincide approximately with the wet and dry seasons, respectively, in western Madagascar and this approach permits comparison across all habitat types, as many cannot be described by two seasons. Furthermore, there is some indication that austral spring and autumnal equinoxes (daylength equal to nightlength) might serve as the triggering mechanism for changes in the ratios of diurnal to nocturnal activity (Figure 1) (Kappeler and Erkert, 2003; Donati and Borgognini-Tarli, 2006).

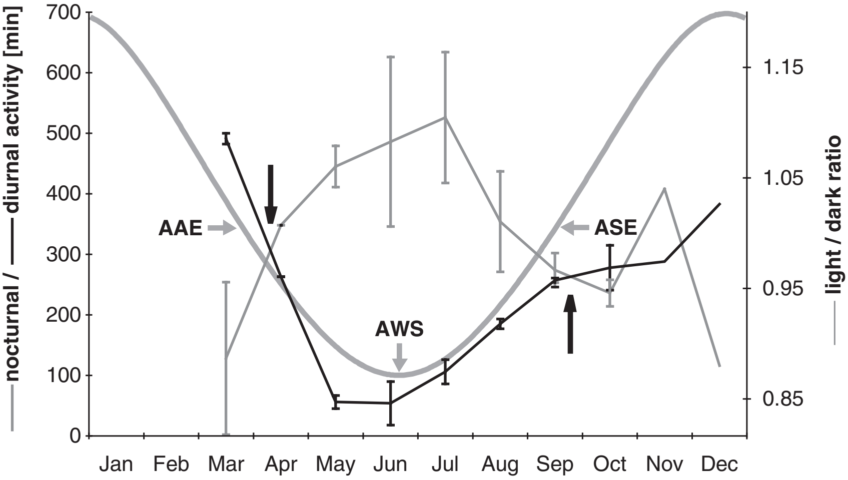

Figure 1. Variation in mean monthly nocturnal and diurnal activity (± SE) in *E. mongoz* at Anjamena, northwest Madagascar (16°03′S; 45°55′E) during a 10-month field study in 1994–1995 (Curtis et al., 1999) and annual changes in the light/dark ratio (Thomas and Curtis, 2001). Nocturnal activity is maximal and diurnal activity minimal around the austral winter solstice (AWS) when daylength is shortest. The austral autumnal equinox (AAE) occurs just prior to the shift from predominantly diurnal activity to predominantly nocturnal activity and the austral spring equinox (ASE) just before the shift back to mainly diurnal activity. The peak in nocturnal activity in November may be connected to predator avoidance, as this coincides with part of the raptors nesting period at Anjamena, low canopy cover, and the onset of infant mongoose lemurs' independent movements (Curtis et al., 1999).

Mode A describes the alternation of day (austral summer) and night activity (austral winter) and has only been observed in *E. mongoz* in the seasonally dry forests of western Madagascar (Figure 2a,b) (Tattersall and Sussman, 1975; Sussman and Tattersall, 1976; Harrington, 1978; Andriatsarafara, 1988; Curtis et al., 1999; Rasmussen, 1999, 2005). The pattern of activity peaks changes from bimodal during austral summer to trimodal during austral winter.

Mode B describes the shift from diurnal activity during the austral summer to 24-hr activity during the austral winter (Figure 2c,d) and is observed in *E. f. fulvus* and *E. f. rufus* in seasonally dry forest (Donati et al., 1999; Rasmussen, 1999; Kappeler and Erkert, 2003), *E. f. collaris* in non-seasonal littoral rainforest (Donati and Borgognini-Tarli, 2006) in Madagascar, and *E. f. mayottensis* in seasonally dry forest on Mayotte (Tarnaud, 2006). Depending on the species and study area, the activity pattern is bimodal or trimodal during the austral summer and trimodal or quadrimodal during the austral winter.

Mode C describes 24-hr activity all year round, with trimodal and/or quadrimodal activity patterns during both the austral summer and winter (Figure 2e,f). This mode is observed in *E. macaco macaco*, *E. rubriventer*, *E. f. rufus* in coastal

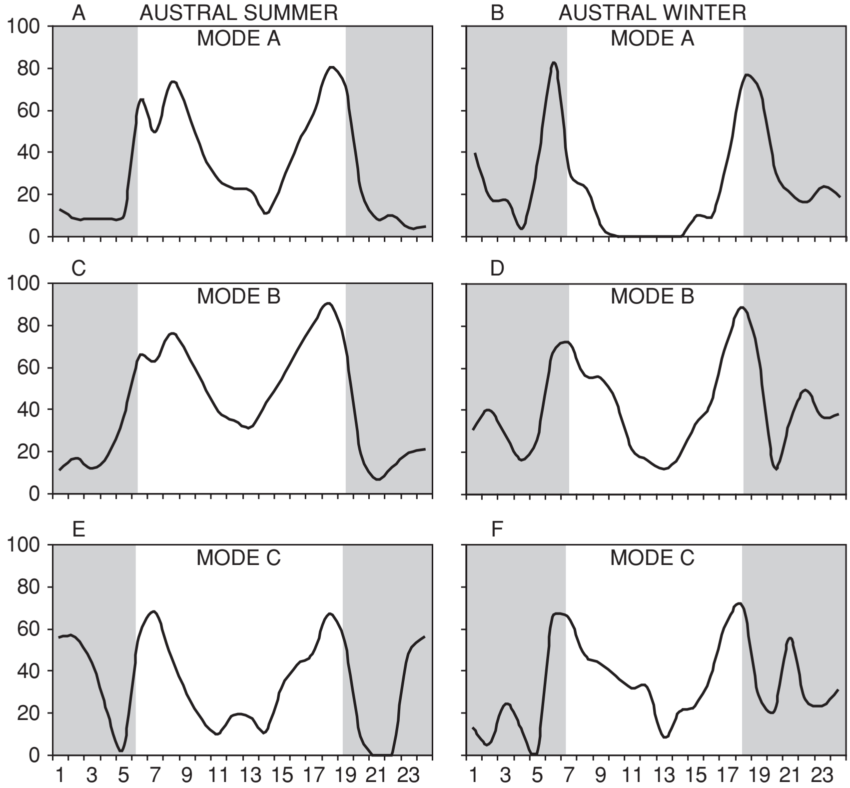

Figure 2. Schematic representations of the three cathemeral modes during austral summer and austral winter. (A, B) Mode A ($n = 2$) combines data from Ampijoroa (16°19′S; 46°49′E) and Anjamena (16°03′S; 45°55′E). (C, D) Mode B ($n = 4$) combines data from Ampijoroa, Kirindy (20°03′S; 45°55′E), Sainte Luce (24°45′S; 47°11′E), and Pointe Saziley, Mayotte (12°58′S; 45°11′E). (E, F) Mode C ($n = 1$) shows data from Andreba (17°38′S; 48°31′E). Gray areas indicate time periods before sunrise and after sunset, the times of which were taken for each location for the summer and winter solstices on December 21 and June 21, respectively, and averaged (Curtis and Rasmussen, 2002).

forests of the Sambirano region and montane rainforests (Overdorff and Rasmussen, 1995; Andrews and Birkinshaw, 1998; Colquhoun, 1998) and in *H. griseus alaotrensis* in lake-side reed beds (Mutschler, 1998). Qualitative descriptions of the activity cycle indicate that *E. coronatus* and *E. f. sanfordi* also exhibit this type of cathemeral activity in Sambirano montane rainforest (Freed, 1996).

Tattersall's definition of cathemerality holds true in the light of data collected since its publication (Tattersall, 1987). The model proposed by Rasmussen (1999) also continues to hold true when more recent data are integrated, but additional data are required to test it further and we must bear in mind that substantial variation exists within the three modes (Curtis and Rasmussen, 2002).

ENVIRONMENTAL CUEING MECHANISMS

Circadian Rhythms, "Zeitgeber," and Masking

The spontaneous period of the circadian rhythm (the internal biological clock) deviates slightly from the 24-hr day and must be synchronized each day by rhythmic environmental cues called "zeitgebers" (from German, meaning "timegiver"). Sunrise and sunset are the main "zeitgebers" that reset the biological clock to the daily light–dark cycle. Illumination, temperature, humidity, rainfall, food availability, and social factors can also entrain activity (Bartness and Albers, 2000). Only diurnal, nocturnal, and ultradian (period length significantly shorter than 24 hr) activity rhythms fulfill the criteria of "true" circadian rhythms that are controlled by one or more internal clocks (Bartness and Albers, 2000). So how can cathemerality be described in chronobiological terms?

Experiments carried out on *E. f. albifrons* indicate that cathemerality results from masking of a true nocturnal rhythm by external factors which override the endogenous clock, either stimulating or inhibiting activity (Erkert, 1989; Erkert and Cramer, 2006). The primary zeitgeber is sunset, controlling the onset of activity, and the secondary "zeitgeber" is sunrise, controlling cessation of activity. Figure 3a shows close synchronization between onset of activity and the primary zeitgeber in a nocturnal primate (*Galago moholi*), while cessation of activity and the secondary zeitgeber are less synchronized (Bearder et al., 2006). Figure 3b shows data for the cathemeral *Eulemur mongoz*, where the negative association between sunset and activity onset is greater, suggesting that sunset acts as the primary zeitgeber and confirming the inherent nocturnality of this species. Furthermore, negative associations between activity onset and cessation with sun-

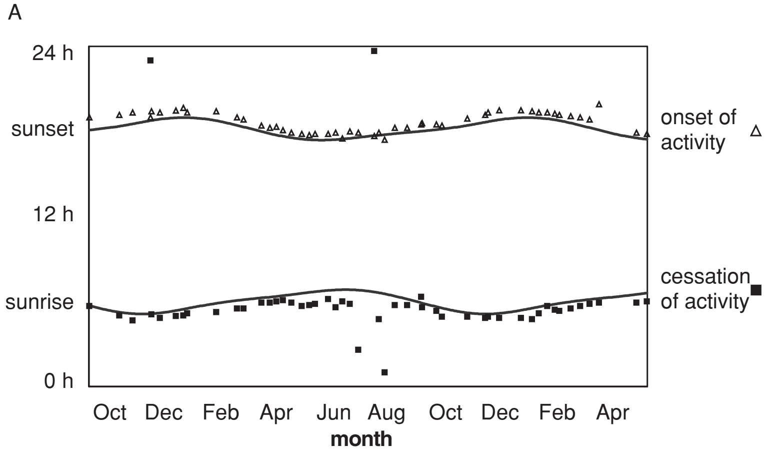

Figure 3. (A) Onset and cessation of activity in a nocturnal primate, *Galago moholi*, Mosdene, South Africa (24°35′S; 28°47′E) and their association with sunset and sunrise.

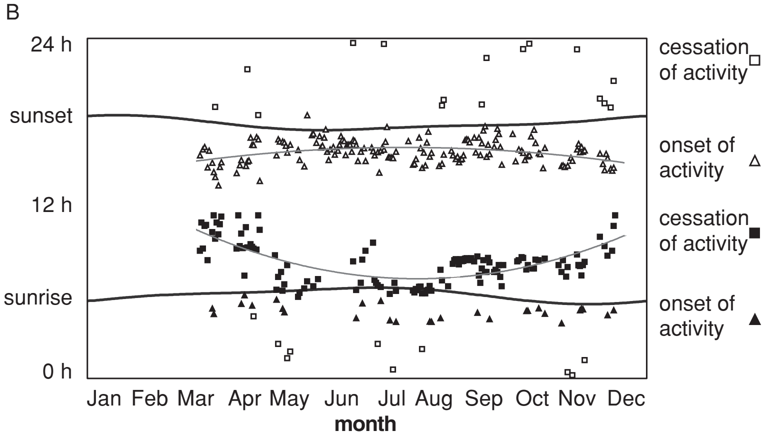

Figure 3. (*Continued*) (B) Onset and cessation of activity in a cathemeral primate, *Eulemur mongoz*, Anjamena, Madagascar (16°03′S; 45°55′E). Trendlines indicate the negative association between onset of activity and sunset in the afternoon and cessation of activity and sunrise in the morning.

set and sunrise, respectively, effectively shift the main activity phase into the night when daylength is short and the day when daylength is long (Curtis et al., 1999). Recent field data on *E. f. collaris* also report dusk acting as the primary zeitgeber (Donati and Borgognini-Tarli, 2006).

Cathemerality is an activity cycle resulting from masking of the genetically predetermined nocturnal activity rhythm. Substantial variability observed within the cathemeral activity cycle (Figure 2) in combination with the persistence of modes B and C across different habitat types and latitudes (Mode B: 12°S–24°S) indicates multiple factors modulating the endogenous rhythm.

Light Intensity

Light intensity varies greatly between day, night, and twilight periods, but also depends on cloud cover, lunar phase, and vegetation cover (Halle, 2000a). In experiments carried out on *E. f. albifrons*, activity changed through variation of the dark-phase light intensity (Erkert, 1989; Erkert and Cramer, 2006). The animals were nocturnal when subjected to full moon light intensities (10^{-1} lux), new moon light intensities (10^{-3} lux) inhibited much nocturnal activity and resulted in cathemeral behavior, and only when it was impossible for the animals to detect any light during the dark phase (10^{-7} lux; physiological darkness) were they fully diurnal.

Masking effects due to low levels of luminosity have been observed in the field in many lemurids in all habitat types and higher levels of nocturnal activity are observed around full moon, with lower levels around new moon (Colquhoun, 1998; Donati et al., 1999, 2001; Olivieri, 2002; Kappeler and Erkert, 2003; Donati and Borgognini-Tarli, 2006). Diurnal activity levels often decrease after full moon nights and increase following new moon nights (Olivieri, 2002; Donati and Borgognini-Tarli, 2006). Detailed analyses show that nocturnal activity is highest when the moon is above the horizon (waxing moon: first half of the night; full moon: all night, activity peaks during brighter middle of the night; waning moon: second half of the night) (Kappeler and Erkert, 2003; Donati and Borgognini-Tarli, 2006). The inhibitory effect of low nocturnal illumination is most dramatically reported on by Donati et al. (1999), documenting complete cessation of *E. f. rufus* activity during a lunar eclipse.

Nocturnal activity in *E. mongoz* is not affected by lunar phase, but variation in luminosity due to variable canopy cover may contribute toward an increase in diurnality when light levels are low. On Anjouan, in the Comoros, luminance was low in highland rainforests, contributing to diurnality in *E. mongoz*, while they were nocturnal at the same time of year in the brighter, seasonal environments of the lowlands (Tattersall, 1976). In Madagascar in seasonally dry forest, 10-fold less light penetrated the canopy during the wet season when *E. mongoz* was mainly diurnal than during the dry season (Curtis et al., 1999). *E. m. macaco* was more active during new moon nights during the dry season (when canopy cover was sparse) than during the wet season (Colquhoun, 1998). Kappeler and Erkert (2003) suggest better nocturnal light availability in higher forest strata may explain frequent observations of cathemeral lemurs feeding in peripheral regions of the canopy at night (Overdorff, 1988; Andrews and Birkinshaw, 1998; Curtis et al., 1999; Donati et al., 1999; Rasmussen, 2005).

Low nocturnal illumination levels are probably the most important masking factor which inhibits activity. Nocturnal activity runs parallel to the moonlit nighttime hours in most cathemeral lemurs, as well as cathemeral populations of *Aotus azarai* (Fernandez-Duque, 2003; Fernandez-Duque and Erkert, 2006)—identical to the situation documented in many nocturnal primates (Bearder et al., 2006). These lemurs are inherently dark-active (Erkert, 1989; Erkert and Cramer, 2006) and common effects of moonlight on cathemeral and nocturnal primates support this further. The effect of lunar light levels on nocturnal activity appears to be an ancient primate trait retained in many cathemeral lemurs and cannot help to further our understanding of cathemerality. A more fruitful avenue of research might be detailed investigations of the effects of light intensities due to variable canopy cover on the cathemeral activity cycle. Given the variability in the effects of illumination on activity cycles in cathemeral lemurs, other masking factors must also contribute to the production of cathemerality.

Temperature, Relative Humidity and Rainfall

Assessing the effect of climatic variables on cathemerality is problematic as they all have a seasonal component and are related to daylength as well as intercorrelated. Daylength plays a role in cathemerality (Figures 1, 2, and 3b) and in seasonal environments we would expect high rainfall, high relative humidity, and higher temperatures associated with the austral summer also to be linked to increased diurnal activity and low values for these variables during the austral winter to be linked to increased nocturnal activity. Chronobiological experiments corroborate this for temperature: According to the "circadian rule," we would expect inherently nocturnal species to be "cold-active," i.e., to increase activity at lower ambient temperatures and decrease activity when temperatures are high (Aschoff, 1979). Erkert and Cramer (2006) demonstrated this for *E. f. albifrons*, recording an increase in activity at ambient temperatures of 20°C and a decrease at 30°C.

There is a trend in *Eulemur* spp. toward diurnality with higher temperatures and nocturnality with lower temperatures in both seasonal and less seasonal habitats (Overdorff and Rasmussen, 1995; Colquhoun, 1998; Curtis et al., 1999; Donati et al., 1999; Rasmussen, 1999; Kappeler and Erkert, 2003; Donati and Borgognini-Tarli, 2006). In other cases nocturnality is associated with high temperatures (Mutschler, 1998) in lake-side reed beds (*H. g. alaotrensis*), diurnality with low temperatures in highland rainforest (*E. mongoz*) (Tattersall, 1976) or no effect is observed in rainforest (*E. rubriventer*) and seasonal habitats (*E. f. mayottensis*) (Overdorff and Rasmussen, 1995; Tarnaud, 2006). In the Neotropics, *A. azarai* increases diurnality when temperatures are low (Fernandez-Duque and Erkert, 2006).

Rainfall as a predictor of diurnal/nocturnal activity was found to be negligible in the two studies that have assessed its effects on cathemerality (Overdorff and Rasmussen, 1995; Kappeler and Erkert, 2003). Donati and Borgognini-Tarli (2006) found rainfall and humidity to be negatively associated with nocturnal activity, but link this to reduced luminosity at night during rainfall, when cloud cover is higher.

Climatic variables, in particular temperature, appear to play some role in masking the nocturnal activity rhythm in cathemeral lemurs, but no consistent pattern is discernible. More detailed data are needed to investigate the individual effects of climatic variables on cathemerality.

ADAPTIVE VALUE

Thermoregulation

Tattersall (1976) first proposed a possible link between cathemerality and ambient temperature and Morland (1993) suggested that lemurs rely primarily on behavioral, rather than strictly physiological mechanisms for thermoregulation. Cathemerality could be such a behavioral mechanism, highly advantageous in "extreme" environments and permitting the animals to shift their activity and reduce thermoregulatory costs by remaining within their taxon-specific thermoneutral zone (TNZ: range of ambient temperatures at which least energy is expended in maintenance of body temperature) (Curtis et al., 1999; Curtis and Rasmussen, 2002, 2006).

E. fulvus has a low basal metabolic rate (BMR), but high body temperature and a TNZ of 22°C to 30°C (Daniels, 1984; Erkert and Cramer, 2006). A low BMR indicates a high capacity for temperature regulation, but high body temperature rules out any capacity to lower body temperature during periods of inactivity in order to conserve energy by decreasing the temperature gradient between the environment and the body (Daniels, 1984; Müller, 1985). *H. g. griseus* has been reported to have a slightly lower and variable body temperature, which would result in a broader TNZ (Bourlière et al., 1956). No other information is available on lemurid BMR or body temperatures. If we extrapolate to other lemurids, then nocturnal activity in *Eulemur* spp. minimizes cold stress and the energetic costs of maintaining a high body temperature when ambient temperatures are below TNZ (Curtis et al., 1999). Thermoregulatory costs for *Hapalemur* spp. are lower during cold periods as they have some capacity for passive adaptation to low ambient temperatures due to their lower body temperature. Ambient temperature during hot periods is likely to create heat stress, requiring inactivity during the daytime and a shift of activity into the nocturnal phase (Mutschler, 1998).

Proposed thermoregulatory advantages to cathemerality are avoidance of heat stress during hot days or cold stress during cold nights by increasing either nocturnal or diurnal activity, but clear shifts in activity rhythms are also observed in the absence of strong seasonality in temperature. There are numerous discrepancies in the interpretation of the potential thermoregulatory advantages of cathemerality, which will only be resolved when we have more data on BMR and body temperatures in these species.

Food Availability, Diet, and Digestibility

Temporal Availability of Food Resources

Tattersall and Sussman (1975) tentatively linked nocturnality in *E. mongoz* to the temporal availability of nectar of the kapok flowers, *Ceiba pentandra*, which only open at night. Andrews and Birkinshaw (1998) found some food items to be more important either during nighttime or during daytime diets in *E. m. macaco*, but other studies on cathemeral lemurs in a variety of habitats have found few or no associations between temporal availability of food and nocturnality/diurnality (Overdorff and Rasmussen, 1995; Colquhoun, 1998; Curtis et al., 1999; Rasmussen, 1999; Tarnaud, 2006). Kappeler and Erkert (2003) suggested that a shift to diurnal activity might constitute an ecological advantage in facilitating visual detection of ripe fruit during the day, but then refuted this as unlikely since lemurs are dichromats. However, fruit consumed by lemurs is colored green, brown, tan, purplish, red (Dew and Wright, 1998). Some of these colors require only dichromatic ability for detection, so Kappeler and Erkert's suggestion might be worth further investigation.

Dietary Quality and Digestibility

Enqvist and Richards (1991) proposed a hypothesis based on the seasonal dietary shift observed in many lemurs to include more leaves in diets during periods of fruit scarcity. They suggest cathemerality is a behavioral strategy to cope with increased fiber intake employed by these small-bodied lemurs with simple digestive systems: Energy and nutrient intake is maximized by optimal spacing of food harvesting through extension of activity across the 24-hr period.

Most field data do not support their hypothesis, as either no increase in nocturnal activity is observed during the dry season (Andrews and Birkinshaw, 1998; Colquhoun, 1998) or the amount of nocturnal activity does not correlate with fibrous foods or fiber content in the diet (Overdorff and Rasmussen, 1995; Mutschler, 1998; Curtis et al., 1999; Donati et al., 1999; Rasmussen, 1999; Curtis, 2004). One study supports the hypothesis (Tarnaud, 2006), where female *E. f. mayottensis* increased mature leaf and fiber consumption during the daytime in the dry season when overall activity was extended into the nighttime. Overdorff and Rasmussen (1995) compared gut passage rate in three cathemeral frugivore-folivores (*E. mongoz*, *E. fulvus*, *E. rubriventer*) with that of a specialized folivore (*H. griseus*). Results indicate a reduced capacity for coping with fibrous foods in the former three species and as all four species exhibit cathemeral activity cycles, the link between cathemerality and the consumption of fibrous foods is not supported. Evidence from studies on molar morphology and digestibility of fibrous material discussed by Overdorff and Rasmussen (1995) indicates that increased fiber intake would not pose any particular problem for nonspecialist lemurids.

Predation

Cathemerality has been proposed as a mechanism to avoid predators and to minimize the risk of predation (Curtis and Rasmussen, 2002; Rasmussen, 2005; Colquhoun, 2006). Raptors, viverrids, boids, and crocodylids have been documented as predators on lemurids (Goodman et al., 1993). The greatest threat, however, is presumed to be posed by the largest living Malagasy carnivore (6.75 kg), the cathemeral fossa (*Cryptoprocta ferox*), which exhibits varying degrees of arboreality, depending on habitat (Hawkins, 2003; Colquhoun, 2006).

Cathemeral lemurs often feed and travel higher up in the canopy at night than during the day and this has been interpreted as a strategy for predation risk minimization, as feeding in exposed parts of the canopy is safest at night when raptors are inactive (Overdorff, 1988; Andrews and Birkinshaw, 1998; Curtis et al., 1999; Donati et al., 1999; Rasmussen, 2005). Feeding and traveling high in the canopy at night may also help avoid threats from below, mainly posed by the fossa. *Cryptoprocta* is highly adapted for arboreal locomotion, but is less adept at moving about in the highest strata of dry forests (Hawkins, 2003) and would be restricted in access to small, peripheral branches of the canopy in all forest types due to its body size. Data on *E. mongoz* demonstrate how the capacity to shift between the diurnal and nocturnal phases of the day might aid in predator avoidance when infants are beginning to move about independently and are most vulnerable to predation by raptors (Figure 1). Other studies have reported no connection between cathemerality and predation: For example, Tarnaud (2004) observes that there are few predators on Mayotte and yet *E. f. mayottensis* is still cathemeral.

Cathemeral species cannot completely eliminate predation risk by shifting activity into either the nocturnal or diurnal phases. Slight adjustments in activity times may, however, be effective in combination with other antipredator behaviors and when the behavior and ecology of predators and other prey species are considered (Rasmussen, 2005). Effective group size is increased in some sympatric pairs of *Eulemur* species through polyspecific associations (Harrington, 1978; Freed, 1996) and increases protection from predation (van Schaik and van Hooff, 1983). Rasmussen (2005) proposed that small group size and cryptic habits in *E. mongoz* may reduce diurnal predation risk from raptors and *Cryptoprocta ferox* during the wet season. This strategy would offer less protection from raptors during the dry season when canopy density is lower so shifting activity to the nighttime could be beneficial. *Cryptoprocta ferox* poses a year-round threat that may be reduced by the different patterns of cathemeral activity exhibited by sympatric species or by the same species at different times of the year, making it difficult for this predator to optimize foraging times. Increased availability of more conspicuous and/or abundant prey species may also relax predation pressure by *Cryptoprocta ferox* on lemurs at certain times of the year (Rasmussen, 2005).

Interspecific Competition

Cathemerality may be one of many factors reducing competition between sympatric species and contributing toward niche separation (Rasmussen, 1999; Curtis and Rasmussen, 2002, 2006). The temporal dimension of niche separation has been neglected and merits further attention (Halle, 2000a). Competition, like predation pressure, is difficult to assess and relationships between resource competition and activity rhythms in primates are equivocal based on studies carried out to date.

The only detailed investigation of niche separation in lemurs found that microhabitat structure and food chemistry separated seven species of sympatric lemurs in rainforest habitat (Ganzhorn, 1989). The two cathemeral species in the area were *E. fulvus* and *H. griseus*, which exhibit little overlap in diet. In contrast, giant bamboo comprises 72–95% of the diets of three sympatric *Hapalemur* spp. in rainforest (Tan, 1999) and the temporal dimension may be an important factor in the coexistence of these lemurids. *Hapalemur simus* has been described as nocturnal or cathemeral, *Hapalemur griseus griseus* as diurnal or cathemeral, and *Hapalemur aureus* as cathemeral (Wright, 1986; Meier et al., 1987; Wright et al., 1987; Santini-Palka, 1994; Ratsirarson and Ranaivonasy, 2002; Mutschler, personal communication), but the activity cycles of these species have yet to be investigated in detail in the wild. For *E. mongoz* in seasonal forests, the most important potential primate competitor was *E. f. rufus* as it not only shared food resources, but also exhibited a similar activity pattern. Therefore, I predicted that for cathemerality to have any function in niche separation, different types of cathemerality would have to exist (Curtis, 1997). This was confirmed by Rasmussen (1999) (Figure 2), who found high levels of spatial and dietary convergence, but distinct patterns of cathemerality that allowed *E. mongoz* and *E. f. fulvus* to shift peak feeding times and minimize competition. In contrast, no differences were discerned in cathemeral activity patterns in eastern rainforests in *E. rubriventer* and *E. f. rufus*, where the two species exhibited little dietary divergence, apart from during periods of food scarcity (Overdorff, 1993). In Sambirano rainforests, Freed (1996) found remarkably similar diets in *E. coronatus* and *E. f. sanfordi*, which also exhibited the same type of cathemerality. The significance of competition in shaping cathemeral activity rhythms in *Eulemur* species is even less clear for those populations that do not co-occur with a congener (Donati et al., 1999; Kappeler and Erkert, 2003; Donati and Borgognini-Tarli, 2006; Tarnaud, 2006).

Tattersall and Sussman (1998) note the overall tendency for pairs of *Eulemur* species to co-occur in northern Madagascar. They suggest that the variation in the activity cycle observed in these morphologically and ecologically similar species may have been an important factor in maintaining sympatry in a number of different habitats. However, evidence from the field is inconclusive and the only indication of a potential link between cathemerality and interspecific competition stems from seasonal forest habitat in Madagascar, where modes A and B have been observed (Figure 2).

CATHEMERALITY IN CONTEXT—DAY–NIGHT ACTIVITY IN OTHER MAMMALS

Day–night activity is widespread in mammals (16 of 24 orders) and common in the artiodactyls, perissodactyls, carnivores, rodents, and monotremes, but rare in primates (2 of 14 families). Day–night active mammals inhabit environments ranging from aquatic to terrestrial, arctic to tropical, forest to desert and are exposed to enormous variability in environmental pressures (Curtis and Rasmussen, 2006). Halle and Stensteth (2000) state this flexibility may (1) permit avoidance of unfavorable environmental conditions; (2) minimize competition; (3) maximize reproductive success; (4) increase predator efficiency; and (5) reduce predation risk. I will elaborate only on those points that permit comparisons between cathemeral primates and other mammals.

Environmental Conditions

Luminosity

High nocturnal luminance suppresses nocturnal activity in most small non-primate mammals, but either enhances or has no effect on nocturnal activity in primates (Bearder et al., 2006; Curtis and Rasmussen, 2006). Large-bodied cathemeral mountain tapirs (Tapiridae) exhibited high levels of nocturnal activity only during full moon nights in primary rainforest, but showed no differences in less dense secondary forest (Lizcano and Cavelier, 2000). This masking effect of low light intensities in dense canopy forest is similar to that proposed for many cathemeral primates.

Possible advantages of activity during periods of higher illumination need to be counterbalanced by the potential for increased predation risk, but many nocturnal primates are themselves visually oriented predators and increased luminosity may aid them in hunting (Bearder et al., 2006). Cathemeral lemurs are prey species rather than predators, but foraging may also be facilitated by higher light levels (Kappeler and Erkert, 2003).

Temperature and Thermoregulation

Daily and annual changes in temperature lead to shifts from one temporal niche to another in many groups of mammals (Curtis and Rasmussen, 2006). Large-bodied herbivores inhabiting arid, hot environments reduce heat stress by being active at night (Grenot, 1992). Sloths (Bradypodidae) are nocturnal when temperatures are high and diurnal when temperatures are low, counteracting thermoregulatory constraints imposed by ineffective body temperature control (Chiarello, 1998). Likewise, echidna (Tachyglossidae) is nocturnal when it is hot and cathemeral when it is cold due to thermoregulatory constraints (Abenspergtraun and Deboer, 1992). Many arctic mammals reduce thermoregulatory costs by shifting to diurnality during cold winter months (Zielinski, 2000). These examples cover a wide range of body sizes and BMRs (Müller, 1985; Martin, 1990), but reveal a trend toward nocturnality in cathemeral mammals when temperatures are high. When temperatures are low, a variety of strategies are exhibited, ranging from diurnality to mixed day–night activity.

These strategies are mirrored to some extent in cathemeral primates: *A. azarai* conserves energy through increased diurnal activity during the cold winter (Fernandez-Duque and Erkert, 2006), resembling sloths, echidna, and arctic mammals. Like sloths and terrestrial herbivores, *H. g. alaotrensis* may reduce heat stress by increasing nocturnality during periods of high temperatures (Mutschler, 1998). The idea that *Eulemur* may reduce cold stress through increased nocturnal activity is not supported (Curtis and Rasmussen, 2002). However, BMR is determined not only by body mass, but may vary according to ecological demands

(Müller, 1985). Strepsirhine BMRs are 30–60% below the mammalian mass-specific standard (Müller, 1985) and this group might exhibit thermoregulatory strategies not present in other mammals. Comparative research on mammals assessing links between body size, physiological variables (BMR, body temperature, TNZ), ecology, and activity rhythms is needed to resolve this, for which further physiological data are required.

Predation Risk

Analysis of the pattern of predation risk throughout the 24-hr day requires consideration of the pooled activity patterns of the entire predator community (Halle, 2000a). Cathemeral mammalian predators often vary diurnal and nocturnal activity levels to maximize access to diurnal, nocturnal, and cathemeral prey, and prey species also exploit temporal strategies to avoid predation (van Schaik and Griffiths, 1996; Zielinski, 2000; Hawkins, 2003). Studies on nonprimate mammals indicate that cathemerality may be effective in minimizing predation risk, can be dependent on habitat structure, but sometimes occurs only in the absence of predators, or, due to their presence.

Mustelids exhibit a tendency toward cathemerality with increasing body size in temperate regions: Small species vulnerable to predation by diurnal raptors are almost exclusively nocturnal and larger species increase diurnality to avoid predation by nocturnal foxes (Canidae) (Zielinski, 2000). Subtropical ursids exhibit intraspecific differences and smaller females and subadults avoid large nocturnal predators (felids) through shifting most activity into the diurnal phase (Joshi et al., 1999). Microtine rodents show an 18-month periodicity in diurnality, which results in predators having no predictable seasonal pattern to which their activity can be adapted. Furthermore, as these rodents are heavily predated on by diurnal raptors a tendency toward increased nocturnality was observed, the more open the habitat became (Halle, 2000b). Diurnal activity in the cathemeral tree hyrax (Procaviidae) in montane tropical forests and cathemeral fruit bats (Pteropodidae) on Pacific islands is probably only possible due to the absence of large avian predators (Milner and Harris, 1999; Brooke, 2001). Nocturnality in cathemeral sloths (Bradypodidae) in some areas may be a response to the presence of large diurnal avian predators (Chiarello, 1998).

Suggested links between cathemerality and predation in primates mirror the functional interpretations of temporal shifts in other mammals. In seasonal habitats, cathemeral lemurs can minimize predation by raptors by moving into the nocturnal phase when canopy cover is sparse, as well as by avoiding exposed areas of the canopy during the day (Overdorff, 1988; Andrews and Birkinshaw, 1998; Curtis et al., 1999; Donati et al., 1999; Rasmussen, 2005). Temporary shifts to nocturnal activity, as exhibited by *E. mongoz* when infants are vulnerable (Figure 1) (Curtis et al., 1999), demonstrate the link between body size and activity observed in some other mammals. Different cathemeral activity patterns in sympatric lemurs may also serve as a "predator confusion strategy," making it difficult for the cathemeral *Cryptoprocta ferox* to optimize its foraging times. Finally, in the Neotropics Wright (1989) suggested that *Aotus azarai* might shift activity to the daytime to avoid predation by the great horned owl (*Bubo virginianus*), but long-term data collected by Fernandez-Duque (2003) provide no support for a link between cathemerality and predation.

Interspecific Competition

The temporal dimension plays a role in niche separation in a number of mammalian species. Studies on carnivores (Mustelidae) in temperate regions and rodents (Muridae and Heteromyidae) in desert habitat emphasize this, and sympatric rodents compete for the most attractive time window, with the dominant species monopolizing preferred portions of the 24-hr period (Halle and Stensteth, 2000; Ziv and Smallwood, 2000; Jones et al., 2001; Marcelli et al., 2003). In temperate regions, sympatric microtine rodents (Muridae) avoid interference competition by fine-tuning activity to different times of the day and night (Halle, 2000b). Finally, Jácomo et al. (2004) found that three cathemeral canids in a seasonal tropical environment exhibited significantly different activity patterns, contributing toward niche separation.

Variation in the cathemeral activity pattern in pairs of *Eulemur* species in seasonal forests in Madagascar may also reduce interference competition (Curtis, 1997; Rasmussen, 1999). Curtis and Rasmussen (2006) proposed that the dominant *E. fulvus* might occupy the more attractive time windows, with the sympatric subordinate species (e.g., *E. mongoz*) adjusting activity to less favorable times, as observed in several sympatric rodents. In eastern rainforests, three sympatric species of *Hapalemur* that exhibit high dietary overlap may avoid competition through activity during different temporal phases (Tan, 1999). In the Neotropics, Wright (1989) suggested that the absence of competition for resources from diurnal monkeys (e.g., *Callicebus*) might result in cathemeral activity rhythms in *Aotus*.

EVOLUTION OF CATHEMERALITY

Two hypotheses have been proposed to explain the evolution of cathemerality in lemurs. The Evolutionary Disequilibrium Hypothesis (EDH) states that cathemerality is of recent origin, representing a transitional stage between nocturnality and diurnality and the result of evolutionary disequilibrium caused by the relatively recent extinction of large-bodied lemurs and large aerial predators (Martin, 1972; Tattersall, 1982; van Schaik and Kappeler, 1996). The second hypothesis proposes cathemerality is more ancient and a stable strategy that may be ancestral for the genus *Eulemur*, or the entire lemurid clade and may have contributed to the radiation of the numerous lemurid taxa in Madagascar (Tattersall, 1982; Tattersall and Sussman, 1998; Curtis and Rasmussen, 2002, 2006).

Evolutionary Disequilibrium Hypothesis (EDH)

EDH argues that ecological release has led to the evolution of cathemerality and diurnality in lemurs (van Schaik and Kappeler, 1996). In the Neotropics, Wright (1989) suggests that *A. azarai* is cathemeral as a result of either ecological release from competition or predation pressure, which is allied to the proposals of the EDH. This is supported by studies on other cathemeral mammals, such as sloths, tree hyraxes, and fruit bats that document diurnality in the absence of aerial predators (Chiarello, 1998; Milner and Harris, 1999; Brooke, 2001), as well as observations on cathemeral lemurs which shift to nocturnality when canopy cover is low and provides little protection from raptors (Overdorff, 1988; Curtis et al., 1999; Donati et al., 1999; Rasmussen, 2005). EDH is not so well supported when we evaluate current predation pressure and competition in the light of the possible situation in the past in Madagascar.

Raptors are present today and exert substantial pressure on day-active lemurs (Goodman et al., 1993). Predator pressure from raptors in the past was probably no higher than today and large aerial predators may have become extinct due to the extinction of their main prey item, the large subfossil lemurs (Goodman, 1994; Wright, 1999). Equally, predation pressure from the cathemeral *Cryptoprocta ferox* is unlikely to be any higher than in the past, when a substantially larger extinct species (*Cryptoprocta spelea*) probably preyed on lemurs (Goodman et al., 2004; Colquhoun, 2006). Recent data on the activity and ecology of *Cryptoprocta ferox* (Hawkins, 2003) indicate that the predation risk posed by this carnivore is possibly far higher for cathemeral lemurs than predation risk from aerial predators. Colquhoun (2006) suggests that cathemeral lemurs were present on Madagascar prior to the arrival of the first carnivores, 24–18 MYA (Yoder et al., 2003), and that cathemerality may have evolved in *Cryptoprocta* as a direct response to the activity rhythm of these prey species. Were this the case, then predation could not have been pivotal in the evolution of cathemerality, but might play a role in the different modes of cathemerality in lemurs, which may aid in "confusing" the cathemeral viverrid.

Ecological release from competition seems equally unlikely to have played a role in the evolution of cathemerality, as there is little evidence the extinction of large-bodied lemurs led to vacation of niches now occupied by cathemeral lemurs: Subfossil lemurs were generally much larger than extant lemurs and mainly folivores or seed predators (Godfrey et al., 1997; Rafferty et al., 2002) that would not have competed with smaller-bodied cathemeral frugivore-folivores or bamboo specialists. *Archaeolemur* was probably adapted to a varied and eclectic diet and might therefore have competed with extant cathemeral frugivore-folivores. However, spatial separation would have sufficed to reduce any potential competition as the large-bodied archaeolemurids are described as more terrestrial than any living lemur (Rafferty et al., 2002). Charles-Dominique (1975) proposed that in the tropics in Africa and the New World every forest econiche can accommodate one nocturnal and one diurnal species and Curtis and Rasmussen (2006) suggest that this might be extended in Madagascar to a third sympatric species for each econiche, namely, a cathemeral species.

Ancient and Stable Strategy

Recent genetic and visual morphological data support an ancient origin of cathemerality in lemurs, as does the greater picture when the adaptive origins of primates and cathemerality in nonprimate mammals are taken into consideration. Genetic data suggest a common ancestry of diurnality and cathemerality in the indriids and lemurids dated between 32 and 52 MYA (Roos et al., 2004). Morphological evidence corroborates this, as the eye morphology of the *Eulemur* clade is intermediate between diurnal and nocturnal strepsirhines and based on this Kirk (2006) proposes that cathemerality characterized their common ancestor, 8–12 MYA (Yoder and Yang, 2004). Visually intermediate characteristics between nocturnal and diurnal morphology are found across the mammals in cathemeral species, leading Kirk (2006) to suggest the convergent evolution of cathemerality in many mammalian clades.

The ubiquity of day–night activity across mammals provides further evidence that this type of flexibility is probably ancient in origin. Day–night activity is present in many types of environment, at different trophic levels in both generalists and specialists, as well as in prototherian, metatherian, and eutherian mammals (Curtis and Rasmussen, 2006). There also appears to be a trend in mammals from nocturnality to mixed day–night activity with increasing body size and at different trophic levels, as shown, for example, for both herbivores and carnivores (Belovsky and Slade, 1986; Zielinski, unpublished data cited in Zielinski, 2000). This is of relevance given recent estimates of body mass in ancestral primates by Soligo and Martin (2006), suggesting that the last common ancestor of extant primates weighed around 1 kg and hence subsisted on fruit in combination with either insects or leaves. Soligo and Martin (2006) suggest that the cheirogaleids represent a dwarf lineage within the lemurs. By extension, this implies a larger body size in the common ancestor to the lemurids and indriids, if not the common ancestor to all lemurs, and hence the possibility for day–night activity.

Predictable and Unpredictable Environments

Wright (1999) and Ganzhorn et al., (1999) have suggested that the unpredictability of the environment on Madagascar may have played a crucial role in lemur evolution and explain many of the traits we see in lemurs which are absent from primates in other tropical habitats. Such unpredictability may be implicated in the evolution of cathemerality in lemurs, but also in *A. azarai*, which inhabits a marginal environment for primates—outside the tropics, highly seasonal and characterized by pronounced changes in temperature. Fernandez-Duque (2003) interprets cathemerality as a thermoregulatory response in *A. azarai* to inhabiting the higher, cooler latitudes of the Argentinian Chaco.

Halle (2000a) suggests that in a highly predictable environment, a genetically fixed temporal program probably constitutes an evolutionary stable strategy (ESS), as it guarantees that activities will be performed at the optimal time of the day. This is not possible in an unpredictable environment where direct responses to environmental variation are required for survival and hence fixed programs are useless. The island environment of Madagascar is unstable, with frequent catastrophic climatic events such as cyclones and droughts in combination with low soil fertility and variability in peaks in abundance and scarcity of foods consumed by lemurs (Ganzhorn et al., 1999; Wright, 1999). While cathemerality is not genetically fixed, it may have evolved as a response to this unpredictability, forcing the ancestors of the extant lemurids away from their biologically inherent nocturnal cycle of activity (Bearder et al., 2006). Alternatively, should this flexibility have already been present in the ancestral lemurs, they would have been well equipped to deal with the unpredictable environment, having the capacity to shift between temporal niches in response to environmental variation.

CONCLUSIONS

It will have become clear in this chapter that there is no unitary explanation for cathemerality in lemurs, but that numerous factors combine to mask the endogenous nocturnal rhythm, dominated by abiotic variables but also ranging from predation through temporal niche separation. The unpredictability of the island environment probably plays an important role in the presence of cathemerality in primates on Madagascar. The ubiquity of day–night activity across the mammals suggests that such flexibility is deeply rooted in mammalian history (Curtis and Rasmussen, 2006). Kirk (2006) suggests convergent evolution of day–night activity in many mammalian orders (also in the Lemuridae and Aotinae). A more parsimonious solution is that the ability of an essentially dark-active mammal to shift some or all of its activity into the diurnal niche may be an ancient mammalian characteristic (Curtis and Rasmussen, 2006). The ancestral lemur is assumed to have been nocturnal (Martin, 1990), but might have displayed this flexibility, facilitating the emergence millions of years ago of cathemerality and diurnality we see today. Regardless of how and when day–night activity evolved, we still have much to learn through further data collection on chronoecology, morphology, and physiology, which will increase our understanding of the underlying proximate mechanisms and the function of this activity cycle and, ultimately, its evolution.

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CHAPTER EIGHT

Adaptations in the Aye-aye: A Review

Eleanor J. Sterling and Erin E. McCreless

INTRODUCTION

The aye-aye is one of the most unique primates in the world. In 1863, Richard Owen, foreshadowing contemporary intelligent design arguments, posited that the aye-aye's unique qualities provided clear evidence that Darwin's theory of natural selection must be wrong (Owen, 1863). Owen, the most eminent British anatomist of his time, detailed the aye-aye's distinctive dental and digital morphology, briefly described how naturalists at the time thought the animal uses these morphological features to acquire food, and concluded that only God could have created an animal so well adapted to its environment. Indeed, the aye-aye has a number of morphological traits that set it apart from other primates and allow it to exploit resources unavailable to most other animals in Madagascar (Figure 1). It also exhibits behavioral characteristics that distinguish it from most other lemurs. Recent research on aye-ayes has begun to overcome obstacles to observing these animals and has started to shed light on the mysterious social habits of this species. As we learn more about the aye-aye, we find more ways in which it is similar to other lemur species, as well as the ways in which it is different.

The aye-aye's unusual morphological characteristics generated a century of controversy, beginning with its introduction to Western science in the 1780s (Sonnerat, 1782), on whether to place *Daubentonia* within the primates, the rodents, or even the marsupials (Sterling, 1994c). Owen's definitive study of aye-aye anatomy (Owen, 1866) finally quelled the debate over the species' taxonomic

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Figure 1. Drawing of a female aye-aye, based on an animal living in the Gardens of the Zoological Society of London, 1862. Drawing by J. Wolf (Owen, 1866).

position, focusing attention away from the animal's rodentlike anterior teeth and towards its primatelike characteristics, such as a postorbital bar, stereoscopic vision, and an opposable hallux (Figure 2). Although its placement within the primates is still being debated, *Daubentonia* is considered a member of the family Indridae (Schwartz, 1986); as a sister taxon to the other Malagasy primates (Pastorini et al., 2002, 2003; Yoder et al., 1996a,b); and as the most basal branch of the strepsirrhines (Delpero et al. 2001; Groves, 1990).

The only living representative of the family Daubentoniidae, the aye-aye is the only primate to have claws on all digits but the thumb, a nictitating membrane ("third eyelid"), and abdominal mammary glands. With a length of 80 cm from nose to tail and a weight of 2.5–3 kg, *Daubentonia* is the largest nocturnal primate species in the world. A distinctive dental formula of 1/1 incisors, 0/0 canines, 1/0 premolars, and 3/3 molars includes incisors that grow continuously like those of a rodent. The aye-aye is probably best known for its slender middle finger, in which modifications to the metacarpal provide extra flexibility in the joint and make the finger appear especially long.

DIET

Many of the aye-aye's adaptations, especially its chisel-like front teeth and probelike middle finger, enable it to gain access to structurally defended food resources that are unavailable to most of the vertebrates in Madagascar (Table 1).

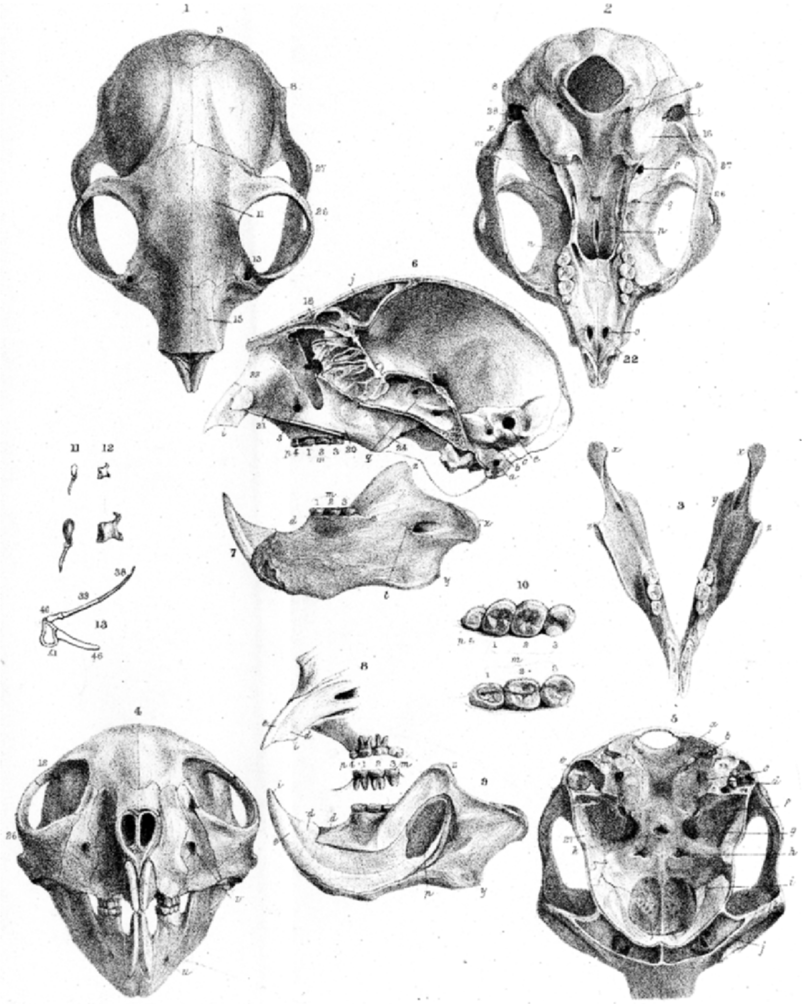

Figure 2. Detailed anatomical drawings of the aye-aye's skull and dental characteristics. Drawings by J. Erxleben (Owen, 1866).

The only long-term study of wild aye-ayes to date was undertaken from 1989 to 1991 on the island of Nosy Mangabe, located off the northeastern coast of Madagascar. This study found the aye-aye's diet to consist of items from three main food types: seeds, fungi, and larvae (Sterling, 1994a). Aye-ayes spent over 90% of their feeding time on only four foods: *Canarium* (Burseraceae) seeds, larvae, cankers from the *Intsia bijuga* cambial layer, and nectar (Figure 3). In the wild, aye-ayes have also been seen to consume seeds of other fruits such as the palm *Orania trispatha* and the tropical almond, *Terminalia catappa*; adult ants;

Table 1. Use of morphological characters for food acquisition by aye-ayes for different food resources (Sterling, 1994a). Used with permission from S. Karger AG, Basel.

Food resource	Incisors	Middle finger
Seeds	Superior incisors are set mid-endocarp and inferior incisors gnaw into endocarp	Scrapes out cotyledon
Canker	Superior incisors serve as point of leverage as the inferior teeth scrape the growth	
Nectar		Inserts finger into flower and brings nectar to mouth with rapid back-and-forth movements
Larvae	Pries off cambium on surface of tree or liana or gnaws into seed	Inserts finger in channel and retrieves larva
Adult insect		Raises ant with middle finger and flicks it into open mouth
Fungus	Scrapes fungus off stem of inflorescence	

a spongy fungus growing on the stems of *Macaranga cuspidata*; and various cultivated crops, including coconuts, litchis, and mangos.

Two species of *Canarium* grow on Nosy Mangabe, one found at the island's higher elevations, from 250 m to 331 m above sea level, and the other found

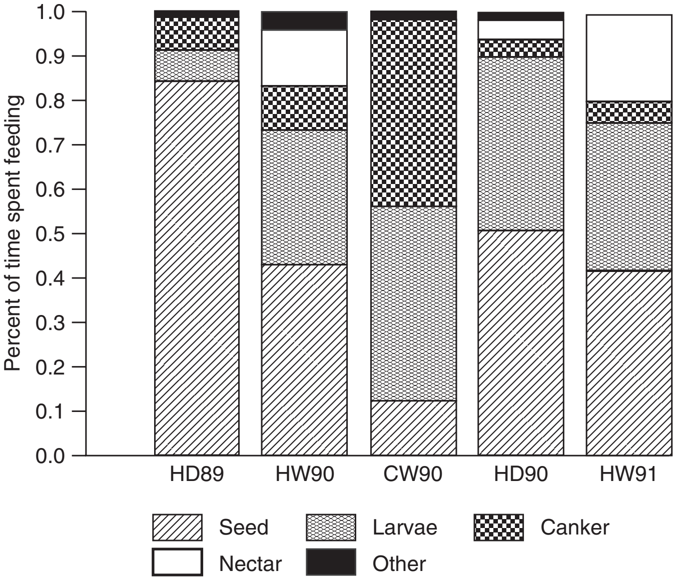

Figure 3. Overall percentage of time spent feeding on different dietary items by season for aye-ayes on Nosy Mangabe from November 1989 to April 1991. Averages of six individuals were used to calculate seasonal means. Seasons are: hot, wet (HW); cold, wet (CW); and hot, dry (HD). Seeds = *Canarium* spp., *T. catappa*; other = fungus, ants, unidentified food sources (Sterling, 1994a). Used with permission from S. Karger AG, Basel.

below 250 m above sea level. Aye-ayes eat *Canarium* seeds by removing the endocarp with their long anterior teeth and then extracting the cotyledon with their slender middle finger (Iwano and Iwakawa, 1988). Individual trees of both species are large-crowned and abundant on the island, and one study showed the lowland *Canarium* species to have the third-highest stem density of all the plants sampled (Sterling, 1994a). Aye-ayes sometimes spent more than 30% of their feeding time consuming *Canarium* seeds, and they appeared to prefer fruits of the lowland species when they were available. Fruit from one species or the other is available throughout the year, although both are less abundant during the coldest of the three seasons. The preferred lowland species is less common during the wet, hot season, causing aye-ayes to turn to fallen, and to a lesser extent, upland *Canarium*.

To gain access to another of their preferred foods, aye-ayes remove cankers from a leguminous tree, *Intsia bijuga*, and then scrape a waxy substance from the underlying cambium with their anterior teeth. The growths are found most commonly on secondary branches and on trunks with more exposure to light and air; it is either a fungus or a gall, but botanists, entomologists, and local forest specialists have not been able to identify it further. This resource is patchily distributed and is restricted to lower elevations on Nosy Mangabe (less than 270 m above sea level). Aye-ayes eat this food most frequently during the cold season, when *Canarium* fruits are less abundant.

Nectar from *Ravenala madagascariensis* (Strelitziaceae) flowers provides a high-energy food source for foraging aye-ayes. The animals scoop the viscous liquid out of the flowers with rapid back-and-forth movements of their thin middle finger. *Ravenala* inflorescenses are few per tree, but the trees are often clumped together in groups of 3 to 12. On Nosy Mangabe, they tend to be most common at higher elevations. In addition, aye-ayes open *Ravenala* fruits to access an unknown food source inside the fruit. The fruit contains seeds that are about 2 cm in length and covered with a blue aril, but aye-ayes do not eat these. Aye-ayes probably open the fruit to reach insects from a diverse array of families (Bruchidae, Pyralidae, Cerambycidae, and Tenebrionidae) that can be found inside the fruits in both adult and larval forms. Larvae (Diptera) have also been found in the *Ravenala* nectar that aye-ayes exploit.

The aye-aye is well-known for its ability to locate and extract wood-boring larvae from several different families with a characteristic behavior called tap-foraging. As it moves along wood surfaces, the aye-aye taps the wood with its middle finger, keeping its nose near the wood and its large ears pointing forward. When it senses a cavity, the aye-aye anchors its upper incisors in the wood and uses the scooping action of its lower incisors to gouge a pit. Larvae from a diverse array of families (Cerambycidae: Lamiinae, Prioninae; Scarabidae: Dynastinae; Passalidae; Pyralidae: Phycitinae) are retrieved from the cavity and brought to the mouth with the slender middle finger (Figure 4). Rich sources of larvae include fallen dead wood, dead branches on a living tree, living trees, dead and living lianas, the underside of bark on living trees, and the insides of bamboo stalks and parasitized seeds. Aye-ayes extract larvae from dead trees, lianas, and the bark of live trees

Figure 4. Drawing of an aye-aye foraging for wood-boring larvae. Drawing by J. Wolf (Owen, 1866).

more often than from any other host types, and they are known to remove larvae from at least 29 different tree species (Figure 5). The periodicity of larval resources is difficult to measure, but large larvae have been found in the bark of medium- to large-sized *Canarium* trees during every month of the year. Bark beetle larvae that live under the first centimeter of bark are also available year-round. Density of larvae resources appears to be high, as aye-ayes eat larvae from beneath the bark of several species that have high stem densities in the forest. Although aye-ayes eat a wide variety of foods throughout the year, insects may represent a stable resource during times when the availability of other resources fluctuates more.

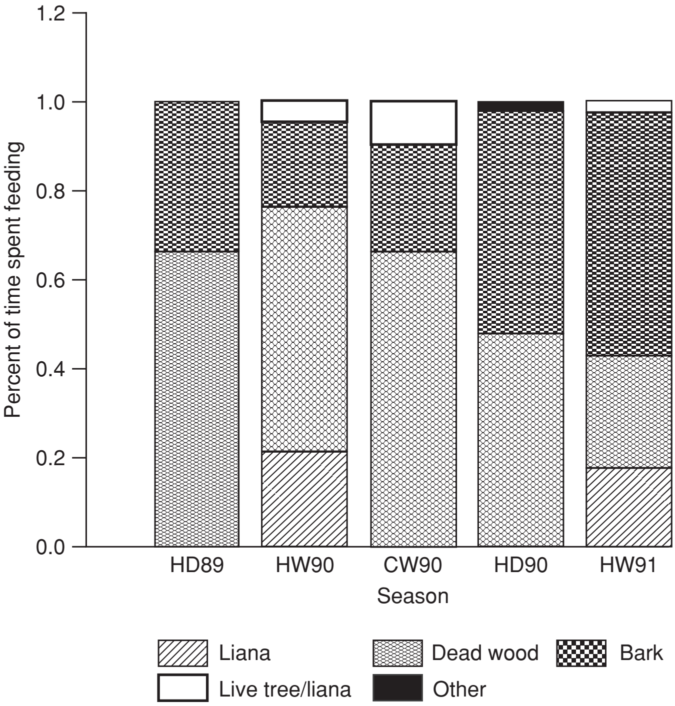

Figure 5. Overall percentage of time spent feeding on larvae from different sources by season for aye-ayes on Nosy Mangabe from November 1989 to April 1991. Averages of six individuals were used to calculate seasonal means. See Figure 3 for sample sizes and abbreviations (Sterling, 1994a). Used with permission from S. Karger AG, Basel.

Morphology and Feeding Adaptations

Many of the aye-aye's preferred foods are highly structurally defended. The animal's long anterior teeth and slender middle finger provide access to foods that are difficult for many of its competitors to reach. Feeding on wood-boring larvae requires aye-ayes to use both of these special morphological features, as an individual must gnaw through live or dead wood and then extend its middle finger into the cavity to hook larvae. The pericarp surrounding *Canarium* seeds is harder than any fruits or seeds that are broken open by primates in South America (Kinzey and Norconk, 1990), but the aye-aye is able to break it open with its strong incisors. The prevalence of these two foods in the aye-aye's diet underscores the species' specializations for, and ability to reach, structurally defended foods.

While the aye-aye's morphology provides access to a variety of food sources that would otherwise be inaccessible, it does not restrict the animal's diet to only structurally defended foods. Nectars and cankers have no known structural defense. Ants may be defended by chitin, but unless the digestive system of the aye-aye contains chitinase, they have no better access to ants than do other animals. Aye-aye specializations and foraging patterns demonstrate that although many ecological specializations may be associated with morphological adaptations, these adaptations are not necessarily associated with ecological specialization. Indeed, in the case of the aye-aye, morphological specialization may confer ecological generalization by allowing the animal to gain access to structurally defended foods in addition to those that are more easily reached.

Although aye-ayes exploit a wide variety of food types, such as seeds, nectar, and larvae, the number of species eaten within each food type is quite small (Table 2). Most primates, including other lemur species, eat a greater variety of species within food types. The reasons for the aye-aye's exploitation of so few species within each food type remain unknown. It is possible that a high dietary diversity exists among the larvae, but sampling techniques have not been able to measure larval diversity. Alternatively, since aye-ayes on Nosy Mangabe specialize on resources that are structurally defended, their choices may be limited if only a few species of structurally defended species grow on the island. However, Nosy Mangabe does not appear to be lacking in structurally defended resources: there are at least five plant species on the island that produce hard-coated seeds, and wood-boring larvae are quite common throughout the island.

The specific factors contributing to *Daubentonia*'s dietary patterns have yet to be fully understood, but there is no question that the aye-aye's morphological adaptations play an important role in its foraging behavior. The aye-aye's hand, which extends up to 45% of its trunk length, is proportionately longer than the hand of almost any other primate — only *Tarsius* equals *Daubentonia* in relative hand length — and exhibits a number of structural modifications that are used in locating and consuming food (Figure 6). The middle finger of the hand differs from the other fingers in its relatively gracile construction and

Table 2. Numbers of species that aye-ayes were observed to feed on, classified by food type, for all individuals on Nosy Mangabe, 1989–1991 (Sterling, 1994a). Used with permission from S. Karger AG, Basel.

Food resource type	Number of species eaten by *Daubentonia*	Taxonomic Designation
Seed	3	*Canarium* spp. (2), Burseraceae; *Terminalia catappa*, Combretaceae
Nectar	1–2	*Ravenala madagascariensis*, Strelitziaceae, and perhaps *Labramia costata*, Sapotaceae
Larvae	6–9	Cerambycidae: Lamiinae, Prioninae; Scarabidae: Dynastinae; Passalidae; Pyralidae: Phycitinae
Adult insect	1	Unidentified ant
Fungus	1–2	Unidentified

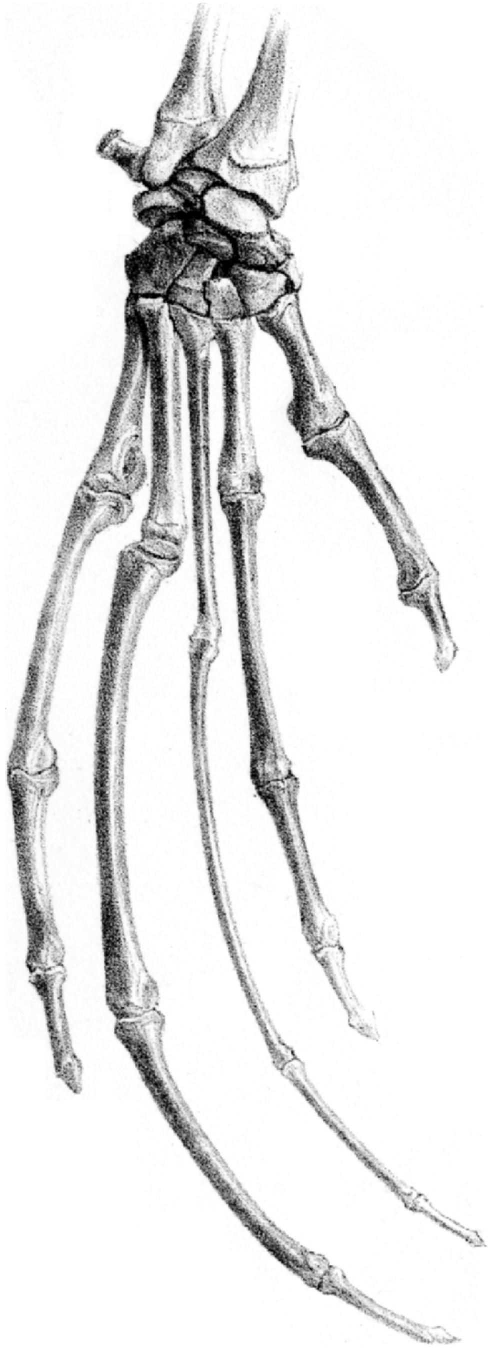

Figure 6. Drawing of an aye-aye's hand skeleton. Drawing by J. Erxleben (Owen, 1866).

greater flexibility in the joints. Though the fourth finger is the longest finger on the hand, the middle finger achieves exceptional reach because the metacarpal to which it is attached acts as an extension base and the web of skin between the second and fourth fingers has been suppressed (Jouffroy, 1975). A ball and socket joint at the metacarpophalangeal articulation allows for extraordinary flexibility in every direction. The aye-aye's hand has evolved in such a way as to allow for increased reach and flexibility, which are especially useful when the animal reaches into a deep or oddly shaped cavity to extract insect larvae (Milliken et al., 1991).

The aye-aye uses this specialized finger to acquire most of its major food resources, including nectar, seeds, and wood-boring insects (Figure 7). When probing a cavity in wood for insect larvae, the middle finger may bend as much as 30 degrees toward the dorsum of the hand, allowing the curved claw to follow the wall of the cavity. In this way, the claw moves past the larva in the cavity instead of pushing it into a deeper, irretrievable location. The finger's ball and socket joint permits excursions in any direction, and Milliken et al. (1991) found that aye-ayes can reach and extract larvae from acute, obtuse, and right-angle cavity orientations. When the flesh of the fingertip comes in contact with a larva, the distal phalanx and claw move ventrally to encircle and balance it for retrieval. Rather than pulping the larva inside the cavity, or impaling it on the claw, the aye-aye hooks it with the claw and lifts it out, permitting the recovery of the entire larva. Aye-ayes seem to possess a highly developed tactile sense, as they typically lift their finger out of a cavity only if there is a larva on the claw.

Figure 7. Photograph of an aye-aye feeding on a seed of *Canarium* spp. Photograph taken by Peter Ersts © AMNH-CBC.

Another striking feature of the aye-aye's hand specialization is independent digit control in the middle finger. When the aye-aye moves along a wood surface and taps the wood with its middle finger, the tapping finger moves substantially faster than the other digits. Similarly, videotapes of aye-aye hands probing cavities showed the movement of the middle digit inside the cavity to be substantially greater than that of the hand and fingers external to the cavity. The aye-aye's hand specializations are remarkable in that a single digit has evolved special capabilities for intricate foraging, while the remaining digits have retained their original form (Milliken et al., 1991).

In addition to its manual specializations, the aye-aye has several other morphological features that make these foraging behaviors possible. The facial skeleton is bent forward relative to the cranial base, possibly as an adaptation for generating and dissipating the large forces needed to chisel through wood and hard fruit carapaces (Cartmill, 1974). While the basic morphology of the aye-aye's facial muscles is clearly that of lemuriform primates, the muscle structure of the oral area and the pinnae more closely resembles that of the Lagomorpha and the rodents (Seiler, 1974). These specialized muscles may assist the aye-aye in using its rodentlike upper incisors for gnawing wood, and to swivel its large ears while feeding. *Daubentonia* also exhibits an unusually high degree of encephalization among primates, comparable only to that of *Homo*, *Pan*, and *Cebus.* Gibson (1986) notes that these genera show a correlation between large brain size, omnivorous extractive foraging, and complex sensorimotor intelligence. Wild aye-ayes have exhibited sophisticated object manipulations while foraging that are indicative of stage five or six of a modified Piagetian scheme of sensorimotor intelligence. However, behavioral studies suggest that aye-ayes may not achieve higher than a level four or five, and that the advanced tool use observed in the field may have been a result of stage five trial-and-error learning or even simpler learning mechanisms (Sterling and Povinelli, 1999).

The apparent lack of advanced sensorimotor intelligence in the aye-aye calls for an examination of other possible explanations for the extreme encephalization of *Daubentonia* relative to other prosimian species. The areas of the aye-aye's brain that are enlarged compared to those of other prosimians, including the pons-ventral area, cerebral hemispheres, and cerebellum, have all been implicated in fine motor coordination, olfaction, or auditory capacities. Many of these brain areas are involved in regulating voluntary, rapid repetitive motions, such as those used by the aye-ayes when tapping with their attenuated middle digit. *Daubentonia*'s enlarged brain size may have more to do with the evolution of a fairly narrowly focused set of sensory-perceptual mechanics supporting its specialized foraging techniques than the evolution of broad, domain general cognitive structures (Sterling and Povinelli, 1999).

Tap-Foraging

Field studies have shown that aye-ayes spend 5–41% of their feeding time tap-foraging for wood-boring insects, compared to 11–85% searching for and feeding on seeds or hard-coated fruits (Sterling, 1994a), but tap-foraging behavior has attracted special attention from researchers because it involves a fascinating combination of specialized senses and behaviors. Aye-ayes appear to belong to a small group of vertebrates that uses self-generated acoustical cues when foraging. Other members of this group include bats, cetaceans, woodpeckers, and the striped possum (*Dactylopsila trivirgata*). The aye-aye's large and flexible ears suggest that hearing plays an important role in an individual's ability to find food. Olfactory signals may also be important, given that the animal sniffs along the surface of the wood as it forages. The sense of touch may play a role as well; the tapping of the third finger is unexpectedly gentle, and it is possible that this extremely slender digit provides an unusual detection of and discriminability among surface vibrations (Erickson, 1991).

Auditory cues are believed to be especially important in prey location by foraging aye-ayes. The pinnae of the aye-aye are more mobile and proportionately larger than in any of the other lemuroid prosimians, and rotate forward when an individual is tap-foraging (Figure 8). In a series of studies on captive aye-ayes, Erickson (1991) found that study animals readily opened cavities in wooden logs, regardless of whether the cavities were empty or contained live or dead mealworms. The aye-ayes gnawed in areas where there were cavities, but not where there were only surface holes, implying that visual cues do not play a role in the decision to excavate. Study animals opened cavities that contained active mealworms slightly more often than they opened empty ones, suggesting that they may be able to identify cavities that contain insects. The tapping may stimulate prey to make audible movements, which would make them easier to detect underneath the wood.

The results of a later study (Erickson, 1998) provide further support for the ability of aye-ayes to locate insects inside a cavity. Captive aye-ayes were presented with wood blocks containing long, narrow channels, designed to resemble the mines of wood-boring insects that an aye-aye would encounter in the wild (Erickson, 1995). Portions of the channels were filled at random with frass or grubs, and other sections were left empty. Aye-ayes captured grubs located in the midsections of the mines as often as they captured those located in the end sectors, indicating that they do not pursue a simple strategy of following the mine to its terminus or to a larva. These results are consistent with those of field data showing that excavations are found both at the mine terminus and in the midsection. Overall, study animals found more than 75% of the grubs in the mines.

DISTRIBUTION

The majority of the information on how the aye-aye's middle digit functions within the cavities formed by wood-boring insects comes from captive studies. Until relatively recently, the aye-aye's nocturnal and largely solitary lifestyle prevented researchers from understanding its behavior, not to mention social structure, in the

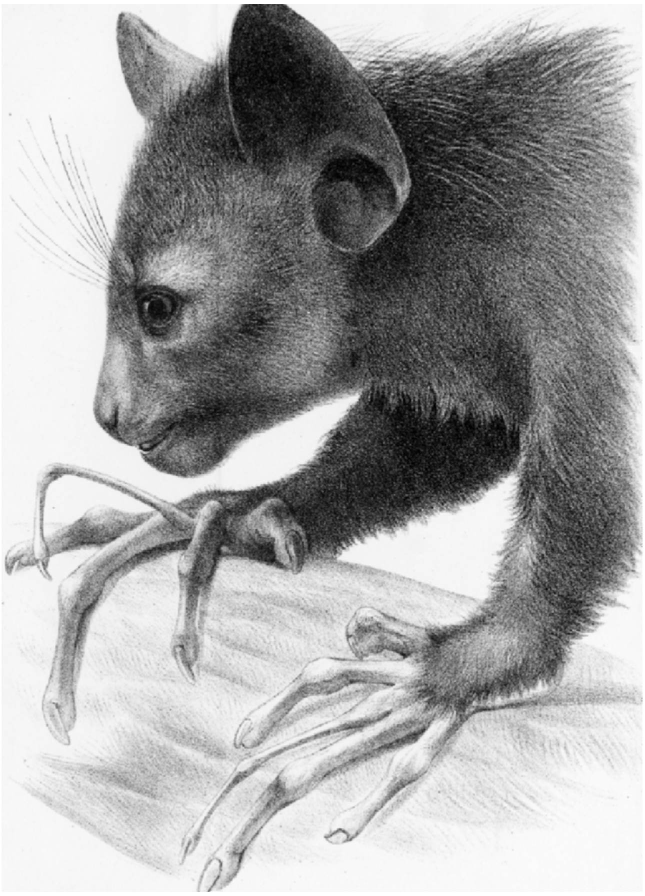

Figure 8. Drawing of an aye-aye tap-foraging, with its large ears pointed forward. Drawing by J. Wolf (Owen, 1866).

wild. In addition, little was known about its habitat preferences or distribution. In the 1970s, aye-ayes were thought to be restricted to eastern coastal forests below 200 m (Petter and Peyrieras, 1970). However, more recent surveys based on identification of secondary signs of feeding or nesting have revealed that aye-ayes seem to be able to adapt to different habitat types, from eastern humid forests (Ganzhorn and Rabesoa, 1986a,b) to western dry forests (Iwano et al., 1991), from primary forest (Andriamasimanana, 1994; Sterling, 1993b) to degraded patchy forests and plantations (Ancrenaz et al., 1994; Andriamasimanana, 1994; Petter, 1977) (Figure 9). To date, little is known about the population density of aye-ayes in any part of Madagascar where the species is found (Sterling, 1994c), mainly because it is extremely difficult to locate them with traditional survey and census techniques.

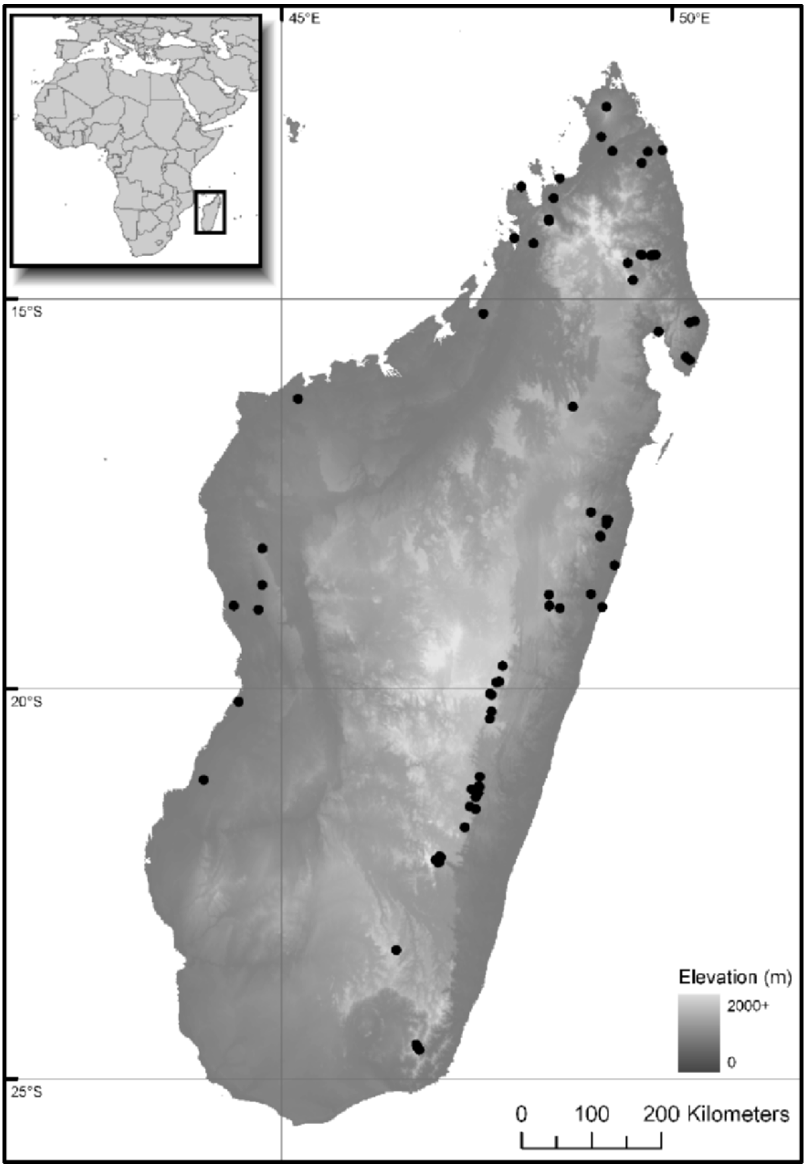

Figure 9. Distributional map of *Daubentonia* based on verified sight records, interviews with villagers, signs of feeding and nesting, and museum specimens. Map by Kevin Koy © AMNH-CBC. Sources: Andriamasimanana et al. (2001); Britt (2002); Britt et al. (1999); Colquhoun (1998); de Roland, R. (personal communication); Goodman, S., and Wilmé, L. (personal communication); Hansen et al. (2003); Rahajanirina and Dollar (2004); Randrianarisoa et al. (1999); Sterling (1998); Tombomiadana and Rakotonravony (2000).

SOCIAL SYSTEM

Systematic study of nocturnal primates in general is difficult due to observation conditions at night and to lack of ability to detect signals that animals may use to communicate with one another. Nocturnal primates, including aye-ayes, often communicate with olfactory signals that are temporally deferred in their delivery, and with vocalizations that researchers cannot always trace to their source (Sterling and Richard, 1995).

Nocturnal primates were long believed to have simpler and more homogeneous social systems than diurnal primates. The vast majority of solitary primate species are nocturnal, and without the ability to observe interactions between individuals, researchers tended to associate a lack of gregariousness with a lack of social complexity. Nocturnal primates tend to be predominantly nongregarious and spend much of their time alone, whereas most diurnal primates live in social groups consisting of individuals that know one another, interact regularly, and spend most of their time nearer to one another than to nongroup members (Sterling, 1993b). Nevertheless, nocturnal primates sometimes form social networks between animals that recognize one another and interact regularly, but that may not spend a significant amount of time in proximity to one another. Richard (1985) suggests that many solitary foragers live in "neighborhoods," in which individuals do not live in distinct social units but are most familiar with those individuals whose home ranges overlap the most with their own home ranges. Nocturnal primates appear to communicate with each other in a variety of ways and to develop complex relationships, but our measurement techniques and sensory capacities remain unable to grasp the majority of these interactions. Nevertheless, research is showing aye-aye social systems to be much more complex than was originally thought (Sterling and Richard, 1995).

Communication

Vocal and olfactory signals are particularly important in the social organization of aye-ayes, as their nocturnal and generally solitary habits preclude the use of visual signals in many situations. Aye-ayes on Nosy Mangabe communicated primarily by means of calls and scent-marks (Sterling and Richard, 1995). No research to date has explored vocal communication between aye-ayes in the wild, but one study of captive animals (Stanger and Macedonia, 1994) has provided information on the number and structural complexity of vocalizations as well as some of the contexts in which they are used. Captive aye-ayes were found to emit six different vocalizations in a variety of situations, and three additional vocalizations have been heard from free-ranging animals. The aye-aye's primary contact call has enormous acoustic variation and is used in many different contexts, whereas most other lemurs use several contact calls, often for spacing purposes. At first glance, this repertoire of nine vocalizations appears to be rather small for a primate, but given that aye-ayes are relatively solitary animals and that other nocturnal lemur species also have small vocal repertoires in captivity, this situation may not represent an aberration among primate vocal patterns (Stanger and Macedonia, 1994).

Olfactory signals, which can provide important information about an individual's age, sex, reproductive status, and territory, can be an effective mode of communication between individuals that may not come into direct contact very often (Kappeler, 1998). Wild aye-ayes on Nosy Mangabe exhibited three kinds of scent-marking: ano-genital rubbing, head and chest rubbing, and overmarking, where individuals urinated or dragged their genital region over an area previously marked by another animal (Sterling and Richard, 1995). Price and Feistner (1994) found evidence that captive aye-ayes can discriminate between the scents of conspecifics from different age–sex classes. The structure of the aye-aye's nasal cavity is unusual when compared to other lemurs in that the maxilloturbinal is somewhat stirrup-shaped, with a single inferior scroll (Tattersall, 1982), and as in many nocturnal species, the olfactory bulb forms a greater percentage of brain volume than in diurnal species. However, many of the details regarding the role that olfactory signals play in social and sexual communication between aye-ayes have yet to be explored.

In addition to communicating across space and time by means of calls and scent-marking, aye-ayes do sometimes interact directly with other members of their species. Sterling (1993a) reported that aye-ayes on Nosy Mangabe generally spent less than 20% of their time within 20 m of another aye-aye of either sex. Males and females differed in their reactions to conspecifics of the same and the opposite sex. Females rarely came into proximity with one another, and when they did, their interactions were usually aggressive and involved fighting or chasing. Interactions between males and females occurred more frequently than those between two females, and the nature of these interactions was highly variable. Tandem foraging, where individuals foraged in the same or adjacent trees and called to one another prior to moving in tandem from resource to resource, made up the largest percentage of time that males and females spent in close proximity. Similarly, affiliative vocalizations between the sexes were heard more frequently than agonistic ones. Males interacted with each other more often than they interacted with females, and certainly much more often than females interacted with each other. Relationships between pairs of males ranged from tandem foraging to avoidance and aggression.

Tandem foraging deserves special attention in a discussion of aye-aye sociality, as it may demonstrate that the species is not entirely solitary, as has long been assumed. Aye-ayes do often forage alone, but Sterling (1993b) documented groups of up to three individuals foraging and traveling together on Nosy Mangabe. Foraging associations were observed between adult males, adult and young males, and adult males and females. Aggregations of several aye-ayes have also occasionally been seen foraging together in Madagascar's mainland forests (Ancrenaz, 1991; Sterling, personal observation). The repeated occurrence of tandem foraging associations suggests that aye-ayes may be more social than was originally thought, and that established relationships may exist between pairs or groups of individuals.

The occurrence and composition of sleeping groups is another major axis organizing the social diversity of solitary primates (Kappeler, 1997a; Müller and Thalmann, 2000). Although aye-ayes show a tendency toward solitary resting, they do sometimes sleep in nests together or near one another. Aye-ayes sleep during the day in oval-shaped nests located 7–20 m from the ground in the fork of a tree or in a tangle of lianas, constructed of branches and lianas from contiguous vegetation. A single individual usually occupies a nest for a few days at a time, frequently refreshing it with new vegetation. Multiple aye-ayes may use the same nest at different times, as previous occupants vacate the nest and move on to new areas. Sterling's field study on Nosy Mangabe (1993b) revealed that females never slept near other females, whereas males slept near other individuals (male or female) only during the mating season. Several aye-ayes on Madagascar's mainland have been seen to build and use nests in a single tree during the same day (Ancrenaz et al., 1994), and males and females have been seen to sleep in nests located only 5 m apart (Andriamasimanana, 1994). Adult males have been observed to share a nest on mainland Madagascar (Sterling, unpublished data). Existing data are not sufficient to draw any conclusions regarding the relationships between individuals or groups of aye-ayes based on choice of sleeping site, but the possibility of social relationships between individuals that sleep near one another should not be ruled out.

Home Range Patterns

Another important factor in determining social organization in solitary primates is the extent of home range overlap with members of the same and the opposite sex (Müller and Thalmann, 2000). Field studies of aye-aye home ranges have provided insights into *Daubentonia*'s social system and how it compares with that of other lemurs. Overviews of nocturnal primate sociality demonstrate that patterns of home range overlap vary greatly both within and between the sexes in a given species (Kappeler and van Schaik, 2002; Müller and Thalmann, 2000). Preliminary data from a 6-month study on a river island near Mananara in northeastern Madagascar show three distribution patterns in male home range size (Lhota et al., 2004). Sterling's (1993b) study of radio-collared aye-ayes on Nosy Mangabe showed male home ranges to have an area of 120–215 ha, which was three to six times the size of females' home ranges (30–40 ha). Male home ranges often overlapped with each other and with female home ranges, whereas females seemed to maintain exclusive home ranges that did not overlap with each other at all (Figure 10). More research is needed, however, to determine whether female home ranges are always fully isolated from one another.

Male and female home range sizes differ primarily because males travel farther during nightly forays than do females. Males on Nosy Mangabe periodically went

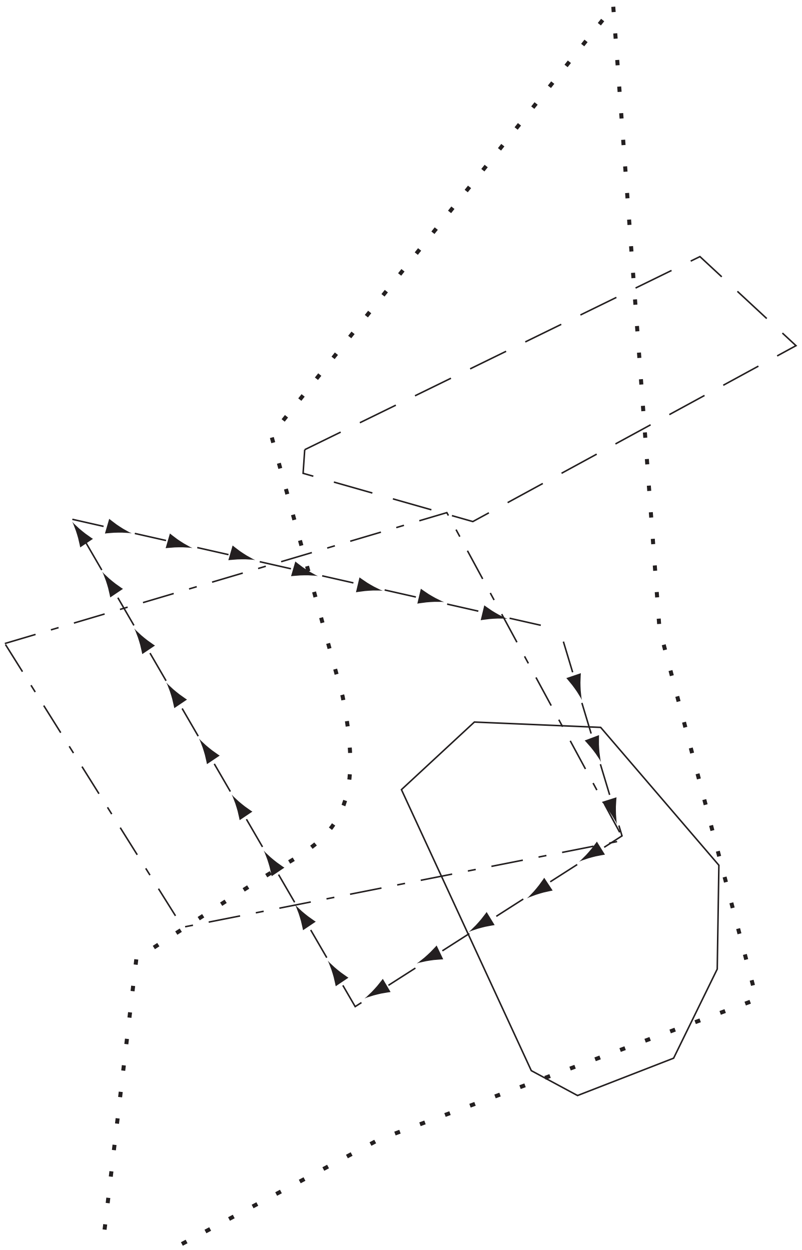

Figure 10. Home range overlap of five *Daubentonia* study animals on Nosy Mangabe, 1989–1991. Females = solid line, dashed line. Males = dotted line, dot/dash line, dash/triangle line (Sterling, 1993a).

on extended forays into outlying areas, often covering between 2.2 and 4.4 km per night on successive nights, sometimes without feeding much on the longer trips. Females generally traveled less than half as far as males did. Nevertheless, female aye-ayes have much larger home ranges than diurnal lemurs of similar body size in the same habitat (Sterling, 1993b).

Several factors may be responsible, singly or jointly, for the distribution patterns of male and female aye-ayes and the differences in foraging travel distances. Resource distribution and defensibility, predation pressure, and the intensity and nature of interspecific competition all may influence dispersion patterns among mammals (Emlen and Oring, 1977; Kappeler, 1997a; Sterling, 1993b; Terborgh and Janson, 1986). These factors influence males and females differently, resulting in sex-specific social and reproductive behavior. Some researchers (Charles-Dominique, 1993; Müller and Thalmann, 2000; Wrangham, 1980) argue that female behavior is influenced more directly by ecological pressures than male behavior because food availability is a major limiting factor on female fitness. Male behavior focuses more on finding mates and achieving mating success, as predicted from sexual selection theory.

The observed distribution patterns of male and female aye-ayes are consistent with the models described above. Females had ranges situated across similar elevation gradients, from 0 to 250 m, possibly in an effort to encompass a variety of both low- and high-elevation food types in their home ranges. Male aye-aye ranges may have exceeded in size and overlapped those of many females because males have greater nutritional requirements than females. However, if *Daubentonia* females can obtain adequate food in 30–40 ha, then males, which are of similar size, should not need 120–215 ha in which to gather food resources.

Mating System

The exploratory sojourns of aye-aye males are striking. Travel over Nosy Mangabe's steep slopes using both terrestrial and arboreal locomotion requires a great expenditure of energy, suggesting that there must be strong incentives for males to travel long distances. The fact that individual male home ranges overlapped those of many females may support the prediction that males are distributing themselves to best take advantage of the distribution of females. Lemurs typically exhibit a strictly seasonal pattern of breeding, with a limited number of successive estrous cycles occurring at a particular time of the year, which varies from species to species. The aye-aye, however, is unique among Malagasy primates in the unpredictability of its breeding events throughout the year. Evidence from the wild suggests that aye-ayes do not exhibit reproductive synchrony: females in close proximity to one another neither cycle nor become pregnant at the same time (Gibson, D., personal communication; Sterling, 1994b). Estrus brevity in individual females and asynchrony across females means that a male aye-aye's ability to detect when the female is in estrus is very important and very difficult. Long forays by males and consequent large home ranges may reflect male efforts to locate estrous females. Indeed, male aye-ayes on Nosy Mangabe did encounter estrous females on a number of their extended foraging excursions.

Resource availability and photoperiod are often cited as important factors in reproductive timing in animals, but aye-aye breeding behavior does not appear to be influenced by either variable. Aye-ayes eat all their major food resources across almost all months of the year, and the timing of peak availability of fruits varies from year to year. It is unclear whether the availability of food resources is highly unpredictable, or if there are patterns that existing data cannot detect. Field observations of aye-aye births occurring throughout the year suggest that photoperiod has little effect on reproductive timing. In addition, aye-ayes maintained on different light regimes in two different captive institutions mated and gave birth at approximately the same time, indicating that breeding was not prompted by changes in the light cycle. It seems that whatever factors contribute to reproductive seasonality in most other lemurs may not affect wild aye-ayes (Sterling, 1994b).

Behavioral signs of reproductive activity become apparent in female aye-ayes about 10 days prior to the onset of full estrus. Females increase the frequency of scent-marking and often visit nests occupied by males, a behavior not seen outside the mating season (Sterling, 1993b). Physiologically, female estrus is marked by vulvar and labial swelling, and a color change in the labia from gray to pink or red (Winn, 1994). Prior to and during mating activity, males exhibit testicular swelling and increase scent-marking frequency. During this time, males cluster around the female during both day and night and, like the females, increase their scent-marking frequency. Males generally mate with a female about a week after testicular swelling is first observed.

During each night of estrus, females exhibit a repetitive pattern of moving swiftly over 500–1000 m, and then sitting still for about an hour and emitting long calls that they use only during the mating period. In response to this call, several males converge on the female from all directions. Males chase and fight with one another near the female, and the female repels some mating attempts while accepting others. The accepted male copulates with the female and maintains hold of her for about an hour, while other males chase each other in circles around the pair and try to dislodge whichever male is copulating with the female. When copulation is complete, the female quickly moves another 500 to 1000 m and repeats the pattern. A female may mate with one or more males during each night of estrus, making it impossible to determine which male is the father of the female's offspring without genetic analysis (Sterling and Richard, 1995).

The aye-aye's home range patterns and breeding behavior suggest that the species exhibits scramble competition polygyny, in which females are solitary and males range widely in search of estrous females (Clutton-Brock, 1989). The females' advertisement calls suggest that they have an interest in attracting more than one male, possibly to provide themselves with a choice of several males on each night of estrus. Individual females may benefit by maintaining reproductive asynchrony, because a large number of males are available to respond to any individual female's call on a given night (Kappeler, 1997c). When a female chooses a mate, the male monopolizes her for a long period, either through single or multiple intromissions. In this way, the male temporarily prevents other males from inseminating the female while increasing his chances for fathering the offspring. Because females mate with more than one male during each period of estrus, *Daubentonia* has a multi-male – multi-female breeding system (Sterling, 1993b). The aye-aye was one of the first lemurs noted to exhibit scramble competition polygyny, but subsequent studies have pointed to other nocturnal lemurs with this system, such as Coquerel's dwarf lemur (*Mirza coquereli*) (Kappeler, 1997c) and the gray mouse lemur (*Microcebus murinus*) (Radespiel, 2000). These species also display similar home range patterns to those found in *Daubentonia*, providing further support for the connection between larger male home ranges and scramble competition polygyny.

Polygynous species often display pronounced sexual dimorphism, with larger, stronger males able to outcompete other males for available females. Sexual size dimorphism is characteristic of many solitary primates, including the Lorisidae, most Galagidae, and *Pongo pygmaeus* (Kappeler, 1997a). However, Malagasy primates, including the aye-aye, generally lack sexual size dimorphism, and some lemur species even show a trend toward larger female size (Jolly, 1998). The wide variety of mating systems and patterns of sexual dimorphism found in lemurs are often seen as a challenge to the general predictions of sexual selection theory (Kappeler, 1997a; Müller and Thalmann, 2000).

In scramble competition polygyny, a male's primary challenge is to locate sexually receptive females. Male attributes such as mobility, perceptiveness, and spatial memory are likely to aid a male in finding estrous females in these systems (Schwagmeyer, 1988). These traits may benefit a male more than would large body size or other defensive traits that are characteristic of males of species that engage in direct combat for females. Studies of other species that use a scramble competition polygyny mating system may help to explain the lack of sexual dimorphism in aye-ayes and other lemurs. Eberle and Kappeler (2004) found that body mass was a poor predictor for mating success in male gray mouse lemurs (*Microcebus murinus*), whereas a high level of spatial familiarity improved mating success. Similarly, the mating success of male thirteen-lined ground squirrels is closely linked to the number of estrous females he finds, while his ability to dominate over his competitors is a poor predictor of mating success (Schwagmeyer, 1988).

Scramble competition polygyny in aye-ayes may correlate with improved spatial ability and mobility in males, as seems to be the case in other species with this type of mating system. Unlike aye-ayes, however, gray mouse lemurs and thirteen-lined ground squirrels tend to exhibit seasonal reproduction, which may limit direct contest competition between males and alleviate the need for males to have a large body size. The lack of seasonality in the estrus cycles of female aye-ayes would be expected to promote direct (contest) competition between males, presumably leading to sexual size dimorphism in addition to improved male spatial ability. The prolonged intromissions and enlarged testes observed in aye-ayes may be a strategy to manage competition. Males of other lemur species with polygynous mating systems exhibit increased testis size, either permanently or through testicular swelling during the mating season (Kappeler, 1997b). Another successful strategy used by males of many polygynous species is the use of copulatory plugs, although this possibility has not yet been explored in aye-ayes. All of these may increase a male's chance of fathering the offspring of a female that mates with additional males (Kappeler, 1997c; Parga, 2003; Schwab, 2000). Clearly, much remains to be understood about *Daubentonia*'s mating system and correlations with male and female morphology and behavior.

CONCLUSION

While great advances have been made in understanding aye-aye ecology and social behavior over the past several decades, there is still much to learn about these animals, their perceived similarities and distinctiveness from other lemurs, and the morphological and behavioral traits that make them unique. In particular, a greater understanding is needed about resource use and social and behavioral ecology of aye-ayes in mainland humid forests and in drier habitats of western Madagascar.

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SECTION THREE

Connecting Ecology and Adaptation: Summaries and New Studies

CHAPTER NINE

Evolutionary Divergence in the Brown Lemur Species Complex

Steig E. Johnson

INTRODUCTION

The brown lemur species group (*Eulemur fulvus*, *E. albocollaris*, and *E. collaris*) is the most widespread of the day-active lemurs, occupying nearly all remaining natural habitats in Madagascar from the extreme north to transitional habitats bordering the arid south, as well as the island of Mayotte in the Comoros (Tattersall, 1982; Mittermeier et al., 1994). The present range in Madagascar is discontinuous, with populations found in coastal and adjacent inland habitats in the north, east, and west (resembling a ring species distribution; Figure 1). However, it is very likely that this vicariance is of recent, anthropogenic origin, as eastern and western populations were once contiguous, occupying the forest mosaics of the high plateau (Tattersall, 1993; Tattersall and Sussman, 1998).

In accordance with their wide distribution, brown lemurs demonstrate a high degree of ecological and behavioral flexibility. In this chapter, I will explore their variability and evolutionary divergence, including aspects of morphology, biogeography, ecology, and social systems. In addition, I will summarize the current conservation status of this diverse species complex. Tattersall and Sussman (1998) reviewed the evolution and ecology of brown lemur taxa in the north of Madagascar

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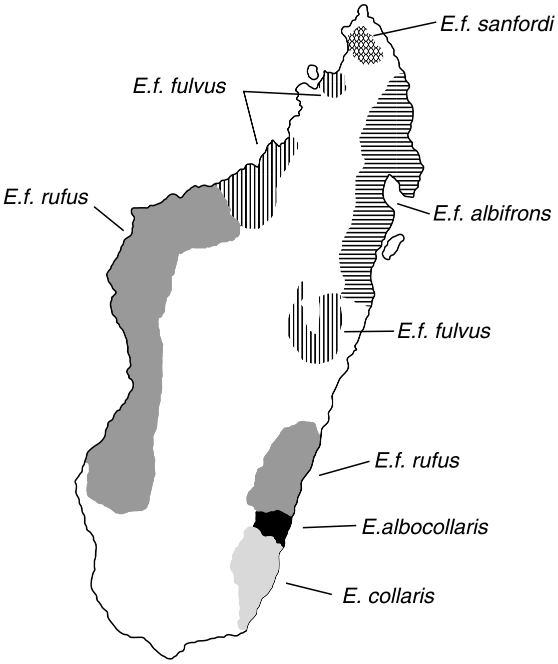

Figure 1. General distribution of brown lemur taxa in Madagascar (from Tattersall, 1982). Actual ranges for all populations are limited by availability of remaining suitable habitat, whose loss is ongoing and rapid (e.g., Green and Sussman, 1990; Irwin et al., 2005).

and the Comoros. Consequently, I will focus here primarily on those populations found in the southeast.

EVOLUTIONARY RELATIONSHIPS AND HISTORY OF THE BROWN LEMUR COMPLEX

Taxonomy

Brown lemurs are among the "true" lemurs (*Eulemur*; Simons and Rumpler, 1988). Their clear evolutionary divergence from other taxa in this group is evidenced by frequent sympatry with the other species in the genus (*E. coronatus*, *E. macaco*, *E. mongoz*, and *E. rubriventer*; Mittermeier et al., 1994; Overdorff and Johnson, 2003), although some hybridization has been noted in the wild (*Eulemur fulvus fulvus* × *Eulemur mongoz*; Pastorini et al., 2001). Traditionally, brown lemurs have been classified as a single species (*Eulemur fulvus*), with up to seven subspecies: the common brown lemur (*E. f. fulvus*), Sanford's lemur

(*E. f. sanfordi*), the white-fronted lemur (*E. f. albifrons*), the red-fronted or rufous lemur (*E. f. rufus*), the Mayotte lemur (*E. f. mayottensis*), the collared lemur (*E. f. collaris*), and the white-collared lemur (*E. f. albocollaris*) (Tattersall, 1982). However, *E. f. mayottensis* likely represents a recently transplanted population of *E. f. fulvus* and should be subsumed in the latter subspecies (Hamilton et al., 1980; Pastorini et al., 2000).

Recent research indicates that collared and white-collared lemurs warrant full species status (Djlelati et al., 1997; Wyner et al., 1999; but see Pastorini et al., 2000; see below). I refer herein to *E. albocollaris* and *E. collaris* by their binomial, species-level designations (cf. Djlelati et al., 1997), while other brown lemur taxa are retained as subspecies of *E. fulvus*. However, to emphasize the close relationships of the taxa within this group, I refer to *E. fulvus*, *E. albocollaris*, and *E. collaris* collectively as "brown lemurs."

Cytogenetics and Molecular Genetics

The brown lemur group varies in karyotypes and chromosome morphology, and these characters may be used to distinguish the three species. All *E. fulvus* subspecies share a common diploid number ($2N = 60$) and have similar morphology in G-, Q-, and R-banding patterns (Rumpler, 1975; Hamilton and Buettner-Janusch, 1977; Hamilton et al., 1980). In contrast, *E. collaris* is polymorphic in karyotype ($2N = 50, 51, 52$), with $2N = 51$ individuals (with a heteromorphic metacentric/acrocentric pair) likely resulting from hybridization between individuals with the other karyomorphs (Buettner-Janusch and Hamilton, 1979). *E. albocollaris* maintains a diploid number of 48; this distinction was the basis for the separation of this taxon from the closely related *E. collaris* (Rumpler, 1975). It has been proposed that *E. collaris* and *E. albocollaris* diverged from an ancestral *E. fulvus* karyotype via the addition of four and six pairs, respectively, of metacentrics (through Robertsonian fusion of acrocentrics), two of which are shared between the two species (Hamilton et al., 1980; Rumpler, 1989).

Similarity in chromosome complements in these groups does not necessarily correspond with reproductive compatibility. As expected, the *E. fulvus* subspecies are fully interfertile in captivity (Rumpler, 1989; Tattersall, 1993). Moreover, both *E. collaris* and *E. albocollaris* produce fertile hybrids when each is crossed with *E. fulvus* subspecies ($2N = 60$) (Rumpler, 1975; Buettner-Janusch and Hamilton, 1979; Hamilton et al., 1980). However, captive *E. albocollaris* × *E. collaris* hybrids are sterile, with meiotic chromosomes arranged in long chains of six (Rumpler, 1990, in Tattersall, 1993). Djlelati et al. (1997) noted severe reproductive breakdown in *E. albocollaris* × *E. collaris* hybrids, citing autosomal-sex chromosomal associations as a cause for impairment of spermatogenesis. Results from this study also support the more recent common ancestry of these two taxa, their karyotypes having developed through different rearrangements of the chromosomes found in an intermediary ancestor (Djlelati et al., 1997). With reproductive isolation apparent in these groups, Djlelati et al. (1997) proposed promoting these taxa to separate species status (*E. albocollaris* and *E. collaris*).

Recent studies in molecular genetics have also examined the brown lemur speciation problem (Wyner et al., 1999; Wyner, 2000; Pastorini et al., 2000). Wyner et al. (1999) investigated evolutionary relationships among the six brown lemur taxa by sequencing mitochondrial DNA (including d-loop, 12S rRNA, and cytochrome *b*) and nuclear DNA (casein kinase II) regions. These authors used population aggregate analysis to segregate the brown lemurs into three distinct evolutionary units: a collared lemur unit (supported by three diagnostic sites), a white-collared lemur unit (with six diagnostic sites), and a group comprised of the four *E. fulvus* subspecies (supported by two diagnostic sites, but with no markers for distinguishing individual subspecies). Based mainly on phylogenetic species concept principles, the findings of Wyner et al. (1999) support the proposal by Djlelati et al. (1997) to elevate the two southeasternmost brown lemur populations to full species status.

Pastorini et al. (2000), however, arrived at opposite conclusions in their study of brown lemur phylogeny. These authors sequenced part of the COIII gene, all of ND3, ND4L, and ND4 genes, and five tRNA genes. White-collared and collared lemurs did indeed form a clade: pairwise distances for these two taxa were among the lowest of subspecies comparisons, and distances were relatively large between this lineage and any other distinguished *E. fulvus* population. Yet because pairwise distances were much greater between *E. fulvus* and the outgroup *E. macaco*, combined with the evidence for some continued interfertility (see above), Pastorini et al. (2000) opted to retain collared and white-collared lemurs as *E. fulvus* subspecies. Four additional brown lemur clades were also identified, but they did not segregate the traditionally recognized subspecies. *E. f. rufus* was sorted into two separate clades (not based on the recent east–west split, but instead on a north–south split in western populations) while *E. f. fulvus* also appeared in two groups (one of which also included *E. f. sanfordi* and *E. f. albifrons*). Interestingly, Wyner et al. (1999) were also unable to identify markers to distinguish the traditionally recognized four northern *E. fulvus* subspecies. Despite this and the potentially polyphyletic nature of the *E. fulvus* clades delineated by Pastorini et al. (2000), collared and white-collared lemurs consistently sorted together in both studies, to the exclusion of other brown lemurs, lending support to their taxonomic separation from *E. fulvus* (see also Yoder and Irwin, 1999, and Wyner et al., 2000, for similar results with reduced sampling).

Natural Hybrid Zones

With the lack of consensus regarding taxonomy in these studies, it may be informative to examine the dynamics of wild populations of brown lemurs at the boundaries of their parapatric distributions. Specifically, natural hybrid zones may provide insight into the history and trajectories of these neighboring but differentiated taxa. Two such brown lemur contact zones have thus far been identified: *E. f. fulvus* × *E. f. rufus* (Lehman and Wright, 2000) and *E. f. rufus* × *E. albocollaris* (Sterling and Ramarason, 1996; Johnson and Wyner, 2000; Wyner et al., 2002).

Lehman and Wright (2000) recorded the possible presence of hybrid groups involving common brown lemur and red-fronted lemurs based on pelage characteristics during a rapid population assessment at Betsakafandrinka. Observations of *E. f. fulvus* and hybrids at this site are noteworthy as Betsakafandrinka lies south of the Mangoro and Oniver rivers, the putative boundary between the two subspecies (Lehman and Wright, 2000). No further investigation into this hybrid zone has been conducted. Yet, should the hybrid zone be confirmed, such intergradation between these two populations would not be surprising, considering their lack of reproductive isolation in captivity and generally close genetic affinities (Wyner et al., 1999; Pastorini et al., 2000).

The second brown lemur hybrid zone, involving red-fronted and white-collared lemurs, occurs farther south, at Andringitra National Park (Sterling and Ramarason, 1996; Wyner et al., 2002). This mountainous region is the source for several major river systems, including the Manampatrana River (noted erroneously by some to represent the *E. albocollaris*–*E. f. rufus* boundary; see Mittermeier et al., 1994; Johnson and Wyner, 2000; Irwin et al., 2005) and the Mananara River (the division between *E. albocollaris* and *E. collaris*; Tattersall, 1982; Mittermeier et al., 1994). During line-transect surveys, Sterling and Ramarason (1996) identified individuals with phenotypes of *E. f. rufus* primarily on the western slope, but also at higher elevations on the eastern slope. In addition, they observed some orange-bearded males (the more diagnostic sex; see below) and suspected the presence of *E. collaris* in this brown lemur population as well. However, the majority of males in the eastern portion of the park had the white beards typical of *E. albocollaris*.

These observations prompted genetic sampling of the brown lemur population on the eastern slope of Andringitra. Wyner and colleagues (Wyner, 2000; Wyner et al., 2002) analyzed sequences of mtDNA (d-loop) and nuclear markers (hemopexin intron 5, microsatellite 26, malic enzyme intron 8, and ceruloplasmin intron 16) to determine if *E. f. rufus*, *E. collaris*, and/or *E. albocollaris* diagnostic haplotypes were present in the Andringitra brown lemurs. These analyses also included a broader comparison of pure parental populations sampled elsewhere. Wyner (2000) found low mitochondrial nucleotide diversity in *E. albocollaris*, suggesting a relatively recent origin for this taxon as well as historically small populations—results supported by the small range (Figure 1) and presently low densities (Johnson and Overdorff, 1999; Irwin et al., 2005).

These studies also determined that the Andringitra contact zone was almost entirely composed of *E. albocollaris* × *E. f. rufus* hybrids (86% of individuals sampled) (Wyner et al., 2002). No *E. collaris* markers were found in the Andringitra population. Those individuals lacking hybrid haplotypes demonstrated only *E. albocollaris* markers, but were phenotypically indistinguishable from individuals of mixed ancestry in their area (with males, in particular, displaying a variety of pelage features, including the bushy white beards of *E. albocollaris* and the reddish crowns and facial stripe of *E. f. rufus*). Moreover, as the number of homozygotes or heterozygotes was not skewed in this population (i.e., no deviation from Hardy-Weinberg equilibrium), the hybrids likely represented multiple generations of intergradation (Wyner, 2000). Perhaps most strikingly, the hybrids of Andringitra maintained private sites (mostly in ceruloplasmin intron 16) *not* found in either pure populations of *E. albocollaris* or *E. f. rufus.* These results denote extensive introgressive hybridization in the Andringitra region (Wyner et al., 2002). Furthermore, as indicated by the apparent localized sequence evolution, the hybrid zone has likely been stable for many generations and is at least partially isolated from parental source populations (Wyner, 2000; Wyner et al., 2002).

The size of the Andringitra hybrid zone has yet to be determined. However, intermediate phenotypes have been noted as far as 32 km to the southwest (Ivohibe) from the putative center of the zone (personal observation). To the southeast, the limit may lie close to Evendra, 34 km from the center. At this site, phenotypes are not dissimilar to some of the hybrids at Andringitra (personal observation) but no hybrid haplotypes were detected in limited sampling (Wyner et al., 1999). Although the northern limit has yet to be sampled, it is likely the Andringitra hybrid zone may be at least 60–70 km in width. These dimensions are very large, particularly in relation to home ranges (a surrogate measure for dispersal) recorded for individual social groups of eastern brown lemurs (12–100 ha; Overdorff, 1991; Vasey, 1997; Johnson, 2002). More strikingly, these estimates for the hybrid zone are equivalent to more than half the length of the probable range of pure *E. albocollaris* (approximately 100–120 km; Figure 1).

The existence of this large hybrid zone provides some support for those who favor maintaining the taxonomic status of *E. albocollaris* and, by extension, *E. collaris* as subspecies of *E. fulvus.* However, the apparently old and stable contact zone is itself developing new genetic variants, evidence for the continued separation of parental populations of *E. albocollaris* and *E. f. rufus* (Wyner et al., 2002). Other differences between parental populations are also apparent, including ecology and behavior (see below). Moreover, there is no evidence for genetic exchange between *E. collaris* and any other brown lemur population (except for introduced *E. collaris* and *E. f. rufus* at Berenty; Jekielek, 2003). Andringitra, where no *E. collaris* markers were found, is the only likely site for overlap with either *E. albocollaris* or *E. f. rufus* within their original range; the Maranara River forms an effective barrier to the south and no suitable habitat remains that could facilitate *E. collaris* dispersal into the Andringitra headwaters region (Wyner et al., 2002). Thus, *E. collaris* is geographically isolated from *E. albocollaris*, which, in addition to the evidence for reproductive isolation from captivity, supports their elevation to full species status.

Given these complex and oft-conflicting lines of evidence, ascertaining whether white-collared and collared lemurs represent species distinct from *E. fulvus* is partly a semantic exercise wherein a biological continuum is arbitrarily separated into categories. Following Jolly (2001), it is perhaps more appropriate to adopt the term "allotaxa" (Grubb, 1999) for such populations that are distinct and diagnosable but may not be completely reproductively isolated. Some criteria for determining species-level designation, such as genetic distance, may not adequately reflect present intergradation or evolutionary trajectories in the brown lemur complex (see also Yoder, 2003). The biological species concept is also difficult to apply to this group, as not all populations are interfertile but reproductive isolation is independent of the degree of relatedness. In contrast, using population aggregate analysis and the phylogenetic species concept, *E. albocollaris* and *E. collaris* may be consistently diagnosed as separate species (Wyner et al., 1999). The phylogenetic species concept may also be preferred for its utility in conservation biology (Vogler and DeSalle, 1994). This method helps underscore the biological significance of critically endangered lemur taxa such as the white-collared lemur (e.g., Harcourt and Thornback, 1990; Mittermeier et al., 1992, 2005).

Phylogeny, Origins, and Diversification

As suggested by the investigations into brown lemur taxonomy, the evolutionary history of the brown lemur group is not currently resolved. Indeed, subfossil evidence may have little utility in clarifying the origins and differentiation of this complex due to the very close relationships of these taxa and the lack of diagnostic morphological features. In an analysis of craniodental characters among *Eulemur* and *Varecia* species and subspecies, Tattersall (1993) found extensive homoplasy and could not identify clear apomorphies to resolve brown lemur (or *Eulemur*) phylogeny.

Nonetheless, combining evidence from karyology, molecular genetics, and biogeographic patterns, tentative evolutionary relationships can be discerned in the brown lemur complex. There is strong consensus that the brown lemur group forms a monophyletic clade (Tattersall, 1993; Tattersall and Sussman, 1998; Wyner et al., 1999; Pastorini et al., 2000). There is evidence from analysis of metachromism that *E. collaris* may be basal to the brown lemur complex (Shedd and Macedonia, 1991). Pastorini et al. (2000) found the *E. albocollaris/E. collaris* clade to be the most primitive clade. Yet, chromosomal studies strongly suggest that it is more likely the *E. collaris–E. albocollaris* clade diverged from *E. fulvus* more recently and subsequently evolved into the two present forms (Hamilton et al., 1980; Rumpler, 1989; Djlelati et al., 1997). Among *E. fulvus* taxa, it appears that *E. f. fulvus* may be the basal form (Tattersall and Sussman, 1998); this population appears to be the least differentiated, at least in terms of gross morphological or pelage characters (Tattersall, 1982, 1993; Shedd and Macedonia, 1991). If this is indeed the case, based on current and likely recent distributions, the brown lemur group would have first appeared in central-north Madagascar (Meyers and Absher, 1994, in Tattersall and Sussman, 1998), perhaps in humid forests (Tattersall and Sussman, 1998). This population would have subsequently expanded into drier western habitats, southeastern rainforests, and the mosaics of the central plateau, diversifying into a northern clade which gave rise to *E. f. albifrons* and *E. f. sanfordi* and a southern group consisting of *E. f. rufus* and later *E. albocollaris/E. collaris* (Tattersall, 1992). It is important to note that these patterns, based on the currently recognized brown lemur subspecies, remain speculative without confirmation from further systematics investigations. Again, the only study to date that potentially resolved *E. fulvus* subspecies phylogeny identified clades that crosscut traditional taxonomic units (Pastorini et al., 2000).

The timing and mechanisms for brown lemur diversification remain obscure. It is perhaps most likely that these taxa originally diverged in allopatry (Tattersall, 1982). Paleoenvironmental studies of the late Pleistocene and Holocene indicate fluctuating periods of increased aridity in Madagascar (Gasse and van Campo, 1998, 2001), associated with forests contracting into isolated refugia (Tattersall, 1982; Richard and Dewar, 1991; Ganzhorn, 1998). With migration routes through the central plateau limited, rivers could have further served (and continue to serve) to subdivide lemur communities. While it appears that these rivers were barriers for already differentiated species (Tattersall, 1982; Richard and Dewar, 1991; Ganzhorn, 1998), it is possible that closely related populations, such as *E. f. rufus* and the ancestor to the *E. collaris–E. albocollaris* group, may have diverged during these more recent drying cycles. Subfossil and extant lemur species assemblages suggest that, while major biogeographic regional distinctions (e.g., between the dry west and humid east and north–south gradients) have long existed, there were numerous routes for faunal exchange among regions prior to the arrival of humans (Ganzhorn, 1998; Godfrey et al., 1999). Present-day parapatry of brown lemur taxa may then have arisen during forest expansion subsequent to the last major period of aridity (e.g., Tattersall, 1982; Richard and Dewar, 1991). Among the significant questions remaining, however, is why the brown lemur group has diversified so extensively while other species have not. For example, the ecologically similar *E. rubriventer* (Overdorff, 1993) is monotypic but maintains a broad distribution which it shares with four distinct brown lemur taxa.

MORPHOLOGY AND LOCOMOTION

Pelage

All brown lemur populations demonstrate sexual dichromatism and sex-specific patterns in facial hypertrichy (ear tufting, ruffs, and collars), although sex differences in pelage are less marked in *E. f. fulvus* (Tattersall, 1982; Shedd and Macedonia, 1991; Mittermeier et al., 1994). In *E. fulvus*, differences among males across taxa are typically greater than among females; males are readily distinguished by head and facial markings, color, and tufting patterns (see Mittermeier et al., 1994; Rowe, 1996). *E. albocollaris* differ from closely related

E. collaris mainly in beard color: *E. collaris* males have reddish-orange collars while *E. albocollaris* males have their namesake white collars. Females of these taxa are largely indistinguishable.

Body Size, Canine Size, and Testis Size

Body mass for brown lemur species is in the middle range for extant lemurs, with populations ranging between 1.8 and 2.4 kg in mean body mass (Kappeler, 1990, 1991; Glander et al., 1992; Gerson, 2000; Johnson et al., 2005; Johnson, unpublished data). Notably, variation is greater within subspecies than among them. Populations in drier western habitats are considerably smaller than those found in humid eastern forests (Albrecht et al., 1990; Godfrey et al., 1990). For example, in *E. f. rufus*, mean body mass in western populations from Anjamba is 1.8 kg (Gerson, 1999, 2000), while mean weight at Ranomafana in the east is 2.2 kg (Glander et al., 1992; Johnson et al., 2005). These ecogeographic size differences have been observed across lemur taxa and may be related in complex ways to variation in climate, seasonality, and forest productivity (Albrecht et al., 1990).

As in nearly all strepsirhines, male and female brown lemurs are typically similar in body size and other morphological traits (e.g., Kappeler, 1990). However, some divergent patterns of sexual dimorphism have been detected in brown lemur populations, again with considerable variation within taxa. Johnson et al. (2005) examined sex differences in three populations of brown lemurs in the southeast: *E. f. rufus* at Ranomafana, *E. albocollaris* at Vevembe, and hybrids of these taxa at Andringitra. They found sex differences in canine size in *E. albocollaris* and the hybrids (with larger canines in males) in conjunction with body-size monomorphism. *E. f. albifrons* (Kappeler, 1996) and western *E. f. rufus* at Anjamena (Gerson, 1999, 2000) also demonstrate this pattern. However, *E. f. rufus* at Ranomafana exhibited significant female-biased size dimorphism and canine monomorphism (Johnson et al., 2005). These differences are suggestive of divergent patterns of intrasexual competition, perhaps linked to local ecological conditions, but further behavioral studies are required to test these associations. Another variable potentially linked to male–male competition in brown lemurs is testis size. All populations examined thus far have demonstrated relatively high testis volume, indicative of high levels of sperm competition and consistent with their multimale/multifemale mating systems (Kappeler, 1997; Johnson et al., 2005).

Positional Behavior

Brown lemurs are typically arboreal quadrupeds, with leaping as the primary form of locomotion (Dagosto, 1995). Vertical postures and support use are not uncommon. In *E. f. rufus* at Ranomafana, vertical clinging represented up to 10% of postures adopted during travel (Dagosto, 1995). Similar positional behavioral profiles have been found in *E. albocollaris* at Vevembe (Johnson, unpublished data). This partial reliance on vertical postures and leaping is reflected in brown lemur anatomy. Fleagle and Anapol (1992) found ischial morphology in *E. fulvus* was consistent with adaptations for pronograde quadrupedalism similar to *Varecia*, as well as for true clinging and leaping, as in the indriids. Like most eastern lemurs, *E. f. rufus* at Ranomafana typically used middle levels of the canopy, ascending to heights above 15 m only 12–28% of the time, depending on the season (Dagosto, 1995). Locomotion can also vary seasonally; quadrupedalism in *E. f. rufus* increased and leaping decreased significantly during the wet season, associated with greater overall travel and use of small feeding trees with small gaps between canopies (Dagosto, 1995).

ECOLOGY AND BEHAVIOR

Diet

The brown lemur complex has been characterized as highly flexible in its ecology, in accordance with its broad geographic distribution which spans many distinct habitat types and elevational zones (Tattersall and Sussman, 1998; Goodman and Ganzhorn, 2004). Brown lemurs have relatively high dietary diversity (Tattersall and Sussman, 1998) and have demonstrated niche contraction and expansion in response to community structure (Vasey, 2000).

Guided by community ecology theory, nearly all studies of brown lemur ecology have assessed adaptations in juxtaposition to those of sympatric presumed competitors. Accordingly, most researchers have investigated brown lemurs in conjunction with a sympatric lemur species (*Lemur catta*: Sussman, 1974, 1977; *Eulemur rubriventer*: Overdorff, 1991, 1993; *E. coronatus*: Freed, 1996; *Varecia variegata rubra*: Vasey, 1997, 2000, 2002; *E. mongoz*: Rasmussen, 1999). Many mechanisms have been proposed to allow brown lemurs to share their habitats with these potential competitors. These include: greater dietary diversity (Vasey, 2000), utilizing higher (Sussman, 1974; Freed, 1996) or lower (Vasey, 2000) vertical microhabitats, feeding in smaller patches (Vasey, 2000), 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).

Except in some highly folivorous western *E. f. rufus* groups (Sussman, 1974, 1977), fruit is the primary resource among brown lemurs, comprising between 66 and 95% of the diet (Tattersall, 1977; Overdorff, 1991, 1993; Freed, 1996; Vasey, 1997, 2000; Rasmussen, 1999; Johnson, 2002). Interestingly, relatively proximate and closely related populations represent the lower and upper limits of fruit dependence: *E. albocollaris* at Vevembe and *E. albocollaris* × *E. f. rufus* hybrids at Andringitra, respectively. Andringitra groups consumed fruit in quantities similar to those observed in lemur species generally considered to be more strictly frugivorous than brown lemurs (e.g., *Eulemur rubriventer*: 81%; Overdorff, 1993; *Varecia variegata*: 71–90%; Morland, 1991; White, 1991; Balko, 1998; Vasey, 2000).

Most brown lemurs also supplement their diets with substantial quantities of secondary food sources (≤ 34% of diet), including leaves (≤ 26%) and flowers and nectar (≤ 20%), as well as other less common items (fungi, soil) (Sussman, 1974, 1977; Tattersall, 1977; Ganzhorn, 1988; Overdorff, 1991, 1993; Freed, 1996; Vasey, 1997, 2000, 2002; Rasmussen, 1999; Donati et al., 2002; Johnson, 2002). Very rare occurrences of invertebrate (Overdorff, 1993) and vertebrate (Pitts, 1995; Mizuta, 2002) prey have also been recorded in brown lemur diets. Diversity appears to be the norm for most brown lemur populations; only *E. f. sanfordi* and Andringitra hybrids infrequently consumed secondary food items (9 and 4–13%, respectively) (Freed, 1996; Johnson, 2002).

Given the differences observed in feeding ecology, as well as the variation in habitat types and food availability across regions, it may also be instructive to examine seasonal influences on diet among the brown lemur groups. Surprisingly, it is often difficult to link diet choices with fluctuations in resource base. In *E. f. fulvus* at Ampijoroa, there was no correlation between seasonal variation in frugivory and fruit production, nor between secondary resources (leaves and flowers) and their availability (Rasmussen, 1999); however, these brown lemurs did feed more on preferred individual species according to availability (Rasmussen, 1999). In the Masoala Peninsula, *E. f. albifrons* and sympatric *Varecia* also remained highly frugivorous during seasonal food scarcity (Vasey, 2000). Vertical stratification and direct contest competition likely served to minimize niche overlap between these species during these periods. Dietary demands of reproductive females in both species also mitigated seasonal diet separation (Vasey, 2000). At Ranomafana, *E. f. rufus* had greater dietary diversity when fruit was most available *and* least available (Overdorff, 1993). However, the most dramatic behavioral response during scarcity was migration: red-fronted lemur groups moved 4–5 km from their normal home ranges to more productive areas (Merenlender, 1993; Overdorff, 1993), a ranging pattern that has never been observed in other brown lemurs (e.g., Freed, 1996; Johnson, 2002). In addition, niche separation between *E. f. rufus* and sympatric *E. rubriventer* fluctuated according to resource seasonality. During peak fruit scarcity, dietary overlap was lowest and the two species varied greatly in time spent exploiting common plant species (Overdorff, 1993). Nevertheless, frugivory remained high for both species in periods of low fruit availability (Overdorff, 1993). This pattern is similar to the year-round obligate frugivory seen in the Andringitra hybrids (Johnson, 2002). There were positive correlations between frugivory and fruit availability in some Andringitra hybrids (as well as in pure *E. albocollaris* at Vevembe), but an inverse association was recorded in other areas of the contact zone (Johnson, 2002).

Thus, it appears that seasonal shifts in resource availability do not directly control food choice in brown lemurs. However, year-round food production may have a substantial impact on diet. For example, availability of all food resources (fruit, flowers, and leaves) is much higher at Andringitra than at Vevembe (Johnson, 2002). This higher overall productivity may permit both the very high population density and the greater degree of frugivory recorded in the Andringitra hybrid populations — despite the richer lemur community at this site (Johnson, 2002; Irwin et al., 2005). Yet, overall resource production may be even higher at Ranomafana (Overdorff and Wright, unpublished manuscript), while diet breadth in *E. f. rufus* here is more like that observed in *E. albocollaris* at resource-poor Vevembe (Overdorff, 1993; Johnson, 2002). Therefore, the abundant and highly frugivorous brown lemur population at Andringitra may be better explained by more specific characteristics of the habitat, such as the availability of critical resources.

The use of specific resources during scarce seasons is important in many primate communities throughout the tropics. For example, keystone resources — particularly asynchronously fruiting *Ficus* species — likely sustain the primates of Cocha Cashu, Peru, during the dry season (Terborgh, 1986). However, the universality of *Ficus* as a keystone resource has been questioned (e.g., Gautier-Hion and Michaloud, 1989). *Ficus* is rare in Madagascar, with 24 total species and only up to 12 species within individual forests (Goodman and Ganzhorn, 1997). Overall fruit availability is also lower in Madagascar, and there is evidence that seasonality is less predictable and more extreme (Goodman and Ganzhorn, 1997; Wright, 1999). Furthermore, the density of individual *Ficus* trees tends to be low in Malagasy forests (Goodman and Ganzhorn, 1997), and thus, rarely consumed by frugivores (Goodman et al., 1997). Therefore, the lack of an important keystone resource like *Ficus* may contribute significantly to the rarity of frugivorous mammals, such as brown lemurs.

Despite the overall rarity of *Ficus* and its presumed effects on frugivores, there may be considerable variation in this pattern within the southeastern rainforest region. At Andringitra, hybrid groups exhibited a striking dietary shift to *Ficus* fruit (≤79% of feeding time), especially in July–September (Johnson, 2002; Dalecky et al., 2003). This period coincides with cold winter months and typically the end of a long period of reduced fruit availability, although eastern rainforests demonstrate great variability in the timing and magnitude of resource production (Hemingway and Overdorff, 1999; Wright, 1999). The apparent abundance of figs in this area may help sustain the very dense brown lemur population during seasonal resource crashes (Johnson, 2002; Irwin et al., 2005). In contrast, Overdorff (1993) found no such seasonal switch to *Ficus* in the diet of *E. f. rufus* at Ranomafana. The seasonal migrations (likely to areas of cultivated or invasive *Psidium*) (Overdorff, 1991, 1993) suggest that *Ficus* cannot sustain the brown lemurs during peak scarcity at Ranomafana. Also unlike in the Andringitra hybrid zone, the relatively low-density *E. albocollaris* populations at Vevembe appeared to rely on *Pandanus* flowers as keystone resources (Johnson, 2002).

Activity and Ranging

Like all *Eulemur* species, brown lemurs exhibit the unusual activity pattern known as cathemerality (i.e., active during both day and night; Tattersall, 1987). All known brown lemur populations forage and move during daylight hours, but the extent of nocturnal activity varies regionally (Rasmussen, 1999; Overdorff and Johnson, 2003). In the west, brown lemurs tend to increase night activity during the dry season (Rasmussen, 1999; Kappeler and Erkert, 2003), while eastern and northern populations remain active across the daily cycle throughout the year (Overdorff and Rasmussen, 1995; Freed, 1996; Johnson, 2002). In semideciduous western forests, the most important proximate determinant of nocturnal activity appears to be light availability, which is dependent on lunar phase (Donati et al., 2001; Kappeler and Erkert, 2003; but see Rasmussen, 1999), while no such relationship is apparent in the dense humid forests of the east (Overdorff and Rasmussen, 1995). The origins for this unusual circadian rhythm have yet to be determined: it may represent a phase in an ongoing transition from nocturnality to diurnality (e.g., van Schaik and Kappeler, 1996; Kappeler and Erkert, 2003) or a stable behavioral pattern, perhaps primitive for day-active lemurs (Tattersall, 1982). Several proposed functions of cathemerality have received support from brown lemur field studies. There is evidence that increased nocturnal activity is an antipredator strategy (largely in response to diurnal raptors), particularly in seasonally defoliated habitats in the west (Rasmussen, 1999; Donati et al., 2001). In addition, cathemerality may be a thermoregulatory response (i.e., to maintain body temperature by moving at night, especially during colder months; Overdorff and Rasmussen, 1995; Donati et al., 1999; Kappeler and Erkert, 2003). Cathemeral activity patterns may also function to mitigate feeding competition with other day-active lemur species (Rasmussen, 1999; Vasey, 2000). Finally, Engqvist and Richard (1991) posited that cathemerality serves to increase feeding time on relatively low-quality food items, such as fibrous leaves, when preferred high quality food items are scarce. Lemurs are relatively small-bodied and lack typical digestive tract specializations for folivory and therefore may be required to consume large quantities of leaves over long periods of time (i.e., across the 24-hour cycle) (Engqvist and Richard, 1991). This function has thus far received little empirical support (Overdorff and Rasmussen, 1995; Donati et al., 1999). However, there was a correlation between nocturnal activity and increased unripe fruit consumption in *E. f. rufus* at Ranomafana (Overdorff and Rasmussen, 1995). It is important to note that all but the last of these proposed functions are based on the assumption that cathemerality represents a shift by an originally diurnal species toward increased nocturnal activity — when instead the reverse may be the case (Kappeler and Erkert, 2003).

Brown lemurs across Madagascar also exhibit variability in time allocation for specific activities. While the most common behavior overall is resting, the frequency varies greatly across populations (47–77%; Sussman, 1974; Overdorff, 1991; Vasey, 1997; Rasmussen, 1999; Gerson, 2000; Johnson, 2002). The large (and variable) proportion of time devoted to resting is undoubtedly partly a response to cathemerality: minimum daily feeding requirements and social demands are more easily met when brown lemurs are active throughout the 24-hour cycle. Brown lemurs also exhibit marked variation in time devoted to feeding (10–26%), travel (6–30%), and social or other activities (1–28%) (Sussman, 1974; Overdorff, 1991; Vasey, 1997; Rasmussen, 1999; Gerson, 2000; Johnson, 2002).

Differences in activity budgets have been suggested to minimize interspecific competition between brown lemurs and other sympatric lemurs (Sussman, 1974, 1977; Overdorff, 1991, 1996; Vasey, 1997). Intrinsic habitat characteristics such as spatiotemporal variation in resources may also affect these behaviors in brown lemurs. During food scarcity at Ranomafana, *E. f. rufus* increased feeding time while reducing time spent traveling and resting (Overdorff, 1996). In some scarce periods, *E. f. albifrons* at Masoala minimized energy expenditure by increasing time spent resting and feeding and traveling less; in other seasons of low resource availability, this population adopted the opposite strategy due to the patchiness of resources and increased direct interspecific competition for particular food items (Vasey, 1997). Vevembe *E. albocollaris* exhibit the latter approach (although without competition from other day-active frugivorous lemurs), while the associations between activity and the availability of important food items are not apparent in the Andringitra brown lemurs (Johnson, 2002). Thus, the relatively low-quality habitat at Vevembe may compel brown lemurs to shift their activities according to changes in resource base and feeding requirements, while the Andringitra hybrids are less constrained (Johnson, 2002).

Ranging patterns also differ across Madagascar. In western dry forests, home ranges are very restricted (0.75–1.0 ha in *E. f. rufus*; Sussman, 1974; 7–16 ha in *E. f. fulvus*; Harrington, 1975; Rasmussen, 1999). Eastern rainforest brown lemurs tend to have larger ranges, but there is tremendous variation (12–100 ha) (Overdorff, 1991; Vasey, 1997; Johnson, 2002). Partly in conjunction with home range differences, daily travel also varies considerably among populations. Again, western brown lemurs have relatively short daily path lengths (*E. f. rufus*: 125–150 m at Antseranomby; Sussman, 1974; 213–368 m at Anjamena; Gerson, 2000; *E. f. fulvus*: 447 m in the wet season at Ampijoroa; Rasmussen, 1999). In the eastern forests, *E. f. rufus* and *E. f. albifrons* both have much longer daily path lengths (962 and 978 m, respectively) despite clear differences in total home range area (85–100 versus 16 ha) (Overdorff, 1996; Vasey, 1997). Divergent patterns are also apparent within sites: Andringitra hybrid groups vary between 286 and 744 m in daily path length, which in this case correlates with home range size (Johnson, 2002). It is difficult to link these patterns with particular ecological constraints or strategies (e.g., in the Andringitra hybrid zone, where ranging differences are not associated with variation in diet, resource availability, population density, or lemur community structure; Johnson, 2002).

SOCIAL STRUCTURE AND ORGANIZATION

Brown lemurs live in multimale/multifemale social systems with group size ranging from 4 to 17 individuals (Sussman, 1974; Harrington, 1975; Overdorff, 1993; Freed, 1996; Vasey, 1997; Johnson, 2002). Long-term demographic studies in the east (Overdorff et al., 1999) and genetic analyses in the west (Wimmer and Kappeler, 2002) indicate that *E. f. rufus* is primarily characterized by female philopatry and male dispersal, although females may also migrate from natal groups (Ostner and Kappeler, 2004). Preliminary data suggest a similar pattern in *E. f. albifrons* (Vasey, 1997) but conclusive information is unavailable for other brown lemur populations.

Equal sex ratios — or perhaps a slight bias in the number of males — appear to be the norm across the brown lemur complex (Overdorff et al., 1999; Kappeler, 2000; Johnson, 2002; Ostner, 2002). Such a proportionally high number of males is unusual among polygynous primates and may be maintained by equal birth and mortality rates for males and females (Overdorff et al., 1999; Kappeler, 2000). Moreover, estrus synchrony may limit male potential for monopolization of females, reducing incentives for males to exclude others from the group (Ostner and Kappeler, 2004). The ultimate causes for even or male-biased sex ratios remain obscure. Overdorff et al. (1999) suggest that increased numbers of males may result from the relatively greater energetic demands of females. Males may also perform some group services such as increased vigilance or aid in intergroup conflicts (Overdorff et al., 1999). Other potential services include support for females in intragroup agonistic conflicts and protection against infanticide, but there is as yet little empirical support for these potential functions (Kappeler, 2000). Indeed, no cases of infanticide have been recorded in brown lemurs. Male strategies may also account for brown lemur sex ratios, as the increased number of males in social groups may be due to the benefits of social and/or mating cooperation among males or joint transfer (Kappeler, 2000, Ostner and Kappler, 2004).

The composition of multimale/multifemale brown lemur groups may also reflect a recent evolutionary development: a transitional stage from nocturnality to diurnal activity (the evolutionary disequilibrium hypothesis) (van Schaik and Kappeler, 1996). In this scenario, the larger, equal sex-ratio social groups are fusions of multiple pair bonds (Kappeler, 2000). Strong bonds between individual males and females within social groups also have been suggested to serve as a mechanism for the prevention of infanticide (van Schaik and Kappeler, 1993). However, in *E. f. rufus* at Ranomafana, Overdorff (1998) found male–female dyads did not consistently maintain greater proximity during critical reproductive seasons (mating and birth) and mating was not exclusive to the dyad (Overdorff, 1998). In addition, subgroups did not exclusively consist of adult male–adult female pairings (Overdorff, 1998), which was also the case in fission–fusion *E. albocollaris* (Johnson, 2002; see below). Ostner and Kappeler (1999) also found no evidence for strong affiliative or mating dyads within *E. f. rufus* social groups at Kirindy. Thus, pair bonding components of the evolutionary disequilibrium and infanticide prevention hypotheses currently lack support from field studies of brown lemurs.

While the composition of brown lemur social groups appears to be similar across populations, the cohesiveness of these units may vary. Typically, brown lemurs are found in stable groups that maintain close spatial proximity (Vasey, 1997; Overdorff and Johnson, 2003). However, *E. f. fulvus* on Mayotte and *E. albocollaris* maintain loose, fission–fusion communities (Tattersall, 1977; Johnson, 2002). In addition, after a 10-year study period wherein social groups were cohesive, *E. f. rufus* groups at Ranomafana recently underwent a complete transition to fission–fusion community structure (D. Overdorff, personal communication). Such fluid group structure has previously been noted only during permanent group division events (Overdorff et al., 1999). This variable expression across populations suggests that flexible grouping patterns are latent in the brown lemur complex. Fission–fusion may be a mechanism for reducing intragroup feeding competition in response to acute resource scarcity in some southeastern brown lemur populations (Johnson, 2002; D. Overdorff, personal communication).

Social dynamics within brown lemur groups may also be fluid. Fixed dominance hierarchies are not present in either sex (Pereira and Kappeler, 1997). Notably, females are not dominant to males in aggressive contexts, as is the case in most other lemurs (Pereira et al., 1990). Wild populations of brown lemurs have been characterized by low rates of agonistic behavior (Kaufman, 1996). Even in captive groups where aggression may be relatively common, brown lemurs lack consistent submissive signals and asymmetry in aggressive relationships between dyads is rare (Pereira and Kappeler, 1997). Pereira and McGlynn (1997) suggest that pair bonding within brown lemur social groups may preclude female dominance in these taxa. Females may accrue benefits such as increased foraging efficiency from coalitions with individual males, thus reducing the impetus to dominate all males, while males may pursue a strategy of special relationships with individual females for increasing mating opportunities (due in part at least to concealed ovulation in these females) (Pereira and McGlynn, 1997). However, the apparently more complex nature of dyadic relationships — or sometimes lack of such special relationships — in wild brown lemurs (Overdorff, 1998; Ostner and Kappeler, 1999) casts some doubt on the importance of male–female pair bonds in determining group social dynamics. Alternatively, consistent dominance relationships may be affected by frequent nocturnal activity, during which social interactions may be constrained (Rasmussen, 1999). However, there are indications that strong male–male competition may persist in this context. For example, recent studies of *E. f. rufus* at Kirindy have demonstrated that a single male may monopolize social interactions and dominate in agonistic encounters within the group – and apparently achieve greater reproductive success (Ostner and Kappeler, 1999; Wimmer and Kappeler, 2002).

Interactions among social groups vary distinctly across brown lemur populations. Brown lemurs are generally described as nonterritorial, with extensive overlap in home ranges (Sussman, 1974; Harrington, 1975; Overdorff, 1991; Vasey, 1997; Gerson, 2000). However, the nature of intergroup encounters can range from passive to highly aggressive. For example, in *E. albocollaris* at Vevembe and in the Andringitra hybrids, the majority of intergroup encounters were neutral, with little or no direct interaction between the groups (57–67%; Johnson, 2002), while in neighboring populations of *E. f. rufus* at Ranomafana, 65% of associations with conspecifics were hostile, with threat displays, chases, and/or direct fighting between groups (Overdorff, 1991, unpublished data). As most conflicts appear to involve food resources, the population differences imply different strategies based on the distribution of preferred food items.

CONSERVATION STATUS

The brown lemur group maintains a broad range across diverse habitats. The more widely distributed populations (*E. fulvus fulvus*, *E. f. rufus*, and *E. f. albifrons*) are at present considered to face a lower risk of extinction (IUCN, 2004). In contrast, with more restricted ranges, *E. f. sanfordi* and *E. collaris* are vulnerable and *E. albocollaris* is considered critically endangered (IUCN, 2004). These populations are threatened primarily by the conversion of suitable habitats into agricultural land (Jolly, 1986; Harcourt and Thornback, 1990), exacerbated in some areas by selective logging and hunting practices (Harcourt and Thornback, 1990; Johnson and Overdorff, 1999). *E. albocollaris* ranks among the most endangered primate species in Madagascar, indeed the world (Mittermeier et al., 2005), with widespread habitat destruction across its range, locally heavy hunting pressure, very low population densities, and a total population size of approximately 7,000 individuals (Mittermeier et al., 1994; Johnson and Overdorff, 1999; Irwin et al., 2005). *E. collaris* maintains higher densities (Johnson and Overdorff, 1999; Banks, 2002) and a larger distribution. However, like *E. albocollaris*, a significant portion of this taxon's range lies in severely threatened littoral forest fragments (Banks, 2002).

Conservation objectives include safeguarding not only taxa and habitats but also underlying evolutionary processes. The dynamics of the Andringitra boundary region may serve important functions in the evolutionary divergence of white-collared and rufous lemurs (Johnson, 2002; Wyner et al., 2002). This hybrid zone is also a potential source for new genetic variation (Wyner et al., 2002). Accordingly, to maintain biodiversity in this group, as well as to better understand lemur speciation processes, it is important to preserve contact zones and the adjoining forest corridors that allow dispersal among brown lemur populations.

SUMMARY AND CONCLUSION

The growing body of research on brown lemurs summarized here demonstrates the striking diversity of this group. Recent studies of cytogenetics and molecular genetics have addressed this diversity, elevating the two southeastern taxa (*E. collaris* and *E. albocollaris*) to distinct species (e.g., Djlelati et al., 1997; Wyner et al., 1999; but see Pastorini et al., 2000). The validity of the traditionally recognized subspecies of

E. fulvus may also be in question, as molecular research has identified distinct clades within both *E. f. fulvus* and *E. f. rufus* (Pastorini et al., 2000). Studies of parapatric southeastern populations suggest that boundaries may be stable and the presence of hybrid zones does not necessarily indicate substantial gene flow between parent taxa, evidenced by the novel genetic variants found in the Andringitra contact zone (Wyner et al., 2002). Morphological variation in this species complex includes ecogeographic variation in body size (Albrecht et al., 1990), as well as population differences in levels and direction of sexual dimorphism (Kappeler, 1996; Gerson, 2000; Johnson et al., 2005).

Ecological and behavioral differences are present as well. There is clear variation across populations in feeding behavior (from folivory to near exclusive frugivory), dietary diversity, and diet switching during resource scarcity (e.g., Sussman, 1974; Overdorff, 1993; Vasey, 1997). Brown lemurs also vary in other niche dimensions, including activity rhythms and ranging. These differences may in some cases be related to particular habitat characteristics, including community structure and seasonal and year-round variation in resource availability. While social behavior in many brown lemur taxa remains poorly understood, distinct patterns of social organization are evident. Group composition is similar across populations, with an even sex ratio — a highly unusual pattern for multimale/multifemale groups among primates (Kappeler, 2000; Ostner and Kappeler, 2004). In contrast, group cohesion differs among brown lemurs. In most populations, groups are stable and cohesive but fission–fusion group structure is found in *E. albocollaris* and, at least at some times and localities, in *E. f. fulvus* and *E. f. rufus* (Tattersall, 1977; Overdorff et al., 1999; Johnson, 2002).

Such variation in behavior and ecology may reflect a high degree of adaptability or, alternatively, localized evolution of individual brown lemur populations or taxa. The relative success of this group in occupying Madagascar's remaining natural habitats, coupled with the apparent evolutionary divergence of some populations, suggests that this complex represents an ongoing adaptive radiation. Nonetheless, several distinct populations face imminent risk of extinction. Conservation concerns for brown lemurs are also elevated because, as prominent frugivores in a broad range of habitats, they may serve critical roles in the maintenance and regeneration of ecosystems across Madagascar (e.g., Bollen et al., 2004). Finally, the ongoing behavioral, ecological, and genetic divergence within this complex represents a dynamic evolutionary process. Thus, preserving brown lemur populations and habitats safeguards both present and future biodiversity in Madagascar.

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CHAPTER TEN

Ecological Diversity and Seasonal Adaptations of Mouse Lemurs (*Microcebus* spp.)

Ute Radespiel

INTRODUCTION

Microcebus is a highly diverse genus with nine described species thus far and more to come (see below). The growing evidence for its taxonomic diversity is the result of intensified fieldwork during the last few decades coupled with the application of modern molecular phylogenetic approaches to this cryptic species group. Although early studies reported different morphotypes of mouse lemurs living even partly in sympatry (e.g., Petter, 1962; Martin, 1972), species status was assigned to them only later following the publications of Petter et al. (1977) and Tattersall (1982). The most influential single field study on the ecology and behavior of mouse lemurs is undoubtedly the ground-laying work of Martin (1972). Since Martin's work, many subsequent field studies were conducted by other researchers on different *Microcebus* taxa and it is now becoming progressively clear that mouse lemurs exhibit a large array of different ecological adaptations to a variety of different habitat types and climatic regimes. Ecological diversity may be expressed interspecifically but can also be detected between different populations

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of the same species. This chapter aims to review the current knowledge on ecological adaptations and their flexibility both inter- and intraspecifically. By doing this, I also want to explore what we can deduce on the biology and ecology of the "ancestral mouse lemur." Any trait that exists in most or all mouse lemur species (assumed starting point of radiation is about 10 million years ago [Yoder and Yang, 2004]) can be assumed to have already been present in their common ancestor. If, on the other hand, traits differ significantly between species, specific ecological adaptations to divergent environments can be assumed. Finally, high intraspecific variation may indicate a high adaptive potential of certain species that may, for example, allow us to explain differential distribution patterns or different susceptibility to human disturbances.

DISTRIBUTION OF MOUSE LEMUR SPECIES

There are currently seven described mouse lemur species inhabiting western Madagascar. Their distribution pattern falls into two categories: species with a broad distribution range such as the grey mouse lemur (*M. murinus*) and species with a regional or even locally restricted distribution range (*M. griseorufus, M. berthae, M. myoxinus, M. ravelobensis, M. sambiranensis, M. tavaratra*) (Figure. 1a,b). The distribution range of *M. murinus* extends from the southern region of Tolagnaro (Martin, 1972; Hapke, 2005) over the west coast (Tattersall, 1982; Mittermeier et al., 1994; Rasoloarison et al., 2000), up to at least the river Sofia in northwestern Madagascar (Olivieri et al., 2005; Olivieri and Radespiel, unpublished results). Previous reports of sightings farther to the north in the Ankarana Reserve (Nicoll and Langrand, 1989; Mittermeier et al., 1994) have so far not been confirmed with molecular data. *M. murinus* occurs sympatrically with other mouse lemur species in southern (*M. griseorufus*), southwestern (*M. berthae*), western (*M. myoxinus*), and northwestern Madagascar (*M. ravelobensis*) (Figure 1a,b). Of these, the distribution ranges of *M. griseorufus* and *M. myoxinus* seem to be the largest and extend from Tolagnaro to north of Toliara (*M. griseorufus*, Rasoloarison et al., 2000; Yoder et al., 2002; Hapke, 2005) and from the Tsiribihina river up to the Betsiboka river (*M. myoxinus*, Rasoloarison et al., 2000; Olivieri and Radespiel, unpublished data), respectively. The four other known western mouse lemur species seem to have much smaller ranges that may cover only the area between two adjacent large rivers (Inter-River-Systems, IRS, Figure 1b), respectively. This could be the Morondava and the Tsiribihina river for *M. berthae* (Rasoloarison et al., 2000; Schwab and Ganzhorn, 2004), the Betsiboka and the Mahajamba river for *M. ravelobensis* (Zimmermann et al., 1998; Radespiel and Raveloson, 2001; Olivieri et al., 2005), the Maevarano and the Sambirano river for *M. sambiranensis* (Rasoloarison et al., 2000; Randrianambinina et al., 2003a), and the Mahavavy river as possible southern border of *M. tavaratra* (Rasoloarison et al., 2000; Rasoloharijaona et al., 2005). The taxonomic classification of mouse lemurs inhabiting other

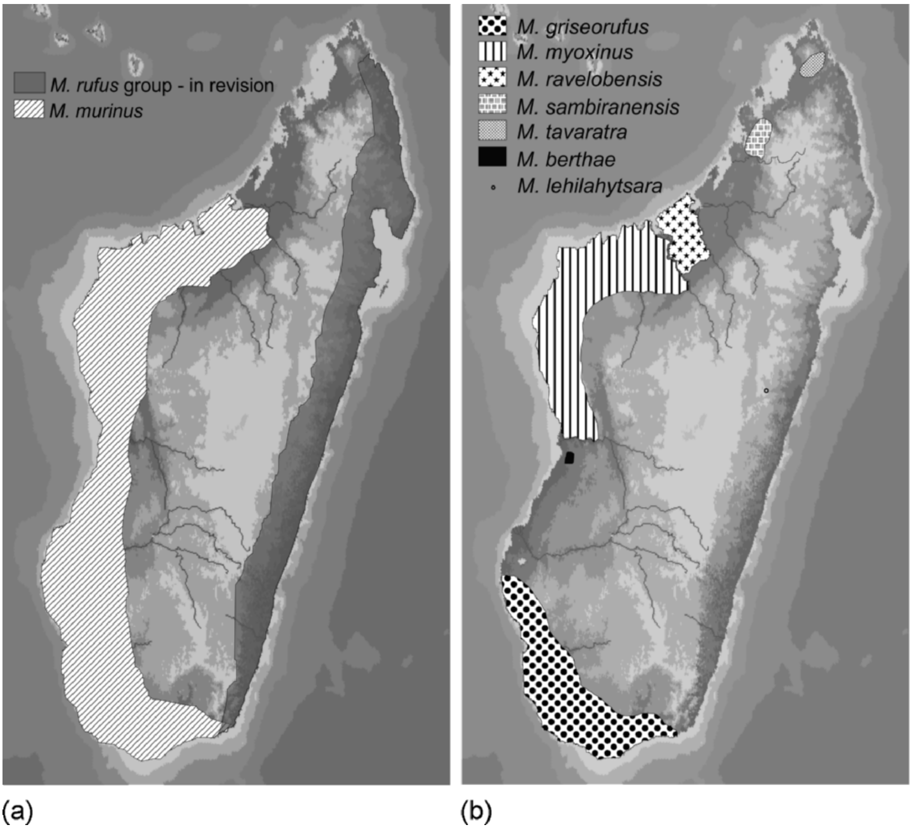

Figure 1. Distribution map of the currently known mouse lemur species. (a) *Microcebus murinus* and the *M. rufus* group: (b) all locally and regionally distributed species.

western IRSs is still under study (Olivieri and Radespiel, unpublished data; Louis, personal communication).

The taxonomy of mouse lemurs from the eastern rainforests of Madagascar is currently under revision (Kappeler, personal communication; Louis, personal communication). Historically, it has been assumed that only one species, *M. rufus*, inhabits all eastern rainforest habitats (Figure 1a; Petter et al., 1977; Tattersall, 1982; Mittermeier et al., 1994). However, there are now indications for deeper phylogenetic splits within this taxon (Yoder et al., 2000; Kappeler et al., 2005; Louis et al., 2006). One new species (*M. lehilahytsara*) has already been described from the region of Andasibe (Kappeler et al., 2005) and more species can be expected to become known within the next few years (e.g., Raharivololona et al., 2003; Louis, 2004). Due to the current lack of detailed ecological and distribution data, however, I will consider these eastern rufous forms the "*M. rufus* group" throughout this chapter and add the locality names whenever suitable.

COMPARATIVE ECOLOGY OF MOUSE LEMURS

Habitat Characteristics and Microhabitat Preferences

Mouse lemurs occur in many different forest habitats of Madagascar and even in those places that have undergone substantial anthropogenic changes (Table 1). On the species level, however, habitat plasticity differs considerably. Whereas

Table 1. Habitat types and environmental characteristics of mouse lemurs

Species	Habitat type (HT)	Rainfall (mm)	Altitude (m)	References
M. murinus	Evergreen littoral forest	1540	<20	1
	Dry deciduous forest	800–1600	10–300	2,5,8,9
	Transitional forest (dry deciduous-humid)		780	6
	Gallery forest	850–1200	20–1200	17
	Arid spiny forest (Didieracea)			13
M. griseorufus	Subarid thorn scrub, thick scrub & gallery forest	230–910[22]	100–200	6,13,23
	Spiny forest	720		13
	Dry deciduous forest	720		13
M. berthae	Dry deciduous forest	800	10	6,8
M. myoxinus	Dry deciduous forest	1100–1600[19]	<140	6
	Mangroves		0	7
M. ravelobensis	Dry deciduous forests, gallery forest, subhumid forests	1200–1600	<300	9,10,16
M. sambiranensis	Mosaic of western (dry) and eastern (humid) forest elements	1400–2300[19]	360–1600	6,15
M. tavaratra	Partially evergreen forest	1900	<400	5
	Dry deciduous forest with gallery forest		180	6
M. rufus group	Lowland & montane tropical humid forest	2500	200–1990	3,12,20,21
	Old Eucalyptus plantations with undergrowth	1700	950	4
	Evergreen rainforest	2600–3700	>100–1200	5,14
	Littoral forest	2700	<50	11,18

[1] Ramanamanjato and Ganzhorn, 2001; [2] Ganzhorn, 1995; [3] Goodman and Rasolonandrasana, 2001; [4] Ganzhorn, 1987; [5] Ganzhorn et al., 1997; [6] Rasoloarison et al., 2000; [7] Hawkins et al., 1998; [8] Schwab and Ganzhorn, 2004; [9] Rendigs et al., 2003; [10] Zimmermann et al., 1998; [11] Ratsirarson and Ranaivonasy, 2002; [12] Irwin et al., 2001; [13] Rasoazanabary, 2004; [14] Irwin et al., 2000; [15] Goodman and Schütz, 2000; [16] Rakotondravony and Radespiel, unpublished data; [17] Hawkins, 1999; [18] Randrianarisoa et al., 1999; [19] Rauh, 1992; [20] Sterling and Ramaroson, 1996; [21] Duckworth et al., 1995; [22] Jolly et al., 2002; [23] Yoder et al., 2002.

some species have been found in as many as five different broad *habitat types* and over a rainfall and altitude gradient (*M. murinus, M. rufus* group), others have been observed in only one (*M. berthae*) or two (*M. myoxinus*) types of forest and seem to lack environmental gradients within their distribution range. However, an interpretation of these findings in terms of higher or lower adaptive flexibility seems to be too premature, since (1) habitat classifications provided in publications are usually very broad, and (2) habitat diversity may also correlate with the number of studies conducted on the respective species. A literature search performed in the Database PrimateLit (http://primatelit.library.wisc.edu/) with scientific species names as search variables revealed a significant positive correlation between the time span since the first record (in years) and the number of hits for each species (range of time span: 5–61 years, range of hits: 25–1389; Spearman rank correlation: $r=0.913$, $n=8$, $p<0.05$).

Detailed studies on *microhabitat characteristics* were so far performed only on three mouse lemur species occurring in sympatric pairs in Kirindy (*M. murinus* and *M. berthae*) and Ampijoroa (*M. murinus* and *M. ravelobensis*). These studies revealed species-specific differences between used and unused microhabitats in all three species, although the findings were ambivalent for *M. murinus.* In some studies *M. murinus* was positively associated with microhabitats in relatively intact primary and diverse forest types (Ganzhorn and Schmid, 1998; Ramanamanjato and Ganzhorn, 2001; Rendigs et al., 2003). Other studies indicated that *M. murinus* may not be very specialized (Schwab and Ganzhorn, 2004), may well survive in disturbed forests (Ganzhorn, 1995; Radespiel and Raveloson, 2001), and occurs even in secondary growth (Ganzhorn and Schmid, 1998) or plantations (Ganzhorn, 1987), although reproductive success and therefore long-term population viability may be reduced under these highly disturbed circumstances. Whereas the first line of argument suggests a considerable vulnerability of *M. murinus* to human disturbances and therefore has important conservation implications, the second line of reasoning implies only low conservation priority for this species. Further studies are urgently needed to decide which of these contradictory conclusions most accurately describes the ecological requirements of this species.

M. berthae was concluded to possess high habitat specificity due to its high affinities to vines (used as sleeping sites) and to relatively open forest in the intermediate layer at 1.6–6.0 m (Schwab and Ganzhorn, 2004). This specificity was taken to explain the small distribution range of this species as well as its vulnerability toward being outcompeted by its larger sister species *M. murinus* which occurs in the same area.

Similar to *M. berthae*, *M. ravelobensis* seems to show a preference for vines (also used as sleeping sites) and was furthermore associated with relatively open microhabitats (i.e., higher cover of herb layer [Rendigs et al., 2003]). In a further study, these findings were interpreted as signs of ecological differentiation between the golden-brown and the sympatric grey mouse lemur in Ampijoroa, since they coincide well with species-specific sleeping site ecology (see below, Radespiel et al., 2003a). The general applicability of these findings needs to be tested by examining more populations from different origins for each of these species.

Feeding Ecology

Quantitative data on the feeding ecology of mouse lemurs are notoriously difficult to obtain, since continuous contact time with focal animals is impossible to maintain due to their small body size and quick locomotion in mostly dense vegetation. Therefore, we rely heavily on qualitative data and sometimes even anecdotal evidence as well as on results from fecal analyses (e.g., Martin, 1972; Atsalis, 1999a; Radespiel et al., 2006). All mouse lemur species studied so far have been reported to have an omnivorous diet.

Most feeding data are available on *M. murinus* (Hill, 1953; Webb, 1953; Petter, 1962; Martin, 1972, 1973; Sussman, 1978; Hladik et al., 1980; Barre et al., 1988; Corbin and Schmid, 1995; Schmelting, 2000; Lutermann, 2001; Génin, 2003; Radespiel et al., 2006). This species consumes animal matter such as insect secretions (of homopteran larvae, Flatidae), arthropods, or even small vertebrates as well as vegetable matter that consists of fruits, flowers, nectar, gum, and even sometimes leaves and buds (Table 2 for a complete list of all published plant species eaten by mouse lemurs). Seasonal variation in the diet is probably high (e.g., Schmelting, 2000; Lutermann, 2001) but remains to be studied in detail. However, it seems to be well supported that insect secretions and gum are of major importance during the dry season when fruits and insects are relatively rare (Corbin and Schmid, 1995; Génin, 2003; Radespiel et al., 2006).

A preliminary study on the feeding ecology of *M. ravelobensis* (Radespiel et al., 2006) also revealed a broad dietary regime with insect secretions and gum constituting the major food components during the second half of the dry season, similar to *M. murinus* (see Table 2 for plant species). Arthropods were regularly found in the feces, whereas fruits and nectar were consumed less frequently during this time of the year. In a neighboring study site (Jardin Botanique B [JBB]) with exclusive occurrence of *M. ravelobensis*, this species was regularly observed to eat leaves during the first half of the dry season (Hagenah, 2001; Weidt, 2001; Table 2).

The diet of the *M. rufus* group has been most intensely studied by Atsalis (study site: Ranomafano National Park, 1999a) and by Ganzhorn (study site: Analamazoatra/Andasibe, 1988). These authors as well as Harste et al. (study site: Ranomafano National Park, 1997) and Ratsirarson and Ranaivonasy (study site: Tampolo forest, 2002) emphasized the major importance of fruits (see also Table 2) and arthropods in the diet of *M. rufus.* As described by Atsalis (1999a), beetles (Coleoptera) were almost continuously present in the feces of *M. rufus* and were therefore defined as a staple food together with the fruit of the epiphytic, semiparasitic, endemic *Bakerella* that appeared year round in approximately 42% of all fecal samples. Martin (1972), Atsalis (1999a), and Ratsirarson

Table 2. Plant species consumed by mouse lemur species

	M. murinus	*M. ravelobensis*	*M. rufus* group
Fruits	*Canthium* sp.[7,10]	*Adenia firingalavensis*[8]	*Alberta humblotii*[1]
	Evonymus pleurostyloides[5]	*Cabucala erythrocarpa*[13]	*Anthocleista amplexicaulis*[1]
	Garessia sp.[9]	*Maerua cylindrocarpa*[12]	*Aphloia theaeformis*[1]
	Grewia sp.[9]	*Mapoutria berizokae*[13]	*Bakerella* sp.[1]
	Grewia trifolia[2]	*Protorhus ditimena*[14]	*Bakerella clavata* subsp.1[1]
	Homollea leandri[11]	*Strychnos spinosa*[13]	*Bakerella grisea*[1]
	Maerua cylindrocarpa[8,9]	*Tamarindus indica*[13,14]	*Canthium* sp.I[4]
	Mapouria boinensis[11]		*Cissus* sp.[1]
	Memecyclon sp[7]		*Clidemia hirta*[4,6]
	Mystroxylon sp.[9]		*Drypetis mad/sis*[4]
	Noronhia boinensis[9]		*Eugenia jambosa*[6]
	Phyllanthus sp.[11]		*Ficus* sp.[1]
	Scolopia sp.[7]		*Gaertnera* sp.[1]
	Tacca leontopetaloides[2]		*Garcinia verrucosa*[4]
	Cf. Tarenna sp.[2]		*Harungana madagascariensis*[1]
	Uapaca sp.[6]		*Ilex mitis*[1]
	Vaccinium emirnense[6]		*Lantana camarra*[4]
	Zizyphus mauritianus[6]		*Maesa lanceolata*[1]
			Medinilla sp.[1,4]
			Memecylon sp.[4]
			Nuxia sp.[1]
			Oncostemum botryoides[1]
			Oncostemum sp.[4]
			Psidium calleianum[1]
			Psorospermum sp.[4]
			Psychotria sp. 1-4[1]
			Rheedia sp.[4]
			Rhipsalis baccifera[1]
			Rubus roridus[6]
			Viscum sp.[1]
Gum	*Acacia schweinfurthii*[8,11]	*Acacia schweinfurthii*[8]	
	Alleanthus sp.[9,10]	*Albizzia gummifera*[8,11]	
	Astrotrichilia astertricha[11]	*Astrotrichilia astertricha*[11]	
	Baudouinia fluggeiformis[8]	*Baudouinia fluggeiformis*[8]	
	Calantica gerasifolia[9,10]	*Cassipourea microphylla*[11]	
	Canthium barorum[8,11]	*Cedrolopsis grevei*[11,14]	
	Commiphora sp[2,8]	*Commiphora* sp.[8,11]	
	Commiphora pervilleana[10]	*Diospyros* sp.1[8]	
	Erythoxylum sp.[8]	*Grewia bailloni*[11]	
	Euphorbia sp.[7]	*Maillardia occidentalis*[8,11]	
	Gaetnera sp.[8]	*Mystroxylon aethopicum*[8]	
	Homollea leandri[11]	*Noronhia boinensis*[11]	
	Hypocratea sp.[11]	*Pourpartia sylvatica*[8]	
	Legumineum sp.[9,10]	*Protorhus ditimena*[14]	
	Linociera topophylla[11]	*Rhopalocarpus similis*[8,11]	
	Mammea punctata[8]	*Terminalia* sp.[8,11]	
	Meliaceae (2sp.)[2]	*Vepris arenicola*[8]	
	Mystroxylon aethopicum[8,11]		

(Continued)

Table 2. Plant species consumed by mouse lemur species—Cont'd.

	M. murinus	*M. ravelobensis*	*M. rufus* group
	Phyllanthus sp.[11]		
	Pourpartia sylvatica[8]		
	Rhopalocarpus similis[8,11]		
	Rothmania reiniformis[8]		
	Sapium melanostricum[11]		
	Terminalia bovinii[2]		
	Terminalia mantaliopsis[2]		
	Terminalia sp.[8,11]		
Nectar	*Canthium* sp.[9,10]	*Karomia microcalix*[8]	
	Ceiba pentandra[3]		
	Evonymus pleurostyloides[5]		
	Karomia microcalix[8]		
Flowers	*Brexia madagascariensis*[6]	*Cabucala erythrocarpa*[13]	*Rubus roridus*[6]
	Vaccinium emirnense[6]	*Combretum coccineum*[13]	
		Maillardia occidentalis[14]	
		Mangifera indica[13]	
		Tarrena sp.[13]	
Leaves	*Uapaca* sp.[6]	*Cabucala erythrocarpa*[13,14]	
		Canthium barorum[14]	
		Cedrolopsis grevei[13,14]	
		Combretum obscurum[13]	
		Dichapetalum bojeri[13]	
		Eugenia sp.[14]	
		Grangeria poposa[13]	
		Maillardia occidentalis[14]	
		Malleastrum gracile[13]	
		Mammea punctata[13]	
		Mapoutria berizokae[13]	
		Molinae retusa[13]	
		Monanthotaxis valida[13]	
		Protorhus ditimena[14]	
		Rourea orientalis[13]	
		Strychnos madagascariensis[13,14]	
		Tina striata[13]	

[1] Atsalis, 1999a; [2] Génin, 2003; [3] Sussman, 1978; [4] Ganzhorn, 1988; [5] Hladik et al., 1980; [6] Martin, 1972; [7] Martin, 1973; [8] Radespiel et al., 2006; [9] Schmelting, 2000; [10] Lutermann, 2001; [11] Rahelinirina, 2002; [12] Reimann, 2002; [13] Weidt, 2001; [14] Hagenah, 2001.

and Ranaivonasy (2002) also noted the consumption of flowers and Ganzhorn (1988) as well as Ratsirarson and Ranaivonasy (2002) documented rare feeding on leaves and buds. Finally, Atsalis (1999a) noted the occasional appearance of gum and insect eggs, larvae, or pupae in the feces and found the remains of one soft invertebrate, possibly an earthworm.

In a first preliminary report on *M. griseorufus* in the first half of the dry season, Rasoazanabary (2004) noted the consumption of insects and gum, but no further details have been given.

Sleeping Site Ecology

All mouse lemur species studied thus far sleep during the daytime in some sort of shelter which may fulfill at least two important functions. It may help in thermoregulation by buffering against high external temperature fluctuations (Schmid, 1998) and should also offer protection against predators (Radespiel et al., 2003a). Two main variables must be addressed when describing the sleeping site ecology of these species: (1) the type and quality of the substrate used as sleeping site and (2) the social grouping pattern and its temporary stability. These variables and the respective references are summarized for each studied species in Table 3.

Again, most information is available for *M. murinus.* Interestingly, throughout its whole distribution range, this species uses tree holes for sleeping whenever they are available. In contrast, other *Microcebus* species appear to use tree holes only as one of several options. Whether these differences can be interpreted as signs of ecological differentiation, as seen in the sympatric species pair *M. murinus/M. ravelobensis* (Radespiel et al., 2003a), or as interspecific competition as seen in sympatric *M. murinus* and *M. berthae* (Schwab, 2000; Schwab and Ganzhorn, 2004) cannot be answered in a generalized way.

The social grouping patterns during the resting period seem to be species-specific but relatively stable in intraspecific comparisons. We find a segregation of sexes with stable female groups/solitary males (type *M. murinus*) or periodic unisex male or female groups (type *M. rufus*) or mixed-sex sleeping associations with unstable (type *M. berthae*) or stable composition (with up to five adult members, type *M. ravelobensis*) over time. It has been suggested that "low-quality sites" may force both sexes either to form sleeping groups with a potential benefit of increased vigilance as in *M. ravelobensis* (Radespiel et al., 2003a), or to follow a solitary lifestyle with the potential benefit of crypsis as seen in *M. berthae* (Schwab, 2000), but these hypotheses still need more rigorous testing on the intra- and interspecific level.

Socioecology

Mouse lemurs have been traditionally categorized as solitary foragers (Bearder, 1987). This term correctly describes their dispersed nocturnal lifestyle but does not take into account periodic or even regular social contacts with conspecifics within or outside the mating context. Based on the available information (see Table 4), all mouse lemur species studied thus far can be categorized as living in an individualized neighborhood. This term refers to the stable nature of a social network with more or less frequent social contacts facilitated by largely overlapping home ranges (within and among the sexes) among individually known neighbors.

Species differ, however, with regard to the smallest social unit within this neighborhood. Whereas some species mostly remain solitary even during the daily

Table 3. Aspects of the sleeping site ecology of the studied mouse lemur species (A: Ampijoroa JBA, B: Ampijoroa JBB)

	M. murinus	*M. griseorufus*	*M. berthae*	*M. ravelobensis*	*M. rufus* group
Substrate	Mostly tree holes[1,2,6,8,12–14] Female sites have better quality than male sites[1] Occasionally: leaf nests or dense foliage[8,14]	Gallery forest: vegetation tangles Spiny forest: tree holes[10]	Bark, nests, branches, vines, tree holes[7] Leaf nests[15]	(A) Tree holes, branches, vines, and others[2] (B) Mostly nests and leaves[17]	Mostly tree holes, but also leaf nests, dense foliage[8,9,11], palm leaf cavities[8], mostly nests, some tree holes[17]
Social grouping (adults)	Females form (matrilineal)[3,5,16] groups, males mostly stay alone[1,3,5,8,14]	Group sleeping observed, composition unknown[10]	Mostly solitary sleeping[7] Regular (47% of days) sleeping groups of variable composition[15]	Mixed-sex sleeping groups[2,4,17]	Solitary sleeping (nonreproductive season), partly unisexual sleeping groups (reproductive season)[17]
Stability of sleeping groups	Long-term stability, changes by deaths, births, or group splitting[3,5]	?	No long-term stability	Long-term stability, changes by demographic events[4]	Stable in composition over several months[17]

[1] Radespiel et al., 1998; [2] Radespiel et al., 2003a; [3] Radespiel et al., 2001b; [4] Weidt et al., 2004; [5] Lutermann, 2006; [6] Schmid, 1998; [7] Schwab, 2000; [8] Martin, 1972; [9] Wright and Martin, 1995; [10] Rasoazanabary, 2004; [11] Ratsirarson and Ranaivonasy, 2002; [12] Petter, 1962; [13] Martin, 1973; [14] Pagès-Feuillade, 1988; [15] Dammhahn and Kappeler, 2005; [16] Wimmer et al., 2002; [17] Randrianambinina, 2001; [18] Weidt, 2001.

Table 4. Socioecological traits of the most studied mouse lemur species (A: Ampijoroa JBA, B: Ampijoroa JBB, K: Kirindy forest, M: Mantadia National Park)

Trait	*M. murinus*	*M. berthae*	*M. ravelobensis*	*M. rufus* group
Size of home ranges (mean)				
Males	(A) 2.2–5.0 ha, seasonally varying[12], (A) 0.7–3.0 ha, seasonally varying[2], (A) 3.2 ha[5], (K) 2.8 ha, seasonally varying[4]	(K) 5.8 ha[27], (K) 4.9 ha[29]	(A) 3.2–7.9 ha[26] (B) 0.4–0.8 ha[25]	(M) 0.3 ha[30]
Females	(A) 1.2–2.6 ha[12], (A) 1.7 ha[5], (K) 0.7 ha[4]	(K) 1.2 ha[27], (K) 2.5 ha[29]	(A) 1.8–2.7 ha[26] (B) 0.5–0.6 ha[25]	(M) 0.3–0.7 ha[30]
Overlap of home ranges				
Male–male	High, many[1–16]	High, many[29]	High[26], many[25]	High[30,31]
Female–female	High[1,3,4,6], selective[1,6], or many[3,4]	Moderate, some[29]	High[26], many[25]	High[30,31]
Male–female	High, many[1–5]	High[29]	High[26], many[25]	High[30,31]
Smallest social unit	Female sleeping group[1,6,7], mixed sleeping groups[8]	Solitary forager[27,29]	Mixed-sex sleeping groups[25,26]	Solitary forager vs. unisexual male and female sleeping groups[30]
Kinship structure	Matrilinear female groups[6–7]	No matrilines[29]	Under study	?
Dispersal regime	Female philopatry, male dispersal[3,7,9–11,13]	Female philopatry, male dispersal[29]	Under study	Possibly male dispersal[31]
Category: social organization	Individualized neighbourhood[1]	Individualized neighbourhood[29]	Individualized neighbourhood[25]	Individualized neighbourhood
Female mate choice (FMC)	Yes: rejection of mates[1,14,22,24], selective escape[22,23]	?	?	?
Male scramble competition (MSC)	Yes: search strategies[1,4,28], no spatial monopolization[1–4,18]	Yes: male roaming behaviour[27,29], no spatial monopolization[29]	Yes: (A) search strategies[26], (A+B) no spatial monopolization[25,26]	Yes: no spatial monopolization[31]
Male contest competition (MCC)	Yes: temporary mate guarding[4,14], male–male aggression[2,4,21,14], spatial monopolization[8]	?	?	?

(Continued)

Table 4. Socioecological traits of the most studied mouse lemur species (A: Ampijoroa JBA, B: Ampijoroa JBB, K: Kirindy forest, M: Mantadia National Park)—Cont'd.

Trait	*M. murinus*	*M. berthae*	*M. ravelobensis*	*M. rufus* group
Sperm competition (SC)	Yes: large testes[15–17], multiple mating[4,14,20,22], multiple paternity[4,20–22], mating plugs[4]	Yes: large testes[17,27,29], mating plugs[27]	Yes: large testes[15,17,26]	Yes: large testes[32]
Modes of sexual selection	FMC+MSC+ MCC+SC	MSC+SC	MSC+SC	MSC+SC
Category: mating system	Dispersed multimale/multifemale system[19]	Dispersed multimale/ multifemale system[27]	Dispersed multimale/ multifemale system[25,26]	Dispersed multimale/ multifemale system

[1] Radespiel, 2000; [2] Schmelting, 2000; [3] Eberle and Kappeler, 2002b; [4] Eberle and Kappeler, 2004b; [5] Pagès-Feuillade, 1988; [6] Lutermann, 2001; [7] Radespiel et al., 2001b; [8] Martin, 1972; [9] Radespiel et al., 2003b; [10] Fredsted et al., 2005; [11] Wimmer et al., 2002; [12] Radespiel, 1998; [13] Fredsted et al., 2004; [14] Peters, 1999; [15] Schmelting et al., 2000; [16] Fietz, 1999; [17] Schülke et al., 2004; [18] Radespiel et al., 2001a; [19] Müller and Thalmann, 2000; [20] Radespiel et al., 2002; [21] Andrès et al., 2003; [22] Eberle and Kappeler, 2004a; [23] Radespiel, unpublished data; [24] Radespiel and Zimmermann, 2003; [25] Weidt et al., 2004; [26] Ehresmann, 2000; [27] Schwab, 2000; [28] Schwab and Ganzhorn, 2004; [29] Dammhahn and Kappeler, 2005; [30] Randrianambinina, 2001; [31] Atsalis, 2000; [32] Randrianambinina et al., 2003

resting period, others form stable sleeping groups of different composition (see Table 3). Most details are known about the social organization of *M. murinus*. Modern molecular techniques such as microsatellite analyses revealed that this species forms matrilinear female clusters (Lutermann, 2001; Radespiel et al., 2001b) that are characterized by preferential kin-biased space sharing and communal infant rearing (Lutermann, 2001; Eberle and Kappeler, 2002a).

With regard to the mating system of mouse lemurs all species seem to have a dispersed multimale/multifemale system with a pronounced importance of scramble competition and sperm competition among males (see Table 4 for details and references). In general, spatial monopolization of estrous females does not seem to be possible due to their dispersed nightly activities and reproductive synchrony. Males rather seem to have evolved search and roaming strategies in order to localize potential mates. Detailed behavioral observations are again only available for *M. murinus*. These have shown that in addition to scramble and sperm competition among males, male contest competition and female mate choice can also influence the reproductive outcome. It therefore appears that this small nocturnal lemur species possesses a complex and variable mating system that allows both sexes to adopt different reproductive tactics (e.g., Radespiel, 2000; Eberle and Kappeler, 2004a,b; Schmelting et al., under review), based on competitive abilities, previous experience, body condition, or receptivity of the partner.

SEASONAL ADAPTATIONS OF MOUSE LEMURS

Reproduction

Most lemur species are well known for their seasonal reproduction (e.g., Jolly, 1984; Richard and Dewar, 1991; Sterling, 1994; Wright, 1999). Although this is also true for all mouse lemur species studied so far, some intra- and interspecific differences have been detected recently. The onset of female cycling activities has been shown to depend largely on photoperiodic changes but also partly on temperature and body condition (e.g., Perret and Aujard, 2001; Randrianambinina et al., 2003b). Free-living *M. murinus* females have been observed or suspected to produce one or two litters per year depending on their geographic origin (Figure 2: Martin, 1972, for Mandena; Schmelting et al., 2000, for Ampijoroa; Eberle and Kappeler, 2004a, for Kirindy). Litter size ranges from one to three with twins occurring most frequently. Interestingly, the lack of a second litter in Kirindy cannot easily be explained with the later onset of the rainy season or the smaller amount of rainfall per year in comparison to Ampijoroa, since there are indications for a second litter in *M. berthae* (co-occurring with *M. murinus* in Kirindy; Schwab, 2000) that should also be constrained by these factors. Future studies should focus more closely on the reasons for such intraspecific variation.

One mouse lemur species differs clearly from all others with respect to reproductive seasonality and this is *M. ravelobensis* (Figure 2). Females of this species start cycling as early as late August (*before* the photoperiodic change to long days)

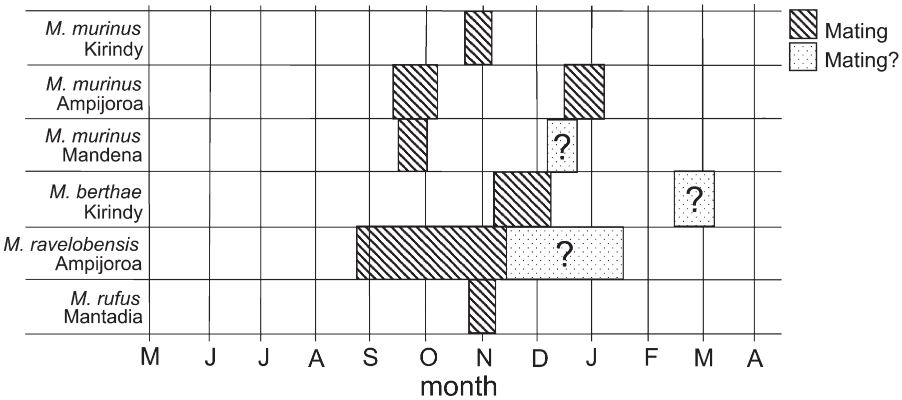

Figure 2. Seasonal mating activities in mouse lemurs (for references see text).

and estrous females can be continuously trapped until November (Schmelting et al., 2000; Randrianambinina et al., 2003b), when capture success usually drops dramatically for this species, preventing further inspections of their reproductive state. Moreover, lactating *M. ravelobensis* females can be captured as late as in early April, suggesting at least partial mating activities until mid January (Schmelting et al., 2000; Radespiel, personal observation). These findings indicate prolonged mating activities and no strict estrous synchrony, which contrasts with the reproductive pattern observed so far in all other species. The physiological and photoperiodic basis for the regulation of the early start and extension of mating activities in *M. ravelobensis* is not yet clear and deserves further attention.

Torpor and Body Mass Variations

Mouse lemurs are well known for seasonal physiological changes that are, for example, expressed in seasonal variations in body mass, general activity, and the ability to enter torpor. Daily torpor has been observed during the cooler months of the year in all mouse lemur species studied so far (e.g., Schmid, 2001, for *M. murinus*; Randrianambinina et al., 2003b for *M. rufus;* Radespiel et al., 2003a, for *M. ravelobensis*; Schmid et al., 2000, for *M. berthae*). Seasonal torpor, i.e., a prolonged state of reduced body temperature with inactive periods of several days to months, is known only from one population of *M. murinus* (Kirindy, Schmid and Kappeler, 1998) and from the *M. rufus* group (Ranomafana: Atsalis, 1999b; Mantadia: Randrianambinina et al., 2003b). The differences between these and the other study sites have been explained as consequences of the respective temperature regimes. Kirindy forest and the eastern mountain rainforests suffer from very low nightly minimum temperatures during the dry season that may impose severe thermoregulatory stress on its inhabitants. Prolonged torpor allows them to save substantial amounts of energy during these harsh months (Schmid, 1999; Schmid and Stephenson, 2003) but on the other hand imposes costs (i.e., loss of body mass) on an individual. It has therefore been argued that only individuals in relatively good body condition (i.e., high body mass of > 50 g) may afford to enter seasonal torpor (Schmid and Kappeler, 1998; Atsalis, 1999b; Randrianambinina et al., 2003b). These seem to be more often females than males with the consequence that populations with seasonal torpor have a seasonally varying sex ratio with a strong excess of males during the cold period of the year (Schmid and Kappeler, 1998; Atsalis, 1999b; Randrianambinina et al., 2003b).

Seasonal variations of body mass have been observed in all mouse lemur species studied (*M. murinus*: Schmid and Kappeler, 1998; Schmelting, 2000; Lutermann, 2001; *M. rufus* group: Atsalis, 1999b; Randrianambinina et al., 2003b) independent of their use of seasonal torpor. These variations can be summarized as follows: Animals usually accumulate fat reserves during the (late) rainy season and lose weight during the subsequent dry season. Seasonally torpid individuals lose proportionally more weight than those that stay active and may feed on a daily basis throughout the year. Males seem to increase body mass prior to the onset of the mating season but lose it soon afterwards, possibly as a result of their mate searching strategies which usually involve high locomotor activities.

THE ANCESTRAL MOUSE LEMUR: WHAT CAN WE TELL BY NOW?

Behavioral traits can be used in order to reconstruct evolutionary scenarios and traits of common ancestors of species groups (e.g., Plavcan, 1999; Nunn and van Schaik, 2002). I will apply this principle to mouse lemur biology in order to detect universal traits in the different habitats of Madagascar that might allow us to learn about their common ancestor.

On the basis of our present knowledge, seasonal reproduction in mouse lemurs appears to be universal. The exact mechanism of reproductive activation seems to vary between different species (photoperiod, body condition, ambient temperatures), but gestation periods and births are not equally likely over the year. Mouse lemurs generally seem to produce litters of one to three offspring and more than one litter per year can be produced if the habitat is favorable. Seasonal reproduction with the potential for several successive litters per season and a litter size of about one to three young therefore seem to be the likely ancestral conditions for mouse lemurs. Such relatively high reproductive potential would have helped to establish populations during their radiation into new habitats.

Daily torpor is common in all mouse lemur species studied so far and may also be an ancient trait that evolved either in the common ancestor or even earlier in primate evolution. Prolonged seasonal torpor, on the other hand, has not been observed in all species and seems to occur only in harsh environments (low ambient temperatures) and in individuals/species with relatively high body mass (above 50 g; Schmid and Kappeler, 1998; Randrianambinina et al., 2003b). Therefore, the presence of this trait in the common ancestor would likely have been tied to its body mass. If it was small such as *M. berthae* (~ 30 g; Schwab, 2000), it is unlikely that it could have used prolonged seasonal torpor. If it was the size of *M. murinus* (~ 60 g; Zimmermann et al., 1998), prolonged seasonal torpor was more likely to occur. It has been suggested that the ancestral lemur crossed the Mozambique Channel on floating pieces of vegetation, surviving this period of presumably low food availability through prolonged periods of hibernation (Kappeler, 2000). This is a possible scenario only for an ancestor of moderate size and this would mean that *M. berthae* has decreased secondarily in size throughout its evolutionary history. Such secondary dwarfism is known from another branch of the primate phylogeny (callitrichids: Leutenegger, 1980; Martin, 1992) but its relevance in the lemur radiation has still to be verified.

Ancestral mouse lemurs were most likely omnivorous, since this mode of feeding can be found in all species studied today. Seasonally varying food availability characterizes all Malagasy ecosystems (e.g., Wright, 1999), therefore, a large variety of potential food sources could have been used: fruits, gum, insects, insect secretions, leaves, flowers, nectar, arthropods, and small vertebrates. Such flexibility allowed the quick colonization of new habitats in Madagascar and may have also facilitated survival during previous times of passage.

All mouse lemur species are arboreal, solitary foragers which scatter themselves spatially during their nocturnal activities. Nevertheless, they all show large degrees of home-range overlap, enabling individuals to regularly interact during their nocturnal activities. On the basis of current knowledge it is not possible to decide whether the *berthae* type (solitary sleeping mode), the *murinus* type (stable matrilinear female sleeping groups), or the *ravelobensis* type (stable mixed-sex sleeping groups) most closely reflects the ancestral condition for mouse lemurs. However, within this genus we see different types of sociality that may well serve as an interesting and suitable model for the evolution of sociality in primates, although these associations are continuously threatened by an enormous predation rate (Goodman et al., 1993) leading to the highest turnover rates known for primate populations (Cheney and Wrangham, 1987; Hill and Dunbar, 1998).

All described mouse lemur species live in a multimale/multi female mating system where monopolization of estrous females is not complete. Sperm competition seems to play a major role, but female interests should also shape the reproductive outcome considerably, since female dominance can be assumed to be an ancestral lemur trait (Radespiel and Zimmermann, 2001). Such a polygamous mating system could also be expected for the ancestral mouse lemur and perhaps even in earlier primates (Müller and Thalmann, 2000).

The comparison of interspecific similarities thus allows us to draw some conclusions about the ancestral mouse lemur condition. Whether this complex of traits may even hold for the ancestral lemur or the ancestral primate condition could only be revealed by further comparative studies (e.g., using small nocturnal galagos, lorises, and small mammalian nonprimate species as outgroups). These comparisons, however, lie beyond the scope of this present overview.

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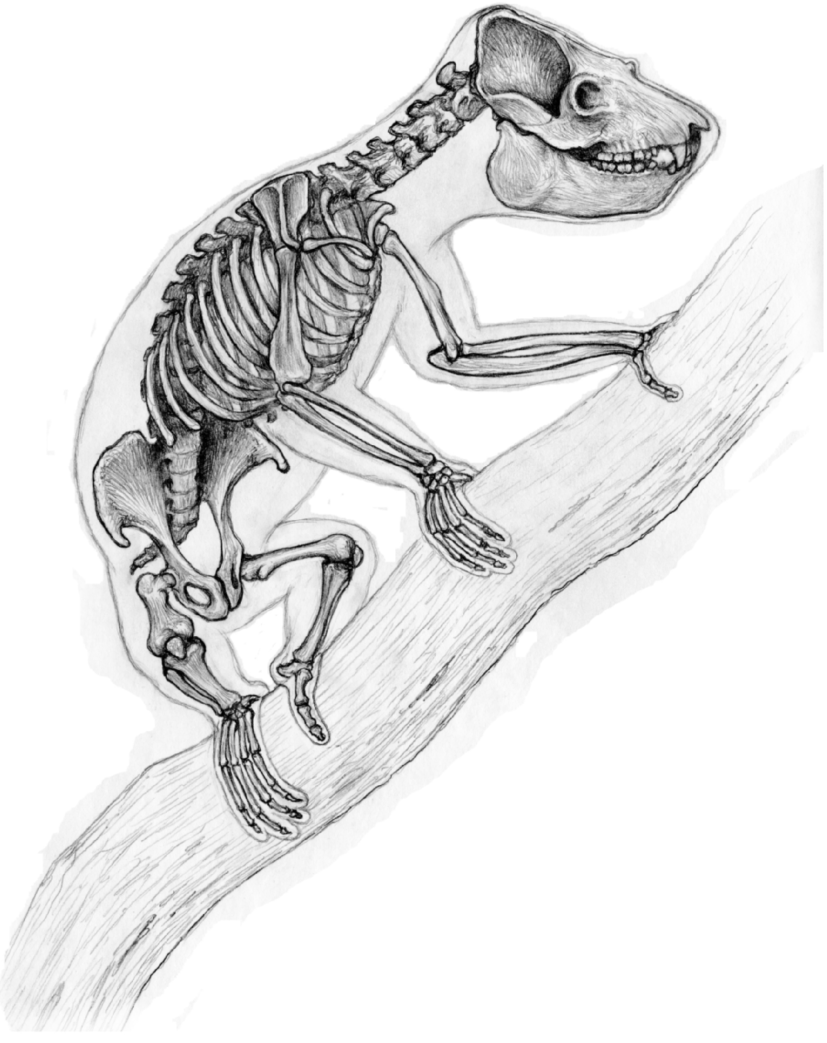

Figure 1. Reconstruction of *Megaladapis edwardsi*, a giant extinct lemur of southern Madagascar, by Stephen D. Nash/Conservation International.

Figure 2. *Eulemur mongoz* (mongoose lemur) juvenile- photo by D. J. Curtis

Figure 3. *Eulemur albocollaris* (white collared lemur)-juvenile- photo by S. Johnson

Figure 4. *Eulemur fulvus refus* (rufous brown lemur) female- photo by D. J. Overdorff

Figure 5. *Eulemur coronatus* (crowned lemur) female- photo copyright B. Z. Freed

Figure 6. *Eulemur rubriventer* (red-bellied lemur) juvenile- photo by S. Tecot

Figure 7. *Lemor catta* (ring-tailed lemur)- photo by M. L. Sauther

Figure 8. *Hapalemur griseus* (gray gentle lemur or gray bamboo lemur)- photo by D. Haring

Figure 9. *Propithecus diadema diadema* (diademed sifaka)- photo by M. Irwin

Figure 10. *Indri indri* (indri)- photo by N. Garbutt

Figure 11. *Varecia variegata* (black and white ruffed lemur)- photo by L. Gould

Figure 12. *Lepilemur edwardsi* (Milne-Edward's sportive lemur)- photo by U. Thalmann

Figure 13. *Cheirogaleus medius* (fat-tailed dwarf lemur)- photo by K. Dausmann

Figure 14. *Microcebus ravelobensis* (golden-brown mouse lemur)- photo by U. Radespiel

Figure 15. *Daubentonia madagascariensis* (aye-aye)- photo by D. Haring

Figure 16. *Avahi occidentalis* (Western woolly lemur)- photo by A. Müller

CHAPTER ELEVEN

Social Pair-Bonding and Resource Defense in Wild Red-Bellied Lemurs (*Eulemur rubriventer*)

Deborah J. Overdorff and Stacey R. Tecot

INTRODUCTION

Pair-bonding among nonhuman primates is rare and the possible selection pressures at work to maintain this type of social grouping have been discussed at great length (Kleiman, 1977; Wittenberger, 1980; Kinzey, 1987; Palombit, 1999; Fuentes, 1999, 2002; Chambers, 2002; Reichard, 2003; van Schaik and Kappeler, 2003). While the behavioral ecology of pair-bonded species has been relatively well studied across radiations, there are fewer studies that examine the nuances of social behavior between pair-bonded individuals and how social behavior is affected by ecological variables such as changes in food availability and feeding competition (but see Curtis and Zaramody, 1997; Bartlett, 2003; Fietz, 2003; Curtis, 2004; Schulke, 2003, 2005). This inhibits researchers' ability to fully evaluate the two main competing hypotheses, mate defense and resource defense (Wrangham, 1980; Dunbar, 1988), that have been put forward to explain the evolution of pair-bonding. Of these two sets of hypotheses, mate defense models have received more attention and empirical support (van Schaik and Dunbar,

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1990; van Schaik and Kappeler, 1997, 2003; Palombit, 1999). The main conclusion of these studies is that mate guarding and infanticide prevention are the main forces that influence the formation of pair-bonded groups in a wide range of species (van Schaik and Kappeler, 1997; Palombit, 1999; Brotherton and Komers, 2003).

Resource defense models, however, may merit further consideration for some groups of primates. For example, in his review of pair-bonding patterns, Fuentes (2002) concluded that pair-bonds, especially among Malagasy strepsirhines, may result due to "male defense against predators and/or defense against resource competition from conspecifics and other species" (p. 958). In this scenario, female reproductive success depends upon receiving help from the male, primarily to maintain exclusive access to food resources. Male aid can also come in the form of care for infants as seen in some of the small New World Primates such as owl and titi monkeys and callitrichids (Wright, 1990; Goldizen, 2003) or siamangs (Palombit, 1996). Although solitary individuals have only themselves to feed, they are likely to be more susceptible to predation, do not gain adequate access to higher-quality food because they are likely to be displaced by social groups, and are likely to accrue little to no gain in reproductive fitness. The addition of more than one male decreases a male's individual reproductive success, increases paternal confusion, and leads to less male investment in range defense and care for infants (Wright, 1990; Goldizen, 2003). Additional females would require a larger home range area to support their increased energetic needs due to reproduction which in turn decreases the group's ability to maintain exclusive access. Pair-bonding is the result of a balance that is struck between the costs and benefits of living a solitary life or group living.

Malagasy strepsirhines in particular are an excellent model taxon to examine the nature of pair-bonding and resource defense for two reasons. First, there is a relatively high proportion of pair-bonded species within the radiation compared with anthropoids (Heymann and Kappeler, 1996; Jolly, 1998) and these species occupy a wide variety of niches. Second, Malagasy primates must cope with severe environmental challenges due to poor food quality, small food patch size, and unpredictable resource patterns, that are influenced by extreme weather patterns (Ganzhorn, 1995; Ganzhorn et al., 1999, Gould et al., 1999; Wright, 1999), and may have evolved traits such as small group sizes to maximize resources and conserve energy (Wright, 1999). As a result of the environmental challenges present in Madagascar, the potential for contest competition for resources within and between species could be quite high (see Mutschler et al., 2000; Schulke, 2003, 2005), thereby placing an upper limit on how many individuals a group can support and explaining the prevalence of pair-bonding within the Malagasy lemurs.

Several predictions can be made if pair-bonding in Malagasy lemurs is driven by resource competition and the need to defend food resources (loosely following Fuentes, 2002). First, the pair-bond will be the common group composition observed within species; these groups will be stable across reproductive seasons and periods of fluctuation in available food. Second, the exchange of affiliative behaviors (nearest neighbor association, grooming, and scent-marking) should be strongest between the adult male and adult female. Third, within-group contest for food should be minimal and rates of aggression should be low. Fourth, between-group contest for food will be more common than within-group contest for food and evidenced through conspecific and intraspecific contest over food. Fifth, both males and females are expected to be active participants in range defense. Finally, given the extreme changes in food availability patterns that have been documented in southeastern Madagascar (Hemingway and Overdorff, 1999), it is likely that within-group and between-group interactions will vary with availability patterns although within-group affiliative behaviors should remain stable (Curtis and Zaramody, 1997; Schulke, 2005).

To test these predictions, we use detailed data on social interactions within three wild groups of red-bellied lemurs (*Eulemur rubriventer*) from a 14-month study and monthly censuses on these groups between 1989 and 1994 (Overdorff, 1993a,b, 1996a,b), and supplement these data with comparable demographic data collected from another long-term study by Tecot (in preparation). In general, red-bellied lemurs appear to maintain small groups, are highly frugivorous, defend discrete home ranges which overlap little with other conspecific groups, and males actively care for infants (Merenlender, 1993; Overdorff, 1993a,b, 1996a,b; Durham, 2003).

First, we address the predictions outlined above by describing the social organization of red-bellied lemurs using data on group composition, affiliative behaviors (grooming, scent-marking, and nearest neighbor patterns), and agonistic patterns within and between groups. In addition, we present data on directionality of social behaviors and how adult males and females participate in interactions with conspecifics and other sympatric species. Finally, we evaluate how food availability and food scarcity patterns influence each of these variables to determine what variables might contribute to the selection for and maintenance of pair-bonding in this species.

METHODS

Study Site

The study site was located in the Ranomafana National Park (RNP) region, a large (43,500 ha) southeastern rainforest in Madagascar (see Wright, 1992). RNP is located between 47″18″–47″37″ and 21″02″–21″25′ S and ranges from montane cloud forest (1500 m) to lowland rainforest (500 m). The 3.5 km^2 site for this study, Vatoharanana, is approximately 5 km south of the Talatakely Research Station and is a high montane rainforest (altitude: 1200 m). Annual rainfall averages from 1500 mm to over 4000 mm (Overdorff and Wright, unpublished data). Ten sympatric species of prosimian primates are found in the area in addition to the study species.

Phenological patterns have been documented previously in Hemingway and Overdorff (1999) and Overdorff et al. (unpublished). Because this species is highly frugivorous (Overdorff, 1993a), it was assumed fruit availability would have the most impact on behavior. Fruit availability typically peaks between August and February and is at its lowest between March and July. The food availability period corresponds to the birth season (mid-September to mid-October) and lactation (through March) while the food scarcity period corresponds to the mating season (mid-May to mid-June) and gestation (mid-June to mid-September/October). Seasonal differences in social behavior, demography, and conspecific and interspecific aggression were examined using these two distinct categories of food availability.

Study Groups and Demography

Two groups of red-bellied lemurs were followed from dawn to dusk at least 8 days a month from July 1988 through August 1989 (1500 observation hours). A third study group was observed on an opportunistic basis. Monthly censuses on each of these study groups continued from September 1989 to December 1994 (see Overdorff, 1993a,b, 1996a,b, for further details).

As part of the long-term nature of this study, groups were censused once a month between September 1989 and December 1994. Additional information on group movements, emigrations, and immigrations was available as other researchers have worked at the site on separate projects (Strait and Overdorff, 1995; Tecot, in preparation). Data from Tecot's study which took place from September 2003 through March 2005 (4800 observation hours), were used to provide supplemental data on two groups at this site, and three groups at the adjacent Talatakely site.

Data Collection

A combination of continuous focal animal sampling, point sampling, and all occurrences sampling was used to quantify social behavior (Overdorff, 1996b). An adult male and female focal animal were each followed by one observer exclusively on each sampling day (8–10 hours in length) and focal samples were balanced between all adult individuals in each study group. In addition, individuals were marked with colored collars and pendants or radio collars. At 5-minute intervals the focal animal's nearest neighbor within 5 m was noted; if two animals were equidistant from the focal, then both animals were recorded. A sign test (Sokal and Rohlf, 1995) was used to determine independence of scan samples and it was determined that samples were independent at 30-minute intervals. These data points were then used to calculate the percent of samples individuals spent near each group member.

All occurrences of the following behaviors were noted: mutual grooming, allogrooming, self-grooming, aggression within groups, aggression between groups, aggression between species, and all forms of scent-marking. The initiator and recipient of grooming bouts and event behaviors were identified and the context of behaviors was also recorded (feed, rest, travel). Detailed *ad libitum* notes were recorded on the adult male and female's behavior when group members interacted with conspecific groups or other species. Supplemental data collected by Tecot followed a similar protocol. Chi-squared tests and Mann-Whitney U tests were used to compare differences between food availability periods. Significance level was set at $p < 0.05$.

RESULTS

Group Composition

During both studies, each study group contained only one adult male and one adult female (Table 1). With the exception of infant births which occurred during mid-September through mid-October, group compositions remained stable. During subsequent censuses we noted that neither males nor females were philopatric and all natal juveniles left social groups between 2.5 and 3 years of age. One of these juvenile females was rediscovered in June 1994 with an adult male and offspring in a home range adjacent to her natal range and was still occupying that range as of September 2003 (Tecot, personal observation).

Replacement of resident adult females by nongroup females has been witnessed four times and we have yet to observe resident males being replaced by nongroup

Table 1. Group compositions for Overdorff's study and Tecot's study

Group ID	# adult females	# adult males	# infants and juveniles	# immigrations	# emigrations	# deaths
Tecot						
A	1	1	2	0	1	2
C	1	1	3	1	1	2
1	1	1	3	0	0	1
2	1	1	2	0	0	0
3	1	1	1	1	1?	1?
Overdorff						
GI	1	1	2	0	1	1
GII	1	1	2	0	1	0
GII	1	1	2	1[b]	1[b]	1[a]

[a] Emigration between 2.5 and 3 years of age (natal juveniles).
[b] Forced emigration by another female, died 2 weeks later.
? Emigrated or died.

males. In three cases, a resident female died or disappeared from her group and a new female joined the remaining male within 3 to 5 weeks. In May 1994, another female from Overdorff's study (Group II) was actively evicted from her group by a nonresident female over a 24-hour period. The first time the nonresident female had been observed was during the week prior to the eviction while she was following the group at a distance (50–100 m). On the day the resident female was evicted, the nonresident female repeatedly chased her, cuffed her, pulled her hair, and attempted to bite her; other group members did not intervene. The day following the eviction the resident female was observed on a trail outside of Group II's home range, approximately 2 km from where she had been seen last. She had sustained several bite wounds on her back and neck and her body was found 3 weeks later. Based on forensic evidence such as puncture wounds to the skull, it was presumed she had been predated on by a *Cryptoprocta fossa* (Overdorff and Strait, 1994).

Affiliative Patterns

Nearest Neighbor Patterns

Red-bellied lemurs almost always had a nearest neighbor and were observed to be alone (i.e., no nearest neighbor within 5 m) in less than 10% of the scan samples. Males and females were alone in 9.1 and 8.7% of the scans, respectively, and offspring were rarely without a nearest neighbor (3%). Males and females were observed slightly less often with each other (42.9% of scans) than with their offspring (male–offspring 48.05%; female–offspring 48.15%) but the difference was not significant. The adult males and females in each group remained in close proximity to each other regardless of season. However, nearest neighbor patterns varied seasonally among other age and sex classes (Figure 1). During food scarcity, the adult male and female were near their offspring less often (Mann-Whitney U test, $n_1=11$, $n_2=14$, male–offspring $Z=4.10$, $p<0.0001$, female–offspring $Z=3.61$, $p< 0.0003$), and all individuals spent more time alone (Mann-Whitney U test male alone $Z=2.85$, $p<0.004$; female alone $Z=2.41$, $p<0.02$; offspring alone $Z=3.7$, $p<0.0002$, Figure 1).

Grooming

A total of 377 mutual-grooming (MGR), 344 allo-grooming (AGR), and 839 self-grooming (SGR) bouts were recorded. Overall, rates of social grooming between adult males and females and their offspring did not vary significantly although adults tended to initiate allo-grooming toward offspring at slightly higher rates than toward each other (Table 2). Social grooming rates (mutual-groom and

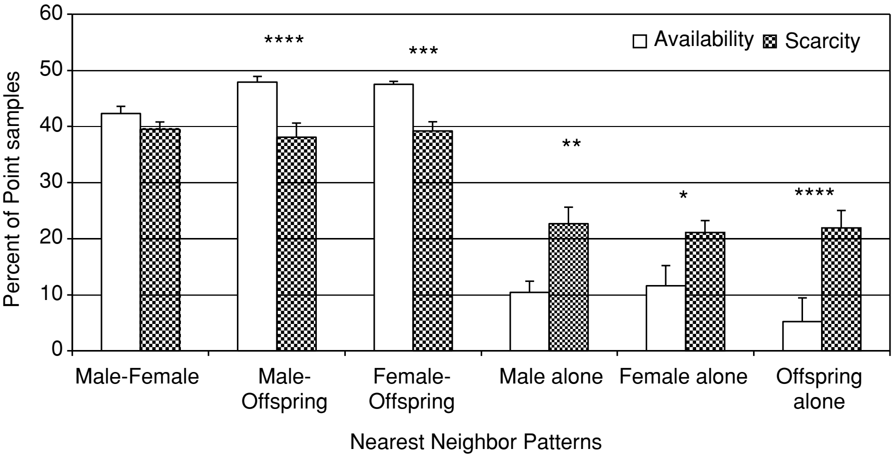

Figure 1. Percentage of point samples that group members spent within 5 m of each other for food availability and food scarcity periods. Significant results indicated by * = 0.02, ** = 0.004, *** = 0.0003, **** = 0.0002.

Table 2. Rates of grooming per hour by director and receiver[a]

Directionality	AGR rate	MGR rate
Female–offspring	0.06	0.05
Female–male	0.02	0.05
Male–female	0.05	0.05
Male–offspring	0.07	0.05
Offspring–adult	0.04	0.05

[a] AGR, allo-grooming; MGR, mutual-grooming. Rates did not vary by category significantly.

allo-groom) also were similar to each other within food scarcity and food availability periods but both rates dropped significantly during food scarcity (MGR: $\chi^2 = 5.07$, $p < 0.04$, $df = 1$; AGR: $\chi^2 = 3.67$, $p < 0.05$, $df = 1$, Figure 2).

The directionality of grooming patterns did not vary seasonally. The male, female, or offspring were equally likely to initiate mutual-grooming bouts with each other and the adult female was least likely to initiate allo-grooming with the adult male ($\chi^2 = 10.23$, $p < 0.03$, $df = 4$, Figure 3). Compared with social grooming, self-grooming rates were almost three times higher during food availability but also dropped to similarly low levels during food scarcity ($\chi^2 = 28.45$, $p < 0.0001$, $df = 1$, Figure 2).

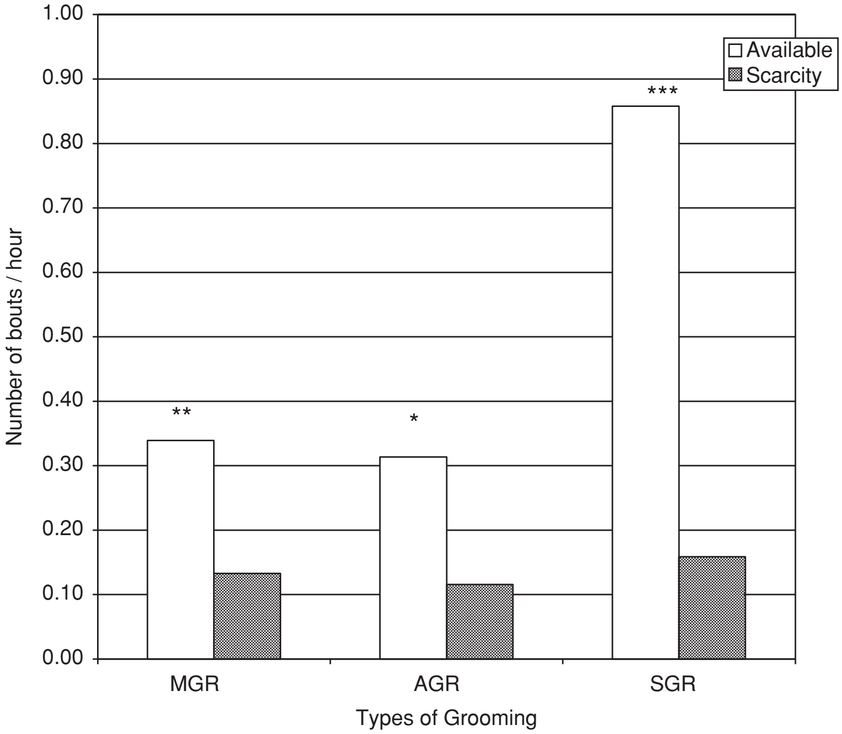

Figure 2. Rates of mutual-grooming (MGR), allo-grooming (AGR), and self-grooming (SGR) for food availability and food scarcity periods. * = 0.05, ** = 0.04, *** = 0.0001.

Scent-Marking

Three kinds of scent-marking were observed: anogenital marking (AGM, $n=1206$), head-marking (HDM, $n=86$), and palmar-marking (PMK, $n=186$). Males anogenital scent-marked almost twice as much as females (male rate 0.51/hr, female rate 0.29/hr $\chi^2=6.54$, $df=1$, $p<0.02$) and only males head-marked and palmar-marked. During palmar-marking, the male quickly rubbed both hands around a branch in a frantic, stereotypical motion like hand washing. Branches were the primary marking surface for both males and females ($n=1170$) but only males were observed to directly mark females ($n=36$ on her back or side). The female, however, was always within 5 m of the male when he scent-marked objects.

Head-marking and palmar-marking rates were slightly higher during food availability, although this relationship was not significant (HDM rate 0.06/hr; PMK rate 0.12/hr). Anogenital marking rates, however, showed significant seasonal

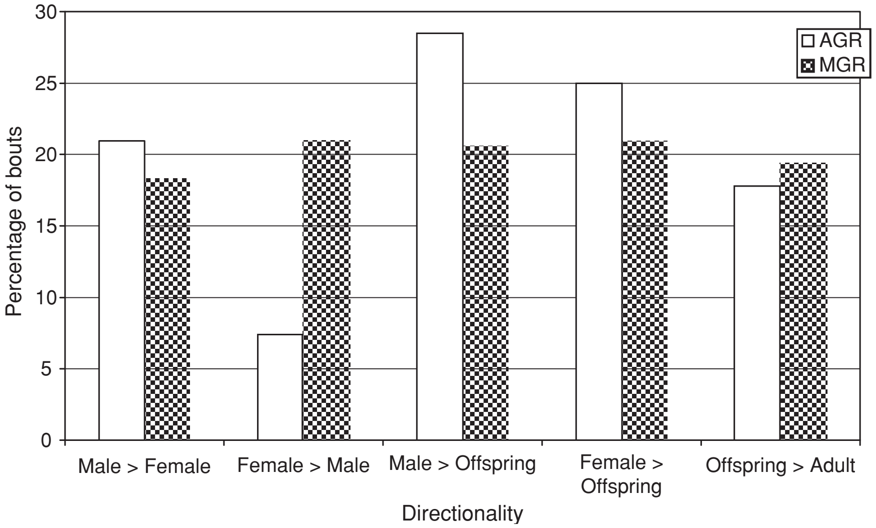

Figure 3. Directionality of grooming patterns for allo-grooming (AGR) and mutual-grooming (MGR). Directionality patterns did not vary with seasonality and did not vary across categories for mutual-grooming. Females were less likely to initiate mutual-grooming than any other individual (p = 0.03).

changes: they were higher during food availability and males marked twice as often as females at this time ($\chi^2 = 5.1$, $p < 0.03$, $df = 1$, Figure 4).

Agonism

Within-Group

The only form of within-group aggression recorded was cuffing and was rarely observed (n = 20, rate 0.01/hr DJO, n = 19, rate 0.007/hr SRT). Only two of these exchanges occurred during feeding in February when food was scarce. The majority of cuffs (n = 20) were observed between parents and unweaned offspring. In each of these cases, the adult female carrying the infant approached the adult male, cuffed him, and turned to rub the infant off her back or belly and onto the male's back. The male would then either carry the infant or rub the infant off his back onto a branch so that the infant was forced to travel on its own. The remaining incidents (n = 17) occurred between an adult and yearling offspring between August (just prior to the birth season) and October (when infants were approximately 1 month old).

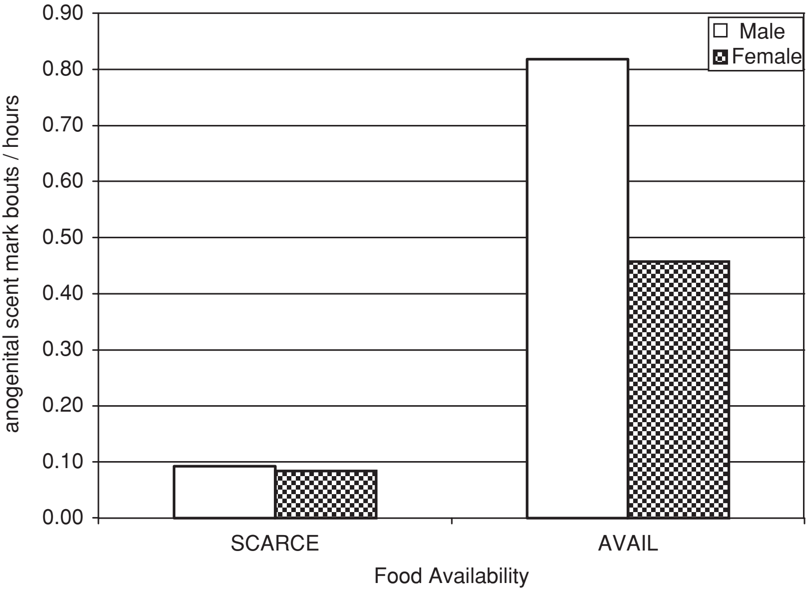

Figure 4. Anogenital scent-marking rates by males and females for food availability and food scarcity periods ($p = 0.03$).

Between Group encounters in results

A total of 18 conspecific interactions (rate 0.01/hr) were observed and rates were ten times higher during food availability (0.03/hr) than food scarcity (0.003/hr). The majority of the encounters ($n = 13$) occurred between neighboring groups; three of these took place in a shared food tree on the border between territories and the remaining ten occurred along territorial borders while groups traveled parallel to one another. In each case, males would lunge at, cuff, and direct bites toward nongroup males while grinding their teeth and palmar-marking. Females would also charge and chase nongroup females. Encounters lasted between 2 and 55 minutes (mean = 17.1 min, SD = 18.8 min).

The remaining encounters ($n = 5$) occurred between established groups and solitary males ($n = 3$) or a male–female pair ($n = 2$) that did not occupy an established home range. In these cases, the nonresident individuals were observed to move slowly and quietly below the study group while they were feeding and were chased by both the resident adult male and female when detected. These encounters were short and lasted 2 min or less.

In comparison, interspecific interactions were observed four times more often ($n = 65$, rate 0.04/hr) and occurred during travel toward a food source ($n = 6$) or while groups were feeding ($n = 59$). Red-bellied lemurs interacted primarily with rufous lemurs (*Eulemur fulvus rufus*, $n = 52$, rate = 0.04/hr), and less often with ruffed lemurs (*Varecia variegata*, $n = 9$, rate = 0.006/hr) and Milne Edward's sifaka (*Propithecus diadema edwardsi*, $n = 4$, rate = 0.003/hr). No interactions with other sympatric species were recorded. Rates of interspecific encounters were twice as high during food availability (0.06/hr) than during food scarcity (rate = 0.03/hr). The majority of encounters ($n = 57$, 88%) took place during food availability, and in all of these red-bellied lemurs were either displaced or actively chased from a food tree. On the eight occasions when red-bellied lemurs stood their ground (which occurred during food scarcity), both the adult male and female would lunge, chase, or try to bite and/or cuff approaching *E. f. rufus* ($n = 5$) or *P. d. edwardsi* ($n = 2$). In all eight cases, red-bellied lemurs remained in control of the food tree.

DISCUSSION

Pair-Bonded Groups

Two-adult groups were by far the most common configuration. Based on the demographic, affiliative, and agonistic data summarized above, red-bellied lemurs can easily be considered a pair-bonded species. This is consistent with the definition that Fuentes (2002) provided after a thorough review of social pair-bonding in nonhuman primates: ". . . a long-term association between 2 non-kin adults characterized by a set of partner specific affiliative behaviors . . ." (p. 969). Implicit in this definition is the fact that pair-bonds will persist for longer than an annual cycle and do not vary with seasonal changes in food or reproductive patterns. This was the case for red-bellied lemur groups in this study.

Pair-Bond Formation

How red-bellied lemur pair-bonds form is less clear and warrants further study. In some species, pair-bond formation occurs through: (1) territorial shift (Easley and Kinzey, 1986), (2) replacement of a group resident by a previously solitary individual through eviction or death of a resident member, or (3) a solitary male or a newly formed pair creating a home range/territory from existing ranges (Brockelman et al., 1998). Although sample sizes are small, examples of each of these have been observed in red-bellied lemurs.

Territorial shift is the subtle and gradual relocation of a group's territory over time which allows for one or more matured offspring to take over the abandoned area. In this study, a female which left her natal range when she was 2.5 years old in 1990 was rediscovered in 1994 occupying a home range which partially overlapped her former natal range (Overdorff and Strait, unpublished data). Short-distance dispersal has been reported in other pair-bonded primates and may contribute to the high degree of affiliation seen between neighboring groups of gibbons (Brockelman et al., 1998; Bartlett, 2003).

Replacement and eviction of resident females by nongroup females has also been observed. In three cases, once a resident female died or disappeared, a new female who was assumed to be previously solitary joined the male within 3 to 5 weeks. In another case, a previously solitary female actively evicted an older female from her group. Together, these observations offer some tentative support for Fuentes's (2002) prediction that there are more costs to a solitary existence, particularly for females if resource defense drives pair-bonding. A solitary female's reproductive success is likely to be more vulnerable if she is not accompanied by a male on an established territory. Additionally, in species where males actively care for infants, infants are more likely to survive when a male is consistently present (Overdorff, 1996b; Fietz and Dausmann, 2003; Goldizen, 2003). Since females migrate out of their natal groups between 2.5 and 3 years of age when they have reached full adult body size and are reproductive, it would be in the female's reproductive advantage to move as quickly as possible into an established group. On the other hand, solitary males have the potential to implement other reproductive strategies such as extra-pair copulations as observed in other pair-bonded species (Palombit, 1994; Reichard, 1995; Schulke, 2004). However, Merenlender (1993) found no evidence that this strategy was implemented in her survey of paternity in multiple groups of red-bellied lemurs at two sites within the Ranomafana National Park.

Finally, we suggest that not only solitary males and females are at a reproductive disadvantage. Pairs of individuals that have not established a defendable home range appeared to be just as vulnerable as solitary females because they lost consistently in conspecific encounters and have never been observed with infants.

Pair-Bond Maintenance: Nearest Neighbor and Grooming

Once a pair bond is formed, an adult male and female can remain together for at least 6 years (e.g., Group 2, DJO). As expected, strong, stable affiliative bonds were evident between the adult male and female based on nearest neighbor, grooming, scent-marking, and within-group agonistic patterns. Groups were highly cohesive and group members were rarely without a nearest neighbor. Adults were observed with offspring as nearest neighbors slightly (but not significantly) more often than with each other but male–female nearest neighbor patterns were the only category that remained consistent across seasonal changes. Unfortunately, because the nearest neighbor data were collected using scan sampling, we could not examine which individuals were more responsible for initiating proximity.

We were able, however, to examine initiation patterns for social grooming (allo-groom and mutual-groom) and these patterns varied depending on the type of grooming observed. Overall, rates for both kinds of grooming were similar; they did not mutual-groom each other significantly more often than allo-groom. Rates and directionality patterns between age and sex classes within groups did not change across fluctuations in food availability, which is similar to reported patterns in hylobatid species (Tilson and Tenaza, 1982; Mitani, 1984; Bartlett, 2003). Group members were equally likely to initiate mutual-grooming with each other. However, the adult male was significantly more responsible for initiating allo-grooming with the adult female which is the reverse of what is seen typically in larger groups of anthropoid primates (Arnold and Whiten, 2003). One contributing factor to this reversal in directionality may be the type of dominance pattern that has been established within the group. In contrast to anthropoids, many lemurid primates are female dominant (Jolly, 1984; Sauther et al., 1999; Overdorff and Erhart, 2001; Pochron et al., 2003; Curtis, 2004). When clear female dominance exists, males typically direct few, if any, agonistic behaviors towards females, receive more agonism from females, and groom more than they receive (Pollock, 1977, 1979). However, it is difficult to label red-bellied lemurs as a female-dominant species with female feeding priority (see Jolly, 1984; Overdorff and Erhart, 2001) due to the fact that agonism occurred so infrequently between adults and females were only observed to supplant males from feeding sources twice (February when food was scarce). Consequently, further study of which sex is responsible for initiating proximity is needed to better understand whether the male, the female, or both are responsible for maintaining the social pair bond.

Pair-Bond Maintenance: Scent-Marking

Adult males scent-marked more often than adult females and had a wider range of scent-marking behaviors (head-mark and palmar-mark). Scent-marking is generally considered an indirect way for males to advertise mated status and mediates competition with conspecifics, particularly among strepsirhines (Epple, 1986; Fornasieri and Roeder, 1992; Kappeler, 1998; Gould and Overdorff, 2002; Pochron et al., 2005). In many species, rates of scent-marking increase during the mating season and scent-marks may serve as an indirect form of mating competition in multimale and female groups (Gould and Overdorff, 2002; Heymann, 2003). However, although males in this study scent-marked more often, scent-marking rates decreased significantly during the food scarcity period which also corresponded to the mating period. Consequently, we propose that scent-marking in red-bellied lemurs may function as an additional way to sustain the pair-bond year round. Although red-bellied females were not the direct recipients of scent-marking very often (3%), they were within 5 m or less of the objects the male marked in all other cases. Scent-marking during the food availability period may also serve as an indirect way of defining and defending a home range and the resources contained therein (Kappeler, 1998; Heymann, 2003).

Within-Group and Conspecific Agonism

As predicted, within-group agonism was low and occurred only twice in a feeding context. This is consistent with levels of intragroup aggression observed in anthropoid pair-bonded species (Wright, 1986; Bartlett, 2003) and other lemur species (with the exception of *Lemur catta*, Erhart and Overdorff, in review). The majority of agonism, in fact, appeared to be related to weaning conflict rather than feeding competition. Although males participate actively in carrying the infants (Overdorff, 1996b; Tecot, personal observation), both parents began to actively discourage infants from riding ventrally or dorsally around 5–6 months of age. This also coincided with the months when food was becoming scarce (February–March) and may serve as an energy conservation strategy for both parents (Wright, 1999). As food becomes scarcer, daily travel between and to food patches becomes longer (Overdorff, 1993a), and food is lower in quality (Erhart, in preparation).

Rates of conspecific encounters were similar to within-group agonistic rates (0.01/hr), interactions with extragroup members were never affiliative, and conspecific encounters occurred most often during food scarcity. Both sexes appear to be equally invested in defending the home range given that adult males and females equally participated in fights with conspecific groups. Aggression with other groups also was exchanged between same-sex individuals which is the case in most other pair-bonded species as well (Fuentes, 2002). Additionally, encounter rates with other red-bellied groups or solitary individuals were ten times higher during food scarcity and occurred primarily at home range borders. Times of food scarcity may force more encounters between conspecifics particularly if ranges are small and food is distributed in large, widely spaced patches (Overdorff, 1996b). In fact, two of the more prolonged encounters with a neighboring group occurred within a *Chrysophyllum madagascariensis* tree that was fruiting out of season and occupied a place where two ranges overlapped.

Between-Group Agonism, Resource Defense, and Energy Conservation

Interspecific encounters differed in two main ways compared with conspecific encounters: they occurred at higher rates overall (0.04/hr) and they occurred more often during higher food availability. Red-bellied lemurs fought more often with groups of *Eulemur fulvus rufus*, their only sympatric congener which is similar in diet and body size but lives in multimale and female groups of up to 16 individuals (Overdorff, 1996b; Overdorff et al., 1999). Larger group sizes clearly offer some advantage regarding food competition as they usually displace smaller groups during contests over food patches. Squirrel monkeys (*Saimiri sciureus*), for example, tend to congregate in groups of 35 individuals compared with sympatric night monkeys (*Aotus trivirgatus*) and titi monkeys (*Callicebus moloch*) which are both pair-bonded (Terborgh, 1985; Wright, 1986). Squirrel monkeys range farther, travel farther between food patches, and easily displace the pair-bonded species from fruit trees. However, both titi monkeys and night monkeys are able to more frequently use smaller, more clumped food patches that squirrel monkeys avoid as these patches are not large enough to support all group members. As a result, all three species are able to effectively coexist.

In the New World monkey example above, these three species are similar and are related at the family level but not at the genus level. Sympatric congeners are substantially more similar in morphology, body size, and diet, and are more likely to compete with each other for access to critical food resources. For both to coexist, some form of niche separation or character displacement must occur and divergence between species may be more pronounced during critical food shortages (Birch, 1957, 1979; Schoener, 1974). Interestingly, encounters between congeners occurred more often during food availability. At this time of year, both red-bellied and rufous lemurs ranged shorter distances, rufous lemurs' core home ranges overlapped considerably with red-bellied lemur ranges, and dietary overlap was higher (Overdorff, 1993a,b). As a result, these two species were more likely to come into contact with each other. When this occurred, red-bellied lemurs were always displaced from the food patches, and in some cases the red-bellied group would withdraw as rufous lemurs entered the patch, minimizing the length and intensity of interaction. Red-bellied lemurs would either move on to a different food source or rest in a nearby tree and revisit the patch once the rufous lemur group departed. Food (fruit in particular) may be abundant enough that it was not worth the cost of retaliating. Indeed, the eight times that red-bellied lemurs did stand their ground to remain in control of a food patch were during food scarcity when the potential cost of leaving and finding alternative food sources would likely be higher. Rufous lemurs will range much farther during food scarcity periods, often migrating more than 8 km away from their core area to find alternative sources of food (Overdorff, unpublished data; Mutschler, unpublished data). Therefore, smaller, pair-bonded groups may allow red-bellied lemurs more flexibility when food is scarce to exploit smaller food patches without having to significantly adjust their ranging patterns. In fact, rufous lemurs in the southeast will also fission-fusion into smaller subgroups of three to five individuals when food is most scarce (Overdorff et al., 2003).

Other aspects of red-bellied lemur behavior such as proximity, grooming, and scent-marking also indicate that food scarcity is a time when energy conservation strategies are of utmost importance (Lee, 1986; Wright, 1999). Although the adult male and female maintained a consistent level of proximity to one another throughout the year, both were observed to be without a nearest neighbor more often during food scarcity. This, in part, is due to the fact that they feed farther apart from one another (Overdorff, 1996a) which may serve as an additional way of minimizing within-group competition for food when food is scarcer. Rates of social grooming and scent-marking also decreased significantly during food scarcity. Seasonal reductions in grooming time and other nonsubsistence activities such as play have been observed in other species as well (Freed, 1996; Bartlett, 1999, 2003) and are presumed to be additional strategies to conserve energy at a time when food resources are severely limited.

In summary, red-bellied lemurs are indeed pair-bonded based on the patterns of social behavior and the consistency of those patterns across seasons of food availability. Solitary individuals or pairs of individuals that have yet to establish a defendable home range are likely to be at a reproductive disadvantage. The lack of within-group competition for food, the higher observed rates of intergroup encounters over food, and the mutual role that males and females play in defending their home range indicate that resource defense particularly from congeners may be an important selection pressure favoring pair bonds in this species.

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CHAPTER TWELVE

Lemur catta Ecology: What We Know and What We Need to Know

Lisa Gould

INTRODUCTION

Ring-tailed lemurs (*Lemur catta*) are probably the best known and most well researched of all Malagasy primates. Populations and subpopulations of this species have been studied since 1963, when Jolly spent a year studying groups of ring-tailed lemurs at Berenty Private Reserve in southern Madagascar (Jolly, 1966). Shortly afterwards, Sussman (1972, 1974) examined ecological distinctions between *L. catta* and *Eulemur fulvus rufus* at Antserananomby, a dry forest in Madagascar's southwest, and so began the legacy of research on this extremely adaptable primate. Since those early studies, a number of researchers from many countries as well as from within Madagascar have travelled to the island's southern forests and even into mountainous habitat to conduct research projects on the behavior, ecology, demography, endocrinology, and population health of this species. Much has been written about their adaptability, their abilities to withstand the marked climatic seasonality of southern Madagascar, and their resilience in the face of natural disasters such as drought and cyclones (e.g., Gould et al., 1999; Jolly, 1984; Jolly et al., 2002; Mertl-Milhollen et al., 2003; Pride, 2005). Jolly et al. (2006:vi) sum it up well when they suggest that ring-tailed lemurs are "at home in discontinuous habitat, and individually, as tough as old boots" (p. vi).

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In this chapter, I review a number of aspects of *L. catta* ecology: what is currently known of its geographic distribution, variation in habitat and population density, diet and feeding ecology, and the importance of the tamarind, or kily tree, a keystone resource. I also summarize some important life-history variables such as sex ratios, fecundity, infant mortality, male dispersal, and life span, and discuss the impact of both anthropogenic and natural change in gallery forest habitat.

GEOGRAPHIC RANGE AND HABITAT VARIABILITY

Goodman et al. (2006) suggest that *L. catta* evolved in dry habitats in the south and southwest of Madagascar, and later dispersed to more mesic highland areas. There is no subfossil record of *L. catta* outside of its current distribution (Godfrey et al., 1999). This is a remarkably flexible primate, found in a range of habitats throughout the south and southwest of the island, including spiny, brush and scrub, gallery and dry deciduous forests, anthropogenic savannah, and in the high-altitude regions of the Analavelona Massif in Toliara province, and the Andringitra mountain range (Goodman and Langrand, 1996; Goodman and Rasolonandrasana, 2001; Goodman et al., 2006; Sussman, 1974; Sussman et al., 2003) (Figure 1). In many of the drier forest habitats, *L. catta* occurs at low densities (Sussman et al., 2003). Higher densities are found in gallery and mesic forest patches, but few of these remain and are disappearing rapidly. Government and private reserves such as Beza Mahafaly, Andringitra, Andohahela, Isalo, Cap Ste. Marie, Anja, and Berenty support populations of varying densities, and scattered sacred forests provide protection to some populations (Sussman et al., 2003).

A broad survey in regions of south and southwestern Madagascar was conducted by Sussman et al. (2003) to document the presence of *L. catta*, current condition of its habitat, and extent of deforestation in areas once inhabited by the species. Approximately 3000 km were covered by vehicle, and comparisons were made of current habitat conditions with aerial topographic maps and Landsat images. Overall, conditions of rapid deforestation were found in many areas, the majority having occurred in the last 20 years. Much of the forest in this region of the island has been cleared in the past two decades for swidden agriculture, and thus, habitat, which previously supported ring-tailed lemur populations, is no longer viable.

The northwestern boundary of this species is not absolutely known; however, Goodman et al. (2006) suggest that it may extend to the Menabe region, between Parc Nationale de Kirindy-Mitea and the Morondava River, and Zinner et al. (2001) found *L. catta* just 60 km south of Morondava. Sussman et al. (2003) note that the forest at Antserananomby, one of the most northern areas in the geographical range of *L. catta*, and where Sussman studied this species in 1972, is still largely intact; however Tongobato, a forest that was near Antserananomby, no longer exists, as it has been cleared for agriculture. Throughout the unprotected dry forests of the southwest, *L. catta* exist at very low densities, and in many cases

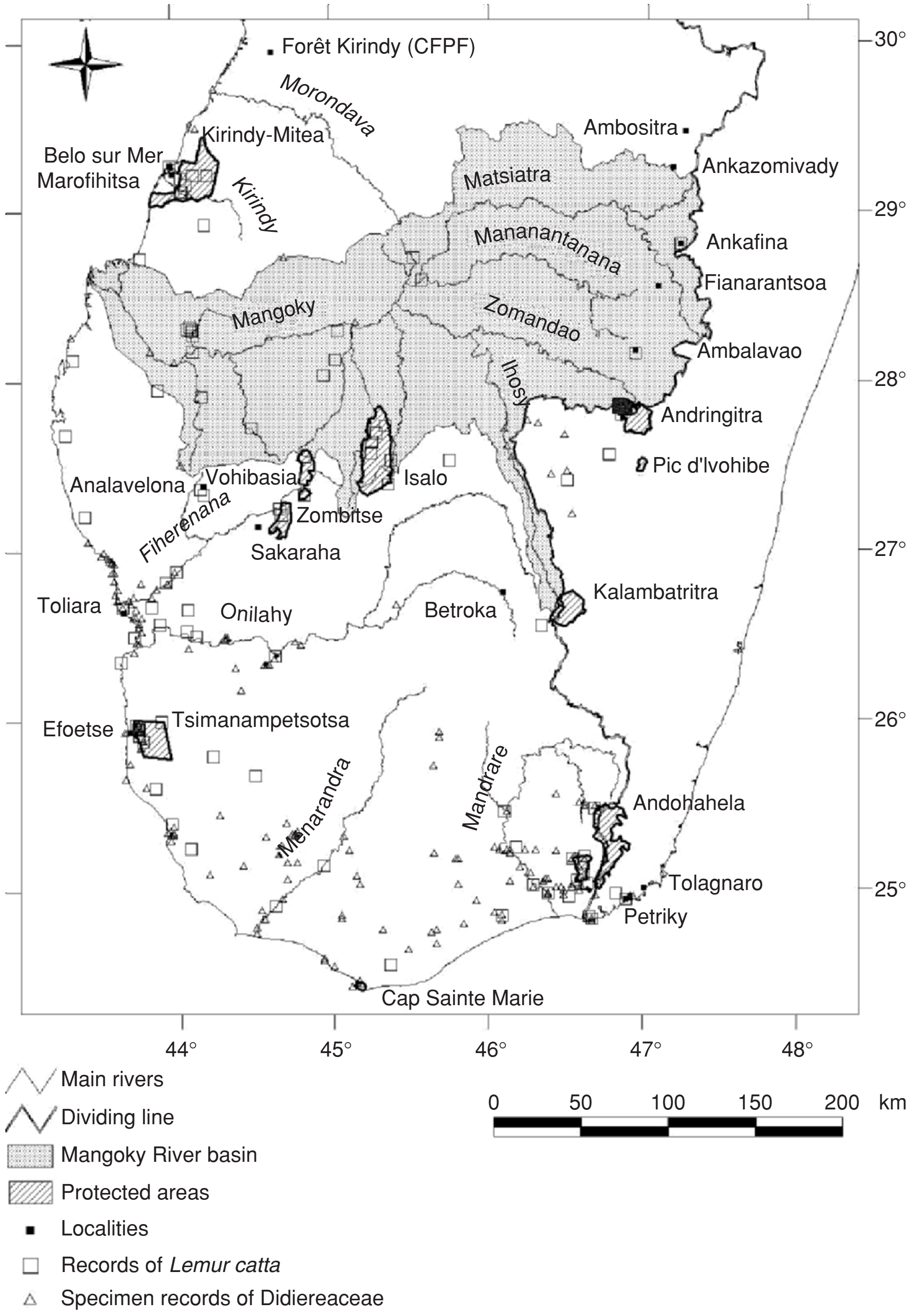

Figure 1. Map of *Lemur catta* distribution. Reprinted from Goodman, S.M., Rakotoarisoa, S.V. and Wilm, L. (2006) with kind permission from the authors.

populations are isolated (Sussman et al., 2003). Densities are somewhat higher in the remaining scattered gallery forest areas. The southernmost population of *L. catta* occurs in the region of Cap Ste. Marie, on the very southern tip of Madagascar. Little is known about this population, but Sussman et al. note that it may be seasonally mobile, as ring-tailed lemurs were observed feeding on seasonal fruits around the Cap Ste. Marie Reserve in October of 2001 and 2002 by a forestry worker, but they are not found there at other times of the year. Four Kilometers from the reserve, they have been seen on a more regular basis (Kelley, personal communication). The habitat in this area is a combination of crops, sacred forests, and introduced *Opuntia* cacti, and the lemurs have been observed most often in the *Opuntia* hedges (Kelley, personal communication).

Moving eastward along the south coast, much of the original natural vegetation was cut before 1950 for both crops and sisal plantations, which now dominate this area. Only a few small patches of gallery forest remain, including Berenty Private Reserve. Throughout this area, Sussman et al. (2003) note the existence of small circular patches of vegetation, which have not changed since at least 1950. These are sacred forests, and some contain lemurs; however, no lemurs exist in the surrounding agricultural areas. In the Andohahela Reserve near the south coast, *L. catta* live both in disturbed dry forest at low densities, and in higher numbers in the gallery forest areas (Raharivololona and Ranaivosoa, 2000). Their southeastern limit occurs at the border of the eastern and western watersheds, with populations living both dry and gallery forests. They have been spotted at Petriky near Tolagnaro (Goodman et al., 2006) and in littoral forest south of Tolagnaro (Sussman et al., 2003).

A high-altitude population of *L. catta* was discovered in the mid-1990s inhabiting an area of the Andringitra mountain range near the eastern edge of its range. This population has been studied by Goodman and Langrand (1996), Goodman and Rasolonandrasana (2001), and Rakotoarisoa (2000), and described genetically by Yoder et al. (2000). These ring-tailed lemurs live in the coldest locality on Madagascar, with nightly temperatures falling to –16°C, but reaching up to 30–35°C during the day. Here, *L. catta* groups live between 900 and 2600 m, well above the end of the tree line at 1950 m (Goodman and Langrand, 1996; Goodman et al., 2006; Rakotoarisoa, 2000). Andringitra *L. catta* exhibit somewhat different pelage coloration from other populations but they are not a subspecies (Yoder et al., 1999, 2000). They have a thicker coat, suggested to be an adaptation to extremely low temperatures, and lighter pelage color, which may result from exposure to intensive solar radiation in their environment. The diet and ranging pattern of this population will be discussed later in the chapter.

In Madagascar's southwest, *L. catta* occurs at very low densities in the remaining areas of the coastal Mikea Forest, and Sussman et al. (2003) note that even before massive cutting of this forest occurred, low densities were recorded, but with the disappearance of habitat in this area, the few remaining populations are now extremely isolated. In the Zombitse forest, between Toliara and Isalo, few *L. catta* exist. The forest here is drier than the gallery forests in the southwest, and does not support tamarind trees, which *L. catta* rely upon in gallery forest habitats.

In the Lake Tsimanampetsotsa region near Toliara (very close to the western coastal area), *L. catta* groups are found in government-protected areas or sacred forests in these regions. Inland, much of the natural dry-adapted vegetation in the Mahafaly Plateau region has been cleared for swidden and subsistence agriculture, although Sussman et al. (2003) found ring-tailed lemur populations to varying degrees in remaining riverine forest areas, and well-protected populations exist at the Beza Mahafaly Special Reserve near Betioky-Sud and at Isalo National Park. Sacred forests also exist in the Beza Mahafaly region, which have been maintained over time, and are inhabited by ring-tailed lemur groups (Sauther, Gould, and Whitelaw, personal observation).

The question of adaptation to extremely arid environments has been discussed by Goodman et al. (2006). They note that the presence of water sources *could* be a limiting factor in the distribution of this species; however, ring-tailed lemur vocalizations have been heard in an area of Kirindy-Mitea National Park in the west where no permanent water source exists. Goodman et al. suggest that they obtain water in this area by licking dew in the early morning and from the water content in some of their food plants. Similarly in and around the Beza Mahafaly Reserve, the home ranges of some groups do not include any freshwater source, yet some of these groups are very large, and in the dry season, no group has access to fresh water because the riverbed is dry. Thus, dew and moisture from food sources in the dry season, and water cachement areas in the wet season can sustain such groups. *L. catta* inhabiting spiny forest must cope with as little as 30–50 cm of annual rainfall, and must obtain water from dew and succulent plants, including *Aloe* (Jolly, 2003).

Goodman et al. (2006) emphasize that because ring-tailed lemurs are a semi-terrestrial species (degree of terrestriality averages 30% [Jolly, 1966; Sussman, 1972, 1977] and ranges from 3 to 75% depending upon season [Sauther, 2002]), they are able to disperse across nonforested areas, and across riverbeds in the dry season, and therefore their geographic range is not constrained by river systems. Nonetheless, the overall population of this species has decreased significantly in the past 50 years due to deforestation (Sussman et al., 2003).

DENSITY OF *LEMUR CATTA* AND HOME RANGE SIZE IN DIFFERENT HABITATS

Biomass and home ranges of *L. catta* vary greatly with habitat. Berenty reserve in southern Madagascar is a 200-ha forest fragment containing four distinct and adjacent habitats: riverine (gallery) forest, second-growth deciduous forest with 15–20 m of canopy, xerophytic scrub forest, and spiny forest (Budnitz and Dainis, 1975; Jolly, 1966; Jolly et al., 2002, 2006). *L. catta* densities vary markedly between habitats from 250 to 500 lemurs/km^2 in gallery and second growth


A
B

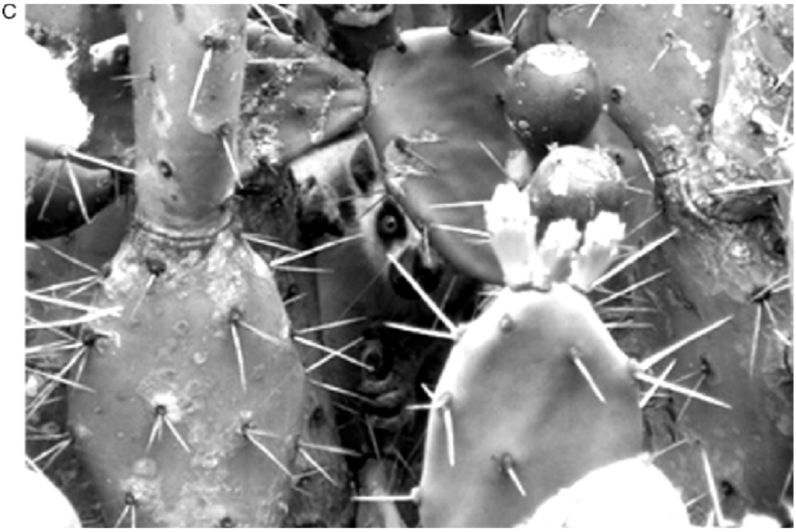

Figure 2. (*Cont'd.*) Photos of *Lemur catta* in 3 different habitats: (a) ring-tailed lemurs in a tamarind tree in gallery forest at the Beza Mahafaly Special Reserve. The ring-tailed lemurs here are collared and tagged as part of a demographic and health study (photo by L. Gould), (b) on a rocky outcrop at Anja private reserve (photo by M. L. Sauther); and (c) in the far south near Cap Ste. Marie in Opuntia cactus hedges (photo by E. A. Kelley).

forest to 100/km^2 in scrub and spiny forest fragments (Jolly et al., 2006). Mean group size at Berenty is also dependent upon habitat with the smallest groups (mean = 8.9 individuals) in the spiny forest, while larger groups average 11.8 animals in gallery forest and 13.9 in the tourist area (Jolly et al., 2002; Koyama et al., 2002). Pride (2005) suggests that *L. catta* at Berenty may live at the highest density of all populations. Pride found that short-term food scarcity in the dry season affected larger groups more seriously in terms of physiological stress (higher cortisol concentrations), as resource competition in a large group was higher than in groups with fewer individuals. Pride suggests that living in intermediate-sized groups may be optimal, particularly for females, in terms of resource competition and availability. Within-group sex ratio at Berenty varies from 9 adult males and 3 adult females to 1 male and 5 females (Jolly et al., 2002). In gallery forest areas, home ranges vary from 3.95 to 16.7 ha, and in the less dense xerophytic/scrub forest, home ranges of 12–25 ha are reported (Jolly et al., 1993).

Beza Mahafaly Special Reserve in southwestern Madagacar consists of two parcels: parcel one is an 80-ha area of undisturbed gallery and xerophytic forest, and parcel two consists of 500 ha of xerophytic and spiny forest. Demographic data were collected between 1987 and 2001 on the ring-tailed lemur population in parcel one (Gould et al., 1999, 2003; Sussman, 1991). The average density of adult animals in this parcel of forest is 87.5 adults/km^2 and 137.5/km^2 when subadults are included (Gould et al., 2003), and actual density ranges from 90 to 135 animals/km^2 depending upon microhabitat (Sussman, 1991). In nondrought years, the Beza population stabilizes at 60–70 adults and 100–110 animals including immatures (Gould et al., 2003), although this is in the reserve itself: groups of *L. catta* live outside the reserve as well, so there is a continuous population in the forested areas of this region. Home ranges vary from an average of 17 ha in the eastern gallery forest area to 32 ha in the drier vegetation-sparse western part of the reserve (Sussman, 1991). Average group size at Beza is 11.5 animals and sex ratio is 0.92. Whitelaw and Sauther (2003) found that lemur density in the degraded gallery forest 1 km north and south of the reserve was just half of that inside the protected area. The population in the reserve forest itself may reflect optimum carrying capacity in that habitat (Gould et al., 2003).

At two other sites, population density varies markedly from that reported at Berenty and Beza Mahafaly. At Andohahela National Park in the extreme south, *L. catta* density ranges from 8 to 64 animals/km^2 with fewer lemurs found in the disturbed dry forest habitat than in nondisturbed gallery forest (Raharivololona and Ranaivosoa, 2000). Ring-tailed lemurs inhabiting the mountainous Andringitra region live at a very low density of 22.8 individuals/km^2 (Rakotoarisoa, 2000). One group studied by Rakotoarisoa lived in an area more than 2000 m in elevation while the other group was found at a lower elevation. The home ranges of these high-altitude *L. catta* occur vertically: the two groups studied by Rakotoarisoa used vertical areas from 1310 to 2360 m and 1250 to 2040 m. They use fissures or overhangs as sleeping sites, which Goodman et al. (2006) suggest may protect them from the fossa (*Cryptoprocta ferox*), a viverrid predator that is present at Andringitra. Day range is large for these lemurs: they cover more than 100 ha daily (1000 m), much of this vertically. Average day range for ring-tailed lemurs at Berenty and Ansirananomby, topographically flat areas, is 1377 and 950 m, respectively (Jolly et al., 1993; Sussman, 1972, 1999).

Jolly and Pride (1999) and Mertl-Milhollen (2000) found that home range sizes in the gallery forest at Berenty have remained stable since first studied in either the early 1960s or early 1970s. At Beza Mahafaly, while some groups dissolved during a 15-year demographic study, others persisted, and home ranges were also stable (Gould et al., 2003; personal observation). Jolly and Pride (1999) suggest that benefits of such stability and detailed knowledge of resources in the range may extend beyond a given season, representing a benefit for future generations. During flowering or fruiting periods, groups at both sites have been observed leaving the home range core to exploit these rare resources (Jolly and Pride, 1999; Sauther, 2002; Sussman, 1991).

SOCIAL ORGANIZATION, GROUP STABILITY, AND GROUP FISSION

Ring-tailed lemur groups consist of a core of adult females and offspring, one or a few central males, and peripheral males, which disperse at sexual maturity and sometimes migrate several times during their lives (Gould, 1997; Jolly, 1966; Sauther, 1992; Sauther et al., 1999; Sussman, 1992). Larger groups sometimes contain more than one matriline, and in such a case, one will be dominant to the other(s) (Nakamichi and Koyama, 1997; Sauther, 1992; Taylor and Sussman, 1985).

In both wild and free-ranging captive populations, when groups become too large, eviction of subordinate females and group fission often occur (Gould et al., 2003; Jolly et al., 2002; Koyama, 1991; Koyama et al., 2002; Sussman, 1991; Taylor and Sussman, 1985). Targetted aggression by dominant females towards subordinate ones usually results in group fission. Such aggression has been documented at both Berenty and Beza Mahafaly Reserves, as well as in free-ranging captive situations (Gould et al., 2003; Jolly et al., 2002; Koyama et al., 2002; Pereira and Kappeler, 1997; Sauther et al., 1999; Takahata et al., 2005; Vick and Pereira, 1989). Jolly et al. (2002) suggest that such evictions may occur because it may be less costly for dominant females to evict their female cousins than to expand their home ranges, since range expansion could result in costs such as increased travel time and resource competition and physical confrontation with other groups.

Group fission at Berenty occurs when group size reaches 15–25 individuals (Jolly et al., 2002). A new group establishes a small home range between the group that expelled them and their competitive neighbors. Costs to a new group arising from fission include increased aggression from neighboring groups and increased infant mortality. At Beza Mahafaly, few groups reach 20 animals, but group fissions have been documented in four of the groups living in the reserve over an 18-year period (Gould et al., 2003; Sauther, personal communication; Sussman, 1991). Home ranges of fissioned groups at Beza are either identical to that of the parent group or part of the parent group's home range is incorporated in the new home range (Gould et al., 2003; Sussman, 1991). Dissolution has also been observed at Beza Mahafaly when groups have become very small, e.g., 2 to 3 individuals (Gould et al., 2003).

DIET AND FEEDING ECOLOGY

The ring-tailed lemur has been classified as a frugivore/folivore and an "opportunistic omnivore" (Sauther, 1998; Sauther et al., 1999; Simmen et al., 2006a) and is able to adapt to marked shifts in diet following the wet and dry seasons. In fact, the feeding ecology of *L. catta* is finely tuned to the seasonality of their food resources and certain key species are relied upon during different phases of the reproductive cycle (Sauther, 1998). Probably the most important food resource for forest-dwelling *L. catta* is the tamarind tree (*Tamarindus indica*), known in Madagascar as "kily." The importance of kily to ring-tailed lemurs will be discussed later in the chapter.

Resource availability is strongly tied to reproduction in this species (Rasamimanana and Rafidinarivo, 1993; Sauther, 1992, 1993, 1998;Yamashita, 2002). Although food resource availability is low during gestation, availability of plant foods increases dramatically with the onset of the rainy season, which corresponds with the period of female lactation and infant weaning. More fruit available at this time means higher energy for lactating females and high-quality foods for weanlings (Jolly, 1984; Sauther, 1992, 1998).

Simmen et al. (2006b) present an exhaustive summary of all plants eaten by *L. catta* at the Berenty, Beza Mahafaly, and Antserananomby sites. Feeding ecology has been studied over annual cycles at both Berenty and Beza Mahafaly; *L. catta* use 82 plant species for leaves, 40 for fruits, and 16 for flowers at Berenty and 40 species for leaves, 28 for fruit, and 16 for flowers at Beza Mahafaly. They use resources as they become available, and key foods (other than tamarind) can change from one month to the next. At both sites, two or three plant species comprise the major part of the diet each month and animals shift to different plants species when they become available (Sauther, 1992, 1998; Simmen et al., 2006b).

Ring-tailed lemurs can handle both ripe and unripe fruit, young and mature leaves, leaf stems, flowers, and unripe seeds, and they regularly ingest dead wood, termite soil, and earth (Rasamimanana and Rafidinarivo , 1993; Sauther, 1992, 1998; Simmen et al., 2003, 2006b; Sussman, 1972). As in other primate species, geophagy in ring-tailed lemurs is likely a strategy to handle and neutralize toxic secondary compounds such as tannins (Krishnamani and Mahaney, 2000; Simmen et al., 2006a,b). *L. catta* do take some animal prey, consuming larvae, locusts, cicadas, spiders, spiderwebs (Sauther, 1992), and occasionally even birds and chameleons (Oda, 1996; Sauther, 1992).

Fruit abundance has been cited as the primary limiting factor in *L. catta* survival (Jolly et al., 2002), but Sauther (1992, 1998), Rasamimanana and Rafidinarivo (1993), and Mertl-Millhollen et al. (2003, 2006) also point out the importance of leaves in such a seasonally variable diet. The importance of herbaceous terrestrial vegetation for groups living in gallery and deciduous forests is noteworthy: at Beza Mahafaly, Sauther (1998) found that 54% of leaf food occurs at or near the ground.

To deal with seasonal food shortages, ring-tailed lemurs decrease their metabolism (Pereira et al., 1999) and travel outside of their home range to find food and water (Jolly and Pride, 1999; Mertl-Milhollen et al., 2006; Sauther, 1998).

Reproduction is closely tied to fluctuating seasonal resource availability in the geographic range of *L. catta*, and both Rasamimanana and Rafidinarivo (1993) and Sauther (1994, 1998) found specific feeding patterns among reproductive females at Beza Mahafaly and Berenty reserves, respectively. During gestation season at Beza Mahafaly, pregnant females fed more on flowers and fruit (excluding tamarind) while males consumed more leaves (Sauther, 1994, 1998). Lactating females focused on easily digestible young leaves, avoiding mature leaves that are high in secondary compounds. Sauther points out that immature leaves contain higher amounts of calcium, protein, and energy, crucial nutrients for nursing mothers. She found that males focused on more fruit and resorted to consuming mature leaves when alternative resources were scarce. In contrast, in gallery forest at Berenty, Rasamimanana and Rafidinarivo (1993) found that pregnant females concentrated mainly on mature tamarind leaves and unripe tamarind fruit, but became more frugivorous during the birth and lactation period. They note that while tamarind fruit is high in tannins, it is also high in protein.

Concentrations of secondary compounds in *L. catta*'s plant foods also correspond with the marked seasonality in this region of Madagascar. Simmen et al. (2006a) found strong seasonal differences in the proportions of protein, phenolics, and tannins in the diet of *L. catta* at Berenty, which reflected differences between the dry season diet composed mainly of leaves and unripe fruit, and the largely ripe fruit diet during the wet season. Tannin content is high in many ring-tailed lemurs foods, but Ganzhorn (1989) and Simmen et al. (2006a) suggest that tannin tolerance is also high. To offset the effects of these secondary compounds, geophagy has been observed at both Berenty and Beza Mahafaly sites.

Goodman et al. (2006) found that the diet of *L. catta* inhabiting the Andringitra high-altitude region is markedly different from that of gallery or dry forest groups. A comparison of plants eaten by *L. catta* at Andringitra and Beza Mahafaly revealed that not one species was shared. The diet of this high-altitude population is comprised of 75% fruit, 8–12% leaves, and 6–12% twigs, stems, and insects (Goodman et al., 2006).

Introduced plants are important resources for the gallery forest *L. catta* at Berenty (Crawford et al., 2006; Soma, 1994). Soma found that when the availability of indigenous plant foods was low, both fruit and flowers of introduced species were abundant, and he suggests that these immigrant plant foods lessen the effect of extreme food seasonality in this part of the reserve. *Leucaena leucocephala*, another introduced tree in this forest, is consumed by gallery forest groups, and has had seriously negative consequences (Crawford et al., 2006). Since the late 1990s, ~25% of the individuals living in gallery forest at Berenty experience extreme seasonal fur and weight loss, which Crawford et al. associate with ingestion of leaves, flowers, and pods of *Leucaena*. This plant contains mimosine, an amino acid that inhibits DNA replication and protein synthesis. *Leucaena* is not found in the scrub/spiny forest habitat at Berenty, and no individuals residing in those areas exhibit the alopecia and weight loss conditions seen in the gallery groups. *Leucaena* consumption peaks during gestation period, and Crawford et al. and Jolly (in preparation) found that ingestion of this plant negatively affects infant survival. In 2004 and 2005 birth seasons, respectively, significantly more females residing in non-*Leucaena* areas had infants, compared with females living in areas where the plant was consumed. Jolly (2006b) notes that it is not simply a matter of infants being unable to cling to mothers suffering from hair loss, but rather the ingestion of *Leucaena* itself is the problem, as she found that even females with good or merely poor fur condition also lost infants in the *Leucaena* areas.

The Importance of the Tamarind, or Kily Tree, in *Lemur catta* Diet

All researchers who have examined *L. catta* feeding ecology in and around gallery forests emphasize the great importance of *Tamarindus indica* (or kily) in the diet of animals found in this habitat. Because tamarind trees produce fruit and flowers asynchronously (Sauther, 1998), this is the only food resource used throughout the entire annual cycle (Simmen et al., 2006b). At Berenty, ripe tamarind pods are relied upon during the late dry and early wet season (birth and lactation periods), and during the dry season, unripe pods and leaves form the staple diet, although many other plants are exploited for much more seasonal fruits, leaves, and flowers (Blumenfeld-Jones et al., 2006; Koyama et al., 2006; Mertl-Milhollen et al., 2003; Rasamimanana and Rafidinarivo, 1993; Simmen et al., 2003, 2006a,b). At Beza Mahafaly, *L. catta* groups also rely heavily on tamarind, but in addition, they consume large quantities of *Enterospermum pruinosum* fruit in the dry season, and *Salvadora augustifolia* during the birth and early lactation season (Sauther, 1998). Yamashita (2002) examining seven groups across microhabitats at Beza (gallery and drier deciduous forest) found a marked preference for tamarind fruit in all microhabitats. She suggests that since tamarind fruit is such a dominant food for all *L. catta* in the reserve, all other foods must be considered secondary. At both sites, when tamarind trees failed as a result of drought, ring-tailed lemur populations decreased dramatically for up to 4 years afterwards (Gould et al., 1999, 2003, Jolly et al., 2002). In 2005, two cyclones hit the Beza Mahafaly region, and tamarind fruiting failures occurred (Sauther, personal communication). Future censuses will reveal how and to what extent the ring-tailed lemur population in the reserve was affected.

In gallery forests, between 35 and 60% of total feeding time is spent on tamarind fruit and leaves (Koyama et al., 2006; Mertl-Milhollen et al., 2003). Mertl-Milhollen et al. (2003, 2006) found that leaves from closed canopy tamarinds closer to the river at Berenty contained more water and protein than did tamarind leaves in the open forest farther from a water source. They also note that water content of new tamarind leaves is more dependent on rain than the water table; but water content of mature leaves correlates strongly with proximity to the river.

Tamarind fruit consumption begins at a very early age. Simmen et al. (2006a) found that infants less than 2 months old are able to lick and feed somewhat on the sour pods, and that mother–infant interactions can be seen as an important step in the ingestion of this keystone resource.

Simmen et al. (2006b) and Sauther (unpublished data) note the *L. catta* play a key role in seed dispersal and germination of kily. Simmen et al. (2006b) found that seed germination is more successful and occurs far more rapidly after passing through the ring-tailed lemur's digestive tract.

LIFE HISTORY VARIABLES

Three long-term demographic studies at Berenty and Beza Mahafaly have revealed much information concerning life history variables and population change over time (Gould et al., 2003; Jolly et al., 2002; Koyama et al., 2001, 2002). Average sex ratio at both sites is similar: 0.92 and 1:1 at Beza Mahafaly and Berenty, respectively (Gould et al., 2003; Koyama et al., 2002). Jolly et al. (2002) note much variation in sex ratio per ring-tailed lemur troop. Similar variation is also seen at Beza Mahafaly, and there seems to be no correlation with habitat, that is, sex ratios fluctuate constantly in both gallery and xerophytic forest (Gould et al., 2003; Sussman, 1991).

Mean fecundity at Berenty over a 19-year period was 75%, whereas at Beza Mahafaly it was 84% over 15 years (Gould et al., 2003; Jolly et al., 2002). Koyama et al. (2001), working in a very densely populated, 14-ha area of Berenty, found that while fecundity among very young (2-year-old) females was low (11%), it increased as a function of age and reached 75–85% for females between 5 and 10 years of age. At Beza Mahafaly, variation in fecundity occurred during and following a 2-year drought, with the lowest percentage at the end of the second drought year (74%) and the highest 2 years later (100%).

Jolly et al. (2002) report fewer infants per female in larger groups at Berenty, and Takahata et al. (2005) found that lower-ranking females in such groups exhibited lower reproductive success.

Infant mortality varies between the two sites and between habitats. In the rich and water provisioned area where Koyama and collegues' (2001) focal groups resided, infant mortality in the first year of life was just 37% in a year of normal rainfall whereas Jolly et al. (2003) report 50% in the scrub forest area of the reserve. At Beza Mahafaly, 80% of infants died in the first 6 months in the second year of a drought. But even in years of normal rainfall, infant mortality averages around 52% (Gould et al., 2003; Sussman, 1991). Such high infant mortality may be related to the suggestion by Gould et al. (2003) that *L. catta* are "income breeders" rather than "capital breeders" (as per Jonsson, 1997), that is, females do not rely upon fat stores during reproduction, rather they use the maximum resources in the environment when pregnant and lactating. Therefore, during natural disasters such as drought periods, when fruiting failures occur, females may simply not have the physiological capacity to adequately nurse their quickly growing infants.

In the wild, adult male *L. catta* become sexually mature around 3 years of age, and some disperse at that time, while others remain in the group until they are four (Gould, 2006; Koyama et al., 2002; Sussman, 1992). Koyama et al. observed some 2-year-old males disperse at his study area at Berenty. Two-year-old dispersal, like 2-year-old female births in that area of Berenty, may be a reflection of the rich resources, and water provisioning which does not occur in other areas of the reserve, i.e., sexual maturity in some animals may occur at an accelerated pace under certain favorable conditions. Also variable is the number of times a male might disperse in his lifetime: Koyama reported that male tenure varied between 1 and 7 years during his 10-year study, and at Beza Mahafaly, some males tend to disperse almost annually, while others can remain in one group for several years (Gould, unpublished data; Sussman, 1992). Sussman (1992) notes that on average, males migrate to another group every 3.5 years. Males usually disperse with one or two migration partners (Gould, 1994, 1997; Jones, 1983; Sussman, 1991, 1992).

Few data exist on maximum life span in wild *L. catta*. Koyama et al. (2002) noted that some females in their study groups lived past 13 years, but only one male reached that age. At Beza Mahafaly, animals were individually identified by means of a collar and numbered tag, and one female of known age survived until the age of 19 (Gould, unpublished data). A few other females, whose ages were known when they were initially collared, lived until 16 and 17 years (Gould et al., 2003). The oldest male of known age was 16 in 2005 (Gould, unpublished data, Sauther, personal communication). However, most animals die before reaching these ages (Gould et al., 2003; Koyama et al., 2002). It would be useful to have data on life expectancy and life span of ring-tailed lemurs living in habitats other than gallery and deciduous forest; however, long-term population studies are difficult to conduct in areas where animals are not easily habituated or protected.

HEALTH OF GALLERY FORESTS AND THEIR IMPACT UPON *LEMUR CATTA* POPULATIONS

Clearly gallery forest is an important habitat for populations of *L. catta* throughout south and southwestern Madagascar. However, in many unprotected, and even protected, areas, these forests are not stable. In fact, Sussman and Rakotozafy (1994) suggest that the southern gallery forest is one of the most endangered forest types in Madagascar, with grazing and overcutting resulting in narrow fragments along edges of existing rivers and streams. Blumenfeld-Jones et al. (2006) note that the well-protected gallery forest at Berenty is strongly tied to the adjacent Mandrare River, and the shape and life history of this forest follows the contours of the shifting current and past riverbeds. Surrounding sisal fields, which were planted in the nineteenth century, contain large, old, widely spaced tamarind trees, which once were likely part of a riverine forest system. Blumenfeld-Jones et al. (2006) suggest that due to rivers shifting their courses and existing forests nearing the end of their life cycles, efforts to protect these small gallery forest fragments may ultimately fail. However, at Berenty, within 10 years of ending cultivation on the lower riverbank, trees now grow where crops once stood, thus gallery forest regeneration is possible. Blumenfeld-Jones et al. caution, however, that conservation plans must be based on an understanding of natural regeneration processes.

DIRECTIONS FOR FUTURE RESEARCH

While we know a great deal about the ecology of *L. catta*, most of our knowledge is derived from studies at only a few sites comprised of gallery and deciduous forests, with the exception of the high-altitude groups residing in the Andringitra mountain range discussed earlier in this chapter. Clearly, to gain an even better perspective on this species, it is important for future researchers to seek out *L. catta* populations in unstudied habitats such as spiny desert forest, savannah, river gorges and canyon areas (such as those found at Isalo National Park and Lake Tsimanampetsotsa). An ecological study of a ring-tailed lemur population at Cap Ste. Marie on the southern tip of the island may be forthcoming (Kelley, personal communication).

Documenting variation in the resource bases used by ring-tailed lemurs in their diverse habitats would be very useful in understanding the complexities of their ecology. For example, while tamarind is considered the primary and keystone resource in gallery forests, and the importance of tamarind has been emphasized in many papers on *L. catta* diet, tamarind is not present in all habitats in which *L. catta* is found, and ring-tailed lemur populations are clearly able to survive in areas without tamarind trees, such as the Andringitra mountains. Isalo National Park and Lake Tsimanampetsotsa are two diverse and well-protected areas in southern Madagascar, which contain populations of *L. catta* (Goodman et al., 2006; Sussman et al., 2003). These would be excellent habitats in which to study not only feeding ecology, but also other ecological variables such as home range extent and use, group size, daily activity patterns, reproduction, demography, and life history.

Future studies in such alternative habitats could also focus on differences in female food intake and feeding behavior across reproductive seasons. Such information is already available from gallery forest habitat at both Berenty and Beza Mahafaly reserves (e.g., Rasamimanana, 1999; Rasamimanana and Rafidinarivo, 1993; Sauther, 1992, 1993, 1998), but no information regarding female feeding ecology in nongallery forest areas exists. Related to this topic, the effects of habitat variability on within- and between-group feeding competition could provide us with further information, which could be tied to variables such as fecundity and infant survivorship. Marked interfemale feeding competition and agonism, both within and between groups, has been well documented at both the Beza Mahafaly and Berenty sites (Jolly et al., 1993; Sauther, 1992, 1993, 1998;Takahata et al., 2005), but again in densely populated gallery forest areas where home range overlap can reach 100%. The extent of within- and between-group feeding competition and range defense in habitats where ring-tailed lemur groups are more widely spaced and populations are far less dense than at Beza Mahafaly or Berenty would provide us with a much broader perspective on the ways in which ring-tailed lemurs make a living.

Examining physiological stress (through fecal glucocorticoid analyses) in relation to habitat, group size, and reproductive variables in wild ring-tailed lemurs is another new area of research (Cavigelli, 1999; Cavigelli et al., 2003; Gould et al., 2005; Pride, 2005), which can help us understand how environmental and social conditions affect these animals. For example, Pride (2005) determined optimal group size for ring-tailed lemurs in three microhabitats at Berenty reserve, by examining mean cortisol concentrations in different-sized groups in the three habitats during periods of higher and lower food availability. Hormonal analyses of fecal samples is a completely noninvasive procedure, and has proven to be an extremely useful tool in furthering our understanding of environmental effects on health and reproductive variables, and future studies could examine such variables in habitats where ring-tailed lemurs have not yet been studied.

Similarly, an ongoing study of population health conducted by Cuozzo and Sauther (2004), Sauther and Cuozzo (2005), and Sauther et al. (2002), is documenting the impact of environmental and seasonal variables at the Beza Mahafaly site on dental health, parasite loads, and morbidity in a relatively large population. Future comparative data on populations in other areas of the geographical range of *L. catta* could allow us to compare health profiles between regions and habitats, and illuminate how both ecological and anthropogenic factors impact *L. catta* populations.

Although *L. catta* populations in alternate habitats in the south and southwest of the island are unhabituated, if they occur in protected areas where hunting pressure is not a factor (e.g., some of the National Parks and Special Reserve areas), it would be worth the effort for future researchers to undertake ecological, health, and behavioral projects in these locales, and attempt to collect data that would allow us to gain an even better understanding of this remarkably adaptable lemur, particularly since much of their unprotected habitat seems to be disappearing at an alarmingly rapid rate.

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CHAPTER THIRTEEN

Impact of Seasonality and Reproduction on Social Structure, Ranging Patterns, and Fission–Fusion Social Organization in Red Ruffed Lemurs

Natalie Vasey

INTRODUCTION

The red ruffed lemur, *Varecia rubra,* is a large-bodied, highly frugivorous lemur that gives birth to litters which are initially nested and then later transported orally to hidden, protected arboreal spots where they are periodically left unattended (e.g., Vasey, in press). A major question arises as to how a primate with such an unusual, costly reproductive pattern, involving simultaneous investment in multiple young, has become adapted to a diet that is seasonally scarce and requires relatively great foraging effort (e.g., in terms of time and/or distance traveled). To address this issue, I examine and compare the ranging patterns of female and

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male red ruffed lemurs according to seasons and reproductive stages. In documenting the geographic patterns of range use in red ruffed lemurs, it has become evident that, like certain anthropoid primates (chimpanzees, spider monkeys), this prosimian species has a fission–fusion social organization.

In proposing that a related species, the black-and-white ruffed lemur (*Varecia variegata*), has a fission–fusion social organization, Morland (1991a,b) presented data on affiliation patterns and subgroup dynamics in two adjacent communities, establishing that the black-and-white ruffed lemur has a multilevel social organization that includes subgroups, affiliates, core groups, and a community social network, listed in order of increasing stability. Although the social criteria Morland (1991a,b) used to describe this multifaceted fission–fusion social system are undeniably strong, they were largely based upon select months of the year, rather than an annual cycle, and quite limited data were collected on its geographic patterning throughout the course of different seasons and reproductive stages. A subsequent study by Rigamonti (1993) partly addressed this issue by presenting ranging data for *Varecia rubra* over a 7-month period. However, the latter study did not sample most hot months, when ruffed lemurs are known to be more gregarious (Morland, 1991a,b). In this article, I present data on the social structure and ranging behavior of wild red ruffed lemurs collected over an entire annual cycle to provide a more comprehensive picture of the ruffed lemur's fission–fusion social system . I focus my analysis on how these factors are impacted by reproduction and seasonal differences in climate and food distribution. These data serve to illustrate the complex fission–fusion social organization of this rainforest lemur in northeast Madagascar.

Background

Food distribution, body size, and reproductive pattern may all potentially impact ranging and foraging behavior. In addition to being governed by abiotic climatic factors, tropical plants have evolved many ways of defending themselves against predation such as rapid leaf expansion, synchronous flushing and masting, production of secondary metabolites, and delayed leaf greening, all of which contribute to the patchy distribution of palatable plant parts (e.g., Coley and Barone, 1996). Thus, edible fruit, flowers, and young leaves are the most clumped and ephemeral plant foods available in a rainforest, and are therefore the most spatiotemporally patchy resources. Having a spatiotemporally patchy diet indicates that a species is selecting foods to avoid toxic plant secondary compounds and optimize nutrient mix and nutritional value given the constraints of its digestive system (Freeland and Janzen, 1974; Westoby, 1974; Oates et al., 1977; Milton, 1980; Glander, 1982; Waterman, 1984; Richard, 1985; Janson et al., 1986). However, being selective in food choice increases the costs of food procurement (e.g., time spent or distances traveled to locate food). A primary consumer with a spatiotemporally patchy diet needs to work out a compromise between being selective in food choice and minimizing the high costs of food procurement. Therefore, the criterion of benefit to be maximized is not simply energy uptake per unit foraging time, as predicted by optimal foraging theory (e.g., Krebs and Davies, 1993). Rather, primary consumers should have evolved ways to minimize the costs of procuring preferred foods. These foraging adaptations should be most evident in the way food is located (i.e., in ranging behavior) and are unlikely to be uniform throughout the year due to seasonal shifts in climate and food availability. In an extensive review of tropical vertebrate frugivores from various geographic regions of the world, Fleming et al. (1987) hypothesized that high spatiotemporal patchiness of food resources will favor the evolution of relatively mobile species that can efficiently travel long distances in search of food, whereas low spatiotemporal patchiness of food will favor the evolution of relatively sedentary species with less emphasis placed on energetically efficient long-distance travel.

A species' ranging and foraging behavior can be associated with body size. The vast majority of primates feed on fruit, with smaller-bodied ones supplementing their diets with insects and larger-bodied ones supplementing with leaves (Gaulin, 1979). Above 300 g, it is not possible for a primate to obtain all of its food energy from insects, and below 700 g it is not possible for it to obtain all of its food energy from leaves (Kay, 1984). These trends are due to scaling relationships. Small primates have high metabolic demands and protein requirements per unit body weight compared to larger animals. Small species cannot survive on a diet of fruit and leaves alone because they cannot extract nutrients quickly enough to supply their tissues even if large quantities are eaten. Therefore, small-bodied primates supplement their diets with high quality, but less abundant, insects. Larger species can obtain sufficient nutrients from bulkier foods that are of lower quality because of their relatively lower metabolic rates and longer gut passage times. Since large species require absolutely more energy than small ones, their population densities are lower and consequently, their home ranges are larger (e.g., Clutton-Brock and Harvey, 1978). Although these scaling relationships are broadly predictive of diet and ranging in many primates, dietary diversity in lemurs appears to be distributed according to taxonomic lineages, not just body size (Richard and Dewar, 1991).

Lastly, there is the potential impact of reproduction on foraging. Gestation and lactation increase nutritional requirements in female mammals (e.g., Loudon and Racey, 1987; Gittleman and Thompson, 1988). Using the rhesus macaque as a model, Portman (1970) estimated that pregnancy and lactation increase energetic and protein requirements of females by 25 and 50%, respectively. Controlled captive studies on primates have demonstrated that females require more food energy during lactation than during other reproductive stages (Kirkwood and Underwood, 1984; Sauther and Nash, 1987; Dufour and Sauther, 2002). Recent field studies on lemurs have suggested specific tactics primates use to meet energetic requirements of reproduction. Morland (1990) demonstrated that lactating *V. variegata* females spent more time feeding than nonlactating females, and Sauther (1998) demonstrated that pregnant *Lemur catta* ate more energy-rich foods than males and timed their most costly reproductive stages with specific resource availability. Particularly germane here, diet, activity budgets, and activity rhythms are all known to vary in *V. rubra* females in tandem not only with seasons, but also with reproductive stages (Vasey, 2000a, 2002, 2004, 2005).

Synthesizing these theoretical and empirical studies, it is cogent to hypothesize that species with spatiotemporally patchy food resources, relatively large body size, and high reproductive costs should have evolved foraging tactics to conserve energy, and should demonstrate sex differences in these tactics due to differing female and male reproductive investment. *Varecia rubra*, the red ruffed lemur, is in all respects a model taxon with which to test this hypothesis.

Body Size, Diet, and Reproduction in Varecia

Varecia has the largest body size (wild weight range = 2.6–4.1 kg, Vasey, 2003), the highest reproductive costs, and quite likely the most spatiotemporally patchy diet among extant lemurids. *Varecia* relies chiefly on ripe fruit (e.g., Morland, 1991a; Rigamonti, 1993; Vasey, 2000a), which is one of the most clumped and ephemeral food resources in a rainforest. At Andranobe, *V. rubra* was shown to have a far more spatially and temporally patchy diet than sympatric *E. fulvus albifrons* (Vasey, 1996, 1997a). A variety of traits increase reproductive costs of *Varecia* relative to other primates. Despite being the largest lemurid, *Varecia* has the shortest gestation period (99–106 days, Boskoff, 1977; Foerg, 1982; Shideler and Lindburg, 1982), the highest mean litter sizes ($x = 2.1$ for *V. rubra*, Vasey, in press), and relatively altricial young that grow extremely rapidly, attaining 70% of adult weight at 4 months (Pereira et al., 1987). *Varecia* has the highest prenatal maternal investment rate of any primate (litter weight divided by gestation length relative to maternal body weight and metabolic rate) (Young et al., 1990). Following their costly gestation periods, they begin lactating, the most energetically expensive reproductive stage for mammals (e.g., Oftedal, 1985; Thompson, 1992; Dufour and Sauther, 2002). Moreover, *Varecia* must produce milk for litters of rapidly growing infants (e.g., Petter-Rousseaux, 1964; Foerg, 1982), whereas other diurnal primates generally nurse singletons. *Varecia* produces milk that is higher in dry matter, fat, protein, and gross energy (kcal/g) than other lemurids, with protein concentrations similar to those of lorisoids whose milks are more concentrated in nutrients than any other group of primates (Tilden and Oftedal, 1995, 1997). Like various nocturnal prosimians, *Varecia* bear their young in nests.

Given the relatively large body size and high reproductive costs of *Varecia*, and the high spatiotemporal patchiness of its diet, predictions that follow are that *V. rubra* will: (1) conserve energy by minimizing forest area used and distances traveled within a large home range during the food-scarce cold seasons and (2) show sex differences in the above tactics during energetically costly reproductive stages (gestation and lactation).

METHODS

Study Site

Location and Climate

A study site was established in northeastern Madagascar on the west coast of the Masoala Peninsula in a region of primary lowland coastal rainforest known locally as Andranobe (15° 40.533' S, 49° 57.800' E to 15° 40.275' S, 49° 57.888' E). The site is located within the recently inaugurated Masoala National Park (Kremen, 1998). There are four distinct seasons in this region: (1) hot rainy (Jan–Mar), (2) transitional cold (Apr–May), (3) cold rainy (Jun–Aug), and (4) hot dry (Oct–Dec) (Table 1). The climatic features of September do not fit any of the four distinct seasons. Therefore, data from this transitional month are not included in seasonal analyses. During the course of the study, average annual rainfall was 5110.26 mm, average monthly temperature maxima ranged from 22.5 to 31.6°C, and average monthly temperature minima ranged from 19 to 23.5°C. Andranobe has more rainfall than any other locality in Madagascar. More extensive descriptions of the study site and climate can be found in Vasey (1997a, 2000a).

Seasonal Food Availability and Reproductive Schedules

Table 1 summarizes plant phenology on the island of Nosy Mangabe (Andrianisa, 1989) and on the Masoala Peninsula (Rigamonti, 1993). These two northeastern Malagasy rainforests are within 25 km of Andranobe and provide a representative view of plant food availability in the region. At both sites, fruit, flowers, and young leaves are more abundant in the hot seasons with additional increases in flower and young leaf availability at the end of the cold rainy season. Peaks in fruit and flower availability are similar in other Malagasy rainforests (Table 1 and references therein). Given the similar patterns in fruit and flower availability in northern and southeastern forests, phenological data from Nosy Mangabe and the Masoala Peninsula are considered reliable indicators of resource availability at Andranobe.

Table 1 also shows the correspondence between seasons, food availability, and reproductive stages. Reproduction in the study population was highly synchronized, with mating occurring in early Jul, gestation Jul–Oct, and lactation Nov–Feb (Vasey, in press). A nonreproductive period followed Mar–Jun, during which time adult females were neither pregnant nor lactating. Thus, seasons and reproductive stages span different, though partially overlapping, sets of months allowing two sets of analyses: by season and by reproductive stage.

Table 1. Correspondence between seasons, reproductive stages, and food availability for *Varecia* in northeastern Madagascar (Phenological data for two other regions are included for comparison. See superscripts. Absence of superscripts indicates that a resource is scarce or unavailable)

Season	Hot rainy			Trans. cold		Cold rainy			Trans. dry	Hot dry		
Reproduction	Lactate and stash		Nonreproductive				Gestation				Lactate, nest, stash	
Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Fruit	peak[a, c, d, e]	peak[a, c, d, e]	[e]			[e]		[c]	rise[b, c]	rise[b, c, e]	peak[a, b, d]	peak[a, c]
Flowers	peak[a]							peak[b, c]	[e]	[d, e]	[c, d, e]	peak[a, c, d]
Young leaves	[c, e]	[e]			[c]	[e]		rise[b, e]	[e]	[e]	rise[b, e]	

[a] Phenological data from Andrianisa (1989), Nosy Mangabe, northeastern Madagascar.

[b] Phenological data from Rigamonti (1993), Ambatonakolahy, Masoala Peninsula, northeastern Madagascar.

[c] Phenological data from Overdorff (1993a,b). Only superscripts are entered in the table as data are from the Parc National de Ranomafana in southeastern Madagascar.

[d] Phenological data from Freed (1996). Only superscripts are entered in the table as data are from the Parc National de Montagne d'Ambre in northern Madagascar.

[e] Phenological data from Balko (1998). Only superscripts are entered in the table as data are from the Parc National de Ranomafana in southeastern Madagascar.

Study Population

The study population comprised one community of *V. rubra*. Ranging data were collected on adult animals on five to eight consecutive days per month over 12 consecutive months (Jan–Dec 1994) using focal animal sampling. Focal animal observation periods usually lasted from 8 to 13 hours per day, depending upon seasonal differences in day length and time needed to locate animals at dawn. *V. rubra* was observed for 672 hours (females, 463 hours; males, 209 hours) during 78 focal animal observation periods. To facilitate location of animals at the beginning of each observation period, three animals were fitted with radio-collars using a live-capture protocol established by Glander et al. (1991); each belonged to a different core group in the community (Table 2). Six of eleven adults in the community were sampled regularly (4 females and 2 males). So that data could be pooled (see Data Analysis), I attempted to equally represent study subjects by following each animal once per month. Because the study population lived in a large fission–fusion community and had a large home range (see Results), it was sometimes difficult to locate the focal animals without radio-collars. Steep terrain, dense forest, and intense rainfall compounded the difficulty of locating a specific member of the community on any given day. Despite these challenges, focal animals without radio-collars were sampled for full-day observation periods in 12 (Pale, female), 7 (White, female), and 5 (Collier Pied, male) months of the study. Two additional focal animals were sampled in the last month of study (Table 2). It was not possible to sample more than one male in every month. *Varecia* males are often solitary and spatially peripheral (Morland, 1991a,b; Vasey, 1997a) and only one male at Andranobe was fitted with a radio-collar. Focal animal data were collected only on the latter male during the hot rainy and cold rainy seasons. However, full-day focal animal observations on two or three different males were collected for every reproductive stage and in the other two seasons (transitional cold, hot dry), thus providing a representative database. All members of the study population, whether focals or not, were individually identified by various means. A more detailed description of the study population can be found in Vasey (1997a, 2000a).

Data Collection

Prior to data collection, my assistants and I became familiar with the forest where the study community was situated. Thereafter we cut trails to facilitate following animals. Cutting a quadrat or coordinate system was not feasible given the steep terrain and the enormous home range used by the community. Twenty-two trails were cut and compass bearings were taken at marked, 25-m intervals. We subsequently mapped trees and other landmarks with reference to the trail system via their distance and bearing from marked trail points. For *V. rubra*, we mapped 3 nest trees, 28 infant stashing trees, 493 feeding trees, and locations of territorial

Table 2. Size and age–sex composition of the *Varecia rubra* community and its core groups[a]

Community size (n = 18–31)	Core group 1 (n = 5–7)	Core group 2 (n = 4–6)	Core group 3 (n = 2)	Core group 4 (n = 4–9)	Core group 5 (n = 9)
Adult females (n = 7–8)	*Glow*[b] *Pale*	*Red** Red NC[c]		*Blue** *White*	Deep Red 1 Deep Red 2
Adult males (n = 3)	*Yellow**	*Petit Blanc*[b]		*Collier Pied*	
Juveniles/subadults (n = 2)			Metisse 1 Metisse 2		
Infants 1993[d] (n = 5)	Barthe (P) Lisa (P)	Socks (RNC) Stockings (RNC)		Be (W)	?[e]
Infants 1994[d] (n = 14)	Marguerite (P) Omar (P)	Ayla (R) Durc (R)		Meanie 1 (B) Meanie 2 (B) Athena (W) Ceres (W) Diana (W)	Lily (DR1) Moses (DR1) Faith (DR2) Hope (DR2) Love (DR2)

[a] Ranging data were collected on adult focal animals in core groups 1, 2, and 4. The names of focal animals are in italics. Individuals with radio-collars are further identified with an asterisk.

[b] Ranging data were collected on Glow and Petit Blanc only in the last month of the study, Dec 1994. In the latter month, Petit Blanc was observed in both core groups 2 and 5 guarding infants (Vasey, in press).

[c] Red NC disappeared from the study area several months after data collection began. Red then adopted Red NC's offspring, Socks and Stockings (Vasey, in press).

[d] The initials of each infant's mother appear in parentheses after the infant's name. The sex of infants and yearlings was not determined during the study.

[e] It is not known whether infants were born into core group 5 in 1993.

battles. A concurrent study of *E. f. albifrons* was taking place, and we additionally mapped 505 feeding trees used by this sympatric lemurid. To reconstruct ranging variables for later analysis, I noted the location of the focal animal each time it entered a new feeding, resting, nesting, or infant stashing tree. For travel that was not directed toward these types of trees, which was rare, I noted the nearest trail marker or marked tree as its locality. If the animal was nowhere near a trail or marked tree, the location was marked with flagging tape and a new landmark was later mapped with reference to the trail system.

Data Analysis

Pathfinder (Winslett, 1989) was used to create a mapping database, derive descriptive statistics for ranging variables, and graph animal travel patterns within the home range. This software application is designed to process data that have been collected using a trail system, rather than a coordinate system. The communal home range area, core areas, and forest areas used by individuals were calculated by Pathfinder from minimum convex polygons enclosing travel routes made by animals during focal animal observation sessions. Daily distances traveled were derived by Pathfinder by summing the linear distance between trees and trail points crossed or visited by focal animals during the course of full-day observation periods (8 hours or more). Data records for ranging variables were pooled according to sex, month, season, and reproductive stage. To test for differences based on sex, month, season, and reproductive stage, I employed *t*-tests assuming unequal variance (two-tailed) or Kruskal–Wallis tests. Standard notation for significance values is used ($^{***} = 0.001$, $^{**} = 0.01$, $^{*} = 0.05$; ns = not significant; Sokal and Rohlf, 1981).

RESULTS

Social Structure: Size and Age–Sex Composition of the Study Community

The study population did not live in a spatially cohesive social group, but rather in a dispersed social network made up of animals that interacted with one another, but whose members were never seen all together in the same place at the same time. Such social networks are commonly referred to as “communities” rather than “groups” (Richard, 1985; Goodall, 1986). The red ruffed lemur community at Andranobe included 18 individuals after the first birth season and 31 after the second birth season (Table 2). These figures represent minimum estimates of community size based upon animals that could be positively identified, aged, and sexed. There were several additional animals that affiliated with members of the community. However, because of infrequent sightings they could not be positively identified. Nor could their core group affiliation be determined. Individuals who shared the same core area (see next section) were considered members of the same core group.

Table 2 shows the size and age/sex composition of the Andranobe study community divided by core groups. There were five core groups, the majority consisting of one adult male, one or two adult females, and immatures. Four of these core groups contained two reproductive females during part or all of the study. Core group 1 had two females that mated, but only one that gave birth. Core group 2 initially had two reproductive females, but one of these females disappeared several months after the study began. Core group 3 was composed of two juveniles or subadults. There were two reproductive females in both core groups 4 and 5, and in each core group the females would stash their infants together (Vasey, in press). There were three reproductive males in the community, and none shared the same core group. In summary, there were multiple reproductive males and females in the community, and as many as two females within a single core group. Therefore, the social structure of *V. rubra* at Andranobe is multifemale/multimale.

Ranging Patterns and Social Organization

Communal Home Range, Core Areas, and Home Range Defense

The communal home range area of *V. rubra* at Andranobe, containing all five core groups, covered 57.7 ha (Figure 1). Members of each core group shared a common core area which they used preferentially throughout the year more often than any other core area. Three of the five core groups contained focal animals and their respective core areas were precisely mapped (Figure 1). To calculate core area sizes, I enclosed the annual ranges for each core group male and the Jun–Oct ranges for core group females within minimum convex polygons. I focused on Jun–Oct because usage of core areas changed seasonally and in relation to reproduction. Core areas were clearly distinguishable geographic entities during these 5 consecutive months which contained the cold rainy season, mating, and gestation (Table 1). Underlying this geographic pattern, during these 5 months animals from different core groups did not socialize. Defined as such, there was little overlap between core areas within the community, but there were no fixed or defended boundaries either (Figure 1). Between communities, on the other hand, ritualized agonistic encounters occurred at the boundaries of communal home ranges (Figure 2). Of 11 intercommunity encounters observed over the 13-month study period, all but one involved agonism: community members allowed a group of strangers to enter the communal home range with little contest during the mating season (Vasey, in press). Of the remaining 10, 6 occurred during hot months, when females, in particular, are ranging widely (see below); and the other

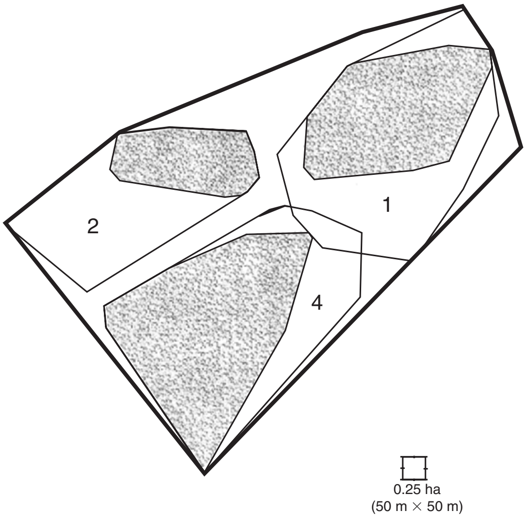

Figure 1. Communal home range and core areas in one community of *Varecia rubra*. The communal home range (57.7 ha) is contained within the most inclusive polygon. Core areas for core groups 1 (17.15 ha), 2 (10.85 ha), and 4 (17.86 ha) are enclosed by three numbered polygons. These polygons enclose male ranges over an entire annual cycle and female Jun–Oct ranges (shading). Core areas for core groups 3 and 5 were not determined.

4 occurred during the transitional cold season. During these encounters, which lasted between 10 and 80 minutes, members of different communities chased each other, scent marked, and performed loud calls. Red ruffed lemurs at Andranobe can therefore be described as territorial in that they have exclusive home ranges that are communally defended from other conspecific communities.

Individual Travel Patterns and Intracommunity Spacing

Though core group members were frequent affiliates, they did not routinely travel through their core areas in a cohesive fashion (see also Morland, 1991a,b). Figures 1 and 3–6 map the spatial patterns created by community members as they moved through their home range and the extent of overlap between individual home ranges at different times of year. Males resided largely within their respective core areas year round. There was slight overlap between the home ranges of two males in June, 1 month before mating took place (Figure 1). Complementing these ranging data, which are based on focal animal sampling, community males were rarely sighted outside of their respective core areas at other times, e.g., while other *Varecia* focals or *E. f. albifrons* were under observation or during random sightings that occurred while collecting botanical samples

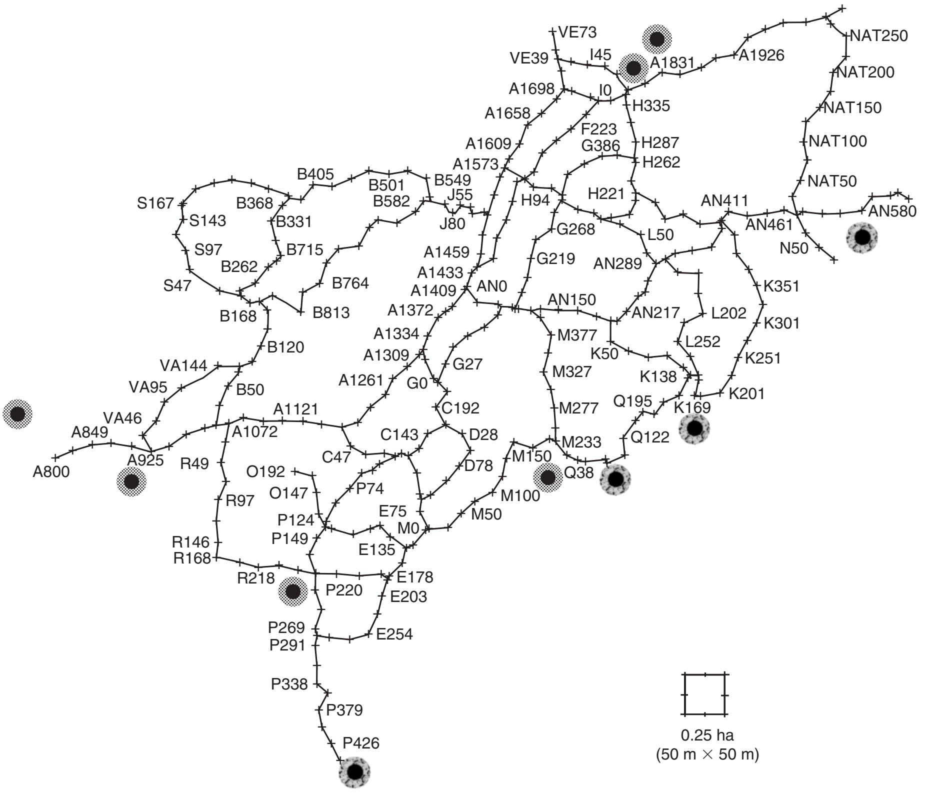

Figure 2. The locations of 10 intercommunity territorial battles, denoted by black dots (●), shown in relation to the trail system installed to track *Varecia rubra* at Andranobe. Dots denoting battles that occurred in hot months show stippling (▨) behind them; dots denoting battles that occurred in the transitional cold season (Apr–May), show forest cover behind them.

or mapping. Of 38 such sightings (which included every calendar month but March), in only 2 cases (5%) was a male seen outside of his respective core area, and in only 2 cases (5%) were community males sighted in proximity to another male; Yellow was sighted once with Collier Pied (in their overlap zone) and once with Petit Blanc. The latter cases all occurred during hot dry/female gestation months (Nov–Dec), and no agonistic behavior occurred.

In contrast to males, female ranging patterns changed during the course of the year. During the hot rainy season (Jan–Mar), female ranges overlapped extensively (Figure 3). Females ranged widely through the communal home range entering other core areas and affiliating with members of other core groups in temporary aggregations (hereafter "subgroups") that varied daily in membership, size, sex

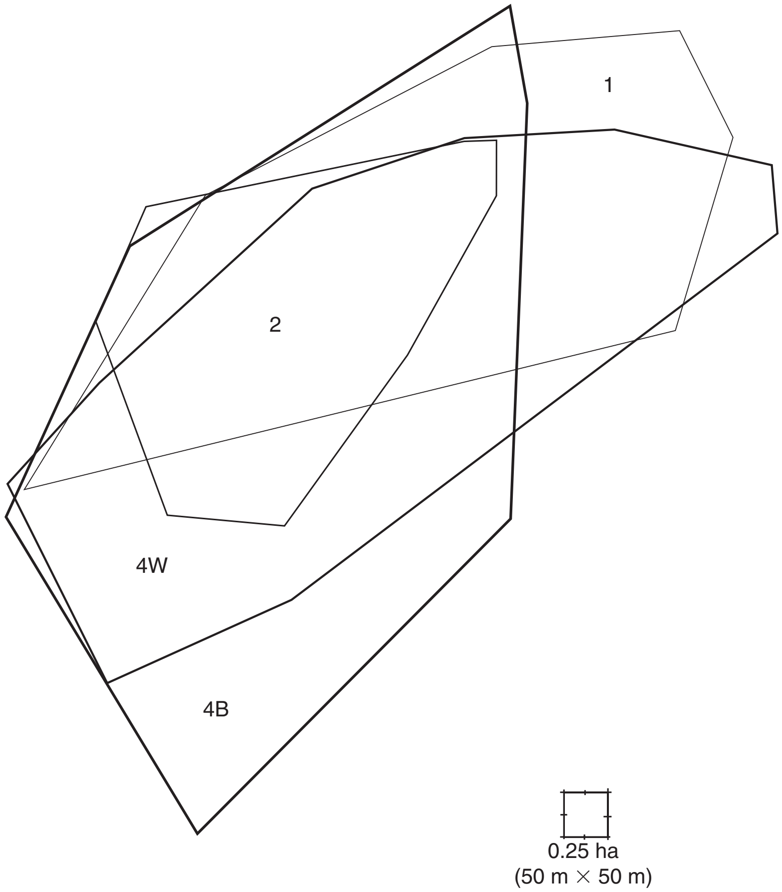

Figure 3. Individual travel patterns and spatial association of *Varecia rubra* females in the hot rainy season (Jan–Mar). Female ranges overlap extensively during this season. Fine-lined polygons enclose female ranges in core groups 1:Pale and 2:Red. Thick-lined polygons enclose female ranges in core group 4: 4W = White, 4B = Blue.

composition, and duration. These subgroups comprise the daily component of their fission–fusion social organization. Affiliative behaviors that occurred in subgroups included female greeting displays, feeding, calling, resting, grooming, and traveling together. The greeting behavior of *V. rubra* females is spectacular, involving anogenital scent marking of each other's backs, jumping over one another in a leapfrog-type fashion, writhing together, and emitting soft squealing sounds. In the subsequent cold rainy season (Jun–Aug), the ranges of females from different core groups did not overlap whatsoever (Figure 4). Females confined themselves to small patches of their respective core areas and affiliation between them ceased; subgroups were formed only by animals from the same core

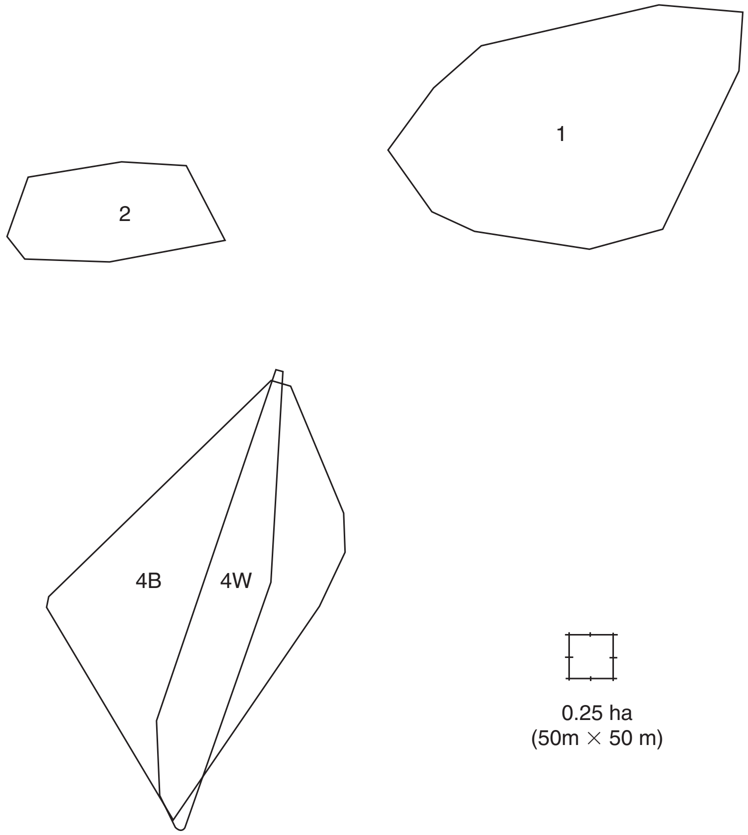

Figure 4. Individual travel patterns and spatial association of *Varecia rubra* females in the cold rainy season (Jun–Aug). Ranges for females in different core groups do not overlap at all during this season. 1 = Pale; 2 = Red; 4W = White, 4B = Blue.

area (except while mating, Vasey, in press). This dispersion of core groups comprises a higher-level component of their fission–fusion social organization.

During gestation (Jul–Oct), *V. rubra* females continued the confined ranging pattern observed during the cold rainy season, traveling only within their respective core areas (Figures 1 and 4). Female gestation coincides with part of the cold rainy season, the transitional month of September, and the first month of the hot dry season (Table 1). After giving birth and commencing lactation (Nov), females began to travel longer distances (see below). However, they remained principally within their own core areas near their nests (Figure 5). Similarly, in the second month of lactation, when infants were starting to travel short distances alongside adults and were stashed for longer periods of time (Vasey, in press), females trav-

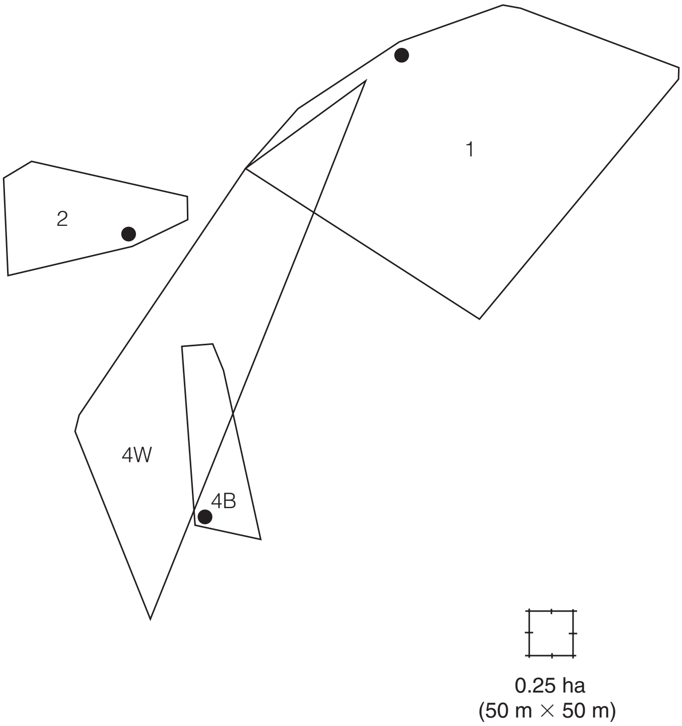

Figure 5. November ranges for *Varecia rubra* females in core groups 1, 2, and 4 are illustrated, including the location of their infant nests, denoted by black dots (●). White's nest was not located. 1 = Pale; 2 = Red; 4W = White, 4B = Blue.

eled farther, yet remained principally within their own core areas near infant stashing depots (Figure 6).

Individual Home Range Areas

Because *V. rubra* lives in dispersed social networks, the communal home range area of 57.7 ha, presented above, does not convey the complexity observed in home range use. Thus, I here compare individual home range areas within and between the sexes annually and according to season and reproductive stage. Mean annual forest area used per female was almost twice as large as that used per male (30.9 ha versus 16.2 ha, $t = 3.05^*$, $df = 3$, Table 3). However, female home ranges were not uniform throughout the year (Figure 7). Home range areas of females were larger in the hot rainy season than in the transitional cold ($t = 2.87^*$, $df = 5$), cold rainy ($t = 4.01^*$, $df = 4$), and hot dry seasons ($t = 3.32^*$, $df = 4$). Large fluctuations are also evident when home ranges are compared according to reproductive stage;

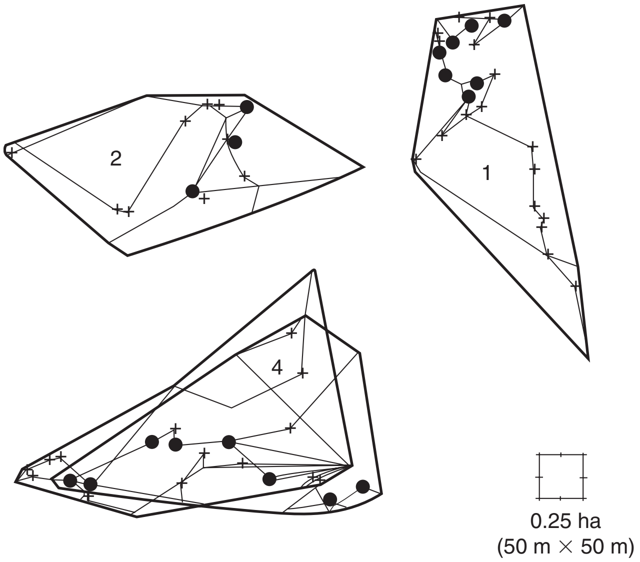

Figure 6. December ranges for *Varecia rubra* females in core groups 1, 2, and 4 including routes followed and the location of infant stashing trees, denoted by black dots (●).

Table 3. Seasonal and annual home ranges (ha) of individuals in one fission–fusion community of red ruffed lemur (*Varecia rubra*)[a]

	Hot rainy	Trans. cold	Cold rainy	Hot dry	Sep	Annual
Female *x*	23.3 (14)	9.1 (7)	5.1 (13)	8.5 (16)	(4)	30.9 (53)
Pale	22.1 (3)	8.7 (2)	7.4 (3)	11.8 (4)	(1)	29.5 (13)
Red	12.2 (4)	4.8 (2)	2.1 (4)	4.2 (4)	(1)	18.3 (15)
White	26.8 (2)		2.4 (2)	12.1 (2)	(1)	35.6 (7)
Blue	31.9 (5)	13.8 (3)	8.6 (4)	7.3 (5)	(1)	40.3 (18)
Glow[b]				6.9 (1)		(1)
Male *x*	(4)	5.4 (5)	(5)	9.1 (8)	(2)	16.2 (22)
Yellow	9.8 (4)	4.2 (3)	12.9 (5)	12.1 (4)	(1)	17.1 (17)
Collier Pied		6.5 (2)		7.8 (2)	(1)	15.2 (5)
Petit Blanc[b]				7.2 (2)		(2)
Community						57.7 (78)

[a] Number of sample days is shown in parentheses.

[b] Glow and Petit Blanc were followed only in December 1994. Animals ranged longer distances in December than during the previous 2 months of the hot dry season (Table 4). Therefore, the figures reported for these two individuals are reasonable minimum estimates of forest area used during the hot dry season. However, these values were not used in computing annual means for females and males.

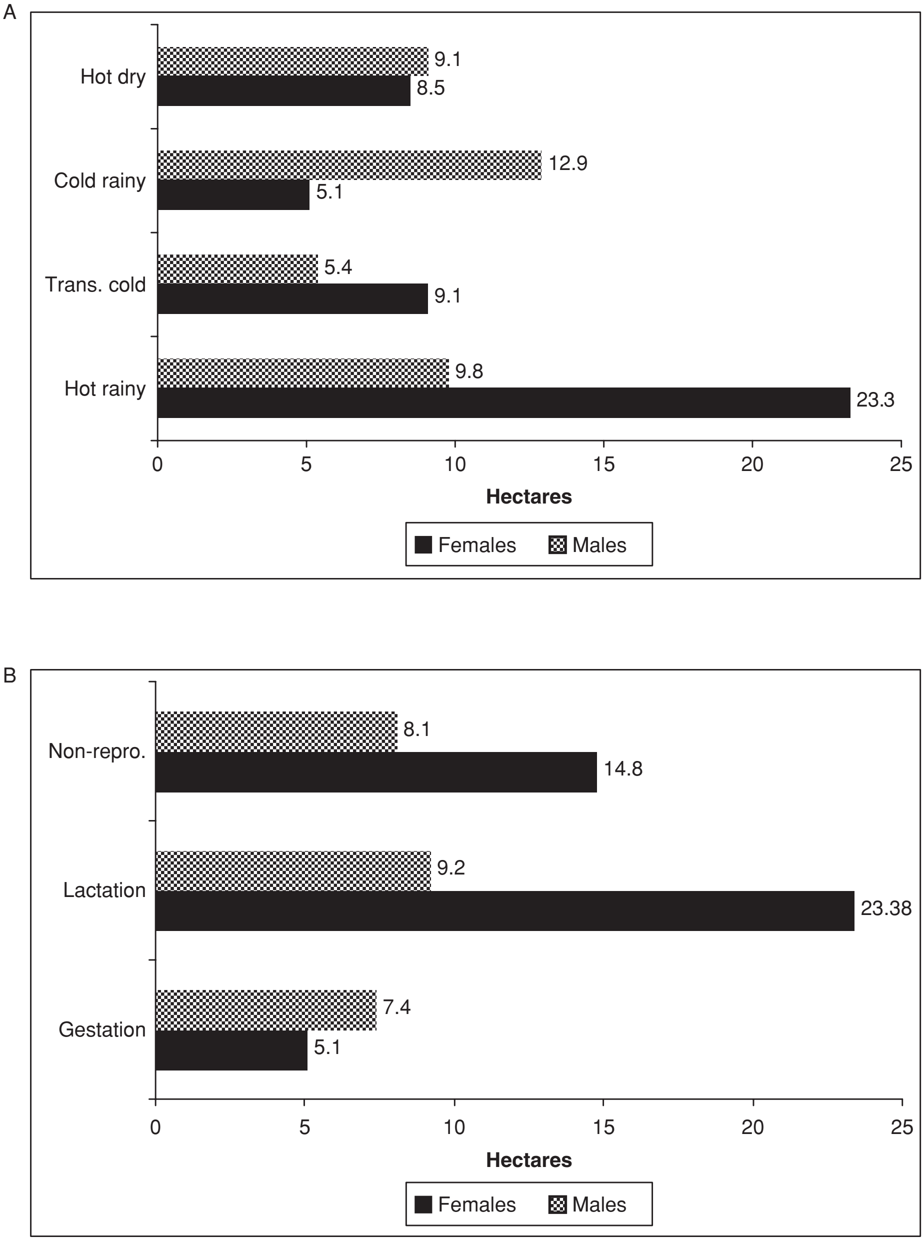

Figure 7. Average forest area used (ha) by *Varecia rubra* females and males according to (A) seasons and (B) reproductive stages.

females had much smaller home ranges during gestation compared to lactation ($t = 4.86^{**}$, $df = 5$) and the period of the year when they are nonreproductive ($t = 3.62^{*}$, $df = 4$). In contrast, home range areas of males did not differ significantly between seasons or reproductive stages, and in particular, for Yellow, the male for which there is comprehensive seasonal data (Table 3). As a result, sex differences in home range area were due to fluctuations in forest area used by females, not males; mean forest area used per female was more than twice that of the male in the hot rainy season (23.3 versus 9.8 ha), less than half the size of the male in the cold rainy season (5.1 versus 12.9 ha), and similar in size to males in the hot dry ($t = 0.28$ ns, $df = 5$) and transitional cold seasons ($t = 1.35$ ns, $df = 3$, Table 3, Figure 7a). In like fashion, females had larger home ranges than males during lactation ($t = 3.51^{*}$, $df = 5$), but not during gestation ($t = 0.91$ ns, $df = 3$) or when nonreproductive ($t = 2.67$ ns, $df = 3$, Figure 7b).

Mean Daily Distances Traveled

Males showed relatively few seasonal differences, traveling shorter daily distances in the transitional cold season than in both hot seasons (hot rainy, $t = 3.01^{*}$, $df = 6$; hot dry, $t = 2.81^{*}$, $df = 9$). On the other hand, females showed marked seasonal variation, traveling longer daily distances in the hot rainy season than in every other season (transitional cold, $t = 2.85^{**}$, $df = 16$; cold rainy, $t = 8.04^{***}$, $df = 23$; hot dry, $t = 2.22^{*}$, $df = 23$). Compared with the cold rainy season, females also traveled farther in the transitional cold ($t = 2.93^{**}$, $df = 17$) and hot dry seasons ($t = 3.58^{***}$, $df = 24$). Despite marked seasonal variation in female travel distances, monthly, seasonal, and annual means did not differ between the sexes, except in the month of June. Nor did the sexes differ within any reproductive stage (Table 4, Figure 8). Yet when data are divided by reproductive stage, the sexes actually show similar longitudinal patterns (Figure 8). For both sexes, daily distances traveled when females lactated were significantly longer than they were during gestation (females, $t = 8.74^{***}$, $df = 30$; males, $t = 4.08^{***}$, $df = 13$) and when non reproductive (females, $t = 3.82^{***}$, $df = 26$; males, $t = 4.38^{***}$, $df = 13$). Females also traveled shorter daily distances during gestation than when non-reproductive ($t = 3.36^{**}$, $df = 28$). Hence, both sexes did not begin traveling longer distances immediately after the cold rainy season, despite improved climate and food availability. Rather, this shift occurred after females gave birth and were finished nesting their young (a month earlier for males). Females dramatically increased distances covered after parturition (Nov) and throughout lactation (Table 4, Figure 8). The one sex difference similarly appears related to reproduction; males traveled significantly farther than females in June, 1 month prior to the mating season when males are known to roam.

Table 4. Mean daily distance traveled (m) by *Varecia rubra* females and males

Season[a]	Hot rainy			Trans. cold		Cold rainy			Trans.	Hot dry			Annual[b]
Reproduction[c]	Lactation		Nonreproductive				Gestation				Lactation		
Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Female *x*	1816	2221	1248	1438	594	477	621	359	377	460	1166	1912	1074
n	(5)	(4)	(3)	(3)	(3)	(4)	(4)	(5)	(4)	(4)	(4)	(5)	(48)
Male *x*	1475	1584	665	676	265	933	595	498	458	910	1056	1946	969
n	(2)	(1)	(1)	(2)	(2)	(2)	(2)	(1)	(2)	(2)	(2)	(3)	(22)
t^d	1.07 ns *df* = 4			2.13 ns *df* = 3	1.96 ns *df* = 3	2.77^* *df* = 4	0.49 ns *df* = 1		0.43 ns *df* = 1	2.70 ns *df* = 1	0.19 ns *df* = 2	0.16 ns *df* = 5	0.59 ns *df* = 68

[a] Female seasonal means: hot rainy, 1809 m; transitional cold, 1016 m; cold rainy, 476 m; hot dry, 1236 m. Male seasonal means: hot rainy, 1300 m; transitional cold, 470 m; cold rainy, 711 m; hot dry, 1396 m. The sexes do not differ in any season: hot rainy, $t = 1.67$ ns, $df = 14$; transitional cold, $t = 1.71$ ns, $df = 8$; cold rainy, $t = 1.5$ ns, $df = 16$; hot dry, $t = 0.50$ ns, $df = 18$.

[b] Annual mean for both sexes combined = 1041 m (range 71–2649 m).

[c] Female reproductive stage means: gestation, 448 m; lactation, 1685 m; nonreproductive, 904 m. Male reproductive stage means: gestation, 632 m; lactation, 1561 m; nonreproductive, 630 m. The sexes do not differ in any reproductive stage: gestation, $t = 1.61$ ns, $df = 22$; lactation, $t = 0.54$ ns, $df = 21$; nonreproductive, $t = 1.26$ ns, $df = 18$. Select monthly values of two females were removed for analysis by reproductive stage. Glow, sampled only in Dec, did not give birth in either year of the study. Blue bore young in the second, but not first, year of study; her Jan and Feb daily distances were not included among lactation values.

[d] Standard notation for significance values are indicated. $^{***} = 0.001$; $^{**} = 0.01$, $^{*} = 0.05$; ns = not significant. *t*-tests were not performed for months where only a single male value was available. Kruskal–Wallis tests were performed instead and none showed significant sex differences (Feb, $H = 2.0$ ns, $df = 1$; Mar, $H = 1.8$ ns, $df = 1$; Aug, $H = 0.77$ ns, $df = 1$).

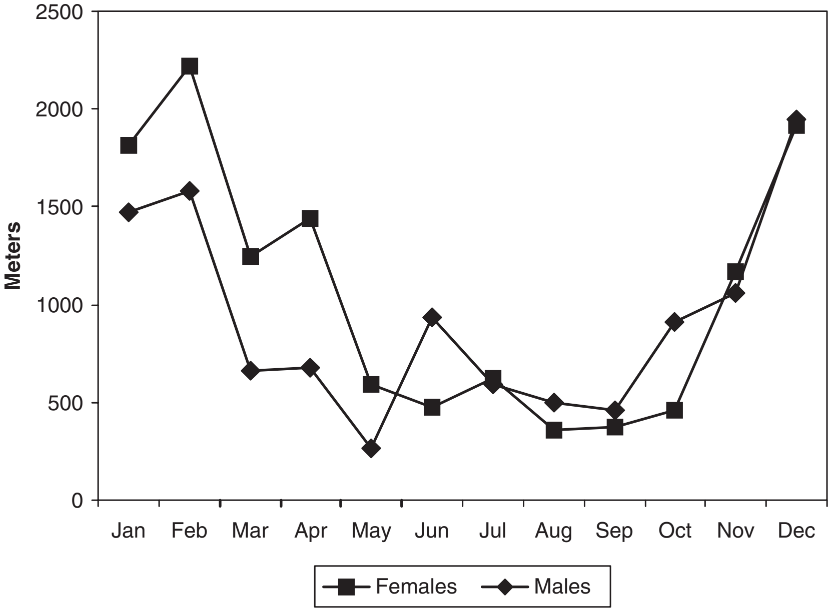

Figure 8. Mean daily distances (m) traveled by *Varecia rubra* females and males by month. For corresponding statistics by month, season, and reproductive stages, see text and Table 4.

DISCUSSION

Based on now classic ecological studies of rainforest primates (e.g., Milton, 1980; Terborgh, 1983) and, more generally, on a comparative review of frugivorous tropical vertebrates (Fleming et al., 1987), I hypothesized that species with relatively (1) high reproductive costs, (2) large body size, and (3) spatiotemporally patchy food resources would have foraging adaptations to conserve energy and would demonstrate sex differences in these adaptations due to differing female and male reproductive investment. I predicted that *V. rubra*, which possesses all three of these traits, would conserve energy by minimizing forest area used and distances traveled within a large home range during the resource-scarce cold seasons. I also predicted that *V. rubra* would show sex differences in these ranging variables that correspond to energetically costly reproductive stages. Ranging data, mainly of females, support the first prediction, while there is only partial support for the second prediction. While there are indeed marked sex differences for most ranging variables when analyzed by season and/or reproductive stage (individual travel patterns and home range areas), in one regard the sexes are alike. Mean daily distances traveled by males fluctuate in tandem with female reproductive stages in a fashion similar to, rather than different from, the pattern shown by females. This result may reflect the investment made by *V. rubra* males in providing care to infants while lactating mothers are away feeding and engaging in other activities (Vasey, 1997a, in press; see also below).

Ranging Patterns, Social Organization, and Reproduction

Data on social structure and ranging behavior presented here also provide insight into the complex social organization of red ruffed lemurs. Below I summarize these data and integrate them with data on food distribution and reproduction, and with observations made on other populations of ruffed lemur (e.g., Morland, 1991a,b; Rigamonti, 1993).

Communities of *V. rubra* at Andranobe are territorial, defending exclusive home ranges from other conspecific communities. Territorial battles occur more often in the resource-rich hot months. Morland (1991a) and Rigamonti (1993) describe similar intercommunity battles in *Varecia* with females as the primary players and males assuming a subsidiary role. Recording dyadic interactions was not a part of the present study, and therefore female-biased home range defense cannot be directly supported for the Andranobe population, though it appeared to be the case. While males scent-marked copiously during these battles, they typically remained on the fringes of the fray; they did not appear to get involved in chases and they often kept silent when other community members were calling.

At Andranobe *V. rubra* has a multilevel fission–fusion social organization that includes subgroups, affiliates, core groups, and a community social network, much like that found in *V. variegata* (Morland, 1991a,b). Ranging variables collected over an annual cycle show that their fission–fusion social organization has (1) a daily component and (2) a higher-level component dictated by both extrinsic seasonal factors and intrinsic reproductive factors. This finding substantiates and augments earlier claims based on social criteria and ranging data of select months (Morland, 1991a,b; Rigamonti, 1993). The daily component of fission fusion involves the formation and disbanding of subgroups and occurs throughout the year. The higher-order component involves the dispersion of core groups into core areas during the food-scarce, cold rainy season and gestation.

Communities of *V. rubra* are composed of core groups each with their own undefended core area. Although core group members affiliate with one another throughout the year, they do not routinely form spatially cohesive groups. Furthermore, the sexes by and large show highly different ranging patterns. The individual ranges of *V. rubra* males overlap little and are stable year round, effectively corresponding to core areas. In turn, forest area used and daily distances traveled by males differ little between seasons, and they form subgroups only with members of their own core group and with community members who enter their core areas. The only departure from this uniform ranging pattern concerns daily distances traveled during female reproductive stages; males resemble females in traveling farther during lactation than gestation. Concomitantly, food resources used by males are farther apart (i.e., spatially patchier) when females are lactating compared to when they are pregnant (Vasey, 1996, 1997a).

In contrast to males, the ranging patterns of *V. rubra* females are complex, shifting in tandem with both seasons and reproductive stages. During the cold rainy season and ensuing gestation months, females use smaller forest areas, travel shorter daily distances, and confine themselves entirely to their respective core areas. This dispersion of core females into their respective core areas adds a higher-level component to their fission–fusion social system, and occurs when their food resources are closer together (Vasey, 1996, 1997a). When females lactate, especially during the food-abundant hot rainy season, they use larger forest areas, travel longer daily distances, and enter other core areas, affiliating with members of other core groups in temporary subgroups that vary daily in membership, size, sex composition, and duration. Correspondingly, food resources used by *V. rubra* females at this time of year are spatially patchier (Vasey, 1996, 1997a).

Pereira et al. (1987) hypothesized that reliance on fruit coevolved with fission–fusion social organization and reproductive traits in *Varecia*. Results presented here validate and greatly expand on this hypothesis. Ranging patterns observed in *V. rubra*, in particular those of females, vary in tandem with reproductive stages and reliance on spatiotemporally patchy resources, not fruit per se (see also Vasey, 2002a,b), producing the daily and higher-level components of fission–fusion social organization.

Further examination of ranging in relation to reproduction is warranted. The limited ranging of *V. rubra* females during many consecutive months of the year (Jun–Oct) appears to be a tactic for conserving (or accumulating) energy not only during the tough winter months when less food is available in the forest, but also as climate improves when females undergo their extremely costly gestations. This low-effort strategy during gestation is in keeping with predictions outlined in the Introduction, but lies in marked contrast to tactics adopted during lactation. Lactation is the most energetically expensive reproductive stage for female primates (e.g., Portman, 1970; Kirkwood and Underwood, 1984; Sauther and Nash, 1987; Dufour and Sauther, 2002). Yet *V. rubra* females adopt a high-effort strategy to meet lactational costs by ranging widely to dispersed resources. To interpret this high-effort strategy, it is necessary to carefully evaluate factors associated with lactation. *Varecia* provides relatively concentrated milk (Tilden and Oftedal, 1997) to litters of infants that grow extremely fast (Pereira et al., 1987). Therefore, energy transfer during lactation must be extremely high, and females may travel farther during the first 4 months of lactation to satisfy high nutritional requirements. However, *Varecia* may save energy during lactation relative to other primates in a variety of ways. First, *Varecia* mothers do not transport their infants full-time. Instead, they routinely stash them in concealed, protected arboreal spots rather than carrying them around (e.g., Morland, 1990; Vasey, in press). Second, *Varecia* mothers benefit from alloparenting (Pereira et al., 1987; Morland, 1990; Vasey, in press), and may even breed cooperatively (Vasey, 1997b, in press), which allows them to leave their infants with other community members while they travel and feed in distant parts of the home range. Third, after the very brief nesting season (1–2 weeks, Morland, 1990; Vasey, in press), ruffed lemur infants are suckled on schedule rather than on demand, which may be less energetically expensive since mothers feed their infants less frequently. A clinging primate infant can and does suckle whenever it wishes (i.e., on demand), but a nonclinging infant feeds only when its mother returns to where she has left it (Martin, 1990). *Varecia*, and other prosimians with absentee parental systems (e.g., *Otolemur, Nycticebus, Cheirogaleus*), may spend less time nursing by providing milk that is more concentrated in energy and nutrients (Tilden and Oftedal, 1997). Fourth, ruffed lemur infants develop quickly, growing independent in terms of nutrition and locomotion more rapidly than other lemurids (Vasey, in press). Lastly, minimizing forest area used and distances traveled during gestation, in addition to modulating activity budgets at this time of year (Vasey, 2005), allows females to accumulate fat reserves, which may buffer energetic deficits experienced during lactation. Wild *V. rubra* do in fact appear fatter during the austral winter and ensuing gestation months. Considered together, reproductive costs of *Varecia* during gestation and lactation are relatively greater than other diurnal primates but they appear to have a variety of behavioral and physiological methods to mitigate them.

Ranging Patterns of *Varecia* in Comparative Perspective

The ranging pattern of *V. rubra* males is similar to that of many nongregarious nocturnal prosimians in that male ranges overlap little (Bearder, 1987). However, unlike many nocturnal prosimians, *V. rubra* males do not appear to defend their core areas against other males, and during many months of the year their home ranges are smaller than those of females. Nor do their ranges overlap those of many females, but rather just those within their own core group. In contrast, ranging patterns of *V. rubra* females depart substantially from nocturnal prosimians in that individual female home ranges are larger than male home ranges and overlap with those of other females and males. Female ruffed lemurs may be philopatric (Morland, 1991a), as are the females of certain nocturnal prosimian species (Nash, 2004). More pertinent here, however, female ruffed lemurs can be highly gregarious, resembling diurnal primates more in this regard. Morland (1991a,b) found that *V. variegata* females were the focus of social activity, giving and receiving the highest rates of affiliative interaction with every age–sex class. They also had more affiliates than males, and interacted socially more often than males in hot months. Both sexes were more solitary in cold months, but males spent more time alone throughout the year and rarely interacted with other males. Although the latter social variables were not quantified in this study of *V. rubra*, nonquantified observations appear concordant with Morland's characterization of *V. variegata*. One noteworthy difference is that of eight core groups in Morland's study, one contained two adult males. Thus, nonoverlapping male ranges may not be a strict rule in ruffed lemurs. Given the alternately dispersed and gregarious forms of sociality and ranging seen in *Varecia*, it is perhaps no coincidence that ruffed lemurs share a suite of reproductive traits with many nocturnal prosimians, in particular, absentee parenting.

Behavioral Variation in Wild Studies of *Varecia*

In previous studies of wild *Varecia*, researchers have described a wide array of community (or group) sizes, social structures, social organizations, and home range sizes, as well as differences in territorial behavior (Table 5; see also Vasey, 2003). In the present study, yet a new combination of features was found. Minimum community size ranged between 18 and 31 individuals, animals had a multifemale/multimale social structure, a fission–fusion social organization, and an exclusive, communally defended home range of 57.7 ha. This home range area falls between estimates from other sites (Table 5). Yet the Andranobe community is larger than any ruffed lemur community known to date, resulting in the highest known population density of *Varecia* (31.2–53.4 individuals/km^2, Vasey, 1997c, 2003).

Previous studies have varied in length, continuity, and in seasons and reproductive stages sampled (Table 5). Some, though not all, of the behavioral variation found among different populations of *Varecia* is likely due to short-term observations and to a lack of sampling during the hot rainy season, when it is possible to clearly distinguish small groups (i.e., of two to four individuals) clearly as part of a larger community network. If not observed in the hot rainy season, small groups could be misidentified as monogamous, pair-bonded family groups rather than as part of a single, larger community with a multimale/multifemale social structure.

In northeastern Madagascar alone, three long-term field studies of *Varecia* (including this one) show remarkable variation in community size, home range size, and territorial behavior (Table 5, Morland, 1991a,b; Rigamonti, 1993; Vasey, this study). Yet despite this variation, all three populations have similar seasonal ranging patterns, and concomitantly, a fission–fusion social organization. For example, in all three studies, *Varecia* communities were formed of core groups with discrete core areas, animals spent more time in their respective core areas in cold months, and individuals traveled shorter daily distances in cold versus hot months. The latter is also evident in a population of *V. variegata* in southeastern Madagascar (Britt, 1997).

Flexible behavior may provide a means of maintaining ecological similarity. In every population studied to date, *Varecia* is highly frugivorous, uses the highest forest strata and the largest feeding trees, is active primarily by day, and is limited to eastern rainforests (Vasey, 2000a, 2003). This ecological inflexibility has undoubtedly contributed to *Varecia*'s vulnerability when it is faced with habitat alteration and loss. Compared with other extant lemur species, *Varecia* has fewer dispersal and habitat options. Factors that elicit behavioral flexibility in *Varecia*

Table 5. Behavioral variation in wild *Varecia*

Site and study[a]	Species	Group structure: community size	Group structure[b]: age/sex composition	Social organization: intragroup spacing	Home range	Territorial
Andranobe (Vasey, this study)	*V. rubra*	18–31	multifemale/multimale	fission–fusion	57.7 ha	yes
Ambatonakolahy (Rigamonti, 1993)	*V. rubra*	5–6	multifemale/multimale	fission–fusion	23.3–25.8 ha	possibly
Manombo[c] (Ratsimbazafy, 2002)	*V. variegata*	2–3	multifemale/multimale	dispersed (semisolitary)	30–70 ha	no
Ranomafana (Balko, 1998)	*V. variegata*	4–9	multifemale/multimale	cohesive	100–150 ha	yes
Betampona (Britt, 1997)	*V. variegata*	2–5	monogamous	dispersed	43.1	
Nosy Mangabe (Morland, 1991a,b)	*V. variegata*	8–16	multifemale/multimale	fission–fusion	30 ha[d]	no
Ranomafana (White, 1991)	*V. variegata*	2	monogamous	cohesive	197 ha	yes
Various sites (Petter, 1962)	*V. variegata* *V. rubra*	2–4	family groups	cohesive		yes

[a] Vasey (this study), Balko (1998), and Ratsimbazafy (2002) sampled contiguous months over entire annual cycles. Morland (1991a,b) sampled 10 months over an 18-month period, excluding the hot rainy/lactation months of Feb and Mar. Rigamonti (1993) sampled seven contiguous months (May–Nov), excluding most hot months of the year. Britt (1997) sampled seven contiguous months (Jan–Jul), including both some hot and cold months. White (1991) sampled only two contiguous cold rainy months (Jun–Jul). Petter's (1962) characterization of sociality in *Varecia* was based on brief surveys at the sites of Perinet, Fanovana, Ambodiriana in the months of Jul and Oct.

[b] Only one aspect of social structure is treated and summarized here: group structure (size and age–sex composition). Another aspect of social structure, namely, population structure (e.g., density), is treated and reviewed for the genus *Varecia* in Vasey (1997c, 2003).

[c] Ratsimbazafy's (2002) study focused on the effects of cyclone disturbance on *V. variegata* ecology in a lowland rainforest fragment. Precyclone group sizes at this site were larger (4–8 individuals).

[d] Broad surveys on Nosy Mangabe provide home range estimates of 30 ha per community, whereas measurements around the perimeter of Morland's study community provide the much smaller estimate of 8.5 ha.

may include differences in population density, resource distribution, the presence of other diurnal, frugivorous lemurs, and perhaps hunting pressure. In a particular region, several of these factors could make defense of a territory, and the resources in it, unprofitable or excessively costly (Krebs and Davies, 1993). Plant resources used by *V. rubra* at Andranobe may prove exceptionally dense and species-rich relative to other rainforests in Madagascar (Vasey, 2000b) and largely explain how such a large community and dense population can be supported within a 57.7-ha home range.

In summary, the ranging pattern of *V. rubra*, especially that of females, shifts during the year consistent with the hypothesis that they would conserve energy during the food-scarce cold rainy season and during energetically costly reproductive stages by minimizing forest area used and distances traveled. Sex differences in ranging correspond to differing reproductive investment by females and males. However, both sexes travel longer daily distances during female lactation than during gestation. This may reflect the ruffed lemur's absentee parenting system and high male parental investment. The ranging pattern and, in turn, the fission–fusion social organization of *V. rubra* appear, therefore, to be the outcome of its reproductive biology combined with its reliance on a spatiotemporally patchy diet. This fission–fusion social system has two components, a daily component and a higher-level component dictated both by seasonality and by reproduction. Where comparisons with other studies of wild *Varecia* are possible, similar seasonal ranging patterns are observed despite variation in community size, home range area, and territoriality.

These summary points suggest a future path of inquiry—one that would more tightly link the least variable (or invariable) ecological traits of ruffed lemurs (such as seasonal ranging patterns, fission–fusion social organization, and reliance on ephemeral rainforest foods) with their suite of reproductive traits, in particular their unusual parenting system. Such an effort will ultimately inform our broader understanding of the evolution and maintenance of traits that are relatively unique to Malagasy lemurs and which ruffed lemurs possess, such as female dominance, the lack of sexual dimorphism, and highly seasonal breeding.

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CHAPTER FOURTEEN

Ecologically Enigmatic Lemurs: The Sifakas of the Eastern Forests (*Propithecus candidus*, *P. diadema*, *P. edwardsi*, *P. perrieri*, and *P. tattersalli*)

Mitchell T. Irwin

INTRODUCTION

The sifakas of Madagascar's eastern forests are some of the most visually distinctive members of eastern lemur communities, by virtue of their unique and often brightly colored pelage combined with their large body size, upright posture, and long, powerful legs. Many serious authors have interrupted their scientific writing to comment on their striking physical beauty; for example: "They are certainly the most beautiful lemurs of Madagascar" (Petter et al., 1977: 344). However, these sifakas' ecology is equally distinctive and enigmatic relative to other lemur groups, a fact that escaped notice until the last few decades. As noted by many authors

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(e.g., Petter et al., 1977), eastern sifakas (particularly rainforest taxa) are much harder to observe than western sifakas, due to lower population density and denser habitat. As might be expected, the earliest in-depth studies of western sifakas (e.g., Jolly, 1966; Richard, 1978) significantly predated similar studies of eastern sifakas (e.g., Wright, 1987).

While eastern sifakas were last chronologically, they certainly are not least in terms of uniqueness among Malagasy lemurs. In terms of diet, eastern sifakas are relatively catholic: not as dedicated to reproductive parts (flowers/fruits/seeds) as *Eulemur*, nor as dedicated to folivory as *Avahi*, *Lepilemur*, or *Indri*. Their social groups are neither as large as the gregarious *Eulemur* and *Hapalemur*, nor as small as the mostly solitary *Avahi*, *Lepilemur*, and other nocturnals. In fact, several aspects of their ecology and life history do not fit neatly into established categories. They have gradually become much better studied, yet the functional significance of, and interrelationships between, these basic elements of their ecology remain poorly understood.

TAXA AND DISTRIBUTION

Originally, two species of sifaka were recognized in Madagascar: *P. verreauxi* occupying the dry southern and western forests, and *P. diadema* occupying the eastern rainforests (Tattersall, 1982). Simons (1988) described a third species, *P. tattersalli* from Daraina in the far north, which appears to be most closely related to *P. verreauxi* (possibly the sister taxon of the subspecies *P. v. coquereli*; Pastorini et al., 2001; Rumpler et al., 2004).

Within *P. diadema*, four subspecies have been traditionally recognized: *perrieri*, *candidus*, *diadema*, and *edwardsi*. These four "types" of diademed sifaka are allopatric, distributed along a north–south gradient, and easily distinguished by virtue of their distinct and colorful pelages. *P. d. perrieri*, the northernmost taxon, has the smallest distribution, being restricted to the Analamera Special Reserve and small forest fragments to the west. *P. d. candidus* has a slightly larger range, from the Marojejy massif in the north to the Antainambalana river in the south. *P. d. diadema* extends from the Antainambalana river in the north to the Onive river in the south; populations in the southwestern part of this range (between the Mangoro and Onive rivers) are morphologically different, and may be taxonomically distinct from *P. d. diadema* (CBSG, 2002; Glander and Irwin, unpublished data). Finally, *P. d. edwardsi* is found from the Onive river in the north to the Manampatrana river in the south.

A fifth "type," *P. d. holomelas*, had been recognized historically based on collection information, but has been subsumed (Tattersall, 1986) into *P. d. edwardsi*, as these two forms appear to have been sympatric. However, the extirpation of populations from areas thought to be inhabited by this variant means that we might well have lost a fifth taxon in historic times.

The taxonomic level at which these "types" of *Propithecus diadema* should be recognized has been subject to debate; all are allopatric in the wild, and therefore reproductive isolation cannot be demonstrated. Karyotypic differences exist (Rumper et al., 2004; Mayor et al., 2004) with *P. d. edwardsi* having a karyotype of $2n = 44$ and all other types having $2n = 42$. Mayor et al. (2004) propose that sequence differences in mitochondrial DNA warrant the elevation of these types to species, following the phylogenetic species concept. Following these authors, I will treat these four taxa as full species, within the "diadema group," which is still considered to be monophyletic on both morphological and molecular grounds.

All told, the distribution of eastern sifakas is extremely broad (Figure 1, Table 1), spanning from 12.75 to 22.75 degrees south, with an altitudinal range between sea level and 1650 m. Most remaining eastern forest is occupied by sifakas, except the extreme southeast (south of the Manampatrana river), the Masoala peninsula in the northeast, and the transitional "Sambirano" forest in the northwest (Mittermeier et al., 1994; Irwin et al., 2005). This broad range harbors marked climatic variation. Average temperature decreases from north to south, while seasonal variation increases; superimposed upon this is a decrease in temperature with increasing elevation (Donque, 1972). Rainfall is high throughout most of the east, owing to the steep ascent of the trade winds striking the eastern escarpment, and annual rainfall is typically 1500–4000 mm/year. However, the northern tip of the island, near Antsiranana and Vohémar (including the range of *P. perrieri* and *P. tattersalli*), has no escarpment; rainfall is much lower (1000–1500 mm/year) and this region's forests are consequently much drier.

Sifaka species have presumably evolved ecological and behavioral adaptations to these varying environments, but these have thus far been underexplored and are a promising direction of future research. For now, it is interesting to note this group's wide range in body mass, which correlates with climatic variables (Lehman et al., 2005); this is suggestive of ecological differences.

FEEDING ECOLOGY

Plant Parts

Although sifakas have morphological specializations for folivory (e.g., long gastrointestinal tract, enlarged cecum) and long gastrointestinal transit time (Campbell et al., 2000, 2004), both western and eastern sifakas actually have a quite varied diet (only in the dry season does foliage truly dominate the diet). The diet of eastern sifakas includes high proportions of foliage, fruits, seeds, and buds/flowers (Table 2). *P. edwardsi* has the most equitable diet, with relatively equal amounts of foliage, fruits, and seeds. *P. diadema* at Mantadia and Tsinjoarivo are more folivorous, with 45–55% of feeding time devoted to leaves.

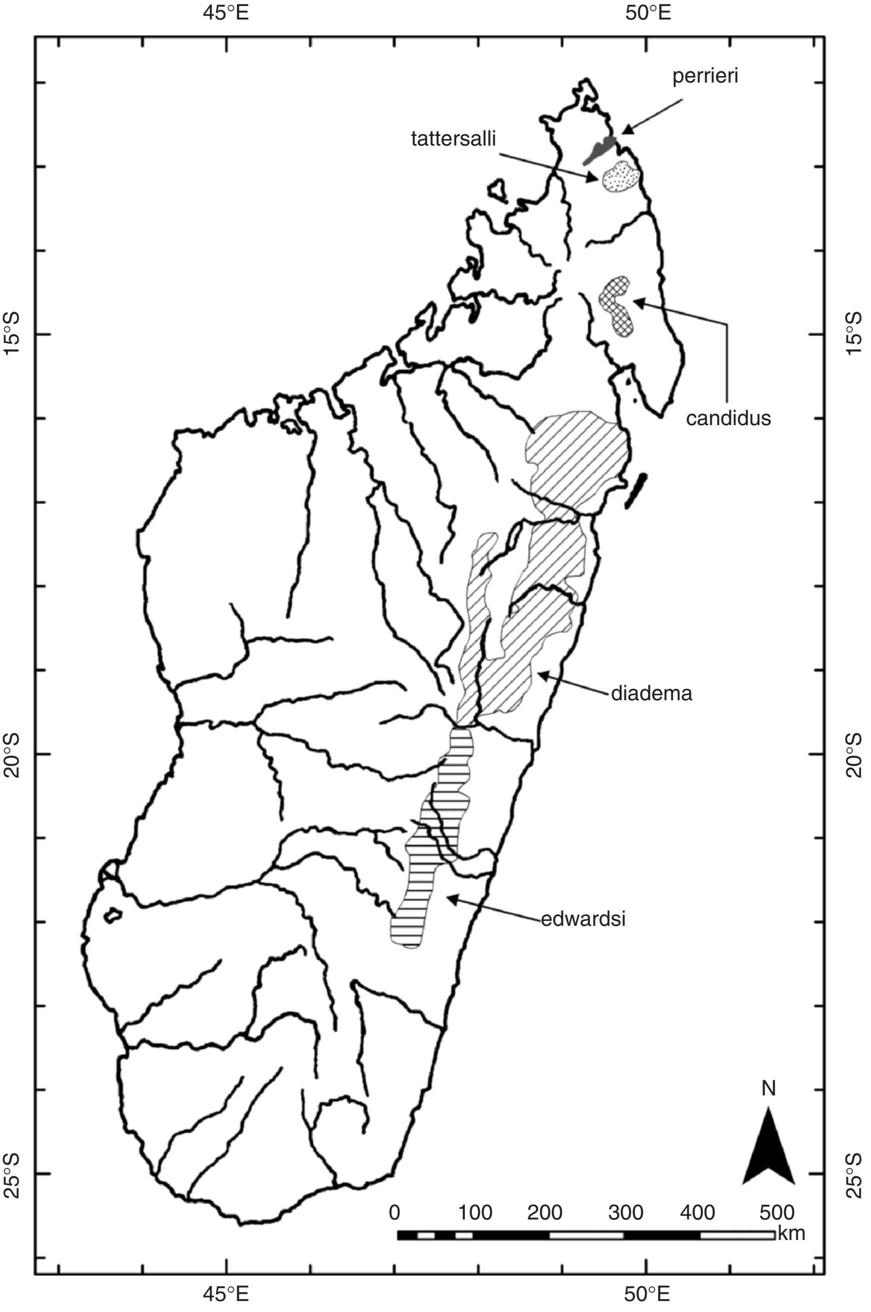

Figure 1. Distribution of eastern sifakas within Madagascar.

Table 1. Sifaka taxa found in Madagascar's eastern forests (from north to south)

Taxon	Geographic range	Altitudinal range (m)	Estimated population size[a]	Protected areas[b]	IUCN Red List status[c]	References[d]
P. perrieri	Analamera Special Reserve and isolated fragments to the west[e]	~56–249[f]	~915	Analamera SR (*P. diadema*)	CR	1,2
P. tattersalli	Daraina, from Loky R. (N) to Manambato R. (S)	0–700	6100–10,000	None	CR	1,3
P. candidus	From Marojejy massif (N) to Antainambalana R. (S)	700–1875	100–1000	Marojejy NP, Anjanaharibe Sud SR	CR	1,4
P. diadema	From Antainambalana R. (N) to Onive R. (S)	300–1650	1000–10,000	Mantadia NP, Mananara Nord NP, Zahamena NP/RNI, Betampona RNI, Ambatovaky SR	CR	1,4,5
P. edwardsi	From Onive R. (N) to Manampatrana R. (S)	625–1600	20,000	Ranomafana NP, Andringitra NP	EN	1,4,6

[a] These figures are from disparate sources and may not be internally consistent. For example, Irwin et al., (2005) found a higher population size for *P. edwardsi* than the earlier estimate of Mittermeier et al., (1994); hopefully further studies will increase the estimated population size of *P. candidus* and *P. diadema*.

[b] Abbreviations: NP, National Park; RNI, Integral Nature Reserve; SR, Special Reserve.

[c] Following IUCN Red List of Threatened Species. www.redlist.org, accessed 9 September 2005.

[d] References: 1, Mittermeier et al., (1994); 2, Banks et al., (in press); 3, Vargas et al., (2002); 4, Goodman and Ganzhorn (2004); 5, Irwin (unpublished); data); 6. Irwin et al., (2005).

[e] *P. perrieri* was previously found at Ankarana Special Reserve, west of Analamera (Hawkins et al., 1990); more recent surveys (Banks et al., in press) failed to locate sifakas at Ankarana, suggesting they have been extirpated.

[f] No study has expressly measured this taxon's altitudinal range; Banks (personal communication) recorded *P. perrieri* census sightings between 56 and 249 m, but as Analamera Special Reserve has an altitudinal range of ~0–750 m, the true range for this taxon could be higher.

Table 2. Relative contributions of different plant parts (measured as percentage of overall feeding time) to the diet of eastern sifakas. Because of strong seasonal variation in diet, only long-term (≥ 1 year) studies are included

	Food type					
Taxon / population	Fruits	Seeds	Flower buds + flowers	Foliage	Other / Unknown	(Soil)[a]
P. diadema, Tsinjoarivo (Irwin, 2006), 4 groups	23.9	7.3	15.1	53.1	0.6	(0.35)
P. diadema, Mantadia (Powzyk, 1997), 2 groups	6.2	30.9	15.0	44.4	3.5	(0.33)
P. edwardsi, Ranomafana (Hemingway, 1995), 2 groups	30.4	35.4	5.3	28.2	0.6	(0.38)[b]
P. tattersalli, Daraina (Meyers, 1993), 3 groups	46.2	0	13.3	38.7	1.7	?

[a] A subset of time devoted to "Other / Unknown."

[b] Value for one group only; second group consumed soil "only rarely."

Among primate groups on other continents, eastern forest sifakas' diet is most similar to the asian colobines (e.g., Davies, 1991; Meyers, 1993; Koenig and Borries, 2001). These colobines also have morphological adaptations for folivory (in this case, foregut fermentation), a diverse diet, and seasonal variation quite similar to that of eastern sifakas.

While all *Propithecus* consume large amounts of foliage, it has been suggested that *P. verreauxi* in western and southern forests tends to be a *frugivore*-folivore, while eastern *Propithecus* tends to be a *granivore*-folivore (Richard, 2003). However, recent evidence does not completely bear out this generalization. While eastern sifakas at some sites (Ranomafana: Hemingway, 1995; Mantadia: Powzyk, 1997) fit this pattern, *P. diadema* at Tsinjoarivo more closely fit the frugivore-folivore model; they often consume fruit pulp and discard seeds (Irwin, 2006). The reason for this discrepancy is unclear, but it is possible that floristic changes related to Tsinjoarivo's high altitude create a fruit guild more like that of drier forests.

The sifakas' relatively catholic diet is in stark contrast to most other lemur groups, which tend to specialize on specific plant parts. Most *Eulemur* taxa in eastern rainforests concentrate heavily on reproductive parts (flowers and fruits), and consume very little foliage (Overdorff, 1993). Most other groups (*Avahi laniger*, *Indri indri*, and *Lepilemur* spp.) are more dedicated to folivory (Ganzhorn et al., 1985; Ganzhorn, 1988; Harcourt, 1991; Powzyk, 1997). In the southern part of their range, rainforest sifakas are the most folivorous of their diurnal lemur communities; in the north they are sympatric with *Indri*, a similar-sized indriid more fully devoted to folivory (Powzyk and Mowry, 2003). In all regions, they are considerably less folivorous than the sympatric nocturnal genera *Avahi* and *Lepilemur*.

There are conflicting reports concerning which plant parts are preferred. *P. tattersalli* at Daraina, *P. edwardsi* at Ranomafana, and *P. diadema* at Mantadia track immature leaf availability (consumption of this resource is positively correlated with its availability; Meyers and Wright, 1993; Powzyk, 1997). In contrast, Irwin (2006) found highly significant positive correlations between fruit availability and consumption in *P. diadema* at Tsinjoarivo, suggesting that fruit is the preferred resource. Finally, newer data from Ranomafana (Wright et al., 2005) also suggest that *P. edwardsi* at Ranomafana track fruit availability. Further research is necessary, particularly to control for such confounding factors as chemical variation among plant species and the preferred maturity level (i.e., ripeness) of selected foods.

Finally, eastern sifakas differ from other sympatric lemurs in their treatment of fruits and seeds (Overdorff and Strait, 1998). *Eulemur* species mainly derive nutrients from pulp, either dropping whole seeds at the feeding tree or ingesting and defecating them whole. Sifakas, in contrast, either consume pulp and drop seeds (Irwin, 2006) or, more commonly, masticate the seeds they consume (some smaller seeds [e.g., *Ficus* sp.] may be consumed whole). *Eulemur* feces often contain multiple whole seeds, while sifaka feces are usually homogeneous with no discernible plant parts. As a result, unlike *Eulemur* species (Overdorff, 1993; Dew and Wright, 1998), sifakas provide limited or no seed dispersal.

Seasonality

All populations for which long-term data are available show extreme seasonal variation in diet composition (Meyers, 1993; Hemingway, 1995; Powzyk, 1997; Irwin, 2006). Generally, sifakas consume high levels of fruit and/or seeds in the rainy season (December–April) when these are most abundant; during this time fruits and seeds can account for 70–90% of feeding time. Diet in the remaining months is more variable but fruit and seeds generally constitute less than 10% of feeding time. *P. edwardsi* at Ranomafana consume more leaves at this time, but still maintain a modest intake of fruit and seeds (including seeds from fallen, rotting fruit; Hemingway, 1995). *P. diadema* at Mantadia consume high levels of leaves, as well as flowers and fern fronds, during this time (Powzyk, 1997).

P. diadema at Tsinjoarivo follow a different strategy (Irwin, 2006). They consume high levels of young leaves at the beginning (May–June) and end (October–November) of the dry season, but rely on flowers during the height of the dry season (July–September), spending up to 50% of feeding time on this resource. Their diet at this time is heavily monotonous, with the buds, flowers, and leaves of a hemiparasitic mistletoe (*Bakerella clavata*) accounting for 45–70% of feeding time. This is an extreme and unusual level of devotion to a single species.

Taxonomic Composition of Diet

The taxonomic composition of diet appears to be relatively flexible, varying widely between study sites (Table 3). Myrtaceae is the dominant plant family for *P. edwardsi* at Ranomafana and *P. diadema* at Mantadia but Loranthaceae

Table 3. Preferred food resources for eastern sifakas, ranked by feeding time

(a) “diadema” group

Study site	Ranomafana	Mantadia	Tsinjoarivo	Tsinjoarivo fragments
Taxon	*P. edwardsi*	*P. diadema*	*P. diadema*	*P. diadema*
Top plant families	Myrtaceae	Myrtaceae	Loranthaceae	Loranthaceae
	Sapindaceae	Euphorbiaceae	Lauraceae	Rutaceae
	Sapotaceae	Clusiaceae	Clusiaceae	Araliaceae
	Erythroxylaceae	Loranthaceae	Pittosporaceae	Euphorbiaceae
	Moraceae	Sapotaceae	Apocynaceae	Myrsinaceae
Top plant species	*Chrysophyllum boivinianum* (Sapotaceae)	*Tannodia perrieri* (Euphorbiaceae)	*Bakerella clavata* (Loranthaceae)	*Bakerella clavata* (Loranthaceae)
	Plagioscyphus louvelli (Sapindaceae)	*Protorhus ditimena* (Anacardiaceae)	*Ocotea* sp. 1 (Lauraceae)	*Melicope* sp. (Rutaceae)
	Erythroxylum sphaeranthum (Erythroxylaceae)	*Chrysophyllum boivinianum* (Sapotaceae)	*Garcinia* sp. (Clusiaceae)	*Schefflera* sp. (Araliaceae)
	Treculia africana (Moraceae)	*Syzygium* sp. 1 (Myrtaceae)	*Pittosporum verticillatum* (Pittosporaceae)	*Macaranga* cf. *ankafinensis* (Euphorbiaceae)
	Eugenia (*Syzygium*) sp. 23 (Myrtaceae)	*Syzygium* sp. 2 (Myrtaceae)	*Salacia madagascariensis* (Celastraceae)	*Embelia concinna* (Myrsinaceae)

Sources: Hemingway (1995), Powzyk (1997), Irwin (2006).

Table 3. Preferred food resources for eastern sifakas, ranked by feeding time—Cont'd.

(b) *P. tattersalli* at three sites in the Daraina region

Study site	Daraina Z (wettest)	Daraina A (intermediate)	Daraina M (driest)
Taxon	*P. tattersalli*	*P. tattersalli*	*P. tattersalli*
Top plant families	Fabaceae	Fabaceae	Fabaceae
	Sapindaceae	Anacardiaceae	Ebenaceae
	Anacardiaceae	Olacaceae	Combretaceae
	Myrtaceae	Araliaceae	Sapindaceae
	Annonaceae	Malvaceae	Anacardiaceae
Top plant species	*Filicium longifolium* (Sapindaceae)	*Baudouinia fluggeiformis* (Fabaceae)	*Pongamiopsis cloiselli* (Fabaceae)
	Cynometra sp. (Fabaceae)	*Albizia boivini* (Fabaceae)	*Diospyros lokohensis* (Ebenaceae)
	Eugenia sp. (Myrtaceae)	*Pongamiopsis* sp. (Fabaceae)	*Terminalia* sp. 1 (Combretaceae)
	Cordyla madagascariensis (Fabaceae)	*Olax lanceolata* (Olacaceae)	*Erythrophysa belini* (Sapindaceae)
	Xylopia flexuosa (Annonaceae)	*Cynometra* sp. (Fabaceae)	*Tamarindus indica* (Fabaceae)

Source: Meyers, 1993

dominates for *P. diadema* at Tsinjoarivo. In the drier forests at Daraina, leguminous trees (Fabaceae) dominate the diet of *P. tattersalli*. Even over small spatial scales, diet composition can vary widely, such as between pristine forest and fragments at Tsinjoarivo (Table 3a) and among drier and wetter sites at Daraina (Table 3b).

SPATIAL ECOLOGY

Home Range

Rainforest sifakas occupy home ranges of 30 to 80 ha. At Mantadia, two *P. diadema* groups used home ranges of 33 and 42 ha (Powzyk, 1997), while *P. edwardsi* at Talatakely have similar-sized home ranges (~ 38 ha; Wright, 1995; Powzyk, 1997), as do *P. candidus* at Marojejy (44 ha; E. Patel, personal communication). *P. diadema* groups in continuous forest at Tsinjoarivo occupy between 70 and 80 ha but groups in fragments occupy 20–37 ha (Irwin, 2006).

In contrast, sifakas in the drier forests of the north have smaller home ranges, similar to those of western sifakas (Jolly, 1966; Richard et al., 1991). Meyers (1993) reports home ranges for *P. tattersalli* at Daraina between 4.4 and 12.3 ha, and *P. perrieri* home ranges at Analamera during the short study of Lehman and Mayor (2004) were even smaller: 1 to 1.1 ha. It thus appears that local ecology determines home range size more than phylogeny: three “diadema group” sifakas in humid forests have large ranges, while two taxa in drier forests (one “diadema group,” one *P. tattersalli*) have small ranges. Why drier forests sustain higher sifaka densities is not entirely clear, but it has been suggested that food quality is a key issue (e.g., Powzyk, 1997). Drier forests in western and northern Madagascar have higher leaf “quality” (measured as the ratio of extractable protein to acid detergent fiber; Ganzhorn, 1992). This difference (surprisingly) may outweigh the cost of food shortages during the protracted dry season.

Day Range

P. diadema at Mantadia have long daily path lengths (1629 m/day; Powzyk, 1997) while those of *P. edwardsi* at Ranomafana are shorter (670 m/day; Wright, 1987). *P. diadema* in continuous forest at Tsinjoarivo (Irwin, 2006) show intermediate values (987 m/day), as do *P. tattersalli* (461.7–1077 m/day; Meyers, 1993) and *P. candidus* (710 m/day; E. Patel, personal communication). These values are similar to those reported for western sifakas (Jolly, 1966; Richard, 1978) which is surprising given the marked difference in home range.

Daily path length is longest during the rainy season (approximately December to March) and shortest during the dry season (July–October) (Meyers, 1993;

Powzyk, 1997; Irwin, 2006). This suggests that it requires more ranging effort to procure an adequate supply of the fruits which are preferred in the rainy season. In contrast, the leaves and flowers used as a fallback in the dry season may be more uniformly available, or sifakas may be less selective about which plant species are used. Further research is necessary to adequately explain this pattern.

SOCIAL ORGANIZATION AND BEHAVIOR

Group Composition

Early field studies noted the variability in sifaka group composition (e.g., Petter et al., 1977). However, they suggested that ". . . the ancestral group structure of *Propithecus* is monogamous, and that a normal group was composed of a pair of adults and two to three offspring of different ages" (p. 379), proposing that the larger observed group sizes may be due to habitat disturbance (possibly representing aggregations of multiple family groups). However, field studies have confirmed for eastern sifakas (as did Jolly, 1966, and Richard, 1978, for western sifakas) that monogamous groups are not the rule.

P. edwardsi at Talatakely (Ranomafana) live in groups of three to nine individuals, with a mean of 4.6[1] (Wright, 1995; Pochron et al., 2004), while those at the Vatoharanana trail system live in groups of 2–8, with a mean of 4.3 (Hemingway, 1995). Groups of 3–6 individuals (mean = 4.8) were observed for *P. diadema* at Mantadia (Powzyk, 1997), while *P. diadema* at Tsinjoarivo have been observed in groups of 4–7 (mean = 4.9; Irwin, 2006, unpublished data). *P. tattersalli* have slightly larger group sizes (3–10; Meyers, 1993), similar to those of western sifakas (Richard, 1978). Such intermediate group sizes open the door for several group types. Assuming that stable groups have at least one breeding male and female, four distinct types are possible: polygynous, polyandrous, polygynandrous, and monogamous pairs. Such variability is less likely in larger groups (usually polygynandrous) or smaller groups (usually monogamous).

Indeed, Pochron and Wright (2003), using data from 46 group-years for *P. edwardsi* at Talatakely (Ranomafana), found an average of 3.2 adults per group and a surprisingly even distribution of the four possible group types. Since the competitive regime would be expected to vary greatly in different group types, these differences may have profound effects on other aspects of social life. However, Pochron and Wright (2003) found no effect of group type on infant birth rate and survival. They argue that feeding competition limits group size, causing small, nonuniform social groups, but mating may occur more freely across group boundaries (as in *P. verreauxi*: Richard, 1985). However, mating season influxes have not yet been observed in eastern sifakas to the same degree known

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[1] Totals include infants and only data from December or January were used whenever possible.

in *P. verreauxi*, and preliminary genetic data provide no evidence for extragroup paternity (Morelli and Wright, in preparation).

The dataset of Pochron and Wright is by far the largest for eastern sifakas, but as it derives from a disturbed (selectively logged) site, one must consider the possibility it does not represent the "natural" state. However, data from *all* other behavioral studies conducted in pristine forests (Meyers, 1993; Hemingway, 1995; Powzyk, 1997; Irwin, 2006) show similar groups sizes and variable composition. It therefore appears that the variable social structure described by Pochron and Wright is typical of eastern sifakas, though further study is necessary to better understand the causes and consequences of this variability.

Dispersal

As with social organization, patterns of natal dispersal do not follow any hard-and-fast rules. In most primates, one of the sexes tends to be philopatric (Pusey and Packer, 1987); only in a few species do both sexes commonly disperse. Based on available evidence, eastern sifakas seem to rank among those rare species having no sex bias in dispersal. In *P. edwardsi*, roughly half of males *and* females disperse, usually at 4–5 years of age (though females may travel greater distances); this dispersal is usually "motivated" by targeted aggression from adults (Wright, 1995; Pochron et al., 2004). Other individuals of both sexes remain, and reproduce, in their natal group.

Pochron et al. (2004) suggest that this opportunism may be due to slow reproduction and high infant mortality. The combination of small groups and slow reproduction means that a given sifaka generally cannot have enough same-sex kin to form the social networks seen in other male- or female-bonded primates. Therefore, animals may be equally willing to stay in their natal group should breeding opportunities become available, or disperse to find breeding opportunities elsewhere. This opportunism may also apply throughout adult life for males; secondary dispersal has been observed among males, but not females (Pochron et al., 2004).

Behavioral studies at other sites have not lasted long enough to provide definitive confirmation of this pattern; the natural rarity of dispersals means that only longer-term studies (i.e., >5 years) can provide a balanced view of dispersal. However, it is worth noting that among *P. diadema* at Tsinjoarivo, the three observed dispersal events have involved two females and one male (Irwin, 2006; Irwin and Raharison, unpublished data).

Intragroup Relations

Sifaka groups tend to have relatively stable dominance relations among individuals (e.g., Meyers, 1993; Hemingway, 1995), but the patterns of dominance vary from group to group. Intersexual relations are difficult to quantify for two reasons: first, aggression rates are extremely low (with a high percentage of undecided encounters), and second, the variable social structure may lead to different social environments and therefore different dominance relationships (Overdorff and Erhart, 2005). Available evidence from various sites is, however, consistent with the definitions of female feeding priority and true female dominance (Pochron et al., 2003), but only under certain circumstances; the situation is still less clear-cut than for some lemurs (e.g., *Lemur catta*). For example, in groups with multiple adult females, the dominant female appears to be consistently dominant over males, but the same is not always true for subordinate females (e.g., Hemingway, 1995).

Patterns of association (as measured by proximity) among males and females are also variable from group to group, and therefore difficult to categorize (Meyers, 1993; Hemingway, 1995). This aspect of group life may also be strongly influenced by the variation in group composition and relatedness of same-sex animals.

Infanticide has been observed in *P. edwardsi* (Wright, 1995; Erhart and Overdorff, 1998), always perpetrated by newly immigrant males. Although infanticide would seem less likely to be adaptive among seasonal breeders, the life history of sifakas (see below) is such that early loss of an infant could increase the chances of conception in the following breeding season.

Intergroup Relations

Despite the maintenance of stable territories (e.g., Wright, 1995), eastern sifakas interact directly with neighboring groups only rarely (e.g., three encounters observed among two groups over more than 1 year at Mantadia: Powzyk, 1997; two encounters among two continuous forest groups over 1 year at Tsinjoarivo: Irwin, 2006). *P. tattersalli* has a higher encounter rate (a few encounters per month; Meyers, 1993), consistent with their smaller home ranges. In general, these low encounter rates may be at least partly due to their low population density. When groups do encounter one another, the interactions are generally agonistic, particularly between same-sexed animals, but they usually involve chasing and vocalizing, without much serious fighting. The primary means of territorial "defense" appears to be scent-marking (Pochron et al., 2005), females using an anogenital gland and males using anogenital and chest glands. Scent-marking is a complex social activity and more research is required to fully understand its causes and consequences, as it likely serves a number of functions (which may differ between males and females; Lewis, 2005). However, indirect evidence for sifakas (e.g., Powzyk, 1997:225; Pochron et al., 2005) indicates that scent marks can serve as "signposts" to conspecifics, marking territorial boundaries.

LIFE HISTORY AND REPRODUCTION

After consistently proving to be unique and enigmatic in all aspects of their ecology discussed thus far, it would seem unfitting if sifakas had an ordinary life history; indeed recent studies have proved that this is not the case. Like all extant lemurs, the reproductive schedule of sifakas is tightly constrained seasonally (most primate species reproduce year-round or show more moderate seasonality; e.g., Koenig et al., 1997). In *P. edwardsi* and *P. diadema* mating occurs in December and January, while birth occurs between May and July, with the majority in June (Wright, 1995; Pochron et al., 2004; Irwin, 2006). *P. tattersalli* breeds slightly later (Meyers, 1993), like western sifakas: mating in January–February, and births in late July.

Average interbirth interval (IBI) at Talatakely, Ranomafana, is 1.56 years (Pochron et al., 2004); in other words, 1 year for roughly half of births and 2 years for most other cases. This is in contrast to many smaller lemurs, which give birth every year. The roughly even split between 1- and 2-year IBIs suggests a possible pressure to speed up infant development (i.e., reduce time to weaning). Sifakas who are metabolically ready to conceive 12 months after a previous conception can do so, but those who become ready at 13 or 14 months must wait until the 24th month postbirth, due to the strict estrous seasonality. This delay might have led to selective pressures to reduce mothers' postbirth metabolic costs, thereby reducing "recovery time."

In terms of infant development, Godfrey et al. (2004) showed that indriids have a slow somatic growth rate relative to other lemurs. This is contrary to the expected pressures of seasonal reproduction, as well as the predictions of the risk aversion hypothesis of Janson and van Schaik (1993). This hypothesis suggests that more folivorous taxa should have rapid development, because the relative lack of food competition lessens the starvation risks associated with rapid growth. However, the slow body growth seen in *Propithecus* and other indriids is paired with an unusually fast rate of dental development (this family is unusual in the extent to which somatic and dental development rates are decoupled). Godfrey et al. (2004) suggest that accelerating the development of adult dentition at the expense of other body tissues may get infants to independence as soon as possible (the high-fiber diet of *Propithecus* requires more dental competence than the softer diet of frugivores). By achieving dental competence earlier than other similar-sized primates, sifakas shorten the dependency period and the mother's overall postbirth metabolic cost, thereby promoting her own survival. It has further been proposed (Wright, 1999) that reproduction is timed to place weaning at the season of peak food availability (March), further reducing the mother's costs at this time. This explanation for sifakas' unusual combination of life history traits fits nicely with what is known about Madagascar's impoverished environments, and with the "Energy Conservation Hypothesis" of Wright (1999).

However, while mothers may succeed at shortening their infants' march to independence, the infants themselves do not fare that well. Roughly half of infants die before 1 year of age at Talatakely, and only about one quarter of females reach reproductive age (Pochron et al., 2004). The only reason this population sustains itself seems to be a long reproductive life span (>20 years; Wright, 1995; Pochron et al., 2004). Adult females seem to follow the "bet-hedger" strategy of Richard et al. (2002), slowing down their reproductive output and reducing investment in individual offspring to aid their own long-term survival. This fits well with what is known about both the paucity *and* the unpredictability of Madagascar's environment; reducing investment makes reproduction possible in average years, and a long life span makes it possible to wait out bad years (Godfrey et al., 2004). However, the unfortunate combination of fast acquisition of adult dentition and a long life span bodes poorly for the state of teeth in elderly individuals. Indeed, observations at Ranomafana indicate that some older animals may suffer from extreme tooth wear, and an impaired ability to feed (King et al., 2005).

PREDATION

Being among the largest of living lemurs, eastern sifakas suffer lower overall predation pressure relative to most lemurs. However, predation by the fossa (*Cryptoprocta ferox*) is ubiquitous, having been recorded for *P. edwardsi* (Wright et al., 1997), *P. diadema* at Mantadia (Powzyk, 1997) and Tsinjoarivo (Irwin and Raharison, in preparation), *P. candidus* (Patel, 2005), *P. perrieri* (Mayor and Lehman, 1999), and *P. tattersalli* (Goodman, 2003). The fossa is the largest Malagasy carnivore, at 6.75 kg (Hawkins, 2003); despite being only slightly larger than adult eastern sifakas, it seems adept at taking both young and adults. No successful predation by birds on eastern sifakas has been recorded (Goodman, 2003), but the presence of antipredator responses indicates that several raptors are considered a threat (Karpanty and Grella, 2001).

RESILIENCE TO HABITAT CHANGE AND FRAGMENTATION

As mentioned earlier, eastern sifakas were studied much later than western sifakas; later still was the development of research programs (in either region) investigating sifakas' responses to habitat fragmentation and alteration. Early studies followed the general trends of primatology, studying groups within habitat which was as pristine as possible. The (valid) reasons for doing so were academic (understand a species' *true* behavior) as well as practical (increase the chances your study groups would last at least as long as your study period). However, the rate of habitat conversion in Madagascar (and elsewhere) has reached crisis proportions: Green and Sussman (1990) estimated that the eastern rainforest cover in 1985 had already diminished to 34% of its original extent, and an extrapolation of the observed disappearance rate predicts a complete loss of this ecosystem ca. 2020. What forest remains is increasingly fragmented and impacted by human activities. The impact of these changes on lemur populations can no longer be ignored.

So what are the prospects for eastern sifakas? Understanding the nature of the threat is the first step. One can conceptualize the threats fragmentation poses to sifaka populations as three sequential challenges. First, direct anthropogenic effects (e.g., hunting) threaten most proximately. Second, fragmentation-related habitat changes may affect the ecological compatibility between sifakas and their habitat—and even if compatibility is maintained, it may be through compromises which affect other aspects of behavior. Finally, on the longest time scale, there is the demographic threat of population subdivision and constrained dispersal.

The immediate anthropogenic effects are hard to estimate and notoriously variable among regions. In many areas, sifakas are protected from hunting by *fady* (taboo); these often apply preferentially to sifakas and indri because of their large size and orthograde posture (resembling humans or human ancestors). However, this protection is by no means universal. *P. edwardsi* is hunted throughout much of its range, especially the northern part (Irwin et al., 2005). Other eastern sifakas seem to be protected in some, but not all, regions. This threat is controllable through human activities (unlike the purely ecological pressures); it is important that education and enforcement of applicable laws (which deem hunting of lemurs illegal) continue to be applied and extended in rural areas where sifakas live.

The second threat, loss of ecological compatibility, is only beginning to be investigated. My dissertation research (Irwin, 2005a,b, 2006) compared the ecology and behavior of two *P. diadema* groups resident in forest fragments and two in continuous forest at Tsinjoarivo. I found that continuous forest groups relied on various tree species to provide fruit during the rainy season, but relied heavily on a small hemiparasitic mistletoe (*Bakerella* cf. *clavata*) during the middle of the dry season (devoting 45–70% of monthly feeding time to this one species). For these groups, mistletoe is a fallback resource. Fragment groups ate fewer fruits, and the loss of preferred fruit trees forced them to consume mistletoe at high levels throughout the year; for them, mistletoe is best described as a *staple*. Arrigo-Nelson (2005) similarly found reduced frugivory and loss of preferred fruit resources in disturbed areas for *P. edwardsi* at Ranomafana, suggesting that this pattern may be consistent across sites.

The fact that groups in fragmented or disturbed habitats can sustain themselves, however, is not in itself reason to discount the threat of habitat change; one must consider the effects of behavioral shifts. One direct line of research involves the nutritional composition of foods; this is currently being studied at Tsinjoarivo. If the altered diet is less nutritious, long-term effects on body condition and reproduction would be apparent. Indeed, reduced body mass of adult sifakas in fragments has already been documented, for *P. edwardsi* at Ranomafana (Dehgan, 2003), and *P. diadema* at Tsinjoarivo (Glander and Irwin, unpublished data). Other effects are also apparent: for example, fragment groups have greatly reduced group cohesion and an increased rate of feeding alone (Irwin, 2005b). The mistletoe on which they rely has an extremely small crown diameter (<2m); animals are forced to spread out because sharing food patches is impractical (and subordinates are unlikely to be tolerated by dominant individuals). These altered resource distributions and decreased group cohesion could lead to altered food competition regimes and changes in social behavior which could affect group structure and reproduction.

The third major threat is the demographic consequence of population subdivision. Even when populations can emerge unscathed from the first two threats, they may be threatened by the longer-term effects of inbreeding and reduced dispersal opportunity. The severity of this threat depends on how reluctant individuals are to cross the nonforested areas between fragments. Most eastern sifakas, in contrast with western congeners, seem extremely reluctant to do so. Dehgan (2003) found that a *P. edwardsi* group in a forest fragment did not leave the forest fragment in which they lived, except to cross distances less than 30 m to smaller satellite patches. Among two *P. diadema* groups in forest fragments at Tsinjoarivo, no crossing between patches was observed during a 1-year study (Irwin, 2006). One adult male did later disperse secondarily across open areas, but only after the rest of his group was decimated by predation. In contrast, Mayor and Lehman (1999) noted that *P. perrieri* regularly crosses open areas, in one instance traversing 600 m. These results suggest that sifakas in drier forest may be predisposed to crossing between fragments, possibly because they have historically lived in more open (possibly mosaic) habitats. Rainforest sifakas, in contrast, may be more suspicious of open areas due to their long evolutionary history in dense forest with little need to come to the ground.

The long time scale of demographic threat means that long-term study is necessary before assessing whether fragmented populations are population sinks, or whether they can be a viable part of the larger population. Given the increasing rarity of pristine forests in Madagascar, the ability to include fragmented populations in effective population sizes would definitely paint a better picture for conservation; only time will tell us for which species this approach is justified.

CONSERVATION SITUATION

Currently, *P. candidus*, *P. diadema*, *P. perrieri*, and *P. tattersalli* are classified as "Critically Endangered" by the IUCN (Table 1), and *P. edwardsi* is classified as "Endangered." Extinction of one or more of these taxa is an imminent possibility, due to their relatively small population sizes, fragmented and discontinuous habitats, and the continuing human threats. The geographic range and population size of *P. edwardsi* and *P. diadema* are still relatively large (though further research is necessary to determine the status of the Tsinjoarivo *P. diadema*); however, *P. candidus*, *P. perrieri*, and *P. tattersalli* all occupy relatively small ranges.

Before comparing the conservation situation of eastern and western sifakas, it is useful to contrast some key aspects of their ecology. On a typical distribution map, the two groups look relatively balanced: four taxa more-or-less evenly spaced along the west and southwest, five more-or-less evenly spaced along the east. However, important differences in ecology may make the eastern sifakas (and particularly the rainforest taxa) much more seriously threatened.

First, eastern rainforest sifakas (*P. edwardsi*, *P. diadema*, and *P. candidus*) as well as *P. perrieri* live at low population densities (2–10 individuals/km^2; Wright, 1995; Irwin et al., 2005; Banks et al., in press). *P. verreauxi* is on the order of 6 to 100 times more densely packed (Richard, 2003) and *P. tattersalli* is intermediate at 17–28 individuals/ km^2 (Vargas et al., 2002). Second, rainforest sifakas appear much less able to live in human-dominated landscapes. It is common, where they are not hunted, to find *P. verreauxi* in small forest patches near villages and water sources. This is likely due to small home range requirements, and tolerance of human-favored tree species (e.g., mango, *Mangifera indica*). The same is not true of rainforest sifakas; *P. diadema* at Tsinjoarivo do not range in human-dominated forest patches (usually dominated by *Eucalyptus* and *Pinus*) but require endemic forest trees and a minimum patch size of around 25 ha (Irwin, unpublished data). Third, the dry forest sifakas' predisposition to cross open areas gives them a demographic resiliency in fragmented habitat which rainforest taxa may not share.

Thus, it is not possible to directly compare eastern and western sifakas based on geographic range, or perhaps even population size. These ecological "disadvantages" of eastern sifakas should be considered when developing conservation priorities and action plans.

SUMMARY

The five eastern sifakas have until recently been poorly studied relative to their western congeners. However, several surveys and long-term studies, starting with Wright's study of *P. edwardsi* in the mid-1980s, have taken great strides to even the playing field. Eastern sifakas share many similarities with western *P. verreauxi*, but differ in their larger body mass, lower population density, and larger home ranges (in rainforest taxa). Many aspects of *Propithecus* ecology, social organization, and behavior remain enigmatic, not fitting well into theory developed for anthropoid primates and even set apart from other lemur taxa. Continuing research is necessary to understand the causes and consequences of these aspects of sifaka life and, perhaps more importantly, to adequately protect their dwindling populations in the face of drastic habitat loss and fragmentation.

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CHAPTER FIFTEEN

Behavioral and Ecological Adaptations in Two Small Folivorous Lemurs with Different Social Organization: Avahi and Lepilemur

Urs Thalmann

INTRODUCTION

Woolly lemurs (genus *Avahi*, family Indridae) and sportive lemurs (genus *Lepilemur*, family Lepilemuridae or Megaladapidae) provide an excellent field model to investigate hypotheses linking behavior and ecology (e.g., Ganzhorn, 1988; Ganzhorn et al., 1985; Thalmann, 1996, 2001, 2002; Warren, 1994). While they are both nocturnal, have comparable body weights and positional behaviors (Vertical Clingers and Leapers), and are both folivorous, they differ in their social organization. In some forests they live sympatrically in the very same

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habitats. As they are phylogenetically distantly related, matching and/or differing eco-ethological pattern may be interpreted as independently derived adaptations related to ecology instead of shared derived characteristics due to common phylogenetic history.

From field studies and anecdotal observations on *Avahi laniger* and *A. occidentalis*, two of the four currently recognized species (Thalmann and Geissmann, 2000, 2005), it can safely be inferred that they are socially and spatially pair-living, in small gregarious family groups (e.g., Albignac, 1981; Harcourt, 1991; Jolly, 1998; Petter et al., 1977; Razanahoera, 1981, 1988; Roth, 1996; Thalmann, 1998, 2001, 2002; Warren, 1994). To what degree this is also matched on the genetic level has not yet been investigated.

In *Lepilemur* the picture is less clear. More thorough field studies focusing on behavior and ecology have mainly been made on three out of eight currently recognized species (Andriaholinirina et al., 2005; Rumpler et al., 2001; Thalmann and Ganzhorn, 2003): the southern *Lepilemur leucopus* (Charles-Dominique and Hladik, 1971; Nash, 1998; Russell, 1977), the western *L. ruficaudatus* (e.g., Ganzhorn, 1993, 2002; Ganzhorn et al., 2004; Hilgartner et al., 2005; Hladik et al., 1980; Pietsch, 1998; Platner et al., 2005; Zinner et al., 2003), and the northwestern *L. edwardsi* (Albignac and Razanahoera, 1982; Ganzhorn, 1993; Rasoloharijaona, 2001; Rasoloharijaona et al., 2000, 2003; Razanahoera, 1981, 1988; Thalmann, 1996, 1998, 2001, Thalmann and Ganzhorn, 2003; Warren, 1994).

Whereas Charles-Dominique and Hladik (1971) inferred a dispersed harem system for *L. leucopus*, Russell (1977) doubted this conclusion. For *L. ruficaudatus*, dispersed pair-living has been inferred as a modal social organization (Ganzhorn and Kappeler, 1996; Pietsch, 1998; Zinner et al., 2003). For *L. edwardsi*, again, dispersed pair-living has been concluded by Thalmann (1998, 2002) and confirmed by Rasoloharijaona et al. (2003) while Warren and Crompton (1997) suggested a kind of "noyau" system—corresponding to a dispersed harem system in the terminology of Müller and Thalmann (2000). In any event, there seems to be more inter- and intraspecific variation in the social organization of sportive lemurs than in woolly lemurs.

In the following I report results of a comparative field study on *A. occidentalis* and *L. edwardsi* over several years to (1) provide basic descriptive data on aspects of their ecology and behavior, (2) explore possible links between behavior, ecology, and seasonality in the two species, and (3) test the hypothesis that *A. occidentalis*'s behavior matches seasonality less than does *L. edwardsi*'s behavior, and are differently adapted. This hypothesis is derived from observations that *L. edwardsi*'s choice of feeding plants matches the forest composition significantly closer than does *A. occidentalis* and, hence, should react on plant food shortage during the lean dry season differently than *A. occidentalis* (Thalmann, 2001, 2002).

MATERIAL AND METHODS

Information on material and methods, study site, precipitation, subject capture, observations, feeding plants, and characterization of forest have been given in Thalmann (2001). Here, it is shortly summarized and complemented with unpublished information on climate and data on forest phenology.

I conducted the study between September 1994 and August 1997 at the Forestry Station of Ampijoroa (northwestern Madagascar; 16°19'S, 46°49'E; 80–330m above sea level) in deciduous seasonally dry western forest. The climate was documented by measuring precipitation and minimum and maximum temperature. Over the whole study period, seven different sportive lemurs were captured (three females, four males), and five different woolly lemurs (two females, three males) with a blowpipe, using 1-ml cold-air pressured narcotic syringe projectiles from Telinject® (Germany) loaded with Ketalar® or Narketan®. Observations using telemetry equipment from Holohil Systems (Canada, transmitters) and Telonics Inc. (Arizona, receivers) focused on one male and one female sportive lemur, and one male woolly lemur. Male and female *Avahi* virtually always move in close spatial proximity through the forest, and feed simultaneously in the same trees and lianas, whereas *Lepilemur* males and females mostly forage independently. For direct observations and follows I established a grid (Figure 1) with small perpendicular trails every 10 m. During regular observations I used instantaneous time sampling and recorded every 2 minutes the quadrat, the location within the quadrat (xy-coordinates and height), and the activity (rest, move, feed [food item and location], groom [self-groom, partner groom]), along with miscellaneous observations (e.g., occurrence of complex vocalizations in *Lepilemur*). Regular observations usually lasted from 18:00 to 24:00 and from 24:00 to the time the animal reached their sleeping site in the morning, and were combined to cover an entire nightly activity period. I observed the focal animals for a total of 590 hours. For reasons of statistical simplicity and to balance sample sizes to some degree I used for most analyses a reduced sample, i.e., one activity period per month per animal totalling 432 hours (144 hours for the focal male *Avahi* individual A1m; 288 hours for the two focal *Lepilemur* individuals, 144 hours each, male L1m and female L2f). Sleeping sites were determined every day as far as possible. For nonfocal animals the sleeping sites were also located on a daily basis whenever possible, and occasional follows or sequential locations of the different individuals were conducted opportunistically during the nightly activity period.

I marked feeding plants during regular observations, collected data (diameter at breast height [DBH], estimate of tree crown volume [TCV]), and identified and permanently tagged the plants during daylight. The forest was characterized by means of a plot method (Figure 1). I randomly chose 40 plots of 25 m^2 each, determined DBH, and identified trees with the help of a reputed local guide.

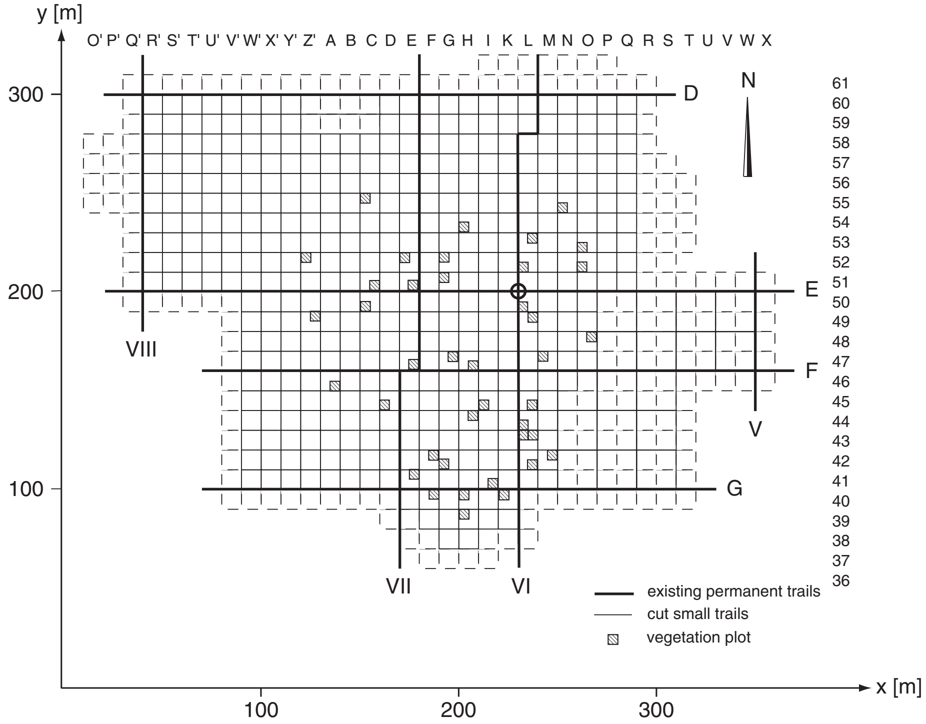

Figure 1. Observation grid. It combined existing permanent trails and small trails established for this study with location of randomly chosen forest plots of 5 m × 5 m used for characterisation of forest. Larger permanent trails (south–north) are indicated with a Roman numeral, east–west with a letter. Small trails divided the forest into quadrats of 10 m × 10 m, each quadrat unambiguously addressed by an Arabic number (south–north) and a letter (west–east), as on a chessboard. For subsequent analyses, locations were transformed into an xy-coordinate system.

Extensive cross checking was necessary, however, to reach consistency of plant identifications within the study. I derived a major axis relationship between DBH and estimated TCV to allow for inclusion of tree crown volume estimates into analyses (for details see Thalmann, 2001).

Phenology data were collected on randomly chosen plot trees ($n = 56$, 50 different species) and all subsequently recorded feeding trees of study animals (*Avahi*: $n = 178$, 33 different species; *Lepilemur*: $n = 137$, 39 different species) from the time they were first used to the end of the study. With a present/absent scheme I recorded the phenology approximately every 10 days (1–10th, 11–20th, 21–30 or 31st day of the month), spaced as evenly as possible: conspicuous buds (B), sprouting buds (sB), sprouting leaves (sL), young leaves (yL), mature leaves (mL), old and deciduous leaves (odL), flowers (Flo), fruits (Fr), relative reduction of foliage (icF), and absence of leaves from a tree (noL). Obviously, categories are not mutually exclusive because a given tree can have at the same time sprouting buds, leaves, and young leaves or other phenological combinations. The overall phenology of the forest (Figure 2, Appendix A-I) was finally inferred based on 64 different tree species in the forest representing 92% of tree stems, and 91% of TCV as calculated from the 40 plots.

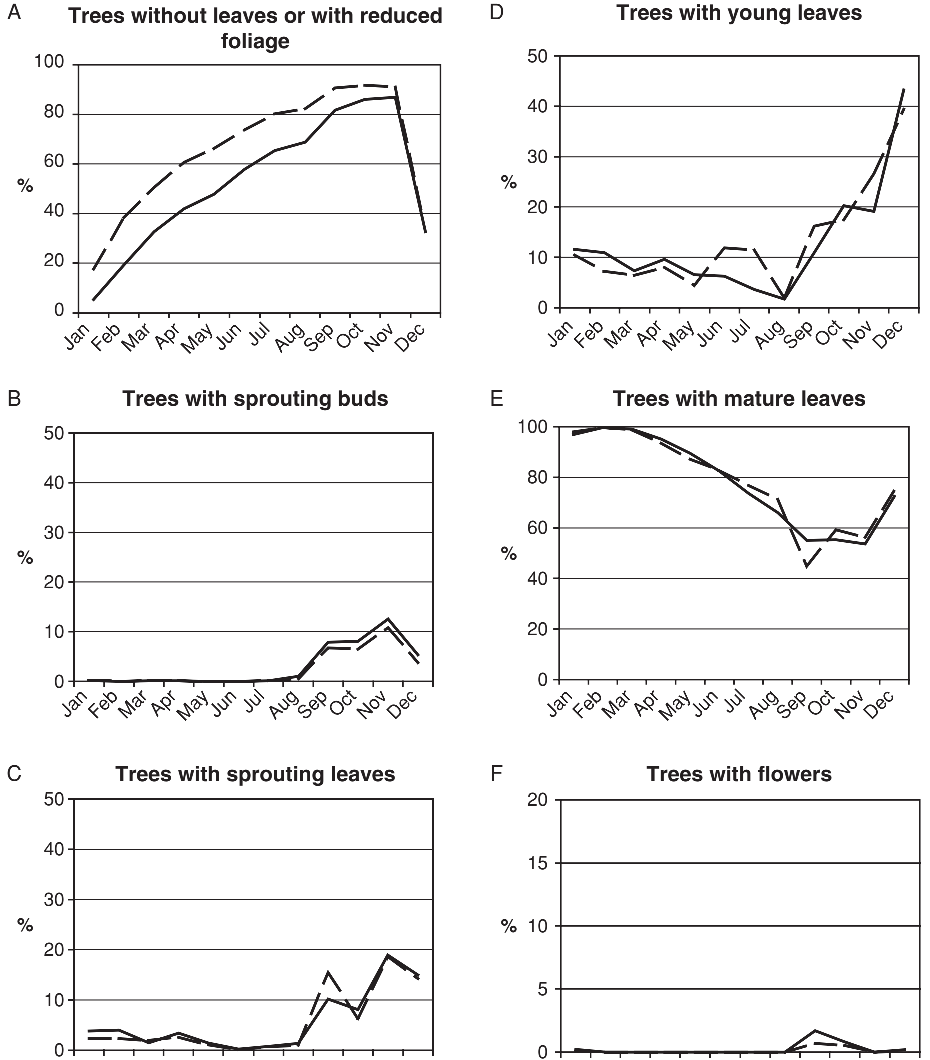

Figure 2. Phenology. (A) Foliage. (B) Sprouting buds. (C) Sprouting leaves. (D) Young leaves. (E) Mature leaves. (F) Flowers. Solid line: percentage in terms of number of trees. Dashed line: percentage in terms of tree crown volume.

Data analyses were performed with Microsoft® Excel 2004 for Mac® v11.1.1, the freeware statistical package R (R Foundation for Statistical Computing 2005 v2.1.0), and InStat 3® on an Apple Macintosh® computer.

RESULTS

Monthly values for the different data are listed in the Appendix.

Climate (Figure 3, Appendix A-II). The climate is highly seasonal and essentially divided into a dry and a rainy season. The dry season usually lasts from mid-April to mid-November (austral winter), and the rainy season from mid-November to mid-April (austral summer).

During the dry season there is a marked deficit in water, while during the rainy season a high water surplus (Figure 3). Total rainfall was 1920mm in the 1995–96

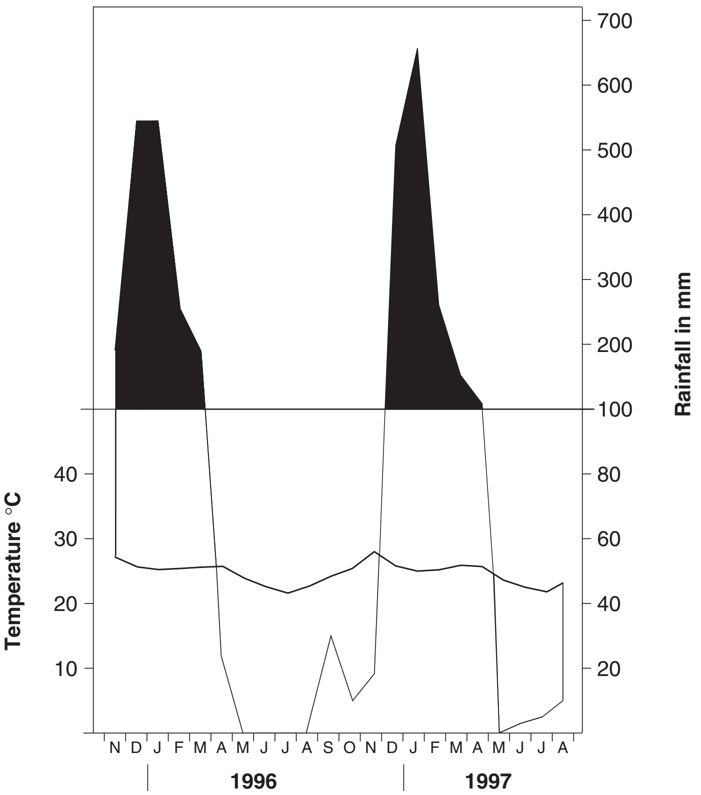

Figure 3. Rainfall and mean temperature recorded at the camp site (Forestry Station Ampijoroa) from November 1995 through August 1997. Black and diagonal hatching indicate periods of water surplus, stippling water deficit (Brower et al. 1997).

rainy season, and 1746mm in the 1996–97 rainy season. Annual rainfall in 1996 (January to December) was 1775 mm. About 60% of rain falls during the night (based on Donque, 1975:427) making continuous observations of nocturnal primates more difficult.

Mean average monthly temperature ranged between 22°C in July and 28°C in November. The highest mean maximum monthly temperature was recorded in November (35°C) and the lowest mean minimum monthly temperature in July (15°C).

Forest. Forest characterization with plant species lists has been reported in detail in Thalmann (2001:296 ff.), and is shortly summarized here. From the plot data it has been extrapolated that 6120 trees/ha with a DBH ≥2 cm of 87 species and 2520 woody lianas/ha (20 species) with a DBH ≥1 cm constitute the major plant biomass in the forest. Eleven tree species and two woody liana species not represented in the plots were additionally used as food species by either *Avahi* or *Lepilemur*, as was 1 nonwoody liana by *Avahi*. The plot samples with additional data from observations reasonably represent the forest for specific richness estimated with jackknife methods (Krebs, 1998; 95% estimate: 96–113 tree species, 21–29 liana species).

Correlations between phenology expressed in terms of number of trees per species and TCV are, with the exception of available fruit, positive and significant. This might lead to the use of tree number per species as proxy for available food. This is inadequate as the correlation between rain data and phenology shows a different pattern. The phenology in terms of TCV is more suitable for further considerations (see below).

Correlations of Environmental Variables

Climate. There is a significant positive correlation between the amount of rain and the mean temperature ($r=0.59$, $p<0.05$). The correlation is not very high, hence, the climate is rather moderately variable in terms of temperature over the year, and the major climatic variable is obviously the amount of rain.

Climate and Phenology (Table 1). As pointed out above, correlations of climate and phenology are most appropriate between rainfall and TCV, with rainfall as the major climatic variable and TCV as best proxy for forest composition and, hence, food availability in general. Surprisingly, results show that correlations between rainfall and potentially preferred food items of folivores such as sprouting buds, sprouting leaves, young leaves, and flowers are not significant (Table 1). This indicates that volume availability of these items depend on more than rainfall, and that accordingly a certain amount of plant items (e.g., young leaves) are available throughout the entire year (Figure 2). However, the major increase occurs after the first substantial rains at the beginning of the rainy season.

Table 1. Correlations between rain and phenology data in terms of tree crown volume: Spearman rank correlations

Phenology	noL	sBsL	sBsLyL	yL	mL	odL	icF	Flo	Fr
Rain	–0.54	0.57	0.38	0.23	0.29	– 0.48	–0.79	–0.12	0.15
p	0.075	0.057	ns	ns	ns	ns	**	ns	ns

noL: no leaves; sBsL: sprouting buds and/or sprouting leaves; sBsLyL: sprouting buds and/or sprouting leaves and/or young leaves; yL: young leaves; mL: mature leaves; odL: old and/or deciduous leaves; icF: reduced foliage; Flo: flowers; Fr: fruit.

* $0.01 < p < 0.05$, **$0.001 < p < 0.01$, ***$p < 0.001$; ns, not significant.

Observations

Visibility (Appendix A-III). Visibility was analyzed to assess comparability of observation data. Overall, visibility is not significantly different between *Avahi* and *Lepilemur*, but there is considerable variation. A larger sample might possibly result in significant differences caused by the fact that a group of animals (*Avahi*) is easier to locate and follow than single individuals as in *Lepilemur*. Indeed, visibility in *Lepilemur* is significantly positively correlated with development of leaf cover (Spearman rank correlation, $p < 0.05$).

Activity Period. Both species were definitely nocturnal, although *Avahi* was sometimes seen moving and feeding during daylight in the rainy season, i.e, when leaf cover was very dense.

Onset and Cessation of Activity. *Avahi* and *Lepilemur* start their activity shortly after sunset when light conditions make it difficult to read. Onset is significantly correlated with the time of sunset in both, *Avahi* (Spearman rank correlation, $n = 12$, $r = 0.99$, $p < 0.0001$) and *Lepilemur* (Spearman rank correlation, $n = 12$, $r = 0.92$, $p < 0.0001$). Conversely, the end of the activity period is not significantly correlated with sunrise.

Length of Activity (Figure 4, Appendix A-III). The length of the active period (sleep tree in the evening to sleep tree in the morning) is significantly correlated with the length of the night (sunset to sunrise) in the male *Avahi* A1m and the male *Lepilemur* L1m. It is not quite significant in the female *Lepilemur* L2f ($p = 0.0586$) but it is significant for *Lepilemur* male and female taken together. The activity period of the male *Avahi* A1m is not significantly longer than the active period of the *Lepilemur* male L1m, female L2f or *Lepilemur* male and female taken together. Within *Lepilemur* there is no significant difference between male and female. Although animals adjust their active time to some degree to the length of the night, this difference is not very obvious. It seems that animals reduce their active time during the rainy season but only slightly increase their active time during the lean dry season. There is a significant correlation between length of the active period between *Avahi* and *Lepilemur* over the year (Spearman

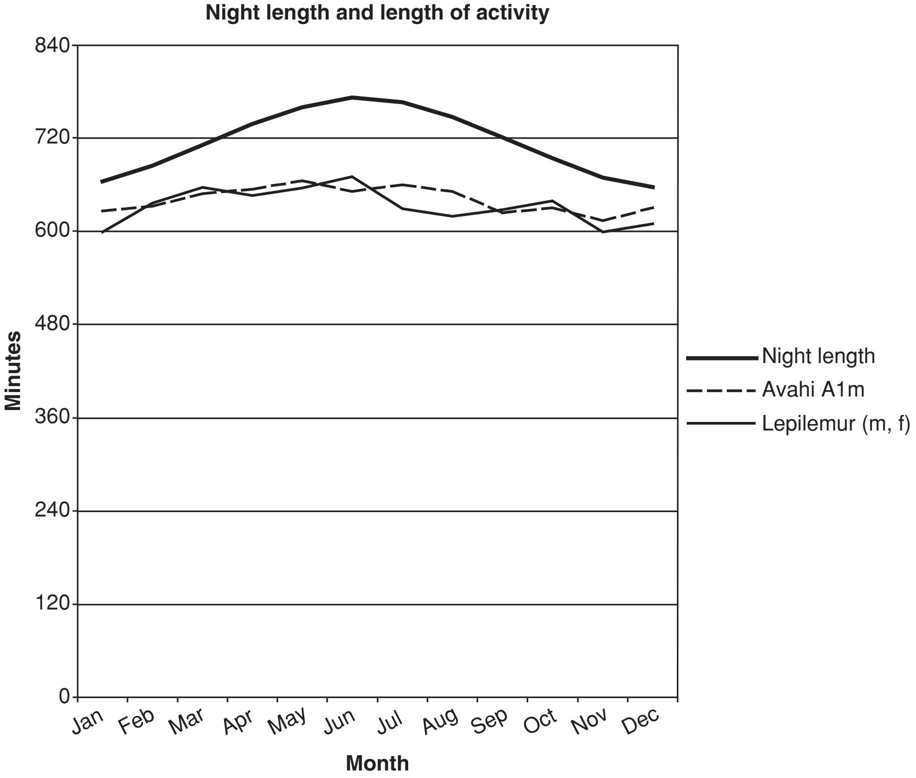

Figure 4. Night length and length of active time for focal animals over an entire year.

rank correlation, $n = 12$, $r = 0.63$, $p = 0.028$), indicating that they react overall in a comparable way to changing night length.

Activity Budget (Appendix A-IV to A-VI). The activity budget was measured by means of the categories rest, feed, move, groom (self-groom, partner groom). *Avahi* spends significantly more time feeding than *Lepilemur* (m, f) and *Lepilemur* male L1m and female L2f separately (Kruskal-Wallis test, $n_{\mathrm{A1m}} = n_{\mathrm{L1m}} = n_{\mathrm{L2f}} = 12$, $p < 0.005$; Dunn post-hoc test, $p < 0.05$, Figure 5) whereas there is no significant difference within *Lepilemur* male and female (Dunn post-hoc test, $p > 0.05$). There are no significant differences with regard to time moving (Kruskal-Wallis test, $p >> 0.05$). Resting is significantly different between *Avahi* and the *Lepilemur* male L1m, but not between *Avahi* and *Lepilemur* (m, f) together nor between *Lepilemur* male L1m and female L2f. No statistically significant interspecific difference is indicated with regard to grooming (including self-grooming and partner grooming) nor the categories separately, self-grooming and partner grooming, respectively.

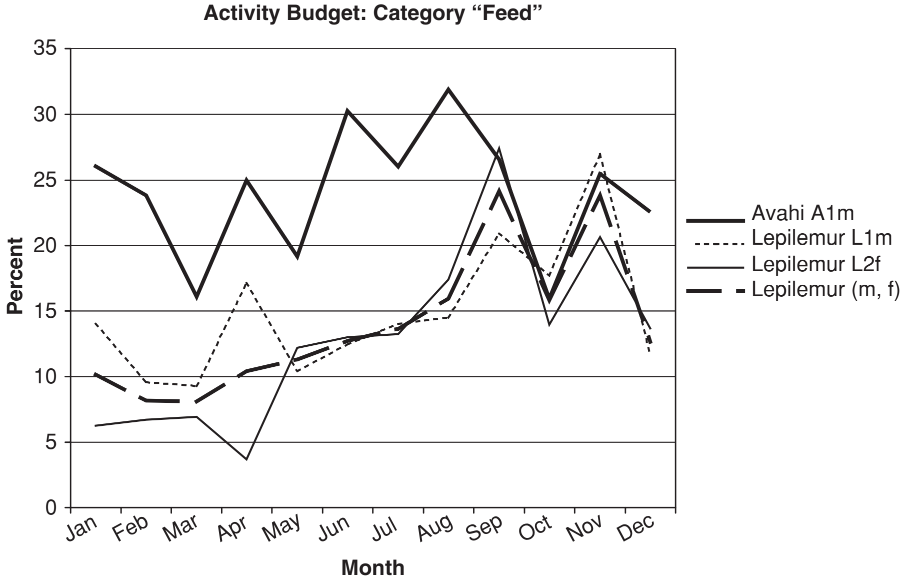

Figure 5. Percentage of feeding bouts during regular observations for focal animals over an entire year.

However, differences are almost statistically significant ($0.05 < p < 0.1$), and would possibly be significant if sample size was enlarged. Hence, statistically significant differences in grooming behavior are expected, if more data were available, and would corroborate subjective impressions from observations.

Food Resources. Food resources in both species have been analyzed in detail elsewhere (Thalmann, 2001) and results are shortly summarized here. Both species fed primarily on leaves over the entire year (77% of feeding bouts in *Avahi*, 74% in *Lepilemur*). In the balanced sample (one night per individual per month), the male *Avahi* A1m used 25 different tree and 5 different liana species at 102 (trees 89, lianas 13) locations. The two focal *Lepilemur* individuals together used 25 different tree and 5 different liana species at 112 locations (trees 101 trees, lianas 11). *Avahi* used on average 2.5 times larger food patches in terms of TCV than *Lepilemur*. Neither *Avahi* nor *Lepilemur* showed a conspicuous preference for clumped plant species. Food resource overlap between the two species is very low, and virtually absent if seasonality and availability in terms of TCV is taken into account. *Lepilemur* select significantly more common trees and liana species than *Avahi* do. *Avahi* have a narrower food niche compared with *Lepilemur* and are, hence, more specialized folivores than *Lepilemur*.

Vocalizations. (Figure 6, Appendix A-VII). Vocalizations have not yet been described and analyzed in detail for the two species (Thalmann, unpublished data). Presented results are hence restricted to the most conspicuous vocalizations in *Lepilemur*. These are loud vocalizations in which most often more than one individual is involved. Here, I call them complex vocalizations. Indeed, these vocalizations seem to be duets between opposite-sex individuals sharing the same home range, such as in the case of the focal animals *Lepilemur* L1m and L2f. In some cases, the female *Lepilemur* individual L18f—living in the same range—contributed too, but it seemed that this individual did not fully participate.

The highest rates of complex vocalizations appear at the beginning and during the rainy season; virtually no complex vocalizations occur during the dry season. The positive correlation (Spearman rank correlation $r = 0.85$, $p < 0.001$) between

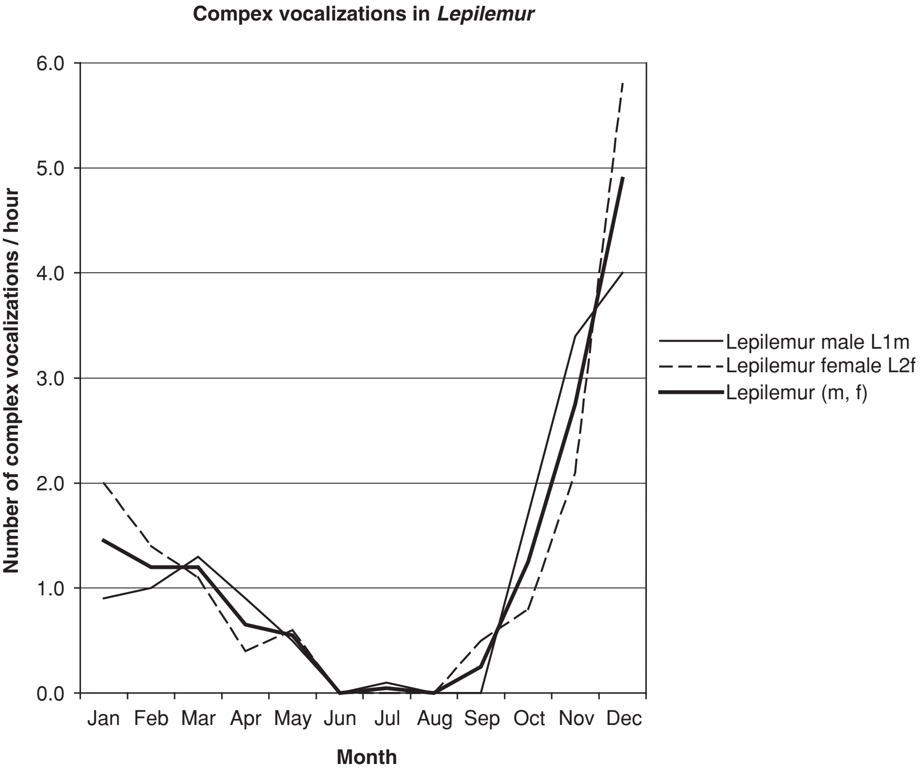

Figure 6. Complex vocalizations in *Lepilemur* over an entire year. Very high rates occur at the beginning and during the rainy season whereas there are almost no complex vocalizations during the dry season.

Lepilemur male and female is highly significant and indicative of coordination between the individuals. Complex vocalizations correlate positively and significantly with rainfall, Nightly Path Length, range size expressed as usage of different quadrats, availability of possibly preferred food items (sBsLyL), and negatively with grooming rates and night length (Table 2).

No comparable complex vocalizations are present in *Avahi*. In *Avahi* there was only a simple loud vocalization, the typical "vou-hì." Neither the focal male Am1 nor the female of the same group was observed uttering this call. It seemed that this vocalization occurred only in special situations, when the male *Avahi* suddenly and very quickly moved away from the group. In this situation it was always lost and out of sight but the conspicuous vocalization was heard.

Ranges (Figures 7–10, Table 3). Home ranges (convex polygons) for neighboring *Avahi* groups ($n = 4$, including the focal *Avahi* male A1m) and individuals of *Lepilemur* ($n = 7$, including focal *Lepilemur* individuals L1m, L2f) belonging to different range associations ($n = 4$) are shown in Figures 7–10. In general, there is little overlap between neighboring *Avahi* groups for which data were available for 1996 (Figure 7). The gaps between the different groups are mainly due to differences in intensity of data collection. Based on the observations of the focal *Avahi* male A1m the range size is approximately 1.1–1.4 ha for a group. The home range remained quite stable in size and location over 4 consecutive years as shown by the comparatively small shift of home range centers and borders for different years (Figure 8). In *Lepilemur*, again, overlap is not extensive between range associations (Figure 9). The focal male L1m and female L2f together with the young female L18f formed a range association. The males L22m and L29m had overlapping ranges as well, and most likely belonged to the same association; L24m and L5f were members of other associations. Because *Lepilemur* individuals often lost their transmitters and changed sleep trees less often than did *Avahi*, less spacing data are available overall. However, the gaps are most probably due to differences in observation intensity, as the different range associations seemed to be neighbors. The ranges of the focal *Lepilemur* male L1m and female L2f

Table 2. Selected correlations between complex vocalizations in *Lepilemur* and environmental and behavioral variables ($n = 12$ for all correlations)

Variable	Spearman's r	p value
Rainfall	0.77	0.005
Nightly path length	0.81	0.002
Range size (quadrats used)	0.91	< 0.0001
Food items (VsbsLyL)[a]	0.58	0.049
Grooming[b]	−0.71	0.013
Night length (min)	−0.93	< 0.0001

[a] Available tree crown volume with sprouting buds and/or sprouting leaves and/or young leaves.

[b] All grooming bouts, including self-grooming and partner grooming.

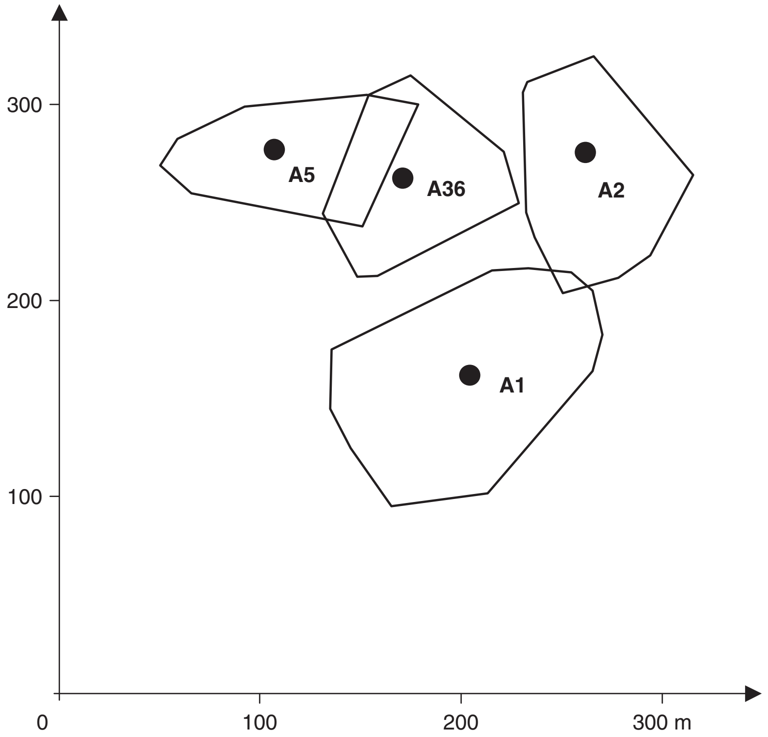

Figure 7. Home ranges with range centers (harmonic mean) of four neighboring *Avahi* groups in 1996 based on direct observations and sleep tree localizations. Most data were available for the focal male of group A1.

remained stable in location over several years as shown by the small shift of home range centers (Figure 10). Differences in home range size are most likely related to observation intensity, the range varying in the *Lepilemur* male L1m between 0.71 and 1.10 ha and 0.57 and 0.94 ha in the female L1f (Table 3). In addition, *Lepilemur* show differences in travel distances according to season (see below). Hence, range size also depends on the season when data are collected. A size around 1 ha may be a reasonable estimate for *Lepilemur edwardsi* in Ampijoroa, both male and female.

Nightly Path Length (Figure 11, Appendix A-VIII). There is no significant difference either across species or individuals (Kruskal-Wallis test, ns) if the entire year is considered. However, there is a conspicuous difference in the distribution of NPL over the year between *Avahi* and *Lepilemur* as shown in Figure 11. Towards the beginning of the rainy season in November/December, there is a major peak in path lengths in sportive lemurs, both male and female. During the rest of the year sportive lemurs have on average a lower NPL than do woolly lemurs.

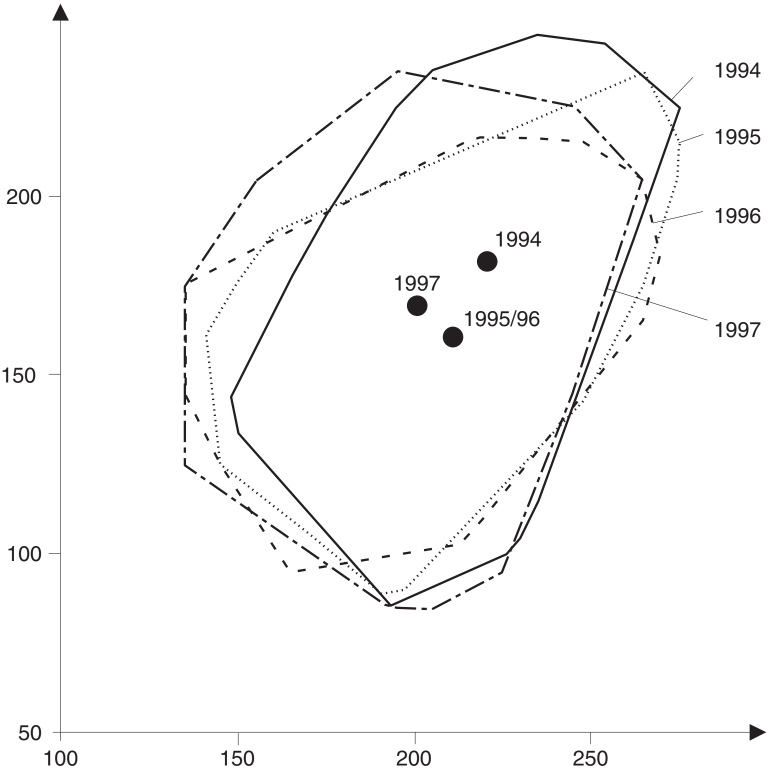

Figure 8. Home ranges and range centers (harmonic mean) of the focal *Avahi* male based on all direct observations and sleep tree localizations for several consecutive years.

DISCUSSION

During the past few years results of field studies on nocturnal primates showed that many species are socially and spatially pair-living (e.g., Fietz, 1999; Müller and Thalmann, 2000; Schülke and Kappeler, 2003). Indeed, the study presented here once started with the premise that *Avahi* and *Lepilemur* provide an exemplary case for behavioral and ecological comparisons between—at the time—a monogamous and a solitary species eliminating body mass, gross diet, and environment as interfering variables. Meanwhile, in the light of all new results, it became clear that it is more appropriate to use the term *pair-living* instead of *monogamous* for the grouping pattern, thus separating genetic and social descriptors for social organizations, and *solitary-but-social* instead of *solitary*, because all nocturnal primates seem to live at least in some kind of social network (e.g., Müller and Thalmann, 2000). In more rigorous terminology, the spacing pattern between individuals was described as gregarious or cohesive for group-living species, and dispersed for

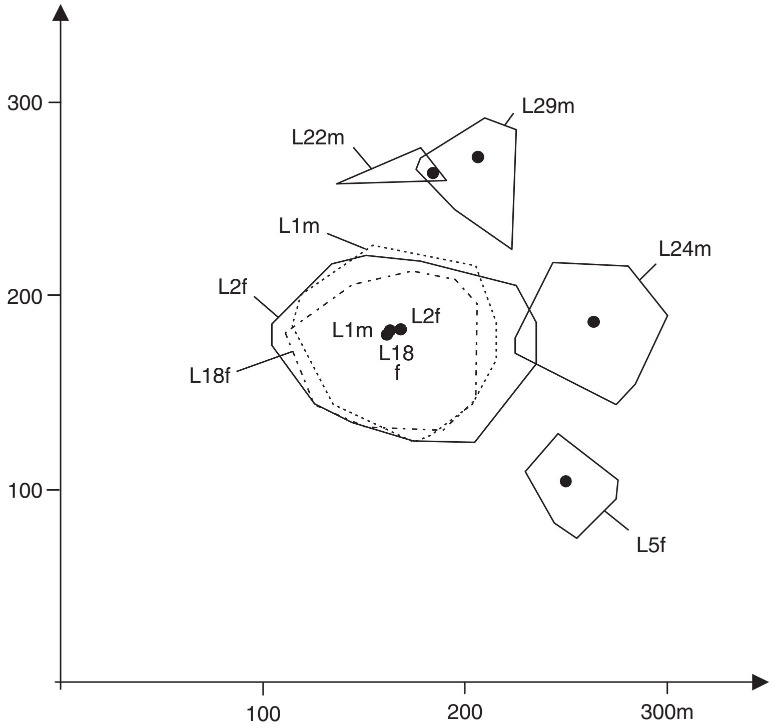

Figure 9. Home ranges with range centers (harmonic mean) for *Lepilemur* individuals in 1996 based on direct observations and sleep tree localizations. Most data were available for the focal animals L1m and L2f, and L18f. All individuals were either neighboring or occupied overlapping ranges when belonging to a range. Gaps between individuals and/or range associations are most probably due to differences in observation intensity.

species where individuals are mostly encountered alone during their active period but obviously live either in the same range or belong to the same social network.

The goals of the study were (1) to provide basic descriptive data on aspects of behaviour and ecology for *A. occidentalis* and *L. edwardsi* to test whether it is justified to use them as a field model to compare a pair-living and a solitary-but-social species, (2) explore possible links between behavior, ecology, and seasonality in view of a supposed change in availability of food resources over the year, and (3) to determine if *Avahi* show different adaptations than do *Lepilemur* in this respect.

The collected descriptive data showed both similarities and differences between the two species. Most surprising was certainly the finding that both species are obviously pair-living, although in different ways. In both species, male and female had coinciding ranges during consecutive years, and ranges were stable in location (Figures 7–10), to the exclusion of other neighboring groups or range associations. *Avahi* lived in spatially gregarious family groups, and it is most probable

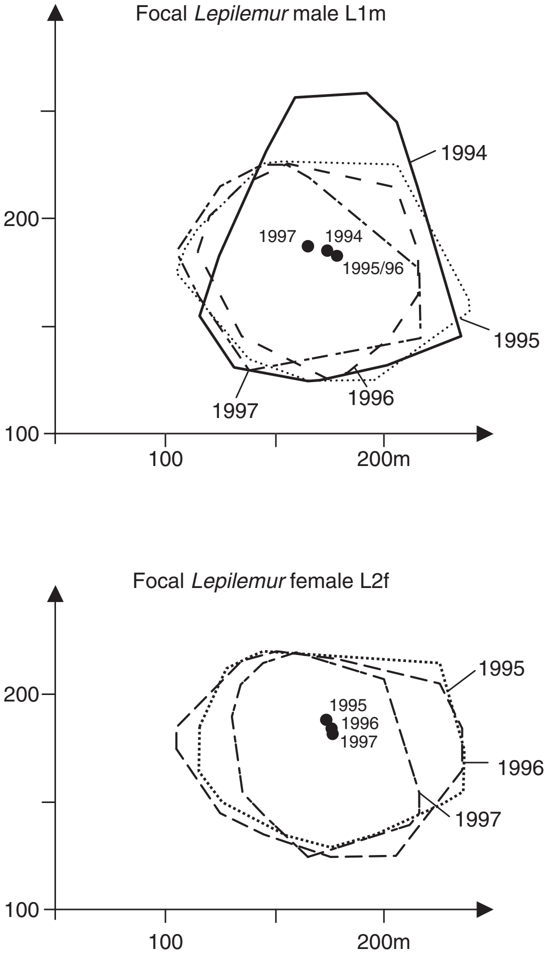

Figure 10. Home ranges with range centers (harmonic mean) in consecutive years for the focal *Lepilemur* male (1994–97) and female (1995–97). Differences in size are mostly due to differences in observation intensity. Ranges overlap across years for both sexes and intersexually, and range centers are close together.

that they conform with the notion of uniform pairs, in the terminology of van Schaik and Kappeler (2003). They define uniform pairs as breeding units in which more than 90% of units have a single breeding female. *L. edwardsi* lived in dispersed family groups. Whether *L. edwardsi* also conforms to the definition of uniform pairs or lives—in the terminology of van Schaik and Kappeler (2003)—in variable pairs (less than 90% of units with single breeding females) remains unknown at the time and needs further investigation. However, all the following comparisons refer

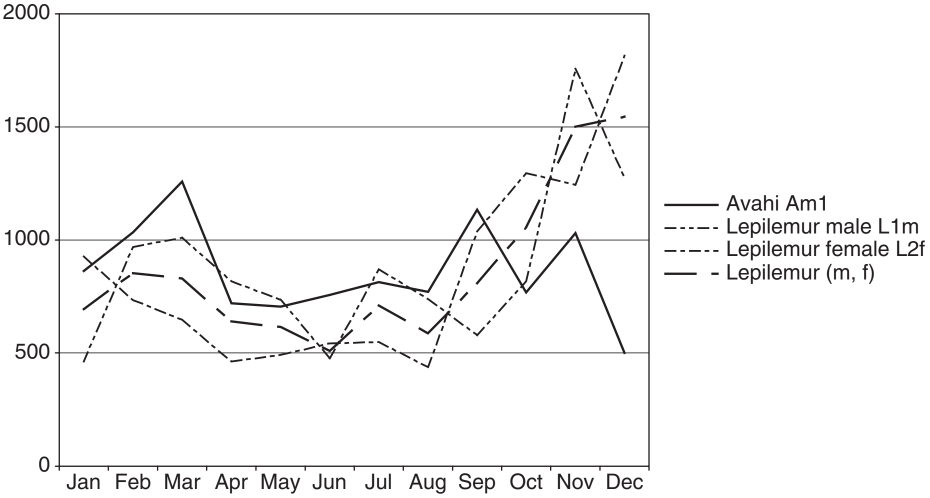

Figure 11. Nightly path length (NPL) in meters for focal animals over an entire year. One NPL per animal per night was available. Average NPL is statistically not different between individuals. However, sportive lemurs show a conspicuous peak towards the beginning of the rainy season in November–December.

thus not to a monogamous and a solitary species but either to gregarious versus dispersed pair-living species, or species living in uniform versus variable pairs. Interestingly, detailed analyses of the feeding behavior showed conformity in feeding hypotheses with predictions derived from a monogamous versus solitary comparative approach (Thalmann, 2001).

Activity. Both species were definitely nocturnal despite the fact that *Avahi* was sometimes seen feeding during the day in the rainy season (Rasmussen, 1999; Thalmann, personal observation) when leaf cover was very dense (Figure 2e). During this season, protection against potential aerial predators of woolly lemurs such as Henst's Goshawks (Karpanty, 2003) might be almost as good as during the night. During the dry season, when leaf cover was weak *Avahi* was never seen

Table 3. Convex polygon range size in hectares for focal animals across several years[a]

		Range size in hectares			
Species	Individual	1994	1995	1996	1997
Avahi occidentalis	A1m	1.33	1.23	1.11	1.37
Lepilemur edwardsi	L1m	1.10	0.99	0.71	0.84
	L1f	—	0.86	0.94	0.57

[a] Size differences within individuals are most probably due to differences in observation intensity.

feeding during the day. *Avahi* seems to have some kind of potential for diurnal activity or cathemerality. *Lepilemur* was never seen feeding during the day but sometimes animals peered out of their tree hole. Both species start their activity shortly after sunset and this is very likely triggered by the low light intensity as indicated by the high positive correlation. However, cessation of activity is not related to sunrise. Thus, it seems reasonable to suggest that, once all needs of individuals are met, activity stops whether it is still comfortably dark or not. The available time for foraging is not entirely exploited. When *Lepilemur* return early to their sleeping hole, they often remain immediately outside of it, and survey the forest before they retire for the day. The length of the active time is related to night length and does not differ over the year between the two species (Figure 4). The positive correlation between night length and active time is lower in *Lepilemur* than in *Avahi*, and it might be possible that *Lepilemur* do adjust their active time more to food availability than do *Avahi* to conserve energy during the leanest months of the dry season (July–October). *Lepilemur* do not use the longer nights to spend more time foraging but instead seem to reduce active time from July to October (after the length of the active time seems to increase till June in line with night length).

Activity Budget. Obvious differences are present in the activity budget in that *Avahi* spends significantly more time feeding than does *Lepilemur*. An increased sample would probably also reveal significant differences in resting time during the activity period and grooming, especially grooming between individuals ("partner grooming"). This would corroborate subjective impressions that the *Lepilemur* male and female groomed each other considerably more often when they met than did the *Avahi* male and female who were always in close spatial relationship. The detailed investigation of food resources (Thalmann, 2001) confirmed that both species are folivores but that there is obviously no direct competition for food. Indeed, dietary overlap is minimal, especially if seasonality and resource size is accounted for. As *Avahi* chooses more high-quality leaves compared to *Lepilemur* (Ganzhorn, 1993), it might be hypothesized that *Avahi* anticipates or finds high-quality food more efficiently than does *Lepilemur*. Indeed, it seemed that *Avahi* returned more often and regularly to the same feeding localities as long as they provided food, and more often chose the very same feeding trees in consecutive years. Whether this matches differences in mapping capacities in the two species is speculative at this time. It may also be hypothesized that *Avahi* have a generally higher basal metabolic rate and a lower ability to adjust their metabolic rate to environmental conditions.

Lepilemur show several behavioral traits, notably complex vocalizations that correlate significantly with environmental variables (Table 2). These complex vocalizations increase dramatically towards the rainy season, evidently in line with increasing rainfall, leaf cover (increased food availability), and simultaneously with an increase in Nightly Path Length and range use. Both sexes show basically the same pattern. This is not too surprising for the complex vocalizations, as they constitute most probably pair-specific duets (Thalmann, unpublished data). More interestingly are the questions as to why such coordinated vocalizations occur at this time of the year, what their function is, and whether they have the same function in both sexes. Several functions have been proposed for coordinated pair vocalizations, including enhancing/advertisement of the pair bond, and territorial advertisement (e.g., Geissmann, 1999). If enhancing and advertisement of the pairbond is the only function, why then should these complex and coordinated vocalizations occur outside of the mating season which is from May to July? If the main function is territorial in nature, what is actually defended? It seems unlikely that these are food resources as they are most probably available in abundance for *L. edwardsi* (Thalmann, 2001). Is it the territory with the female that is defended by the male, or, quite unlikely, vice versa? The complex vocalizations do, however, overlap to some degree with the birth season (September – November) and continue over a period when newborn *Lepilemur* are cached and do not follow their parents. Hence, it could be suggested that this coordinated vocal behavior occurs in the context of infanticide prevention, as infanticide has been reported in *L. edwardsi* (Rasoloharijaona et al., 2000). This might explain the participation of both sexes in such vocalizations during this particular time of the year. Further investigations are certainly needed to investigate this particular behavior, which is obviously not present in *A. occidentalis* where the mother always carries the offspring until it can move independently.

CONCLUSION

1. *A. occidentalis* and *L. edwardsi* are both pair-living: *A. occidentalis* in small cohesive family groups, *L. edwardsi* in dispersed family groups.
2. *A. occidentalis* and *L. edwardsi* show comparable home-range sizes, travel distances, and activity patterns across the entire year, but distribution within the entire year differs. This is most notable in travel distances and vocal behavior.
3. The activity budget of *A. occidentalis* differs from that of *L. edwardsi*. *Avahi* spends significantly more time feeding than does *Lepilemur*. It may be hypothesized that *Avahi* has a higher basal metabolic rate.
4. *Avahi* selects larger food patches and leaves of rarer tree species than does *Lepilemur*.

This fits predictions based on a resource-defense model for uniform pairs (*sensu* van Schaik and Kappeler, 2003). In this respect, *Lepilemur* fits predictions for solitary-but-social species despite being pair-living. Whether this is due to its dispersed pair-living, the mode of pair-living (uniform *vs.* variable pair-living *sensu* van Schaik and Kappeler, 2003), or other factors remains unknown.

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APPENDIX

Table A-I. Phenology in terms of tree crown volume (all values in percent)

Month	noL	sBsL	sBsLyL	yL	mL	odL	icF	Flo	Fr
Jan	0.0	2.5	12.9	10.4	97.9	49.0	17.7	0.0	2.5
Feb	0.1	2.4	9.5	7.1	99.5	75.2	38.3	0.0	11.8
Mar	0.5	2.0	8.5	6.4	98.6	94.0	50.1	0.0	3.9
Apr	3.3	2.7	10.6	7.9	93.4	95.6	57.3	0.0	2.7
May	7.9	1.0	5.5	4.4	87.1	91.7	58.5	0.0	2.6
Jun	10.5	0.1	11.9	11.8	82.7	89.5	63.3	0.0	2.8
Jul	14.8	0.7	12.1	11.4	76.9	84.8	65.5	0.0	3.3
Aug	22.0	1.5	3.5	2.0	71.2	77.6	60.3	0.0	2.7
Sep	46.7	22.1	38.3	16.1	44.8	52.8	44.0	0.7	2.6
Oct	34.4	12.7	30.2	17.5	59.3	62.5	57.4	0.5	4.0
Nov	28.4	29.4	55.9	26.6	56.3	59.8	62.8	0.0	6.0
Dec	7.0	17.9	57.4	39.4	74.8	48.8	26.2	0.0	3.1

Tree crown volume in percentage without leaves (noL), sprouting buds and/or sprouting leaves (sBsL), sprouting buds and/or sprouting leaves and/or young leaves (sBsLyL), young leaves (yL), mature leaves (mL), old and/or deciduous leaves (odL), incomplete foliage cover (icF), flowers (Flo), fruit (Fr).

Table A-II. Night length and climate in Ampijoroa Forestry Station

Month	Season	Night[a] [min]	Rain [mm]	Tmean[b] [°C]	Tmax [°C]	Tmin [°C]
Jan	Rain	664	601	25.1	28.2	21.9
Feb	Rain	684	258	25.3	28.7	21.9
Mar	Rain	711	270	25.7	29.3	22.1
Apr	(Dry)	738	66	25.7	30.0	21.4
May	Dry	760	0	24.1	29.3	18.8
Jun	Dry	772	1	22.5	30.0	18.5
Jul	Dry	766	3	21.7	30.5	15.1
Aug	Dry	747	5	22.9	32.0	16.0
Sep	Dry	721	30	24.7	32.9	16.6
Oct	Dry	694	10	25.8	33.3	18.6
Nov	(Dry)	669	92	27.3	33.9	20.7
Dec	Rain	657	526	25.7	29.6	21.8

[a] Average night length in minutes.
[b] T: temperature. Tmean = (Tmax + Tmin)/2.

Table A-III. Visibility and length of activity (sleep tree in the evening to sleep tree in the morning)

	Visibility [% of bouts]				Length of activity [min]			
Month	A1m	L1m	L2f	L (m, f)	A1m	L1m	L2f	L (m, f)
Jan	53.3	31.7	26.7	29.2	626	582	616	599
Feb	41.9	26.1	28.9	27.5	632	640	632	636
Mar	41.4	47.8	28.1	37.9	648	670	643	657
Apr	50.0	50.3	37.5	43.9	654	664	628	646
May	72.5	58.6	56.9	57.8	665	666	646	656
Jun	54.2	71.4	61.9	66.7	651	652	689	671
Jul	67.2	63.3	37.8	50.6	660	628	630	629
Aug	58.3	51.7	55.8	53.8	651	614	624	619
Sep	57.5	54.4	54.7	54.6	624	604	652	628
Oct	76.7	65.8	47.8	56.8	630	620	658	639
Nov	44.7	49.4	57.8	53.6	613	594	604	599
Dec	36.9	40.6	38.6	39.6	630	596	622	609

A1m: focal male *Avahi*. L1m: focal male *Lepilemur*. L2f: focal female *Lepilemur*. L (m, f): average for focal *Lepilemur* individuals.

Table A-IV. Activity budget of focal animals in percent of observed bouts: categories "Rest" and "Feed"

	Rest				Feed			
Month	A1m	L1m	L2f	L (m, f)	A1m	L1m	L2f	L (m, f)
Jan	65.6	73.7	80.2	76.9	26.0	14.0	6.3	10.1
Feb	58.9	77.7	83.7	80.7	23.8	9.6	6.7	8.2
Mar	76.5	52.9	78.2	65.6	16.1	9.3	6.9	8.1
Apr	62.2	63.0	88.1	75.6	25.0	17.1	3.7	10.4
May	60.9	78.7	72.7	75.7	19.2	10.4	12.2	11.3
Jun	54.9	77.0	75.3	76.2	30.3	12.5	13.0	12.7
Jul	64.5	78.5	72.1	75.3	26.0	14.0	13.2	13.6
Aug	55.7	66.7	53.2	60.0	31.9	14.5	17.4	16.0
Sep	60.4	65.8	67.5	66.7	26.6	20.9	27.4	24.2
Oct	71.4	71.7	80.2	76.0	15.9	17.7	14.0	15.8
Nov	51.6	52.8	67.8	60.3	25.5	27.0	20.7	23.8
Dec	57.9	74.7	68.3	71.5	22.6	11.6	13.7	12.7

A1m: focal male *Avahi*. L1m: focal male *Lepilemur*. L2f: focal female *Lepilemur*. L (m, f): average for focal *Lepilemur* individuals.

Table A-V. Activity budget of focal animals in percent of observed bouts: categories "Groom"[a] and "Self-groom"

	Groom				Self-groom			
Month	A1m	L1m	L2f	L (m, f)	A1m	L1m	L2f	L (m, f)
Jan	0.5	0.0	0.0	0.0	4.7	5.3	3.1	4.2
Feb	0.0	0.0	0.0	0.0	11.3	8.5	3.8	6.2
Mar	0.0	0.0	0.0	0.0	2.0	8.7	4.0	6.3
Apr	0.0	1.1	0.0	0.6	6.7	12.2	4.4	8.3
May	1.5	0.9	2.4	1.7	13.4	3.8	7.8	5.8
Jun	1.0	0.0	1.3	0.7	10.8	9.3	5.4	7.4
Jul	0.0	0.0	3.7	1.8	7.0	2.6	3.7	3.2
Aug	0.5	0.0	0.0	0.0	6.2	12.9	22.4	17.6
Sep	0.0	0.0	0.0	0.0	9.2	7.1	0.5	3.8
Oct	2.5	0.0	0.0	0.0	7.2	8.0	2.3	5.2
Nov	0.0	0.0	0.0	0.0	7.5	0.6	6.3	3.4
Dec	3.0	0.0	0.0	0.0	12.8	5.5	1.4	3.5

[a] The category "Groom" contains bouts that could not be classified as either "Self-groom" or "Partner groom."

A1m: focal male *Avahi*. L1m: focal male *Lepilemur*. L2f: focal female *Lepilemur*. L (m, f): average for focal *Lepilemur* individuals.

Table A-VI. Activity budget of focal animals in percent of observed bouts: categories "Partner groom" and "Move"

	Partner groom				Move			
Month	A1m	L1m	L2f	L (m, f)	A1m	L1m	L2f	L (m, f)
Jan	0.0	0.9	0.0	0.4	3.1	6.1	10.4	8.3
Feb	0.0	1.1	0.0	0.5	6.0	3.2	5.8	4.5
Mar	0.0	1.7	0.0	0.9	5.4	27.3	10.9	19.1
Apr	0.0	0.6	0.0	0.3	6.1	6.1	3.7	4.9
May	0.8	0.5	0.5	0.5	4.2	5.7	4.4	5.0
Jun	0.0	0.0	0.4	0.2	3.1	1.2	4.5	2.8
Jul	0.0	0.0	0.7	0.4	2.5	4.8	6.6	5.7
Aug	0.0	3.8	0.0	1.9	5.7	2.2	7.0	4.6
Sep	0.0	0.0	0.0	0.0	3.9	6.1	4.6	5.3
Oct	0.0	0.0	0.0	0.0	2.9	2.5	3.5	3.0
Nov	0.6	0.0	0.0	0.0	14.9	19.7	5.3	12.5
Dec	0.0	0.0	0.0	0.0	3.8	8.2	16.5	12.4

A1m: focal male *Avahi*. L1m: focal male *Lepilemur*. L2f: focal female *Lepilemur*. L (m, f): average for focal *Lepilemur* individuals.

Table A-VII. Complex vocalizations per observation hour in *Lepilemur* (*Avahi* have no corresponding vocalization)

Month	L1m	L2f	L (m, f)
Jan	0.9	2.0	1.5
Feb	1.0	1.4	1.2
Mar	1.3	1.1	1.2
Apr	0.9	0.4	0.7
May	0.5	0.6	0.6
Jun	0.0	0.0	0.0
Jul	0.1	0.0	0.1
Aug	0.0	0.0	0.0
Sep	0.0	0.5	0.3
Oct	1.7	0.8	1.3
Nov	3.4	2.1	2.8
Dec	4.0	5.8	4.9

L1m: focal male *Lepilemur*. L2f: focal female *Lepilemur*. L (m, f): average for focal *Lepilemur* individuals.

Table A-VIII. Nightly path length and range size [number of visited quadrats × 100 m^2] in focal animals

	Nightly path length [m]				Number (n) of quadrats used [range size = $n \times 100$ m^2]			
Month	A1m	L1m	L2f	L (m, f)	A1m	L1m	L2f	L (m, f)
Jan	862	463	927	695	38	27	49	38
Feb	1035	971	733	852	44	36	34	35
Mar	1258	1011	648	829	52	52	29	41
Apr	720	817	463	640	44	51	25	38
May	705	736	492	614	40	34	27	31
Jun	757	476	542	509	34	25	26	26
Jul	814	870	549	710	38	25	24	25
Aug	770	738	438	588	40	22	22	22
Sep	1135	578	1039	809	45	29	29	29
Oct	768	817	1296	1057	36	37	35	36
Nov	1031	1757	1245	1501	56	76	37	57
Dec	500	1276	1815	1546	36	48	63	56

A1m: focal male *Avahi*. L1m: focal male *Lepilemur*. L2f: focal female *Lepilemur*. L (m, f): average for focal *Lepilemur* individuals.

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CHAPTER SIXTEEN

The Feeding Ecology and Related Adaptations of *Indri indri*

Joyce A. Powzyk and Christopher B. Mowry

INTRODUCTION AND PHYSICAL DESCRIPTION OF *INDRI INDRI*

Indri indri is a large-bodied lemur with numerous adaptations to facilitate its ecological niche of folivory within the rainforests of eastern Madagascar. More precisely, *Indri* is well adapted to life in the trees: its limb morphology allows for a highly arboreal lifestyle, while digestive specializations permit a diet that is almost extensively folivorous with limited frugivory. An adult male and female live together as a monogamous pair and quickly identify their presence in a forest with a deafening duet of long calling. This remarkable vocalization can last over 3 minutes and is typically introduced with a communal "roar" followed by a song proper of both ascending and descending notes, with a male and female timing their phrases to attain a stable dueting pattern (Powzyk and Thalmann, 2003). The long call is termed "contagious": as one group finishes their long call, a neighboring group commences and so the calling continues sequentially through the forest. Yet despite their loud vocalizations, *Indri* can be difficult to view since they rely heavily on crypsis. Crypsis works well to camouflage a lemur that spends long periods of the daylight hours resting on tree branches in the dappled light of a forest. This has earned *Indri* the reputation of "ghost of the forest," often heard

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but not seen. Yet, once sighted, *Indri* is easily identified with its distinctive black, gray, and creamy white pelage, dark, cublike ears (often tufted), and a penetrating gaze from its light yellow irises. In addition, *Indri*'s near lack of a tail (tail length just 5–7 cm) sets it apart from all other lemur species (Glander and Powzyk, 1995). Adult pelage coloration can vary; some individuals are almost entirely black, while others have extensive amounts of white on their arms, legs, lower back (inverted V in pygal region), top and back of the head and on their facial disk. Born nearly all black except for a light pygal patch, an *Indri* typically gains more white in its overall coloration as it matures.

Indri indri is able to move through the trees with alacrity as its long arms and even longer legs assist them in what is termed "ricochetal leaping" (Oxnard et al., 1990), a form of locomotion that also comes under the description of "vertical clinging and leaping" (Napier and Walker, 1967). Their body is held in a near vertical position during the leap with the arms extended where the lateral skin serves as a sort of "flying membrane" (Oxnard et al., 1990). In order to grasp their substrate, both hands and feet show extensive elongation in their digits (i.e., metatarsal and phalange bones) (Tattersall, 1982), and are similar to gibbons in having a deep cleft separating the thumb from the other digits, an adaptation that may facilitate climbing large vertical supports (Cartmill, 1974) with a "vicelike grip." The head is balanced over the neck vertebrae in a position that facilitates the head having a wide range of movement, especially when scanning the forest in a vertical cling position (Napier and Napier, 1985; Rigamonti et al., 2005). All of these adaptations make *Indri* one of the most arboreal of lemurs with a heightened avoidance of the ground. Even when descending a tree for geophagy, *Indri* often maintains a vertical cling position while straining its neck to consume soil from an exposed bank (Powzyk, 1997).

Although *Indri indri* has long been heralded to be the largest extant lemur (Petter and Peyrieras, 1974), reported body weights of 12.5 kg were based on visual estimations (Pollock, 1977). We previously described the sympatric *Indri indri* and *Propithecus diadema* as the two largest extant lemurs on Madagascar with mean body weights of 6.48 kg ($n = 4$) and 6.50 kg ($n = 11$), respectively (Powzyk and Mowry, 2003; Powzyk and Thalmann, 2003). When sexes were compared, *Indri* females averaged 7.14 kg ($n = 2$) while males averaged 5.83 kg ($n = 2$) (Glander and Powzyk, 1995). Britt et al. (2002) weighed eight adult *Indri* (four females, four males) and recorded a mean body weight of 6.93 kg, although females averaged 1.1 kg heavier than the males (overall range: 6.1–8.8 kg). Therefore, *Indri* may well be the largest extant lemur, but additional body weights of both *Indri* and *P. diadema* need to be collected from the field to substantiate this claim.

Indri indri has been studied extensively at three sites. One site is located in the Eastern Domain, within the Betampona Nature Reserve (low-altitude secondary humid forest), while the Central Domain has two *Indri* sites, Mantadia National Park (midaltitude dense rainforest) and Analamazaotra Special Reserve (low-altitude secondary humid forest) (Mittermeier et al., 1994). Only the Mantadia study site, which was approximately 100 ha in size and located in the northwest sector of the park, had been undisturbed by human activities such as trail blazing, logging,

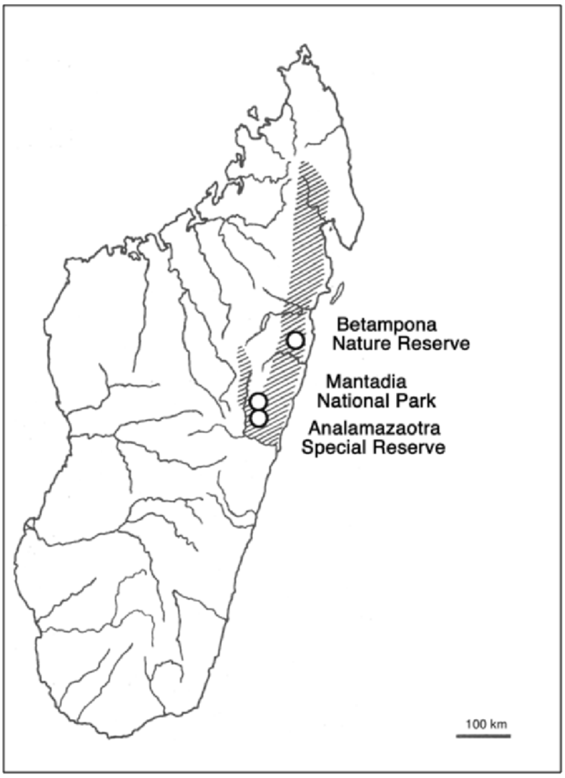

Figure 1. Current range of *Indri indri* in Madagascar indicated by crosshatching. Locations of Betampona, Mantadia, and Analamazaotra study sites are indicated by circles. (Redrawn from *Lemurs of Madagascar* by Mittermeier et al., 1994.)

and/or rice cultivation. Current population numbers of *Indri* are unknown but Figure 1 indicates *Indri*'s distribution throughout Madagascar and the location of major study sites, while Table 1 provides a summation of important parameters on data collection and physical makeup of the *Indri* sites.

Table 1. Ecological studies of *Indri indri*

Study site	Dates of study	Elevation (m)	Territory size (ha)	Indri groups (individuals)	Hours of observation	Disturbance
Analamazoatra	June 1972–June 1973	930	15–30	2 (8)	2300	selective logging/hunting
Mantadia	Sept. 1993–Feb. 1995	1000–1220	34–40	2 (4)	993	none
Betampona	Feb. 2000–Feb. 2001	275–650	21–32	3 (9)	652	selective logging/hunting

MORPHOLOGICAL AND PHYSIOLOGICAL FEEDING ADAPTATIONS

All members of the Indriidae (*Avahi laniger*, *Propithecus* spp., *Indri indri*) have specializations to accommodate a folivorous diet. Early dissections showed them to be anatomical folivores with hypertrophied salivary glands, voluminous stomachs, sacculated ceca, and looped colons, which facilitates efficient digestion of leaf parts (Hill, 1953). Anatomical folivores can be classified as either foregut (e.g., colobine monkeys) or midgut fermenters (previously known as hindgut fermenters) (Chivers, 1994). All indriids are the latter, exhibiting increased surface area in the midgut where nutrients are made available through fermentation of fiber by symbiotic gut flora (protozoan and bacterial) (Bauchop, 1978; Hladik, 1978; Parra, 1978). During fermentation, volatile fatty acids are released and then passed into the bloodstream where they are taken up by the animal as a form of assimilable energy. Compared to foregut specialists, midgut fermenters are able to consume more fibrous forage but need larger volumes to pass through their digestive tract to ensure sufficient extraction of nutrients (Janis, 1976). Within the indriid clade, *Indri* shows the highest degree of specializations for foliage digestion over any other confamilial (Hill, 1953).

The teeth of *Indri indri* are also indicative of a folivorous lemurid. All indriids have a reduced dentition, with just 30 teeth rather than the lemur-typical 36 teeth (Swindler, 1976). The molars of *Indri* have high crowns and long shearing blades (Kay and Hylander, 1978) to slice up fibrous plant matter and fruit seeds. In addition, *Indri*'s molars are squared off with a bilophodont morphology that only the Indriidae and Cercopithecoidea exhibit (Maier, 1977). The large crushing basins of these molars are highly effective at breaking down plant matter to even finer grades, the first step toward efficient digestion (Kay and Hylander, 1978).

Indriids have a toothcomb comprised of a single set of incisors and canines (four teeth total) rather than the two sets of incisors and one set of canines (six teeth total) that are typically found in other lemurids. *Indri indri* uses its toothcomb for both grooming and feeding purposes. At Mantadia, *Indri* utilized its toothcomb to pry out the large seeds from the leathery exocarp of *Beilschmiedia* fruits (Lauraceae) (Powzyk, 1997). This fruit resembles a small avocado with an oversized cotyledon without the fleshy fruit. *Indri* would first pluck a fruit with its front teeth and then, while clenching it in one hand, slice through the skin with its cheek teeth. Once the fruit was opened, the toothcomb was used to scoop out the seed by moving the lower jaw in an upward motion to release the hard seed from the outer skin. Toothcomb grooves were clearly observed on the fallen debris (Powzyk, 1997). Since *Indri* fully masticates all food items, it should be considered a seed predator rather than a seed disperser (Powzyk, 1997).

DIETARY PROFILE

All field studies indicate that *Indri indri* is highly folivorous with the majority of its feeding time spent on immature foliage. At Mantadia, 72.3% of feeding time was devoted to immature leaves with a reduced emphasis on fruit seeds/whole fruits (16.4%) and flowers (6.7%) (Powzyk, 1997; Powzyk and Mowry, 2003). *Indri* observations at Betampona yielded similar results: 73.4% of total feeding records were on immature foliage, followed by 8.2% on fruit/fruit seeds and 5.3% on flowers (Britt et al., 2002). Pollock (1977) reported 34.3–43.8% of feeding time at Analamazaotra on unknown plant parts, yet when food items were identified, the majority were on leaves (32.4–37.0%), followed by fruits (23.8–26.4%) and flowers (0.0–2.3%).

Other notable items in *Indri indri*'s diet were galls (1.37%) and other plant parts (3.22%), including bark, stems, leaf petioles, and new branch tips (Powzyk, 1997). Plant galls were a much sought after food item at Mantadia for *Indri,* but were more ephemeral in their availability than either fruit or flowers. A plant gall is a tumorous growth of cells typically initiated by a microscopic insect (or a bacterium or fungus), which then feeds on the nutritious tissue (i.e., amino acids) (Koyama et al., 2004). *Indri* likely consumes galls for the same vital nutrients. *Indri*'s consumption of plant galls and fruit were nearly indistinguishable from one another because of similarities in the shapes and handling of these items. Confirmation of gall feeding was only made after collecting gall-infested foliage directly from a food tree (Powzyk, 1997).

Overall, phenological monitoring at the Mantadia site showed that palatable immature leaves were both available and abundant year round for *Indri,* as were palatable fruit and flowers, albeit at comparatively lower levels (Figure 2) (Powzyk, 1997; Powzyk and Mowry, 2003).

Indri indri did consume mature leaves, although their contribution to the annual diet varied between research sites. At Betampona, 7.2% of total feeding records were on mature leaves (Britt et al., 2002), while *Indri* at Mantadia ate mature foliage just 1.4% of feeding time (Powzyk, 1997). Although not a major food constituent, Mantadia *Indri* fed on mature foliage from 12 different plant species, including "kijiabonaka" (*Symphonia fasciculata*, Clusiaceae) whose mature leaves were so thick and crunchy, they mimicked the sounds of fruit consumption (Powzyk, 1997). In contrast, Betampona *Indri* consumed mature leaves from 25 different plant species, with peak consumption in April and October when young leaf availability was reduced (Britt et al., 2002). It is unclear whether this disparate finding is due to observer differences in the classification of mature foliage, or differences in available food items within a forest type. Nevertheless, *Indri* in Betampona appeared to rely more heavily on mature leaves than *Indri* at other study sites.

An unusual food item consumed by *Indri indri* at both Mantadia and Betampona was tree bark. *Indri* consumed bark at Mantadia 2.86% of the total feeding time

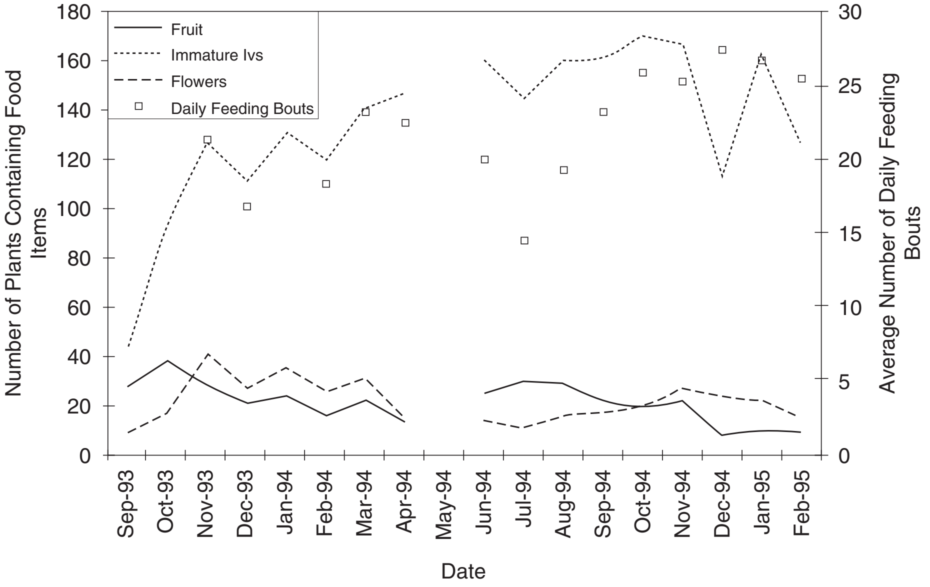

Figure 2. Food item availability and mean number of daily feeding bouts for *Indri indri* at Mantadia National Park from Sept. 1993 to Feb. 1995.

from a single *Ocotea* tree species (family Lauraceae), which they would girdle by removing strips of bark from a 5- to 10-cm-diameter tree branch. Feeding bouts on bark were lengthy: one recorded bout lasted 1 hour and 17 minutes (Powzyk, 1997). Bark consumption at Betampona was more common and involved nine different tree species, also including *Ocotea*. *Indri* exhibited a monthly maximum of 12.7% total feeding records on bark during September 2000 at Betampona, during the cool-dry season. Phenological monitoring showed this time of year to be one of limited young leaf and fruit availability (Britt et al., 2002). Richard (1977, 1978) reported that *Propithecus verreauxi* also ate bark during the dry season, using it as an important source of water. Overall, it appears that *Indri* residing in Betampona relied more heavily on mature leaves and bark, items that may contain high levels of plant fiber yet are clearly less preferred by Mantadia *Indri*.

Preferred Foods and Phytochemical Analysis

Only *Indri indri* food items from the Mantadia research site have undergone phytochemical analysis (Powzyk and Mowry, 2003). A list of the top ten preferred food items consumed by *Indri* based on time spent feeding at Mantadia was compiled, and field samples were collected/dried and analyzed for nutrient and secondary compound content. Of the top ten preferred food items for *Indri*, each was a

Table 2. The ten most frequently consumed items by *Indri indri* at the Mantadia study site

Genus/species	Item	Family	% of feeding time
Uapaca densifolia	imm lvs	Euphorbiaceae	8.4
Haematodendron glabrum	imm lvs	Myristicaceae	7.5
Uapaca thouarsii	imm lvs	Euphorbiaceae	6.5
Beilschmiedia oppositifolia	imm lvs	Lauraceae	4.1
Uapaca sp.	imm lvs	Euphorbiaceae	4.1
Cryptocaria sp.#1	imm lvs	Lauraceae	2.3
Ochrocarpos mad/sis	imm lvs	Clusiaceae	2.2
Calophyllum milvum	imm lvs	Clusiaceae	2
Symphonia fasciculata	imm lvs	Clusiaceae	1.9
Cryptocaria sp.#2	imm lvs	Lauraceae	1.9
TOTAL			40.90%

new/young tree leaf species, and these items collectively made up ~41% of its total feeding time, a further indication of *Indri*'s strong preference for immature foliage (Table 2). However, it should be noted that the eleventh most preferred food item was *Hematodendron glabrum* (Myristicaceae) fruit (Powzyk, 1997).

Nutritional analysis of *Indri indri*'s top ten foods found them to be significantly lower in fats and water-soluble carbohydrates (sugars) than the top ten food items for the sympatric *Propithecus diadema* (Powzyk, 1997; Powzyk and Mowry, 2003). *P. diadema*'s top ten food items were an assortment of flowers, fruit seeds, whole fruits, and immature leaves (Powzyk, 1997), so the nutritional differences between the two indriids' diets were not surprising. Protein (crude, bound, available) levels were slightly higher for *P. diadema*'s preferred foods, although not significantly (Powzyk and Mowry, 2003). Both *Indri* and *P. diadema* ate high-fiber diets, especially when compared to less folivorous primates. For example, *Indri*'s preferred foods at Mantadia had a mean neutral detergent fiber (NDF) value of 56% dry weight compared to 31–34% for foods eaten by chimpanzees (*Pan troglodytes schweinfurthi*), blue monkeys (*Cercopithecus mitis stuhlmanni*), red-tailed monkeys (*C. ascanius schmidti*), and mangabeys (*Lophocebusalbigena johnstoni*) in Kibale National Park, Uganda (Conklin-Brittain et al., 1998; Powzyk and Mowry, 2003).

Fiber (NDF and ADF) values in Mantadia *Indri indri* foods are similar to those reported for other indriid diets (Ganzhorn, 1988; Ganzhorn and Abraham, 1991). These values likely reflect the anatomical specializations of the indriid midgut and their inclusion with colobines as morphological folivores (Milton, 1980). In fact, ADF values for foods consumed by *Indri* and *P. diadema* at Mantadia are comparable to foods eaten by colobines (Waterman and Kool, 1994). Table 3 shows the nutrient composition of *Indri*'s preferred foods at Mantadia.

Tests for secondary compounds were conducted on the same subset of preferred *Indri indri* foods from Mantadia, as well as an additional 37 plant samples.

Table 3. Nutrient composition of top ten most frequently consumed food items by *Indri indri* at Mantadia National Park

Rank	Genus/species	Item	Ash	CP	BP	AP	NDF	ADF	Ls	WSC	Fat
1	*Uapaca densifolia*	il	4.25	10.26	9.03	1.23	73.13	78.62	55.86	0.57	0.87
2	*Haematodendron glabrum*	il	2.37	9.54	8.4	1.14	68.44	68.58	51.4	1.58	0
3	*Uapaca thouarsii*	il	5.58	10.67	9.17	1.5	63.3	61.62	44.5	0.44	1.41
4	*Beilschmiedia oppositifolia*	il	2.94	12.13	4.47	7.66	41.35	27.34	19.1	1.66	1.16
5	*Uapaca* sp.	il	3.43	6.32	6.48	—	67.4	66	41.24	2.25	1.7
6	*Cryptocaria* sp.#1	il	3.65	17.99	6.72	11.3	55.36	40.47	26.35	3.2	0.88
7	*Ochrocarpos mad/sis*	il	6.66	8.14	1.4	6.74	28.51	20.98	8.31	2.92	6.24
8	*Calophyllum milvum*	il	8.24	11.12	8.87	2.25	58.26	51.46	37.33	5.85	1.54
9	*Symphonia fasciculata*	il	4.56	9.68	8.58	1.1	68.91	63.36	46.4	2.47	4.6
10	*Cryptocaria* sp.#2	il	—	—	—	—	—	—	—	—	—
	Mean		4.63	10.65	7.01	4.11	58.3	53.16	36.72	2.33	2.04
	S.E.		0.63	1.08	0.87	1.38	4.9	6.55	5.25	0.54	0.67

CP = crude protein, BP = bound protein, AP = available protein, NDF = neutral detergent fiber, ADF = acid detergent fiber, Ls = sulfuric acid lignin, WSC = water-soluble carbohydrates. Mean values are % dry matter. il = immature leaves.

These additional food samples were eaten by either *Indri* or *Propithecus diadema* and included important seasonal food items such as tree bark, ferns, and fruits. Plant samples were assayed for total phenolics, hydrolyzable tannins, condensed tannins, and alkaloids. Ecological theorists have long proposed a defensive role for such plant secondary metabolites (Karban and Baldwin, 1997; Rosenthal and Berenbaum, 1992) and studies have suggested that these compounds act as deterrents in primate (as well as other mammalian) food choices (Glander, 1978; Hladik and Simmen, 1996; Hume, 1999; Lawler et al., 1998; McKey et al., 1981; Oates et al., 1977, 1980; Simmen et al., 1999). Tannins and alkaloids have been the most widely studied classes of secondary compounds in relation to folivory (Rosenthal and Berenbaum, 1991). Plant tannins can form indigestible complexes with digestive enzymes and ingested proteins and thus limit nitrogen assimilation by folivores (Hagerman and Butler, 1991); they may also have an antibiotic effect on gut microflora (Waterman and Mole, 1994). Nitrogen-based alkaloids can be potentially toxic by crossing cell membrane barriers and disrupting metabolic activity (Harborne, 1982) and include compounds such as strychnine and cyanide.

Nevertheless, no significant correlations between the preference of a particular food item by *Indri indri* and the item's corresponding level of putative antifeedants (total phenolics, hydrolyzable and condensed tannins, or fiber) were found. However, *Hematodendron glabrum* fruit, the only fruit eaten by *Indri* that was assayed, was quite low in phenolics and lacked alkaloids, and none of the other *Indri* food samples tested contained alkaloids, even though these items represented nearly half of *Indri*'s total annual diet. In contrast, sympatric *Propithecus diadema* routinely ate two alkaloid-containing species of fruit (not within the top ten preferred food items) and consumed soils twice as often during the study as did *Indri*. Soil consumption by *Indri* occurred on 22% of the sample days on which they were followed for full-day data collection (Powzyk, 1997). Geophagy can detoxify deleterious compounds (Diamond, 1999; Gilardi et al., 1999; Hladik, 1977a,b; Krishnamani and Mahaney, 2000; Oates, 1978). Results that show *Indri*'s limited intake of digestion-inhibiting carbon-based compounds (e.g., tannins) are either inconclusive or nonexistent, but they do appear to be avoiding potentially toxic alkaloids in their dietary choices. The entire secondary compound data set can be found in Powzyk and Mowry (2003).

Plant Species Consumed

Indri indri consumed 76 different plant species within the Mantadia research site, with an average of 11.19 ± 2.52 on a daily basis (Powzyk, 1997). At Betampona, *Indri* consumed a total of 42 plant species (Britt et al., 2002). This difference in plant species choice may be a reflection of forest type (plant species diversity) and/or a reflection of disturbance levels. Mantadia has not been selectively logged while Betampona has experienced both logging and hunting (Welch, personal communication) Lauraceae (35.5%), Clusiaceae (29.3%), and Myristicaceae (16.3%) were the most preferred plant families at Betampona and accounted for 78% of all identified feeding records. At Mantadia, the most preferred plant family was Lauraceae (26 plant species consumed, 34.2% of feeding time), followed by Euphorbiaceae, with four "Uapaca" species eaten (22.3%), including their immature leaves, galls, and seasonal flowers. The third most preferred plant family at Mantadia was the Clusiaceae with 13 species representing 16.8% of total feeding time (Powzyk, 1997). Thus, the top three plant families accounted for 73.3% of total feeding time observed. Interestingly, the fourth most popular plant family at Mantadia was Myristicaceae with a single species, *Haematodendron glabrum*, known locally as "Rara." This tree species represents a vital food resource of immature leaves and fruit for Mantadia *Indri*. Britt et al. (2002:235) found this plant species to be the "most preferred single food source" at Betampona and labeled it a "keystone species" for *Indri*. Betampona *Indri* consumed every aspect of this tree, including its mature foliage, immature foliage, fruit, bark, seeds, flowers, and petioles (Britt et al., 2002). Knowing which plant species are most preferred by *Indri* will have direct applications to its conservation (Britt et al., 2002). Pollock (1977) reported that *Indri* fed upon 62 plant species, yet this number was derived from several forest locations in and around the Special Reserve Analamazaotra.

Preferred Plant Types and Forest Height When Feeding

Indri indri fed 5–15 m above ground level for the majority of feeding records at Betampona with only 0.7% above 25 m (Britt et al., 2002), while at Mantadia, feeding heights varied from 1 to 32 m with a preferred height of 12.7 m (Powzyk, 1997). Clearly, *Indri* chooses most of its food from trees: 98.3% of foods consumed at Mantadia came from trees, followed by 0.8% from lianas, and 0.1% from parasitic plants. *Indri* was not observed to feed on any ground herbs, hemiepiphytic plants, or ferns, all of which are eaten by *Propithecus diadema* at Mantadia. *P. diadema* spent more time on or closer to the ground than *Indri*. *P. diadema* often came down to the ground to feed on fallen fruit in the leaf litter, as well as browsing on low-growing herbs, ferns, and lianas. One particular parasitic plant genus, *Bakerella*, comprised 17% of *P. diadema*'s flower eating feed time while *Indri* spent just 0.11% of its feed time on this plant genus (Powzyk, 1997). Following a cyclone in 1994, numerous canopy gaps formed in Mantadia from the loss of large mature trees. Lianas were often the first colonizers in these new sun-lit patches, and *P. diadema* spent long periods of time feasting on the new foliage from these quick-growing vines. *Indri* did not appear to benefit from this sudden resource availability, but rather incurred a cost since many of the fallen trees had been their food trees (Powzyk, personal observation).

Feeding Behavior and Activity Patterns

Ecological comparisons between sympatric *Indri indri* and *Propithecus diadema* at Mantadia provided insight into the effects of diet on behavior. The more folivorous *Indri*'s feeding bouts were fewer in number but longer in duration than those of *P. diadema*, whose diet was more varied in both the number and types of foods eaten. *Indri*'s average number of daily feeding bouts changed seasonally and ranged from 14.5 to 27.4, with fewer feeding bouts occurring during the dry months (Figure 2). *P. diadema* usually had twice as many daily feeding bouts as *Indri* in any given month. The availability of food types also corresponded to the duration of *Indri*'s feeding bouts: feeding bouts were shortest on ubiquitous young leaves with increasingly longer bouts occurring on more ephemeral flowers and fruit (see Figure 2). *Indri*'s longest feeding bouts were observed in an adult female who fed continuously on a *Cryptocarya* (Lauraceae) fruit; one bout lasted 2 hours and 37 minutes, while another bout lasted for 1 hour and 27 minutes. This individual carefully chewed and softened the tough exocarp, causing the husk to tear open, whereby the seeds were squeezed out while the remaining fruit was dropped (Powzyk, 1997).

Indri indri also had significantly shorter daily path lengths (yearly means for dpl: *Indri* = 740 m, *Propithecus diadema* = 1629 m) and shorter active periods than *Propithecus diadema* (Powzyk, 1997). The *Indri* is highly diurnal; on one *Indri* sample day, the focal pair awoke at 9:12 and settled into a sleep site at 13:18, while *P. diadema* typically spent an additional 2–3.7 hours active per day than *Indri* (Powzyk, 1997). *Indri* established/defended their territories using long call vocalizations and appeared to avoid all intergroup contact with no observed intergroup fighting within the Mantadia site. Within the smaller Analamazaotra Special Reserve, intense intergroup fighting has been observed, although this may be an outcome of a "hyperconcentration" of *Indri* owing to a lack of viable corridors for animal transfer (Petter and Peyrieras, 1974). Not surprisingly, Analamazaotra *Indri* had smaller territories than Betampona or Mantadia *Indri* (Glessner and Britt, 2005; Pollock, 1975a,b, 1977; Powzyk, 1997) (Table 1). In contrast to *Indri*, *P. diadema* maintained their territorial defense with more energetically costly behaviors such as extensive territorial patrols, scent marking, and intergroup fighting. *P. diadema* also exhibited significantly more play behavior than *Indri* both in the trees and when *P. diadema* ventured down to the ground to wrestle (Powzyk, 1997). Finally, *Indri*'s daily defecation rate was half that of *P. diadema*'s (2 versus 4.7), while *Indri* spent significantly more time resting during the 12-hour daylight period than did *P. diadema* (Powzyk, 1997). These are important behavioral adaptations since increased resting facilitates efficient fermentation of plant fiber. Such "inactivity" allows blood to be relegated to its digestive tract; when a primate is traveling, its sympathetic nervous system sends blood from its gut out to the limb muscles and heart (Smith, 1977). Based on *Indri*'s digestive anatomy, dietary choices, and behavioral patterns, we classified it as an animal who makes efficient use of its cecocolic fermenting ability while conserving energy (Powzyk and Mowry, 2003).

CONCLUSIONS

Madagascar is a refugium insomuch that many conservative eutherians that colonized the island have since undergone spectacular radiations (Eisenberg, 1981; Yoder, 2003; Yoder and Flynn, 2003). *Indri indri* may well be the largest folivore on the island and in this chapter we have detailed numerous adaptations that reveal the ecological specificity of this remarkable indriid. One of the major selection pressures acting upon *Indri* is its preference for a food source that likely yields less energy when compared to a diet of fruit. This may predispose *Indri* to a lifestyle that can be described as an "energetic minimizer."

Indri does not actively patrol its territorial boundaries, nor does it scent mark judiciously from its glandular anogenital region but achieves territorial defense (and individual recognition) through long calling. The rate of anogenital scent marking by *P. diadema* spiked during the breeding season at Mantadia, and remarkably *Indri* showed this same spike but in the number of long calls given (Powzyk, 1997). In contrast to other lemur species, *Indri* lack scent glands on the throat, chest, head, arms, and wrist, with glandular fields in evidence around the anus region (Petter et al., 1977; Pollock, 1975a,b; Powzyk, 1997). *Indri* does appear to cheek mark with salvia throughout their territory (Powzyk, 1997), a marking system that can also be found in *Microcebus* with its unspecialized salivary glands (Glatston, 1983). Although anogenital scent marks by *Indri* were observed, they were significantly lower in frequency than for the sympatric *P. diadema* (Powzyk, 1997).

Indri appears to rely more on the auditory (long calling) rather than the more lemur-typical olfactory (scent gland marking) form of communication. The two types of signals can achieve similar results, yet vocalization may be far less costly (energetically) for a 6.5-kg animal that must travel via vertical clinging-leaping throughout a relatively large (34–40 ha) territory. In studies of bird vocalizations, the cost of singing was found to be relatively "cheap" when compared to most other activities, especially patrolling territorial boundaries (Gaunt, 1987). Remarkably, when the olfactory region of the *Indri* brain was examined, researchers (Stephens and Andy, 1969, 1970; Stephens et al., 1982) found that *Indr*i showed the highest reduction of all 20 prosimians tested. Therefore, *Indri* has less olfactory tissue with which to interpret scent marks when compared to other lemur species, further evidence that it may be emphasizing a territorial defense that is less costly energetically when compared to the territorial behaviors of *P. diadema*.

Many of *Indri's* behaviors relate to its dependence on immature leaves. Although these food items are ubiquitous within the Mantadia study site (Powzyk, 1997), they may levy a cost in that it predisposes an animal to limited movement and protracted bouts of resting which in turn enhance fermentation efficiency.

Overall, *Indri indri* has a body type well suited to life in the trees. It is an exceptional leaper with the ability to move through and search for palatable food in its forested home. Coupled with these external morphological features, *Indri* has internal specializations that allow it to efficiently convert its fiber-rich diet into assimilable energy. In this chapter we have detailed *Indri*'s feeding behaviors and dietary preferences, all of which have had major repercussions on other aspects of its behavioral repertoire.

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CHAPTER SEVENTEEN

Behavior and Ecology of Gentle Lemurs (Genus *Hapalemur*)

Chia L. Tan

INTRODUCTION

Gentle lemurs (genus *Hapalemur*) are peculiar lemurs. They are the ecological equivalent of pandas in the primate world. No other extant primates are known to subsist almost exclusively on bamboo and/or grasses. Therefore, it comes as no surprise that these primates are also known as bamboo lemurs. Currently, the genus includes three species: *H. griseus*, *H. aureus*, and *H. simus* (Table 1). *H. griseus*, with several geographic variants, is distributed widely in Madagascar. *H. aureus* and *H. simus*, in contrast, have extremely narrow ranges limited to the southeastern central rainforests. Groves (2001) recently promoted *H. g. occidentalis* and *H. g. alaotrensis* to full species status and resurrected *Prolemur* as the genus for *simus*. Due to controversies involving *Hapalemur* phylogeny (see Fausser et al., 2002; Pastorini et al., 2002, 2003) and to avoid taxonomic confusion, Groves's nomenclature is not adopted here.

Because bamboo features prominently in the diet of *Hapalemur*, one cannot understand the animals without knowledge about the plant. Bamboo belongs to the grass family (Poaceae or Gramineae), which includes rice, millet, and reeds. The true bamboo (subfamily Bambusoideae) can be divided into woody and herbaceous bamboo (Clark, 1997). Approximately 32 endemic woody bamboo species,

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Table 1. Extant *Hapalemur* taxa[a]

Scientific name	Common name	Body weight (kg)	Distribution
H. g. griseus	Gray Gentle Lemur or Eastern Lesser Bamboo Lemur	0.9[b]	Eastern rainforests
H. g. alaotrensis	Alaotran Gentle Lemur	1.2[c]	Surrounding marshes of Lac Alaotra
H. g. meridionalis	Southern Gentle Lemur or Southern Lesser Bamboo Lemur	—	Lowland rainforest of Station Forestière de Mandena, near Fort Dauphin
H. g. occidentalis	Western Gentle Lemur or Western Lesser Bamboo Lemur	—	Central west and northwest dry and subhumid deciduous forests
H. aureus	Golden Bamboo Lemur	1.4[b]	Southeastern central rainforests
H. simus	Broad-nosed Gentle Lemur or Greater Bamboo Lemur	2.6[b]	Southeastern and possibly central-eastern rainforests

[a] General reference: Mutschler and Tan (2003).
[b] Species average, based on individuals captured at Ranomafana National Park (Tan, in preparation).
[c] Mutschler et al. (2000).

provisionally assigned to 10 genera, are recognized in Madagascar (Dransfield, 2000). This diversity and high degree of endemism of woody bamboo reflect Madagascar's long geographic isolation. Undoubtedly, the evolution of *Hapalemur* is intimately linked with the evolution of bamboo in Madagascar and the anthropogenic effect on this plant after colonization of the island. Today, the majority of Malagasy woody bamboo species are found in the remaining eastern humid forests, although some have adapted to the drier climate of the west (Dransfield, 2000). In the southeastern central region, for example, *Hapalemur* spp. (specifically *H. g. griseus*, *H. aureus*, and *H. simus*) feed on a variety of bamboo plants, some of which contain cyanogenic compounds in the actively growing parts (Glander et al., 1989; Tan, 1999, 2000, and unpublished data) (Table 2). The mechanism by which the three species of *Hapalemur* manage to prevent cyanide poisoning has not been determined. Processing cyanogens to avoid the toxic effects may involve a specific enzymatic pathway that is unique to the lemurs and may yield insights into *Hapalemur*–bamboo coevolution.

Since the first field study of *Hapalemur* began in the 1960s, there have been several subsequent investigations, including one that made the discovery of *H. aureus* in 1986 (Meier et al., 1987; Petter, 1962; Petter and Peyriéras, 1970; Petter et al., 1977; Pollock, 1986; Wright, 1986; Wright et al., 1987). More recently, a new generation of researchers has expanded our knowledge about these primates with in-depth studies of *H. g. alaotrensis* and *H. g. griseus* (Grassi, 2001; Mutschler et al., 1998, 2000; Nievergelt et al., 1998; Overdorff et al., 1997; Waeber and Hemelrijk,

Table 2. Bamboo species consumed by *Hapalemur* in southeastern central Madagascar

Scientific and vernacular name	Culm	Location	Presence of cyanide (and parts tested)[c]
Cathariostachys madagascariensis[a] Volohosy	Woody	Talatakely, Ranomafana National Park (RNP) Ambatolahy Dimy Antsenavolo	Yes (young leaf bases, branch shoots, and ground shoots)
Cephalostachyum cf. *perrieri*[b] Tsimbolovolo lavalavaravina	Viny	Various sites in RNP Tolongoina	No
Cephalostachyum sp.[b] Tsimbolovolo boriboriravina	Viny	Various sites in RNP	No
Nastus elongatus[b] Volofitsiokafo	Woody	Various sites in RNP Tolongoina	Yes (branch shoots)
Nastus sp.[b] Tsimbolovolo maitso	Viny	Various sites in RNP	No
Arundinaria ambositrensis[b] Volotsangana	Woody	Various sites in RNP (excluding Talatakely) Tolongoina	No
Valiha diffusa[a] Volojatsy (or vologasy)	Woody	Ifanadiana Kianjavato	Yes (ground shoots)

[a] Dransfield (1998).
[b] S. Dransfield (personal communication).
[c] Qualitative assay using Feigl-Anger test strips (C. Tan, unpublished data).

2003) and for the first time, simultaneous comparison of three *Hapalemur* species living in sympatry (Tan, 1999, 2000). The scope of this chapter, therefore, is to provide an overview of *Hapalemur* behavior and ecology, using information gathered from these studies. The focus will be on key aspects such as habitat, diet, activity, ranging, social organization, and reproduction. Finally, the chapter concludes with an update on the current conservation status of *Hapalemur* taxa.

HABITAT

Populations of *H. griseus* ssp. are found in a variety of habitats in Madagascar. *H. g. griseus* occurs in the eastern lowland and montane rainforests (Mittermeier et al., 1994; Tattersall, 1982). This subspecies is sympatric with *H. aureus* and *H. simus* in parts of Ranomafana National Park (RNP) and Andringitra National Park (ANP) (Sterling and Ramaroson, 1996; Tan, 1999, 2000; Wright, 1992). In RNP, *H. g. griseus* inhabits both undisturbed and disturbed forests where bamboo is interspersed with other vegetation (Tan, 1999, 2000). *H. g. alaotrensis*, in contrast, is confined to the marshes surrounding Lac Alaotra. The dominant vegetation growing in these wetlands is papyrus (family Cyperaceae) and reeds (family Poaceae), and bamboo is absent (Mutschler, 1999a; Mutschler and Feistner, 1995). Though lacking a well-defined geographic range, *H. g. meridionalis* is found in the south, specifically in the lowland rainforest of Station Forestière Mandena (10 km north of Tolagnaro) (Warter et al., 1987). Mandena is a degraded littoral forest with patchy areas of bamboo, and a relatively high density of *H. g. meridionalis* has been reported in an area without any bamboo (Mutschler and Tan, 2003). *H. g. occidentalis* has a disjunct distribution with isolated populations in the central west (Tsingy de Bemaraha, Forêt de Tsimembo, Bongolava Massif, Namoroka National Park, Baly Bay, and Tsiombikibo) and northwest (Manongarivo Special Reserve, Sambirano River valley, and along the coast between Maromandia and Beramanja, including the Ampasinidava peninsula) (Curtis et al., 1995; Goodman and Schütz, 2000; Hawkins et al., 1998; Petter and Andriatsarafara, 1987; Petter et al., 1977; Rakotoarison et al., 1993; Raxworthy and Rakotondraparany, 1988; Tattersall, 1982). In addition, an unconfirmed *H. griseus* ssp., which may be *H. g. occidentalis*, has been sighted in Ankarana Special Reserve in the north (Hawkins et al., 1990). These populations have been reported to live in dry to subhumid deciduous forests where bamboo may or may not exist (Mutschler and Tan, 2003).

H. aureus is known from few sites in southeastern central Madagascar, and its range is extremely restricted. Besides RNP and some forest fragments to the east (e.g., Tolongoina), this species occurs in ANP and in the forested corridor connecting these two protected areas (Goodman et al., 2001; Irwin et al., 2005; Mutschler and Tan, 2003; Sterling and Ramaroson, 1996; C. Tan, unpublished data). At Talatakely, RNP, *H. aureus* coexists with *H. g. griseus* and *H. simus*. This site was selectively logged in the mid-1980s and contains both woody and viny bamboos (Tan, 1999, 2000).

Current populations of *H. simus* occur in limited localities in southeastern central rainforests, including the aforementioned RNP and ANP (Mutschler and Tan, 2003; Sterling and Ramaroson, 1996; Tan, 1999, 2000). Although *H. simus* may be associated with the presence of large woody bamboo, small remnant populations have been encountered in highly degraded areas, such as Kianjavato and Karianga, where there is little or no bamboo (Tan, 1999, 2000; C. Spoegler, personal communication). A recent survey in the central eastern region near Torotorofotsy (ca. 10 km northwest of Andasibe) revealed indirect evidence of *H. simus* (Dolch et al., 2004). If confirmed, this would be the northernmost population of *H. simus.* It should be noted, however, that both museum collection and subfossil records indicate that *H. simus* had been widely distributed throughout northern, northwestern, central, and eastern Madagascar, overlapping in ranges with *H. griseus* ssp. As recently as about 130 years ago, *H. simus* occupied the eastern rainforests, from the Bay of Antongil in the north to Vondrozo in the south (Godfrey and Vuillaume-Randriamanantena, 1986).

DIET

In comparison with the other subspecies, the diet of *H. g. griseus* is the best known and includes a diverse array of plants. In Analamazoatra Special Reserve (ASR), Wright (1986) reported that bamboo (*Bambusa* sp.) constitutes 90% of the animals' diet during the austral winter months. Like Pollock (1986), Wright also found *H. g. griseus* eating leafy parts of other plants and some fruit. Long-term studies conducted in RNP confirmed that bamboo is the mainstay of *H. g. griseus* (Grassi, 2001; Overdorff et al., 1997; Tan, 1999, 2000). In particular, at Talatakely, approximately 80% of the lemur's annual diet is comprised of bamboo (*Cathariostachys madagascariensis*, *Cephalostachyum* cf. *perrieri*, *Cephalostachyum* sp., *Nastus elongatus*, and *Nastus* sp.); parts ingested include the base of young leaves, immature pseudopetioles, branch shoots (i.e., emerged from the nodes), and ground shoots. The animals also consume a variety of nonbamboo foliage, fruit, and flowers (Tan, 1999, 2000). In fact, ongoing research (1996–2006) at Talatakely shows that the total number of food plants has exceeded 40 species for *H. g. griseus* (C. Tan, unpublished data).

By contrast, *H. g. alaotrensis* is strictly folivorous, relying solely on leaves and grasses around Lac Alaotra marshes. In a 15-month study, Mutschler (1999a,b) documented the animals eating 11 plant species; of these, 4 represented >95% of the total feeding records. Pith of papyrus stems (*Cyperus madagascariensis*) as well as reed shoots (*Phragmites communis*), southern cut grass (*Leersia hexandra*), and millet (*Echinochloa crusgalli*) make up the principal diet (Mutschler, 1999a,b; Petter et al., 1977; Pollock, 1986).

Little is known about the feeding habits of the other subspecies of *H. griseus.* Petter et al. (1977) reported *H. g. occidentalis* eating fruits of Madagascar plum (*Flacourtia ramontchi*) and wild dates in Forêt de Tsimembo. Additionally, in

Bemaraha and Sambirano, the animals were observed feeding on items such as liana flowers and pseudopetioles of a woody bamboo (Mutschler and Tan, 2003). There is no published dietary information on *H. g. meridionalis* to date.

The diet of *H. aureus* is known only from Talatakely, RNP. Nearly 90% of the animals' diet is comprised of bamboo, primarily the giant bamboo (*Cathariostachys madagascariensis*) (Tan, 1999, 2000). Whereas young leaf bases and young pseudopetioles of bamboo are consumed throughout the year, branch shoots and ground shoots are seasonal food items. *H. aureus* also supplements its diet with leaves, stems, fruit, and flowers of other plants and mushrooms. There is extensive dietary overlap between *H. aureus* and *H. g. griseus*; however, the food diversity of *H. aureus* is relatively lower.

Bamboo culm pith and shoots represent the main components of the diet of *H. simus* (Petter et al., 1977; Tan, 1999, 2000; Wright and Randriamanantena, 1989). At Talatakely, RNP, *H. simus* specializes on the giant bamboo, which accounts for 95% of the annual diet (Tan, 1999, 2000). Unlike *H. aureus* and *H. g. griseus* that feed on only the tender sections of bamboo leaves (i.e., base of young leaves and immature pseudopetioles), *H. simus* consumes all parts of leaves, including mature leaf blades. Furthermore, *H. simus* differs from the two sympatric congeners in having a strikingly seasonal diet—shifting from eating mainly ground shoots in the warm-wet season to culm pith in the cold-dry season (Tan, 1999, 2000). In highly disturbed forests, *H. simus* has been observed to survive on various plant materials. For example, in Kianjavato, animals were seen raiding rice crops and feeding on shoots of a woody bamboo (*Valiha diffusa*), young leaf bases of a viny bamboo, flowers of traveler's palm (*Ravenala madagascariensis*), jackfruit (*Artocarpus integrifolius*), mango (*Mangifera indica*), figs (*Ficus* sp.), palm (*Dypsis* sp.), and leaves of African ginger (*Aframomum* sp.) and kikuyugrass (*Pennisetum clandestinum*) (Meier and Rumpler, 1987; C. Tan, unpublished data).

ACTIVITY PATTERN

Even though captive individuals of *H. g. griseus* are known to exhibit nighttime activities (Pollock, 1986; Santini-Palka, 1994), field investigations carried out during daylight hours and nocturnal surveys all suggest that the animals are diurnal (Grassi, 2001; Overdorff et al., 1997; Pollock, 1986; Tan, 2000; Wright, 1986). Except in the degraded forest of Maroantsetra, *H. g. griseus* individuals have been observed to travel after dusk (16:00–21:00) (Petter et al., 1977). In Talatakely, RNP, a recent study involving 24-hour observations lends further support that the animals are strictly diurnal in the southeast (C. Tan, unpublished data). Daytime activity budget shows that *H. g. griseus* spends about 41% resting, 48% feeding, and 9% traveling (Figure 1) (Tan, 2000).

H. g. alaotrensis demonstrates cathemerality, or day and night activities (Mutschler, 2002; Mutschler et al., 1998). Although the animals are active mainly during the day, they exhibit significant activity at night that does not seem to be

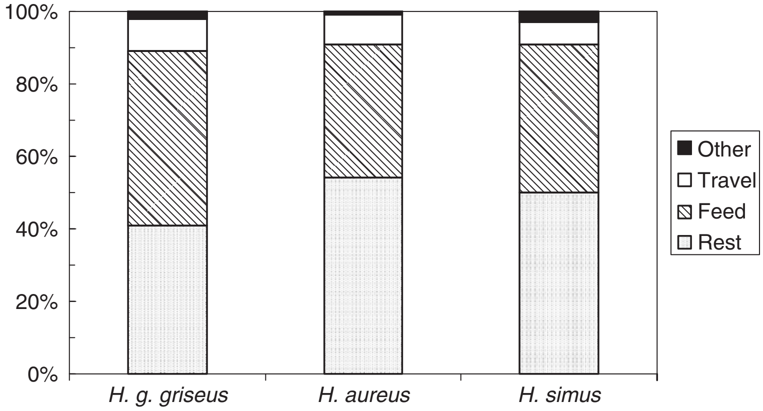

Figure 1. Activity budget of three sympatric *Hapalemur* species in Talatakely, Ranomafana National Park.

affected by moonlight conditions. Additionally, year-round nocturnal surveys indicate that they have at least one activity bout per night and each bout lasts ≥30 minutes (Mutschler et al., 1998; Mutschler and Tan, 2003).

The activity pattern of *H. g. meridionalis* and *H. g. occidentalis* is poorly known. Opportunistic sightings suggest that *H. g. meridionalis* may be diurnal (Mutschler and Tan, 2003). In Bemaraha and Sambirano, *H. g. occidentalis* individuals were found to be active primarily at night during the dry season (July–September) (Mutschler and Tan, 2003).

In Talatakely, RNP, *H. aureus* is diurnal as indicated by 24-hour observations (C. Tan, unpublished data). The activity pattern shows a distinct midday rest period between 09:00 and 13:00. *H. aureus* spends approximately 54% of the daytime resting, 37% feeding, and 8% traveling (Figure 1) (Tan, 2000).

Petter et al. (1977) suggest *H. simus* individuals are active only in the daytime. However, in Talatakely, RNP, the animals exhibit a cathemeral activity pattern throughout the year (Tan, 2000 and unpublished data). Diurnal time budget data show that *H. simus* spends 50% of the time resting, 41% feeding, and 6% traveling (Figure 1) (Tan, 2000).

RANGING

In RNP, the home range of *H. g. griseus* groups measures 15–20 ha (Grassi, 2001; Overdorff, et al. 1997; Tan, 1999, 2000). Groups are highly territorial; both adult males and adult females have been observed to actively defend their territory against neighboring conspecific groups. Territorial defense behaviors may include scent-marking, vocal display, and chasing. In the proximity of sympatric *H. aureus* and *H. simus*, *H. g. griseus* behaves indifferently (Tan, 2000).

H. g. alaotrensis groups are territorial and occupy small home ranges varying in size from 0.6 to 8 ha (Mutschler, 1999a; Mutschler and Tan, 2003; Nievergelt et al., 1998). Currently, no such information is available for the other two subspecies.

In Talatakely, RNP, *H. aureus* groups have home ranges averaging about 30 ha (Tan, 1999, 2000). Like *H. g. griseus*, they are also extremely territorial. In fact, they are the only *Hapalemur* species that produce complex, sex-specific vocal duets as a form of territorial defense against conspecifics. *H. aureus* individuals are unperturbed around *H. g. griseus* but have been observed to chase *H. simus* (C. Tan, unpublished data).

The home range of *H. simus* in Talatakely, RNP, encompasses over 60 ha (Tan, 1999, 2000). Whereas *H. g. griseus* and *H. aureus* utilize their home ranges more or less evenly, *H. simus* shows intensive use of core areas. Specifically, areas dominated by the giant bamboo are heavily utilized whereas other areas are mostly used during travel (Tan, 2000). Because only one group of *H. simus* is present in Talatakely, it is unclear whether or not the animals are territorial against conspecifics.

SOCIAL ORGANIZATION

The majority of *H. g. griseus* groups contain 2 to 7 individuals, although some may have as many as 11 individuals (Grassi, 2001; Overdorff et al., 1997; Petter et al., 1977; Pollock, 1986; Tan, 1999, 2000; Wright, 1986). The social organization is variable: groups may consist of a breeding pair or a breeding male with two breeding females (Pollock, 1986; Tan, 1999, 2000). Both sexes are known to disperse from natal groups (Grassi, 2001; Tan, 2000). Preliminary data suggest that females are socially dominant over males (C. Tan, unpublished data).

H. g. alaotrensis are found in small groups with no more than 9 individuals. About 50% of the groups are family groups but a considerable number (35%) include two breeding females. In addition, the dispersal pattern shows that males and females both migrate (Mutschler et al., 2000; Nievergelt et al., 2002). There is clear female dominance in *H. g. alaotrensis*, and more than 90% of all conflicts are over food (Waeber and Hemelrijk, 2003).

Small group sizes (of up to 6 or 7 individuals) have been reported for *H. g. meridionalis* and *H. g. occidentalis* (Goodman and Schütz, 2000; Mutschler and Tan, 2003; Raxworthy and Rakotondraparany, 1988). No additional social information is available.

H. aureus generally lives in small family groups (Meier et al., 1987; Tan, 1999, 2000; Wright and Randriamanantena, 1989). In Talatakely, RNP, 80% of *H. aureus* groups contain a breeding pair; however, there can be two breeding females and up to 8 individuals in the group. Long-term demographic data collected between 1996 and 2006 show that both sexes migrate. There is no clear dominance hierarchy between the sexes (C. Tan, unpublished data).

The *H. simus* group in Talatakely, RNP, consists of one breeding male and two breeding females (Tan, 1999, 2000). The maximum number of individuals in the group at one time is 13. In highly disturbed areas, multimale/multifemale groups (of up to 30 individuals) have been reported (Andriaholinirina et al., 2003; C. Spoegler, personal communication). In RNP, only males disperse and females remain in their natal group (Tan, 2000). Furthermore, there is evidence supporting male dominance, particularly during feeding context, in this species (C. Tan, unpublished data).

REPRODUCTION AND INFANT DEVELOPMENT

In RNP, *H. g. griseus* individuals primarily mate in June–July and give birth in October–November, with a gestation length of about 137 days (Tan, 2000). Elsewhere, in Maroantsetra and ASR in particular, births can occur as late as January (Petter and Peyriéras, 1970; Pollock, 1986). Females generally produce a singleton but twinning has been reported in captivity. The interbirth interval is 1 year (Tan, 2000). Furthermore, *H. g. griseus* exhibits infant parking behavior. Infants are orally transported from birth to 2 weeks of age before they are capable of clinging onto their mother. At 3 weeks, infants begin tasting solid foods, and at 6 weeks, they begin eating bamboo and other plants. Weaning occurs after 4 months (Tan, 2000).

Around Lac Alaotra, the birth season of *H. g. alaotrensis* starts in September and ends in February (Mutschler, 1999a). In both captive and wild populations, the rate of twinning is high (≥40%) (Mutschler et al., 2000; Nievergelt et al., 2002). The reproduction of the other *H. griseus* ssp. is unknown.

In RNP, *H. aureus* individuals have been observed to mate in July and August with births occurring in late November and December. The gestation length is approximately 138 days and females give birth to a single infant, once a year. Like *H. g. griseus*, *H. aureus* also parks and transports infants orally (Tan, 2000; Wright and Randriamanantena, 1989). Infants show interests in solid foods as early as 6 weeks old; they begin ingesting bamboo and other plant materials after 10 weeks of age. At 6 months, infants are weaned (Tan, 2000).

The mating season of *H. simus* in RNP is between May and June. After a gestation period of about 149 days, infants are born in October and November. The litter size is one and interbirth interval is 1 year. Unlike the two congers, *H. simus* does not practice infant parking. Mothers continuously carry their young for the first 4 months. Infants were observed feeding on bamboo at 8 weeks but they continue to suckle until they are 8 months old (Tan, 2000).

CONSERVATION STATUS

One of the overwhelming threats to *Hapalemur* and all other lemurs in Madagascar is habitat loss. Because of their dietary specialization, *H. g. alaotrensis*, *H. aureus*, and *H. simus* are particularly vulnerable to microhabitat changes. Protecting key habitats from human development, therefore, is paramount to these lemurs’ survival. Currently, *H. g. alaotrensis*, *H. aureus*, and *H. simus* are listed as "critically endangered" based on the updated IUCN Red List criteria, and *H. g. griseus, H. g. meridionalis*, and *H. g. occidentalis* are placed in the low conservation priority categories, largely due to insufficient data for accurate evaluation.

Urgent attention is needed for *H. g. alaotrensis*, presently limited to 220 km^2, or merely 3% of the wetlands surrounding Lac Alaotra, Madagascar's most important rice-growing region. Agricultural expansions into the shallow reaches of the lake and hunting have decimated this lemur's population dramatically in the past decades (Mutschler and Feistner, 1995). At present, the population is estimated to only be around 3500–5500 individuals. Several conservation organizations, most notably Durrell Wildlife Conservation Trust, have demonstrated long-term commitment in the region by promoting awareness and maintaining a steady stream of research and monitoring programs. However, the survival of the Alaotran gentle lemur cannot be ensured without incorporating Lac Alaotra into Madagascar's national park system. A breeding program managed by Jersey Zoo is currently in place.

The conservation status of *H. aureus* and *H. simus* may be worse than previously reported (Mittermeier et al., 1994). Both species not only have restricted ranges but also occur in extremely patchy distribution (Irwin et al., 2005; Mutschler and Tan, 2003). Consequently, there is no reliable population estimate for either species. Deforestation and fragmentation continue to be a major cause for concern. Hunting and exploitation of bamboo by local people also have contributed to the general population decline. In the case of *H. simus*, a conservation action plan is needed immediately to develop management strategies safeguarding the species from extinction. In RNP, *H. simus* may be the rarest diurnal lemur. Despite numerous survey efforts aimed to locate additional groups outside of Talatakely (Parcel III), only one other group was found in Miaranony (Parcel I) (Arrigo-Nelson and Wright, 2004; Ratelolahy et al., 2006; C. Tan, unpublished data). Currently, there are no viable captive breeding programs for either *H. aureus* or *H. simus.*

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SECTION FOUR

Lemur Adaptations to a Changing Environment, Natural and Anthropogenic Stress

CHAPTER EIGHTEEN

Considering Climate Change Effects in Lemur Ecology and Conservation

Patricia C. Wright

INTRODUCTION

Lemurs are a diverse and varied group of primates of over 70 species which occupy a wide variety of niches (Richard and Dewar, 1991; Wright, 1999; Mittermeier et al., 2006). The niche breadth is even greater if the subfossil lemurs are considered (Godfrey et al., 1997; Simons, 1997; Jungers et al., 2002). Lemurs show many "special" traits not seen in other primates, such as hibernation (Wright and Martin, 1995; Schmid, 1998a; Dausmann et al., 2004), female dominance (Jolly, 1966, 1984; Pollock, 1979; Young et al., 1990; Radespiel and Zimmerman, 2001; Pochron et al., 2003), low basal metabolic rate (Schmid and Ganzhorn, 1996; Schmid, 1998b), and long lifespan coupled with high infant mortality (Overdorff et al., 1999; Sauther et al., 2001; Gould et al., 2003; Pochron et al., 2004; King et al., 2005). The breadth of the primate niche and the peculiar characteristics of these more primitive primates may be a result of their long isolation sympatric with a special subset of taxa on this micro-continent (Wright, 1999). This paper reviews what we have learned from studying Madagascar plant phenology, weather patterns, and effects on lemur behavior and

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ecology. There appears to be a delicate balance between plants and lemurs mediated by climate. Cyclones, droughts, and extreme rain can affect the balance, limiting reproductive success. Although the lemurs have evolved resiliency strategies (hibernation or multiple litters or low metabolic rate) we are finding that small changes in the forest composition or the amount of rainfall can impact on lemur populations. These changes are presently amplified by human disturbance.

GEOGRAPHY AND CLIMATE

Madagascar, the fourth largest island in the world, rifted from Africa more than 150 million years ago, and has been isolated in its present position for over 88 million years (Krause et al., 1997). This location with the great expanse of ocean stretching to Australia, leaves Madagascar vulnerable to frequent annual cyclones from the east (Donque, 1975, Ganzhorn, 1995). The combination of ENSO (El Niño) cycles of drought and excess precipitation and these severe cyclones results in unpredictable weather patterns (Wright, 1999). Annual rainfall can vary tenfold across primate habitats with over 5 m in the Masoala (Vasey, 2004) to less than 500 mm in Berenty (Jolly, 1966). Annual variation in total rainfall even in one site can range from 1700 to 4300 mm (Wright and Andriamihaja, 2002). Severe droughts occur approximately once a decade (Richard et al., 2002). The fact that a fifth of Madagascar forest lies south of the Tropic of Capricorn results in fluctuations between hot and cold maximum and minimum temperatures. In addition, there is a lack of large tracts of lowland humid forests, compared to other continents (Goodman and Ganzhorn, 2004).

GEOGRAPHY AND FRUIT

Over 1500 km long, Madagascar supports as rich and varied a flora as can be found anywhere in the tropics (Reitsma, 1988; Gentry, 1993; Lowry et al., 1997; Schatz, 2002), including rainforest, dry subtropical forest, and spiny desert. Many animal taxa are absent from Madagascar because of biogeographical history and ungulates, monkeys, many birds, and many bat taxa simply never reached the island. What effect does this absence have on the ecology of the rainforest? In most rainforests the primary pollinators and seed dispersers are insects, birds, and bats (Fleming et al., 1987; Bawa et al., 1990). Terborgh (1986) estimated that as much as 80% of Amazonia's mammalian biomass depends on fruit resources. In contrast, in Madagascar 8% of the birds are frugivores (Fleming et al., 1987). Bats are also relatively depauperate in diversity with 28 species, and almost all are insectivorous (Peterson, 1995). Lemurs may be the primary pollinators and seed dispersers in the rainforests of Madagascar (Kress et al., 1992; Overdorff, 1992; Nilsson et al., 1993; Wright and Martin, 1995; Balko, 1998; Ratsimbazafy, 2002; Wright et al., 2005a). Black-and-white ruffed lemurs, red-bellied lemurs, and brown lemurs, medium-sized (2–4 kg) diurnal primates, pass vine and tree seeds intact, and these sprout faster and with less mortality than seeds not passed through a primate gut (Dew and Wright, 1998). Indeed, in the Malagasy ecosystem it is actually possible to single out one animal group, lemurs, which have the greatest biomass of frugivores and may qualify as "keystone mutualists" (Gilbert, 1980).

Although in other tropical rainforests, such as Kibale Forest, Africa (Struhsaker, 1997; Chapman, 2005), Colombia, South America (Stevenson, 2005), and Barro Colorado Island, Central America (Milton, 2005), long-term phenology data show that fruit production varies greatly for individual trees, there are fruits available throughout those forests all year. And in rainforests such as Manu Park in the Peruvian Amazon, keystone resources such as figs (large-crowned) or nectar (abundant patches) provide food for frugivores during extended periods of fruit scarcity (Terborgh, 1983; Wright, 1989). Madagascar rainforests, unlike other forests with 12–14 species of sympatric primates (Table 1; see Figure 1 and 2), have a much longer period without fruits, up to 6 months a year (Wright, 1999). And Madagascar has fewer fig species, a staple during months with scarce fruiting in other rainforests (Goodman and Ganzhorn, 1997). These long periods without fruits are reflected in the fact that few lemurs are obligate frugivores (Fleming et al., 1987; Goodman and Ganzhorn, 1997; Balko and Underwood, 2005) but nonetheless, fruits, seeds, and flowers compose 40–90% of the annual diet of *Eulemur, Varecia, Eulemur* ssp., *Propithecus, Microcebus, Cheirogaleus*, and perhaps *Mirza* and *Phaner* (Overdorff, 1991, 1993; Wright and Martin, 1995; Ganzhorn and Kappeler, 1996; Hemingway, 1996, 1998; Balko, 1998; Atsalis, 1999; Ganzhorn et al.,

Table 1. Lemur species in the rainforest site of Ranomafana National Park[a]

Species	Body mass (g)	Biomass (kg/km2)
Avahi laniger, woolly lemur	900	18
Propithecus edwardsi, Milne-Edward's sifaka*	5800	125
Cheirogaleus major, fat-tailed dwarf lemur*	350	18
Microcebus rufus, rufous mouse lemur*	42	4
Daubentonia madagascariensis, aye-aye	3500	7
Lepilemur sealii, sportive lemur	970	1.6
Hapalemur griseus, grey gentle lemur	935	20
Hapalemur aureus, golden bamboo lemur	1550	9.6
Prolemur simus, greater bamboo lemur	2450	12
Eulemur fulvus rufus, brown lemur*	2200	66
Eulemur rubriventer, red-bellied lemur*	2000	48
Varecia variegata, black-and-white ruffed*	3650	9

[a] Lemurs with an annual diet of at least 30% fruits are marked with an asterisk. Only one diurnal species (*Varecia variegata*) eats fruits for over 85% of its diet (Balko, 1998; Balko and Underwood, 2005).

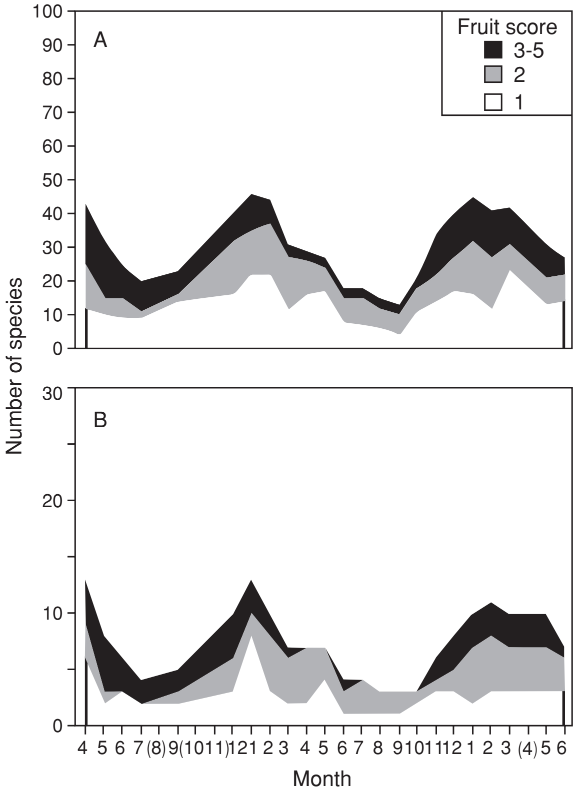

Figure 1. Phenology of fruit availability in 98 species (A) and a subset of 31 species eaten by sifakas (B) in the rainforest of Ranomafana National Park during April 1997 to June 1999. Note how changes in number of fruit species eaten by *Propithecus* track the overall richness of fruiting taxa. Fruit score 1 represents even one fruit observed in a tree, fruit score 2 represents up to a quarter of the branches having fruit, and fruit score 5 describes branches having abundant ripe fruits. Months in parentheses lack data. (Adapted from Wright et al., 2005a.)

1999; Powzyk and Mowry, 2003). *Varecia* stands out as the only lemur that eats fruits for about 90% of its diet (Balko, 1998; Vasey, 2004, 2005; Balko and Underwood, 2005). The evolution of three species of bamboo specialists (Tan, 1999) and many nocturnal leaf specialists (Ganzhorn, 1993; Warren and Crompton, 1997; Thalmann, 2001) may be a direct result of the adaptations of lemurs to these long periods of fruit scarcity (Wright, 1999). And this in turn may influence other traits such as unusually low metabolic rates of these primates (Ganzhorn, 1993; Schmid, 1998b; Pereira et al., 1999; Schmid and Speakman, 2000).

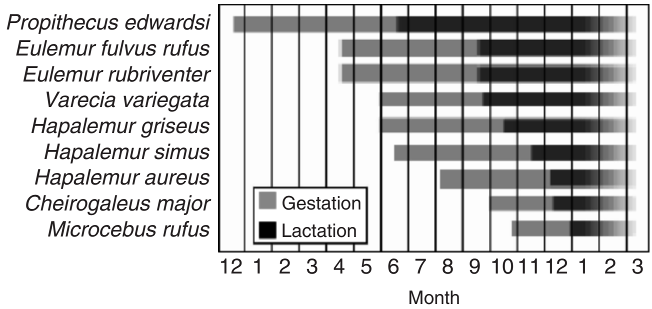

Figure 2. In Ranomafana National Park, the percentage of plant species fruiting, lemur species gestating, and lemur species lactating over a 2-year period. Note how lactation and fruiting peaks coincide. (Adapted from Wright et al., 2005a.)

Seasonality in Fruiting and Fruit Feeding

Despite the similarity of Madagascar in number of species and number of stems found in tropical forests of other geographic areas (Sussman and Rakotozafy, 1994; Abraham et al., 1996; Lowry et al., 1997), the fruiting patterns in Madagascar contrast with many rainforests (Ganzhorn et al., 1999; Wright, 1999; Wright et al., 2005a). Madagascar phenology plots in the eastern humid forest show a prolonged season of 4–6 months with few trees in fruit (Sauther, 1991; Overdorff, 1993; Hemingway, 1995; Powzyk, 1997). In addition, in Malagasy rainforest many canopy species produce flowers and fruit on irregular, asynchronous, or alternate year cycles (Morland, 1993a; Overdorff, 1993; Hemingway, 1995; Powzyk, 1997). A phenology study of 98 rainforest tree species showed that the number of species that carried fruit varied between 10 and 50 (Wright et al., 2005a). In fact, during the austral winter June–September of 1997 and 1998, the number of fruiting species remained below 25 and 20, respectively (Wright et al., 2005a). In contrast, the times of abundant fruiting of individual trees are typically during austral summer (Figure 1). Thus, Malagasy winters are not only characterized by a drop in the number of trees producing fruit but also a lack of species producing fruits.

In this study of rainforest tree phenology less than half of the 98 sampled plant species carried fruit in any single month, and the overall turnover of fruiting species calculated by cumulative fruiting curves showed from a fruiting peak when roughly 42% of species carry fruit, in 12 months over 70% of the species have fruited, and in 24 months up to 85% of species have fruited (Wright et al., 2005a). These numbers suggest a relatively high turnover rate of fruiting species which suggests that the flexible fruit feeding of most lemurs may be a good strategy in a Malagasy forest where species richness and composition of fruiting plants changes through time.

The seasonal cycling of Malagasy rainforest fruit diversity is strongly reflected in the diet of *Propithecus edwardsi*. During an annual cycle, these sifakas ate fruits of 31 out of the 98 species studied (Wright et al., 2005a). Fruiting of the 31 species resembled closely the overall seasonal patterns. However, sifakas appear to increase the relative diversity of fruit species consumed during the summer season compared to winter. Roughly 20% of concurrently fruiting species were eaten during the winter while up to 30% were eaten during the summer. This suggests that sifakas are opportunistic frugivores that track the overall fruit richness in the forest. In Figure 3 the percentage of fruit feeding minutes is plotted for one annual cycle. Sifakas spend about half of their feeding time on fruits during the summer while the proportion of fruit feeding drops to zero in July (Figure 3). The majority of sifakas' feeding time is spent eating leaves.

In contrast, in this same rainforest habitat, *Varecia variegata* specialized on a few species of fruits each month, and ranged widely to find these fruiting trees (Balko and Underwood, 2005). In fact, over an annual cycle the majority of feeding minutes was on four tree species at one site and two tree species at another (Balko and Underwood, 2005). Balko also found that the fruiting phenology was tied to patterns and distribution of rainfall with the peak of fruiting occurring after a 4-month period of consistent rainfall including consecutive cyclones in the months prior to the peak. The behavioural response to the lack of fruits during the winter months, is reduction of activity and energy expenditure (Morland, 1993a,b; Balko, 1998; Vasey, 2005).

In the dry western forests, there is a dramatic contrast in rainfall compared with the eastern rainforests. The dry season extends 6–8 months (Sorg and Rohner, 1996; Scholz and Kappeler, 2004). At Kirindy Forest there are 8 months with no rain, with a total annual rainfall of 800 mm (Scholz and Kappeler, 2004). The Beza Mahafaly Reserve and Berenty Reserve have less than 500 mm annual

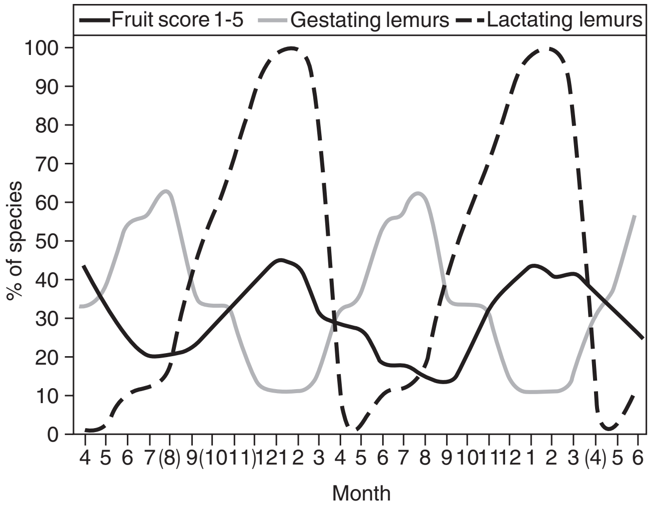

Figure 3. Fruit productivity and lemur lactation and gestation of 12 species over a 2-year period in Ranomafana National Park. (Adapted from Wright et al., 2005a,b.)

rainfall, and potentially throughout the south, droughts occur about once every 10 years (Gould et al., 1999; Jolly and Pride, 1999; Richard et al., 2002).

Lemur Response to Scarce Food Periods

Many lemurs respond to scarce fruits by eating more leaves. For example, *Propithecus edwardsi, Eulemur fulvus rufus*, and *Eulemur rubriventer* replace fruit feeding by increasing leaf eating (Overdorff, 1993). The seasonal shift in sifaka diet does not, however, indicate that these lemurs are completely able to replace fruits with leaves in terms of energy. *Propithecus edwardsi* lose up to 20% of their weight during winter season (Pochron and Wright, 2002; Wright et al., 2005a) suggesting that fruits play an important role even in this relatively folivorous lemur. At least 30% of sifaka feeding time is on fruits annually while species of the most frugivorous lemur genera, *Eulemur rubriventer* and *Varecia variegata*, spend 70 and 90% of their annual feeding time on fruits, respectively (Overdorff, 1991; Balko, 1998; Balko and Underwood, 2005). *Varecia*, a highly arboreal lemur weighing 3 to 4 kg, can be regarded as the only diurnal living lemur that is an obligate frugivore. It is also relatively specialized because fruits from five species make up to two-thirds of its annual diet (Balko and Underwood, 2005). This specialized frugivory is reflected in *Varecia* having large territories and extreme seasonal shifts in territory use (Balko and Underwood, 2005). However, even *Varecia* has been reported to survive on leaves after total loss of fruit productivity due to cyclone damage on trees, albeit with a substantial weight loss and lack of reproduction.

In addition to dietary shifts, all lemur species appear to be able to deal with the season of scarce resources by conserving energy (Ganzhorn, 1993; Morland, 1993b; Wright and Martin, 1995; Schmid and Ganzhorn, 1996; Warren and Crompton, 1997; Nash, 1998; Schmid, 1998a,b; Thalmann, 2001). Extreme responses to winter season are seen in small-bodied lemurs. *Cheirogaleus* spp. go into hibernation for 4–6 months every year (Wright and Martin, 1995; Schmid, 1998a; Fietz and Ganzhorn, 1999; Dausmann et al., 2004) and *Microcebus* also enter torpor for several days at a time (Fietz, 1998; Schmid, 1998b; Atsalis, 1999). *Lepilemur ruficaudatus* has the lowest basal metabolic rate recorded for any folivorous mammal (Schmid and Ganzhorn, 1996). Additional lemur traits that can promote energy conservation are thick insulating fur, increased resting behavior, maintenance of small group size, birth of low-weight infants, and relatively small brain size (Wright, 1999).

Fruits as Keystone Resources for Reproductive Output

Individual lemur species have strict breeding synchrony with a mating season typically lasting less than 2 weeks (Rasmussen, 1985; Sauther, 1991, 1998). This breeding synchrony is triggered by changes in photoperiodicity which makes lemurs among primates uniquely coupled with seasonal changes (van Horn, 1975; Pereira, 1993). Furthermore, in contrast to most primate communities in the Neotropics, Africa, or Asia (Terborgh, 1983; Gautier-Hion et al., 1985; Struhsaker, 1997; Chapman et al., 1999), lemurs do not have synchronous birth peaks across species. In Ranomafana sympatric lemurs show that while individuals within a species have synchronized births, different species gave birth at different times of the year (Wright, 1999; Wright et al., 2005a). However, while mating and birth seasons are not synchronized across lemur species, weaning appears to happen in all species during March–April (Wright, 1999; Wright et al., 2005a) in the rainforest.

One effect of the weaning synchrony is that all lemur species lactate during the period of increasing fruit availability (Figure 3). The smallest lemurs are able to fit their whole breeding cycle into the peak fruiting season, whereas sifakas, the largest of the living lemurs, lactate for the first 2 months without fruits. It is noteworthy that while lactation is the most energy-demanding stage of reproduction (Lee, 1997; Tilden and Oftedal, 1997), lemur newborns are small relative to their mothers. A newborn sifaka weighs around 100 g which is less than 2% of the mother's weight. Therefore, the initial cost of lactation is far less than during the peak fruiting season when the infant is 15–22% of the mother's weight (Wright, 1999). This will allow the infants to find abundant fruits, when the inexperienced forager needs to gain weight by eating large quantities of this abundant resource. The peak lactation synchrony among sympatric lemurs suggests that even sifakas, while relatively opportunistic fruit eaters, may rely on fruits as key resources for reproductive success. A close relationship between tree phenology and lemur reproductive success has also been found in the dry forest areas (Sauther, 1991, 1998; Gould et al., 2003).

HUMAN IMPACT, CLIMATE CHANGE, AND LEMUR SURVIVAL

If lemurs as a guild are adapted to rely on the timing of the phenology of fruits in order for lactation and weaning to succeed, what are the long-term effects should the climate parameters change causing the fruiting patterns to change? It is important to note that many of the fleshy-fruit plant species used by lemurs are also hardwood species favored by selective loggers in undisturbed forest (Wright et al., 2005b). These same species are eliminated first from fragments (Dehgan et al., 2000; Dehgan, 2003; Irwin, 2005). While loss of key fruit trees may not drive lemurs into extinction immediately, it may adversely affect reproductive success years after logging (Arrigo-Nelson and Wright, 2004a,b; Pochron et al., 2004; Dunham et al., 2005). Female body mass and successful reproduction are linked and there is strong evidence that females in selectively logged, fragmented as well as in cyclone-disturbed forest (Ratsimbazafy, 2002; Irwin, 2005; Arrigo-Nelson, 2006) weigh less than in undisturbed forest. This kind of "energetic debt" can affect reproduction decades after the logging has ceased. Ultimate survival of populations may be at risk even though the forest cover is present.

Although we know that there has been a dramatic desiccation of western and highland regions in the past thousand years (Gade, 1996; Simons, 1997; Godfrey et al., 1997), there are indications that deforestation and fragmentation of forests are presently continuing to produce a drier climate in Madagascar (Madagascar Weather Bureau, 1960–2005). Although drought is known to be a natural phenomenon, especially in the south of Madagascar (Gould et al., 1999), droughts may be becoming more frequent. Southern Madagascar underwent a severe drought in 1990–1991 (Sauther, 1998; Gould et al., 1999, 2003; Jolly, 2004). The impact on lemur populations in the spiny desert was dramatic. For example, the population of *Lemur catta* at Beza Mahafaly dropped from 85 individuals in early 1991 to 51 in 1994, with 21% of adult females, 80% of infants, and 57% of juveniles dying during the 6 months of drought (Gould et al., 1999). Ten years later the population had recovered to be 61 adult individuals, far below the 1991 figure of 85 adults (Gould et al., 2003). Additional droughts in 1997 and 2005 have been recorded. There is some indication that tooth morphology in recent generations may be evolving to cope with this drier environment (Cuozzo and Sauther, in press). If droughts continue to occur with greater frequency, there will be less opportunity for lemur populations to recover.

Recently, a study of Milne-Edward's sifakas has shown that dry years can even have an effect on lemur reproduction in a rainforest (King et al., 2005). The surprising result showed that older females (14% of the population) with worn teeth lost infants if the months of early lactation had low rainfall. It is hypothesized that the elder females cannot shear the leaves, which are more fibrous in dry months, to obtain moisture and nutrition necessary for successful lactation. This study showed how even a slight decrease in rainfall can have an impact on lemur populations.

CONSERVATION IMPLICATIONS

Ganzhorn and colleagues (1999) showed that low-level disturbance can have a large impact on forests and lemur populations. Recent surveys and censuses of lemurs have shown that there has been continued deforestation, fragmentation, and hunting in unprotected forested areas of Madagascar (Irwin et al., 2000, 2005; Lehman and Wright, 2000, 2005, Sussman et al., 2003). In a 2005 global mammal assessment, critically endangered species of lemurs were assessed, and these included *Eulemur albocollaris, Hapalemur aureus, Prolemur* (*Hapalemur*) *simus, Propithecus perrieri, P. candidus, and Varecia variegata* (Banks, in press; Mittermieier et al., 2006). These lemur species in particular are on the brink of extinction with the number of adult individuals perhaps in the hundreds, and these species will be challenged by any changes in climate.

Conservation action, such the Durban Vision of increasing the protected areas of Madagascar by three times in 5 years, has become a Madagascar governmental goal (Mittermeier et al., 2006). New tools such as GIS and satellite images are assisting with a landscape view to conservation to provide a more comprehensive approach to targeting populations at risk (Green and Sussman, 1990; Sussman et al., 2003; Irwin et al., 2005; Unruh et al., 2005). There is hope that long-term research on behavior, ecology, and demography is providing better data to target the issues to address that will assist in lemur conservation (Richard et al., 1991, 2002; Jernvall and Wright, 1998; Sauther, 1998; Overdorff et al., 1999; Sauther et al., 1999; Ganzhorn, 2002; Jolly et al., 2002; Wright and Andriamihaja, 2002, 2003; Pochron and Wright, 2003; Wright, 2004; King et al., 2005). Implementing programs that build on this knowledge may preserve the most endangered species into the future. However, the dangers of climate change including increased temperatures, continued desiccation, and increased frequency of cyclone and drought cycles must be closely monitored, as these findings increase the hidden and apparent dangers of losing lemur populations and eventually species survival.

It is hypothesized that the lemur's traits have evolved to cope with the unpredictable and climatically difficult island of Madagascar (Wright, 1999). Many of these traits are adaptations to either conserve energy or maximize the use of scarce resources (Gould et al., 1999; Vasey, 2005). Lemurs are resilient, but this resiliency has its limits. The effects of rapid climate change on the ecology and long-term survival of lemurs may be large, and further amplified by human disturbance and we need to consider these factors in our conservation planning.

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CHAPTER NINETEEN

Diet Composition, Foraging, and Feeding Behavior in Relation to Habitat Disturbance: Implications for the Adaptability of Ruffed Lemurs (*Varecia v. editorium*) in Manombo Forest, Madagascar

Jonah Ratsimbazafy

INTRODUCTION

The effects of hurricanes and the process of forest recovery have been well-studied in the Caribbean, especially in Puerto Rico (e.g., Sanford et al., 1991; Walker et al., 1991; Walker, 1995). However, long-term investigations of the effects of severe

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natural disaster upon forest recovery processes have received only limited study to date in most tropical rainforests. Behavioral strategies used by species or groups of species experiencing natural disasters are important with respect to their subsequent recovery in the particular forest affected. It can be extremely useful to determine how different species have responded to the cumulative impact of human activities and natural disturbances of their natural habitats (e.g., cyclone, flooding, windstorms, fires, or drought) in order to improve species management for conservation purposes. Primates are an excellent group of animals to study when attempting to understand the impact of habitat alterations on the fauna of a tropical forest (Struhsaker, 1997). They can be relatively easy to census, and individual species in a given community often respond differently to habitat disturbance (Lovejoy et al., 1986; Ganzhorn, 1994; Estrada and Coates-Estrada, 1996; Tutin et al., 1997). Indeed, primates respond in complex and varied ways to different types and levels of disturbance (Dunbar, 1988). Obviously, the effects of habitat disruption on a primate population depends upon the nature and extent of forest alteration, the time since such alteration took place, as well as the requirements and adaptability of each primate species inhabiting an area (Wilson and Wilson, 1975; Cowlishaw and Dunbar, 2000). Nevertheless, studies on primate communities show that some species are more adaptable and resistant than others in response to habitat disturbance (Cody, 1981; Ganzhorn et al., 1999).

It is also important to remember that dietary flexibility is an important feature of ecology of all primates, even though species can be characterized as favoring one type of diet (Cowlishaw and Dunbar, 2000), as dietary category of a particular species can vary from one habitat to another. For example, gorillas in Rwanda are typically terrestrial folivores, whereas those in Gabon are typically arboreal frugivores (Tutin et al., 1991).

Obtaining food of appropriate quality and quantity, and avoiding predators are often considered to be conflicting goals for animals living in the wild (van Schaik and van Hooff, 1985; Koivula et al., 1995). The difficulty of reconciling these conflicting goals may be aggravated when pristine forests become fragmented and/or altered. Currently, there is growing interest in learning how primates cope with extreme forest degradation and destruction (see Johns, 1986, 1991; Estrada and Coates-Estrada, 1996; Cowlishaw and Dunbar, 2000).

Empirical studies have demonstrated that the combined effects of natural catastrophe (e.g., cyclone or wind storm) and anthropogenic disturbance can cause levels of habitat destruction to increase spatially and temporally. Consequently, favored foods become less abundant, and different primate species must employ different behavioral strategies in response to environmental change. de Ruiter (1986) demonstrated that large groups of *Cebus olivaceus* may travel farther than small groups, and forage less on fruit, and large groups can compensate for loss of fruit by foraging more on invertebrates. Such behavior demonstrates the ability of *C. olivaceus* to feed opportunistically on available food resources. Research on *Callithrix flaviceps* indicates that this species can substitute gum for fruit as a source of carbohydrates during periods of food scarcity. This strategy enables *C. flaviceps* to survive in small patches of highly disturbed habitats (Ferrari and Diego, 1995).

The rainforest habitats of Madagascar constitute a good starting point for studying behavioral responses in lemurs, as habitat disturbance is not restricted to anthropogenic pressures. Indeed, natural disturbances are common, and are of great concern (Jolly, 1989; Richard and Connor, 1997; Wright, 1997). However, little has been written about the impact of natural disasters of this island, or the adaptive responses of lemurs to highly altered habitats. Therefore, in this study, I am interested in behavioral response strategies used by black-and-white ruffed lemurs (*Varecia variegata*) to the combined effects of human-induced pressures and natural disturbances. Long-term studies of ruffed lemurs have only been conducted in pristine, less disturbed forests and in captivity. It appears that *V. variegata* is susceptible to habitat disturbance to a far greater degree than are most other lemur taxa (White et al., 1995; Ratsimbazafy, 1999).

The ruffed lemur is one example of a group-living prosimian that exhibits great flexibility in grouping patterns (group size: 2–31) (Morland, 1991a,b; Rigamonti, 1993; Balko et al., 1995; Vasey, 1997; Balko, 1998; Ratsimbazafy, 2002a; Louis et al., 2005; Lehman et al., 2005). Ruffed lemurs are highly frugivorous (nearly 75% of their diet is fruits), but they can supplement fruits with varying amounts of other food resources (e.g., leaves, flowers, nectar) during times of food shortage (see Morland, 1991a; Rigamonti, 1993; White et al., 1995; Balko, 1998; Ratsimbazafy, 2002a,b; Ratsimbazafy et al., 2002; Mittermeier et al., 2006). *V. variegata* has been described as the most reproductively stressed of all primates because of its high maternal investment (Tilden, 1994). In other words, *Varecia* is an ideal candidate for this natural experiment (Ratsimbazafy and Ratsirahonana, 1998).

From June to July 1997 and from February 1999 to July 2000, research was conducted on the southernmost population of black-and-white ruffed lemurs, at Manombo forest, in southeastern Madagascar. Manombo is a good location to carry out investigations on lemur behavioral responses, as this environment combines human pressures with a history of stochastic windthrow damage from the annual cyclone season.

In this chapter, I discuss foraging and feeding behavior in relation to food availability used by *Varecia v. editorium* living in an abruptly disturbed habitat. In addition to collecting data on activities such as feeding, foraging, traveling, resting, and others (e.g., social and agonistic), I examined the relative use of different plant species by each individual during different seasons and throughout the study. In this way, I could document not only the proportions of fruits, leaves, nectar, and other items in the diet, but also individual preferences for certain plant species and families, and the role of alien plant species in the *Varecia* diet. My data were also compared with data on the same species collected in undisturbed habitats.

METHODS

Study Site Description

The study was conducted in a southeastern lowland rainforest in Madagascar, the Manombo forest. Manombo forest is comprised of the Manombo Special Reserve (MSR) and the Manombo Classified forest (MCF). Manombo is located in the province of Fianarantsoa at 23° 02'S and 47° 44'E (Figure 1). The MSR and CFM cover 14,000 ha, but only 9000 ha remains forested (Ratsimbazafy, 2002a). The elevation of the forest ranges between sea level and 137 m.

The climate of Manombo is characterized by high rainfall throughout the year, with heaviest rainfall during the cyclone season, from January through March. During this period, the area is subject to cyclones from the Indian Ocean, causing flooding, stream-course changes, and extensive tree falls (Donque, 1975).

In January 1997, cyclone "Gretelle," with winds up to 245 km, hit Manombo forest for 12 hours causing extensive damage: uprooting trees, breaking trunks

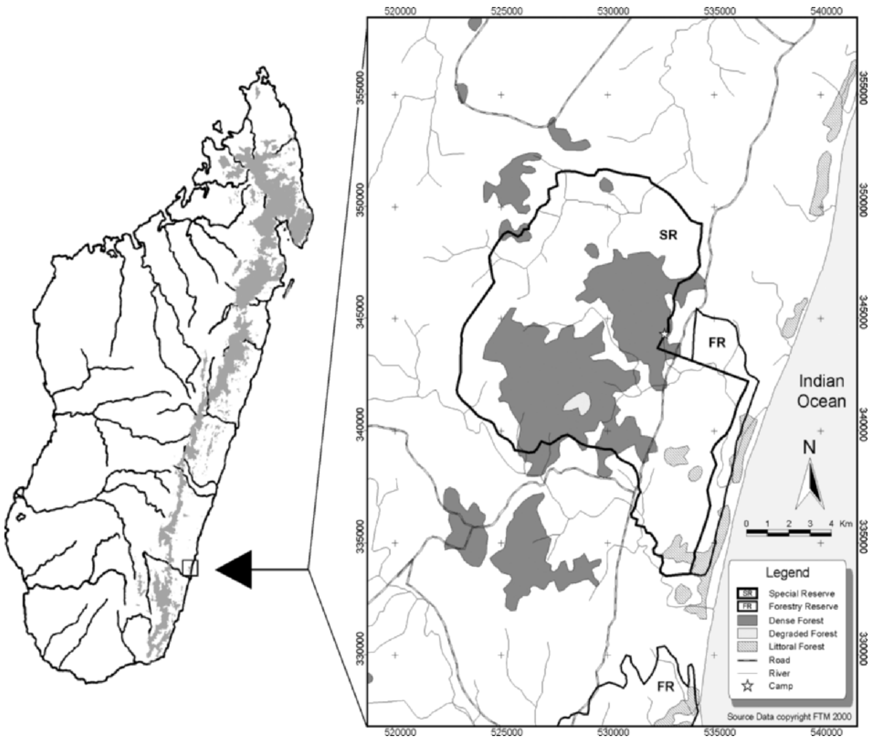

Figure 1. Location of Manombo Forest study area in Madagascar. Madagascar map: forest cover after Green and Sussman (1990). Inset: GIS data courtesy of ANGAP (Laborde Projection)

and large branches, toppling the canopy trees, and defoliating most of the remaining canopy. Postcyclone botanical transect studies revealed 85% canopy loss. Three years after the cyclone, alien plant species have invaded more than 40% of the total forested area. Currently, seven species of plant invaders have become potential threats to the native vegetation, especially in forested areas already subject to anthropogenic disturbances. As such, Manombo forest provides a unique environment in which to study habitat disturbance.

Study Individuals

Following a 2-month habituation period, I continuously studied two groups of *V. variegata* for a period of 18 months. Although the composition of each group did not change during the study, only one adult male that was present in Group I during a 3-month survey in 1997 survived to 1999. Group I comprised three members (one male, Redy-M, and two females, Boloa-F and Silvera-F), while neighboring Group II consisted of two members (a male, Grina-M, and a female, Kolara-F).

Individual scans on the study groups were taken 10 days each month for a total of 1431 hours of observations on 188 days (total scans = 17,171). Data are unavailable on Grina-M for the months from April to June 1999, and in July 2000. In addition, Kolara-F was missing during the months of April and May 1999, and in July 2000. Boloa-F disappeared during June 1999 and again in April 2000. Comparisons between groups were not always possible (as each group has relatively few individuals in each age/sex class); therefore, comparisons were made between individuals in statistical analyses.

Behavioral Methods

Data collection procedures involved focal animal sampling (Altmann, 1974). With the help of field assistants, groups were followed for a full day's activities whenever possible. Each day, a different focal animal was chosen in order to obtain a representative sample among individuals and across sexes. Individual scans on the study groups were taken 10 days each month for a total of 1431 hours of observations on 188 days (total scans = 17,171).

The activity of a focal animal was recorded at 5-minute intervals during daylight hours ("instantaneous" samples, Altmann, 1974). Behaviors were described at a general level (forage, feed, travel, rest, other). Specific behaviors provided more detailed records of these general activity categories. Each of the activity states was scored as an activity record for the corresponding 5-minute interval. The percentages of time spent at each activity were then calculated in relation to the total activity records for each 5-minute interval (Milton, 1980).

Feeding activity was defined as: reaching for, picking, placing in the mouth, chewing, and swallowing food items, whereas foraging was defined as moving slowly with attention directed toward a food source or manipulating substrates in search of foods (Whitten, 1983; O'Brien and Kinnaird, 1997). As feeding data are based on scans, they are measures of the frequency in which the focal animal fed on each item every 5 minutes. The food item and the part eaten were categorized and described as ripe or unripe fruit (only the fleshy part and/or the seed or both), young or mature leaves, flower parts, or miscellaneous materials (e.g., sap, bark) (see Overdorff, 1993).

The availability of different food was estimated using Importance Values (IV) (Curtis and McIntosh, 1951). The IV takes into account *relative tree density*, distribution (*relative frequency*), and *relative dominance* (basal area). The IV data were taken from a postcyclone survey of 665 trees. The IV are calculated by the equation

Importance value ($IV_{\text{tree species } i}$) = $RD + RF + RDo$
where
RD = (number of individuals of species i/total individuals of all species) x 100
RF = (number of species at which species i occurs/total number of points sampled) x 100
RDo = (total basal area of species i/total basal area of all species) x 100
[Basal area (cm^2) = $(\text{dbh})^2$ x (0.7854)]

Rainfall and temperature (maximum and minimum) were recorded daily at the study site and the mean monthly values were calculated. Combining these two climate parameters resulted in a total of eight seasons. The following criteria were used to define seasons:

"Rainy": average monthly precipitation (AFM) > 400 mm; "Moist" if AFM 400 – 200 mm; and "Dry" if AFM < 200 mm.

"Hot": temperature (T) > 20°C; "Cool" if (T) 20–15°C; and "Cold" if (T) < 15°C.

RESULTS

Dietary Patterns

Overall: Combining data from five individuals, black-and-white ruffed lemurs were observed to feed on a total of 83 different plant species during the dry and rainy seasons combined (see Table 1). This is about 12% of the total number of species recorded in my seven sample transects. Among the species eaten, 70 were used as fruit sources, 17 as leaf sources, 2 as nectar sources, and 4 as other item sources. Thus, the number of species used as fruit sources is more than four times the number of leaf species and more than 11 times the number of nectar and other items together. As Table 1 shows, only 1% of those 82 species was used for food sources in all three categories (fruit, leaf, and nectar), 4% for foods in two categories (fruit and leaves), and 79% for foods in only one (fruit), 12% only

Table 1. List of food species eaten by *Varecia variegata* at Manombo forest

Family	Scientific name	Vernacular name	Part eaten[a]	Importance value
Annonaceae	*Monanthotaxis pilosa*	vahatsimatra	Fr	—
	Polyalthia oligosperma	ramiavitoloha	Fr, Lv	73.1
	Xylopia sp.	fotsivony	Fr	—
Apocynaceae	*Landolphia platyclada*	vahateso	Fr	—
	Plectaneia sp.		Fr	—
Aspleniaceae	*Asplenium nidus*	betoboka (velomiato)	Lv	—
Burseraceae	*Canarium madagascariensis*	ramy	Fr	72.6
Clusiaceae	*Symphonia urophylla*	haziny	Fr, Lv	—
	Garcinia aphanophlebia	kimba	Fr, Lv	14.8
	Mammea sp.	kimba	Fr	43.3
	Garcinia chapelieri	kimba	Fr	—
Combretaceae	*Hirtella tamenaka*	tamenaka	Lv	—
	Terminalia mentaly	masomposaina	Fr	—
Connaraceae	*Agelae pentagyna*	vahibe	Lv	—
Cunnoniaceae	*Weinmania rodoxylon*	varikanda	Fr	—
Cyperaceae	*Cyperus latifolius*	harana	Fr	—
Ebenaceae	*Diospyros platicalyx*	hazomainty	Lv	43.6
Erythroxylaceae	*Erythroxylon sphaeranthum*	menahihy	Lv	28.8
Euphorbiaceae	*Uapaca louvelii*	voapaky	Fr	75.7
	Anthostema madagascariensis	baby (raloto)	Fr	79.8
	Cecropia peltata	tanatana	Fr	—
	Cleisthanthus bovianum	taimbarika	Lv	28.9
Fabaceae	*Cynometra cloiselii*	variotra	Lv	—
	Calliandra alternans	ambilazona	Lv	—
Flacourtaceae	*Aphloia theaformis*	fandramanana	Fr	—
	Hemalium sp.	tsimbotry	Fr	—
Hypericaceae	*Harungana madagascariensis*	harongana	Fr	—
Icaninaceae	*Apodytes* sp.	malanimanta	Fr	58.0
Lauraceae	*Cryptocaria* sp.	vitano	Fr, Lv	—
	Ocotea sp.	varongy	Lv	43.4
Linaceae	*Hugonia* sp.1	vahamavo	Fr	—
Melastomaceae	*Clidemia hirta*	voatrotrokala	Fr	217.5
	Memecyclon sp.	tomizo	Lv	86.8
Menispermaceae	*Burasia madagascariensis*		Fr	29.0
Moraceae	*Ficus baroni*	amontana	Fr	14.4
	Ficus reflexa	laza	Fr	—
	Ficus rubra	vahinonoka	Fr	—
	Bosqueia boiviniana	kivozoala	Fr, Lv	—
	Pachytrophe dimepate	andrimena	Fr	—
	Treculia sp.	hazosavoa	Fr	—
Myrtaceae	*Eugenia emimense*	rotra	Fr	—
	Syzigium sp.1	rotra fotsy	Fr, Lv	—
Oleaceae	*Norohnia myrtoides*		Fr	—
	Norohnia sp.2	silaitra	Fr	15.9
Palmae	*Dypsis gracilis*	varaotry	Fr	—
	Dypsis nauseosa	mangidibe	Fr, Ex	—
	Vonitra thouarsii	vonitra	Fr	—
	Dypsis sp.1	vakaky	Fr, Br, Ex	—

(Continued)

Table 1. List of food species eaten by *Varecia variegata* at Manombo forest—Cont'd.

Family	Scientific name	Vernacular name	Part eaten[a]	Importance value
Pandanaceae	*Pandanus* sp.1	tsiriky	Fr	57.7
	Pandanus sp.2	tsiriky	Fr	—
Polyporacea (fungus)	*Polyporus* sp.	olatra	other	—
Rubiaceae	*Coffea* sp.1	maranitrantany	Fr	—
	Rothmania sp.1	bevoa	Fr	29.2
	Rothmania sp.2	fotsikatry	Fr	—
	Gaertnera stipula	belakevo	Fr	43.7
	Breonia chinense	valotra mainty	Fr	87.0
	Breonia sp.1	valo— drano	Fr	—
	Gaertnera sp.	hazondambo	Fr	43.7
Rutaceae	*Vepris* sp.1	kalavelo	Fr	—
Sapindaceae	*Sapindacus* sp.	hazomby	Lv	—
	Macphersonia madagascariensis	sanirafotsy	Fr	59.7
	Prothorus ditimena	sandramy	Fr	—
	Prothorus sericea		Fr	—
	Tina sp.1	lanary	Lv	—
Sapotaceae	*Labramia louvelii*	nato	Fr	1.0
	Gambeya madagascariensis	harongampanihy (rahiaka)	Fr	—
Sarcolaenaceae	*Schizolena cauliflora*	foto	Nr	—
Sterculiaceae	*Dombeya lucida*	hafomena	Fr	—
	Dombeya sp.	hafotra	Fr, Lv	—
	Sterculia tavia	aboladitra	Fr	—
Strelitziaceae	*Ravenala madagascariensis*	ravinala	Nr	43.3
Tiliaceae	*Grewia* sp.	hafopotsy	Fr	—
Ulmaceae	*Trema orientalis*	andrarezina	Fr	—
Verbenaceae	*Vitex cauliflora*	mazambodiala	Fr	—
Unknown	11 unknown sp.		Fr	—

[a] Fr: fruit; Lv: leaves; Nr: nectar; Br: bract (modified leaf in the inflorescence); Ex: exudates.

leaves and 5% only nectar (if data collected in 1997 also included). *Varecia* were never observed to eat animal matter or soil, but they were seen licking exudates. Furthermore, they consumed only flower nectar, not sepals or petals. From general observations, there was a significant loss of both flowers and fruit, and even shrubs declined after the cyclone. *Varecia* drank water occasionally in the morning from tree holes when the temperature was very hot. Eighty-four percent of the *Varecia* food sources came from trees, 6% from lianas or vines, and the remaining 10% from epiphytes, shrubs, and shelf fungi.

Thirty-five percent of available food species were used as food sources on only one day during the entire study. More than half of the food sources of *Varecia* were eaten over fewer than 4 days during the entire study. In contrast, only three species of food sources were consumed more than one-fifth of the total number of the study days. The fruits of a nontree species, *Clidemia hirta*, were eaten most frequently by *Varecia* (80 days or 42% of the total days of study), followed by the leaves of two tree species, *Polyalthia oligosperma* (40%) and *Cynometra cloiselii* (23%).

The average percentage of each food type used was calculated for each individual using instantaneous sampling at 5-min intervals containing feeding data throughout the sample period (Redy-M *n* = 849, Grina-M *n* = 551, Boloa-F *n* = 449, Kolara-F *n* = 746, and Silvera-F *n* = 687). For all five focal animals, there were no consistent differences between seasons in time spent foraging or feeding. However, when considering the use of individual food species, there were consistent differences in intensity of use across focal animals from day to day and month to month. In other words, on different days of the month and different months of the year, *Varecia* devoted different amounts of time feeding on particular species. Overall the dietary diversity ranges from 1 to 11 species per day and 5–26 species per month. Generally, the number of species eaten was greater during the hot rainy season.

***Fruit*:** At Manombo forest, fruit was a basic part of the *Varecia* diet and was eaten on nearly every sample day throughout the study. *Varecia* were observed eating fruit on 165/188 study days (or 88% of the total observations). In addition, a great proportion of the feeding time each day was devoted to fruit eating. When data from the five focal animals were combined, fruits constituted 75% of the amount of time spent feeding (Figure 2). Seven of the ten top foods during the total 18 months were fruits. Because of the low relative density of preferred food trees, most fruits eaten by *Varecia* were consumed while still unripe. Unripe fruits comprised 22.5% of all observations. Some fruit trees were depleted before fruits ripened. Although *V. variegata* are primarily frugivorous, they were not ripe fruit specialists, at least not at Manombo during this critical time.

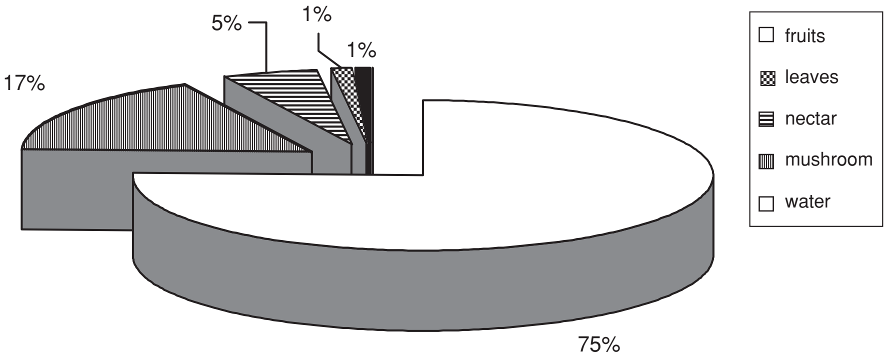

Figure 2. Representation of food types in the diet of *Varecia variegata editorium* at Manombo forest.

Seventy-eight percent of *Varecia* food trees consisted of berries and 22% were drupe. While *Varecia* fed on a wide range of fruit colors (seven different colors), most fruit consumed were green. Black-and-white ruffed lemurs at Manombo utilized fruits of all sizes as did the *Varecia* groups on Nosy Mangabe (Morland, 1991a).

During the study, the mean percentages of fruits in the diet of each individual were as follows: Redy-M male, 72% from 34 different species; Grina-M, 81% from 30 species; Boloa-F, 57% from 25 species; Kolara-F, 83% from 42 species; and Silvera-F, 77% from 33 species. Overall, *Varecia* fruit sources were obtained from 70 species of trees, shrubs, and vines.

Leaves**:** Combined data on all individuals revealed that 17% of *Varecia's* diet consisted of leaves, but only of a few tree species. A great proportion of time was spent eating the leaves of two plant species, *Polyalthia oligosperma* and *Cynometra cloiselii*. Young leaves were overwhelming preferred over mature leaves. Leaves were consumed on 45 of the study days (24% of total observations, n = 188). Only six food species were exclusively leaf sources. During the sample period, the mean percentages of folivorous material in individual diets were: Redy-M 20%, Grina-M 14%, Boloa-F 21%, Kolara-F 11%, and Silvera-F 17%.

Nectar**:** Although the mean average of nectivory was low overall (5%), it was an important food source from September 1999 to February 2000. *Varecia* did not feed on the nectar of all of the flowers available in the forest, but specialized on two species, *Humbertia madagascariensis* and *Ravenala madagascariensis*, which flowered at the end of the dry season. During one day, a single *R. madagascariensis* tree could be visited four to five times. It appears that *R. madagascariensis* trees were visited only to feed, as I never saw any individuals using those trees as resting places.

Shelf fungi**:** Shelf fungi comprised only a small percentage (1%) of the Varecia diet. The mean percentage of shelf fungi in the diet of each individual was as follows: 0.4% for Redy-M, 1.1% for Grina-M, 1.3 for Boloa-F, 2.1% for Kolara-F, and 1.5% for Silvera-F, and the focal animals ate only one species, *Polyporus* sp. (Polyporaceae), which occurred at low densities throughout the forest. Shelf fungi were eaten on 22/188 days, by both females and males.

Miscellaneous items**:** (bark and exudates): Bark and exudates played a very small role in the diet of *Varecia*. The total amount of those two items combined was insignificant (0.5%), perhaps because they were eaten opportunistically, and not by all animals. Grina-M was seen feeding on bark of *Dypsis* sp. in the wet and hot season. Kolara-F was observed consuming the bark of *Garcinia aphanophlebia* in a dry month (November 1999). Redy-M, Boloa-F, and Silvera-F were also seen feeding opportunistically on plant exudates around the pedicels in the moist, cool season (September–October 1999).

***Water*:** Water was used especially during the hottest season, between the months of February and April of 1999. I did not observe *Varecia* drinking water directly from a stream, but they did drink water from holes within trees, either by leaning their heads into larger tree holes or by placing their hands into holes too small for the head to fit into, and licking the water off of their hands.

Family and Species Preferences

As noted earlier, *Varecia* at Manombo were observed to eat at least 83 plant species. Seventy-nine of these species were identified to family level. In total, *Varecia* food trees are distributed throughout 43 families (about 2 species per family on average). The families most frequently represented were Moraceae (7 of the 10 species recorded), Rubiaceae (7 of the 27 species recorded), Annonaceae (4 of the 4 species recorded), and Clusiaceae (4 of the 9 species recorded).

DISCUSSION AND CONCLUSIONS

Severe drought years have been shown to impact dry, western forests in Madagascar (Gould et al., 1999). But droughts also affect the rainforest by extending the dry season and reducing annual rainfall (Wright, 1999). Drought in rainforests has resulted in high canopy tree mortality (Milton et al., 1994; Condit et al., 1995), reproductive failure (Struhsaker, 1997), fruit crop failure (Foster, 1980; Leighton and Wirawan, 1986), and decrease in young leaf abundance (Leighton and Wirawan, 1986; Struhsaker, 1997). No long-term studies have been conducted yet on the effects of natural disasters such as drought and cyclones on fauna and flora in the Manombo region. However, direct cyclone hits can result in complete defoliation, blowdowns of all canopy trees, landslides, and flooding (Ganzhorn, 1995a,b). As a consequence, neither fruits nor leaves may be available for consumption until the following spring, leaving only crisis foods, such as epiphytes, for the lemurs to eat (Ratsimbazafy, 1999).

In the pristine forests of Madagascar, the mean tree crown diameter (patch size) of fruit trees fed in by lemurs is 12 m (Overdorff, 1996; Balko 1998; Hemingway, 1998). In Manombo, cyclone Gretelle had two effects on the food supply of *Varecia*. First, surviving native trees suffered an average crown loss of 85%, and broad crowned trees are generally toppled first by the high winds generated by a cyclone (Wright, 1999). Six months after the cyclone of 1997, the mean crown diameter of trees from the seven sample plots was 3 m (range: 0.5–9 m; $n = 439$). These losses represent a greater than 70% reduction in the fruit-producing vegetation of the forest. Ninety percent of the few remaining trees forming the upper layers of the forest are still producing new leaves and new branches. Moreover, after the cyclone, there were significant losses of flowers and fruits among trees, and shrubs. The recovery of endemic species after this natural disaster is still very slow, but *Varecia* are able to survive in this highly disturbed forest by adjusting their feeding strategies.

It has been well-demonstrated that seasonal peaks in the abundance and scarcity of food used by lemurs are variable from year to year in Malagasy rainforests, as many canopy species produce flowers on prolonged, irregular, and asynchronous or alternate year cycles (Morland, 1991a, 1993; Hemingway, 1995; Powyzk, 1997). In the rainforest at Manombo, a study of the phenological sequence of 120 trees of 24 plant species consumed by *Varecia* over almost 2 years demonstrated that this irregularity of fruiting pattern is reflected in variable annual food availability, i.e., more species produced fruits in May 1999 than in May 2000. As noted by Wright (1999), this pattern of unpredictability requires lemurs to be able to adapt to energetic constraints at almost any time of the year. Manombo presents an extreme case of the effects of habitat disturbance; therefore, it is important to determine how an obligate frugivore like *V. variegata* copes in such a highly disturbed habitat. Did the ruffed lemurs at Manombo exhibit diet similarities with their conspecifics living in undisturbed forests?

Comparisons with undisturbed forests indicate that there are general similarities in the ruffed lemurs' diets in different habitats with regards to the overall food categories eaten. Field research on the diets of *Varecia* at different sites have shown that this species is highly frugivorous (see Table 2). When the data for both sexes are combined from studies on wild *V. rubra*, diets are similar from season to season, comprised mainly of fruits (Vasey, 1997). In the present study, it was expected that *Varecia* living in highly disturbed habitats would have general dietary patterns different from those living in undisturbed habitats. My results demonstrated that they remain predominantly frugivorous regardless of habitat type. This confirms that *Varecia* is an obligate frugivore (Balko, 1998). While dietary diversity fluctuated monthly, the percentage of fruit in the diet always outnumbered the percentage of nonfruit items, except during the month of November 1999 (the second driest month of the study). *Varecia* could feed heavily on young leaves when they were available. In other words, it is not necessary that *Clidemia hirta* be consumed when other foods are available. As fewer trees bore fruits (due to serious cyclone damage), *Varecia* at Manombo devoted much of their feeding time on fruits from shrubs and vines. For instance, the exotic shrub species *C. hirta* can provide a fairly constant source of fruits throughout the year. This became a staple food source and an essential fruit for 3 years after cyclone Gretelle hit Manombo. Ruffed lemurs living in undisturbed sites have not been reported to feed on *C. hirta*, although it is eaten by *Hapalemur griseus* in Valohoaka/Ranomafana (Grassi, 2001). As noted by Vasey (1997), during the transitional cold season *V. rubra* feeds exclusively on fruit.

Results from this study indicate that *Varecia* are able to diversify their diets in terms of the number of fruit species consumed, but the ability to digest and detoxify leafy material and other nonfruit items is limited. A comparative study of the gastrointestinal tract of five lemur species (*Propithecus tattersalli*, *Propithecus verreauxi coquereli*, *Varecia variegata*, *Hapalemur griseus*, and *Lemur catta*)

Table 2. Diets of *Varecia variegata* at different sites

Study Site[1]	Species	Seasons observed	Fruit	Nectar	Flowers	Leaves	Young Leaves	Other
Nosy Mangabe Morland (1991)	*V. v. variegata*	all	74%	21%			5%	2.7%[2]
Ranomafana White (1991)	*V. v. editorium*	cold rainy	71%	15%	3%	11%		
Ambatonakolahy Rigamonti (1993)	*V. v. rubra*	cold rainy, hot dry	74%		5%	18%	3%	[3]
Ranomafana Balko (1998)	*V. v. editorium*	all	90%	4%			6%	
Andranobe Vasey (1997)	*V. v. rubra*	all	88%		6%	1%	3%	2%[4]
Manombo (This study)	*V. v. editorium*	all	74%	6%		17%		3%[5]

[1] Study lengths vary: Morland (1991), 12 months over 18-month period; White (1991), 2 months; Rigamonti (1993), 7 months; Balko (1998), 18 months over four-year period; Vasey (1997), 13 months; Ratsimbazafy (this study), 18 months White's percentages are based on percent food patches used. Percentages for other studies are based on time point samples.

[2] Flowers, buds, shoots, shelf fungus, unidentified (0.9%).

[3] Mushroom.

[4] Unidentified (2%).

[5] Bracts, exudates, fungus.

shows that *Varecia* has the least structural complexity, as determined by the lack of tenaie and subsequent sacculations (Campbell et al., 2000). These authors suggest such a lack of sacculations may explain the inability of this species to subsist on a diet high in secondary compounds, such as those found in leaves. Compared with other sites, *Varecia* living at Manombo had the highest percentage of folivorous material in the diet through every season, yet they concentrated on the leaves of only two plant species, *Polyalthia oligosperma* (ramiavitoloha) and *Cynometra cloiselii* (hazomby). These two species are present in Ranomafana, but only ramiavitoloha is listed in the food species of *Varecia* in that site.

Even living in a harsh environment, *Varecia* spent an overwhelming percent of their feeding time on seasonal rather than perennial foods, as demonstrated by the high percentage of feeding time spent on fruits and young leaves, and a preference for nectar and shelf fungi. The abundance, distribution, and availability of a given food in the habitat may influence feeding behavior, but there is strong evidence in *Varecia* that seasonal foods are much preferred.

Comparing food species in disturbed (Manombo) and pristine (Nosy Mangabe, Ranomafana) forests, ruffed lemurs concentrated their feeding on relatively few tree species in the undisturbed forests. At these different sites, total food species utilized by ruffed lemurs were as follows: In Ranomafana, the three study groups used 27 plant species in 17 different families, 16 species in 12 families, and 14 species in 9 families; on Nosy Mangabe, 67 species in 24 families; and in Manombo, 83 species in 43 families. Preliminary data from a plant inventory study of the Nosy Mangabe rainforest indicate that this forest has very high species diversity (Gentry, 1988). In Manombo, although long-term effects of logging activities limit food choices, there is increased plant diversity due to massive invasions of various new plant species. This allows animals to diversify the number of food species ingested. Additionally, because different species fruit asynchronously, but within a species-specific 2- to 3-month period, feeding diversity is important to any animal with a small home range (Milton, 1980). The two study groups used mainly four small core areas of about 3 or 4 ha during this study, but the entire area used by each group was summed, and the home range was quite large: estimated at 70 and 30 ha for Groups I and II, respectively. Nevertheless, the food species chosen by *Varecia* at Manombo indicates that they were opportunistic feeders. Results of this study demonstrate that 35% of food species were used on only 1 day, and more than half of all food sources were eaten on less than 4 days of the entire study. This further underscores the opportunistic strategy used by ruffed lemurs at Manombo.

Varecia may travel less, and broaden the species they ingest as a strategy to cope with disturbed habitats (Milton, 1980; Terborgh, 1983; Dunbar, 1988). There are two possible explanations for this strategy: (1) to better guard and control food patches both from intraspecific competitors, and from other species at Manombo such as the brown collared lemur (*Eulemur albocollaris*) and frugivorous birds; and (2) to minimize use of the home range and distance traveled thereby conserving energy. It is important to note that the two study groups at

Manombo were not prevented from ranging farther and could have adopted an alternative strategy, traveling and foraging more if needed. Moreover, solitary foraging seemed to be another strategy for *Varecia* at Manombo, to avoid or reduce direct competition between group members, thus maximizing foraging success. Indeed, this allows a species to survive in areas where the distribution of resources would not support a cohesive group (de Thoisy and Richard-Hansen, 1997).

It is also important to note that even though the use of *C. hirta* tallied higher than any of the other food sources during the whole study, this does not necessarily mean that *C. hirta* was preferred, because when other food sources became available, its role was reduced. However, the two alien species, *C. peltata* and *C. hirta*, could be considered as "important foods," because these two species were eaten on many days during the study. Neither of these species is listed in the diet of *Varecia* at other sites. Overall, 38% of the total amount of feeding time was spent on those two species at Manombo. The survival of this frugivorous lemur in the highly disturbed Manombo forest seems to be related mainly to the availability of fruits of these two exotic plant species, because many of the endemic plant species did not produce fruits.

In comparing the five most important food families among the three sites (Manombo, Ranomafana, and Nosy Mangabe), no single family was present in all three (Table 3). Individually, Manombo shared one family (Clusiaceae) with Ranomafana and one family (Moraceae) with Nosy Mangabe. That Clusiaceae family at Ranomafana was consumed by the group living in selectively logged areas. Once again, this demonstrates changes in diet composition correlated with changes in the forest quality.

Some of the foraging strategies exhibited by the ruffed lemurs at Manombo forest can be explained by the high relative abundance of few plant species within the animals' territory. For instance, each time a preferred tree-food became less

Table 3. Comparison of top five plant families exploited by *Varecia variegata* groups at various sites in Madagascar

	Site		
	Nosy Mangabe (Morland, 1991b)	Ranomafana [a] (Balko, 1998)	Manombo (Ratsimbazafy, 2002a)
Plant family	Ebenaceae	Anacardiaceae	Annonaceae
	Lauraceae	Clusiaceae	Arecaceae
	Moraceae	Lauraceae	Clusiaceae
	Myrtaceae	Monimiaceae	Moraceae
Sapotaceae	Myrsinaceae	Rubiaceae	
		Proteaceae	
		Sapotaceae	
		Tiliaceae	

[a] Combined top five food families for three separate study groups.

abundant, *Varecia* supplemented their diets with the nontree food *C. hirta* and/or sometimes with *Pandanus* spp. Likewise, *Varecia* may have reduced their daily range by feeding on these shrub food sources. Moreover, during this study, Kolara-F was seen in the same *Ficus rubra* tree the entire day for 10 successive days, and Boloa-F was found in an unidentified fruit tree for 8 days. It is also the case that a single *Ravenala madagascariensis* tree was visited four to five times in 1 day by Boloa-F.

In this study, I did not have clear evidence as to whether *Varecia* at Manombo fed before dusk, or outside of daytime observation periods in general. It is possible that they did, as they were sometimes heard calling in warm seasons while it was still very dark in the early morning hours, but nocturnal vocalizations alone do not confirm nocturnal activity. No systematic nocturnal studies of ruffed lemurs in the wild have been conducted. On only two occasions did I see *Varecia* continuing to feed after dark (at 6:30 pm and 7:30 pm). Morland (1991a) also made limited observations of nocturnal activity in ruffed lemurs. She described seeing one female feeding and another feeding and moving. If *Varecia* does exhibit significant nocturnal activity, it will be interesting to investigate how such behavior may correlate with other ecological factors (e.g, food availability, food competition, or predation).

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CHAPTER TWENTY

Overview on the Health and Disease Ecology of Wild Lemurs: Conservation Implications

Randall E. Junge and Michelle L. Sauther

INTRODUCTION

The significance of health and disease on the preservation and management of endangered species has been recognized for many years (Scott, 1988; Thorne and Williams, 1988; Gilmartin et al., 1993; Lafferty and Gerber, 2002). The discipline of conservation medicine involves documenting, evaluating, monitoring, modifying, and/or preventing the impact of disease on wildlife. It also includes the study of the multiple two-way interactions between health and disease on the one hand and species and ecosystems on the other (Tabor, 2002). In large stable populations, disease is a normal part of population dynamics. However, when populations are extremely small or fragmented, stochastic events such as disease outbreaks and epizootics may have catastrophic effects. In some cases, veterinary intervention during a disease outbreak is essential to prevent extinction of the population (Thorne and Williams, 1988). The monitoring of occurrence and spread of disease is also a sensitive indicator of a change in the ecology of a species, often secondary to human intervention (Daszak, et al., 2000).

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There are a variety of factors that are involved in the ecology of disease. For lemurs, a few of these have particular importance. *Geographical isolation* is an important factor in disease presence, absence, and significance. With regular migrational movement, species are exposed to a wider variety of pathogens and are given the opportunity to develop a degree of resistance or commensalism. Also with immigration, population numbers may be augmented after significant disease events. Likewise, overpopulation and its effects on stress, nutrition, and disease transmission may be less likely to occur when emigration is possible. Isolation does have positive effects as well. Novel pathogens are much less likely to be introduced (by natural means), and pressure from new competitors and predators is unlikely. However, such immunologically naive populations may be at higher risk from introduced pathogens. For example, it has been suggested that disease may have played a major role in the Pleistocene megafauna extinctions (McPhee and Marx, 1997). If humans or human associated animals carried disease agents of high virulence (so-called hyperdisease), first contact epidemics may have resulted in elimination of Madagascar megafauna shortly after human arrival (McPhee and Marx, 1997).

A disease is considered *endemically stable* when a balance is reached between host and pathogen. The disease, while present and exerting some morbidity and mortality, does not have overwhelming effects on the population. A disease becomes endemically unstable when the balance is disrupted. Disruption may occur with the introduction of stress, competition, decreased food availability, or new pathogens that may compromise the host. Invasive species may bring novel parasites, viruses, or disease to naive species, often with devestating effects. The introduction of canine distemper virus to African wild dogs from domestic dogs is an example of such a situation (Alexander and Appel, 1994). The anthropogenic introduction of novel pathogens (with or without their hosts) into naive populations has been referred to a *pathogen pollution* (Daszak et al., 2000). Pathogen pollution effects are especially strong when domestic animal hosts are introduced, as they provide a constant reservoir for pathogen introduction.

ANTHROPOGENIC FACTORS AND PRIMATE DISEASE

Given the tendency of the human species to directly and often dramatically alter and impact their environment, the potential for disease to affect humans, their domestic stock, and adjacent wildlife is high, and can have significant conservation, economic, and health effects (Daszak et al., 2000; Cleaveland et al., 2001, 2002). Indeed, nearly 61% of human diseases can also infect animals (Taylor et al., 2001). The connection between emerging human diseases and wildlife has been widely discussed (e.g., Daszak et al., 2000, Jessup, 2003) and descriptive accounts indicate that human movement into new habitats can be linked to human disease emergence (Peters et al., 1994; Mahy and Murphy, 1998;

Daszak et al., 2000). From a literature-based database of infectious disease pathogens, it was found that viral pathogen emergence in humans and domestic animals was twice as likely when there were wildlife hosts (Cleaveland et al., 2001). Literature reviews also indicate that anthropogenic alteration is the most important variable associated with wildlife disease outbreaks (Dobson and Foufopolous, 2001).

IMPORTANT FACTORS IN LEMUR DISEASE ECOLOGY

The time of arrival of domestic animals in Madagascar has been inferred through the fossil dung spore, *Sporomiella* (Burney et al., 2003), and suggests that domestic animals arrived early after humans began inhabiting the island about 2000 years ago. Such human encroachment has had a dramatic effect on Madagascar's endemic flora and fauna. Today, a rapidly increasing human population is forcing primates and humans into more direct contact. In particular, transmission of diseases between wild lemurs, domestic animals, and humans is possible, but the actual patterns remain unknown. Such relationships are not static, as changing ecological conditions can increase the risk of disease transmission in animal populations (Deem et al., 2002). For instance, habitat degradation can increase crowding so that the potential for transmission of infectious disease increases. Such habitat degradation can also compromise the nutritional status of a population, increase stress, and adversely affect other factors that are important in immunity to disease. These are all factors that can increase a species' susceptibility to infectious diseases (Woodroffe, 1999; Daszak et al., 2000; Lafferty and Gerber, 2002).

Over the past 60 million years, extant lemurs have evolved only in Madagascar, in the absence of many disease pathogens found on continents. Because humans and their commensals have only recently inhabited the island, lemurs may be especially susceptible to pathogen pollution from human-introduced species such as rats, domestic animals, and the human populations themselves. Indeed, as one of the most ubiquitous mammalian groups on the island of Madagascar, lemurs may have an exceptionally high exposure. As humans and their domestic and pest species (e.g., the common rat) are brought into increasing contact with lemurs, the potential for a "virgin ground epidemic" increases, e.g., an explosive spread of novel pathogens among immunologically naive wildlife populations (Dobson and Foufopoulos, 2001). A number of potential disease risks from anthropogenic effects are known. Rodent – reservoir diseases introduced into Madagascar include plague (*Yersinia pestis*), murine typhus, schistosomiasis, *Angiostrongylus*, and salmonellosis. Other introduced diseases include rabies (domestic dog reservoir), Rift Valley Fever, and borreliosis (Duplantier and Duchemin, 2003). Both *Yersinia* (species *enterocolitica*) and *Salmonella* spp. have been documented in captive lemurs, but not wild lemurs. However, the possibility of these diseases affecting lemurs exists.

OVERVIEW OF LEMUR HEALTH AND DISEASE

In considering the significance of disease in wild lemurs it is useful to consider what is currently known about both wild and captive lemur health. A number of biomedical surveys document a variety of natural maladies. In many cases individuals are able to survive quite dramatic natural health insults, including severe otitis externa (ear infection) (Figure 1), and facial trauma (Figure 2), probably of predator origin. Wild lemurs are often able to cope well with such maladies. For instance, the ring-tailed lemur with otitis was reevaluated one year later and was found to still have otitis; however, she had gained weight and was an active

Figure 1. Ear infection with drainage in a wild ring-tailed lemur at Beza Mahafaly Special Reserve.

Figure 2. Nasal trauma in a wild white-fronted lemur (*Eulemur fulvus albifrons*) at Betampona Special Reserve with significant trauma to the face. The wound margins are healed and clean, suggesting that the wound occurred some time previously.

member of the population (Miller et al., in press). The white-fronted brown lemur with facial trauma was a dominant member of her troop (Junge, personal observation).

A review of the current literature provides scant information on the diseases of wild lemurs. No major epizootics have been reported. A few systematic surveys have been carried out (Garell and Meyers, 1995; Junge and Garell, 1995; Junge and Louis, 2002, 2005a; Dutton et al., 2003; Junge, 2005; Miller et al., in press); however, most reports consist of clinical description of illness in a single lemur. The literature on lemur pathogens provides a foundation for understanding disease susceptibilities of both captive and wild lemurs. Reports from wild lemurs describe parasites (enteric, systemic, hemoparasites), viral exposure, and bacterial infections. Ectoparasites include ticks (*Haemophysalis lemuris*), lice (*Trichophylopterus babakotus*), and mites (Table 1). Endoparasites include both nematodes and pinworms (Table 2). There are few published reports of fecal cultures from wild lemurs, but recent lemur biomedical surveys have expanded this database (Table 3). Comparative information on health and disease exists for captive lemurs (Griner, 1983; Benirschke et al., 1985; Flügger and Pfeiffer, 1992; Junge, 1999, 2003) and includes documentation of parasites, viruses, bacterial infections, enteric pathogens, and fungal diseases (Table 4).

Several current health issues in wild lemurs have been identified that may have ecological and conservation significance. In most cases, parasite infestations can

Table 1. Wild lemur diseases and conditions

Disease	Etiology	Reference
Malaria	*Plasmodium*	Landau et al., 1989
West Nile virus	Arbovirus	Fontenille et al., 1988
Alopecia	*Leucaena*	Crawford et al., in press
Endoparasites	Various	Coulanges et al., 1979; Laakkonen and Goodman, 2004
Dermatitis	Various	Junge, personal observation; Sauther et al., in press
Ectoparasites	Ticks, lice, mites	O'Connor, 2003; Klompen, 2003; Sauther et al., in press
Toxoplasmosis	*Toxoplasma gondii*	Sureau, et al., 1962
Caries, abscesses, gingivitis	Bacterial	Sauther et al., 2002, in press
Eye pathologies	Unknown, possibly associated as secondary infection from *Pseudomonas* and/or *Staphylococcus* after eye trauma	Porteus, 1998

Table 2. Wild lemur endoparasites.[a]

Species	Parasite	Reference
Avahi laniger	*Bertiella lemuriformis*	Deblock and Capron, 1959
Cheirogaleus major	*Lemuricola*	Hugot et al., 1995
Daubentonia madagascariensis	*Lemuricola, Trichurus lemuris, Ascaris petiti*	Chabaud et al., 1964; Petter et al., 1972
Eulemur fulvus albifrons	*Lemuricola, Lemurostrongylus, Trichurus, Nochtia, Enterobius*	Junge, unpublished data; Chabaud et al., 1965
Eulemur fulvus rufus	*Trichurus, Strongyloides*	Junge and Louis, 2006b
Eulemur macaco	*Callistoura brygooi, Lemuricola, Enterobius lemuris*	Chabaud and Petter, 1958; Sandosham, 1950
Eulemur rubriventer	*Lemuricola*	Junge, unpublished data
Hapalemur griseus	*Strongyloides, Lemurostrongylus residuus*	Chabaud et al., 1961a; Junge, unpublished data
Indri indri	*Strongyloides, Parahabdonema longistriata, Courduriella courdurieri*	Chabaud et al., 1961a
Lemur catta	Cestodes, *Strongyloides*	Dutton et al., 2003
Propithecus verreauxi deckeni	*Lemurostrongylus*	Junge and Louis, 2006a
Propithecus diadema candidus	Cestodes	Junge, unpublished data
Propithecus verreauxi verreauxi	*Strongyloides, Biguetius trichoides*	Chabaud et al., 1961b
Lepilemur dorsalis	*Callistroura, Lemuricola*	Junge, unpublished data
Lepilemur edwardsi	*Strongyloides, Lemuricola, Lemurostrongylus*	Junge, unpublished data
Lepilemur mustelinus	*Ingloxyuris inglisi*	Chabaud et al., 1961b
Lepilemur ruficaudatus	*Parahabdonema longistriata, Pseudostertagia*	Chabaud and Anderson, 1955
Varecia rubra	*Lemurostrongylus*	Dutton et al., 2006

[a] This is not an exhaustive list but provides a good overview.

Table 3. Bacteria isolated from fecal cultures of wild lemurs

Species	Enteric bacteria	Reference
Avahi laniger	*E. coli, Enterobacter, Klebsiella pneumoniae, Acinetobacter*	Junge, unpublished data
Eulemur fulvus albifrons	*Enterococcus, Staphylococcus intermedius, E. coli, Escherichia, Acinetobacter, Pseudomonas, Bacillus, Klebsiella oxytoca*	Junge, unpublished data
Eulemur fulvus rufus	*E. coli, Klebsiella ozaenae, Acinetobacter lwofii, Enterobacter amnigenus*	Jung and Lewis, 2006a
Eulemur macaco	*Enterococcus, Staphylococcus, E. coli, Streptococcus, Klebsiella ozaenae, Bacillus cereus*	Junge and Lewis, 2006a
Eulemur rubriventer	*Bacillus, Klebsiella oxytoca, Klebsiella pneumoniae, Enterobacter, Enterococcus, E. coli, Pseudomonas*	Junge, unpublished data
Hapalemur griseus	*Bacillus, Enterobacter, Acinetobacter, Escherichia, Klebsiella pneumoniae*	Junge, unpublished data
Indri indri	*Staphylococcus, Bacillus, Enterococcus*	Junge and Lewis, 2003
Lemur catta	*Enterococcus, Enterobacter, Staphylococcus, E. coli, Acinetobacter, Pseudomonas, Micrococcus, Bacillus, Citrobacter*	Dutton et al., 2003
Microcebus	*Staphylococcus, Acinetobacter, Enterobacter, Enterococcus*	Junge, unpublished data
Propithecus diadema candidus	*E. coli, Enterobacter*	Junge, unpublished data
Propithecus diadema diadema	*Streptococcus*	Junge, unpublished data
Propithecus verreauxi deckeni	*E. coli, Citrobacter, Enterococcus faecalis, Bacillus cereus*	Junge and Lewis, 2006b
Propithecus verreauxi verreauxi	*E. coli, Klebsiella, Enterobacter, Staphylococcus, Corynebacterium*	Junge, unpublished data
Varecia rubra	*Enterobacter, Staphylococcus, Enterococcus, Acinetobacter, Aeromonas hydrophila, Escherichia vulneris, E. coli, Pseudomonas putida*	Dutton et al., 2006
Varecia variegata	*Bacillus, E. coli, Enterobacter*	Junge, unpublished data; Junge and Lewis, 2003, 2005b
Unidentifed "lemurs"	*E. coli, Enterobacter, Citrobacter, Proteus, Pseudomonas aeruginosa*	Coulanges et al., 1978

be considered endemically stable or commensal. In some cases, ectoparasites that transfer to a novel host may produce more significant problems, or may also do so in situations of stress or other health compromise. Clinical signs of dermatitis associated with mite infestation have been diagnosed in both black lemurs and ring-tailed lemurs (Sauther et al., in press; Junge, unpublished data) (Figure 3a,b), and may be the result of stress and human exposure. The common observation of mesostigmatid mites on ring-tailed lemurs of Beza Mahafaly (Miller et al., in press)

Table 4. Captive lemur diseases and conditions

Disease	Etiology	Reference
Viral		
Meningoencephalitis	*Herpesvirus*	Kornegay et al., 1993
Herpes simplex	*Herpesvirus hominis*	Flügger and Pfeiffer, 1992
Bornavirus	Bornavirus	Schuppel et al., 1995
Encephalomyocarditis	Encephalomyocarditis virus	Reddacliff et al., 1997
Callitrichid hepatitis	Lymphocytic choriomeningitis virus	Scanga et al., 1993
Hepatitis	Hepadnavirus	Worley and Stalis 2002
Bacterial		
Enterocolitis	*Salmonella, Campylobacter, Yersinia, Clostridium*	Luechtefeld et al., 1981; Bresnahan et al., 1984; Williams, 2002
Septicemia	Various agents; *Klebsiella*	Junge, 1999; Richard, 1999
Tularemia	*Francisella tularensis*	Calle et al., 1993
Tuberculosis	Mycobacterium	Knezevic and McNulty, 1967
Parasitic		
Ehrlichiosis	*Ehrlichia chaffeensis*	Williams et al., 2002; Yabsley et al., 2004
Cryptosporidiosis	*Cryptosporidium*	DaSilva et al., 2003
Trypanosomiasis	*Trypanosoma cruzi*	Pung et al., 1998
Toxoplasmosis	*Toxoplasma gondii*	Dubey et al., 1985
Fungal		
Coccidioidomycosis	*Coccidiodes immitis*	Burton et al., 1986
Nutritional		
Hemosiderosis		Spelman et al., 1989

indicates that potential vectors for *Bartonella* spp. and *Ehrlichia* spp. are present. Anthropogenic causes may also be related to an alopecia condition of wild ring-tailed lemurs at Berenty. Behavioral observations have indicated that in this area, ring-tailed lemurs are consuming an introduced plant *(Leucaena leucocephala)* that contains compounds associated with arrested hair follicle activity, resulting in severe alopecia (Figure 4) (Crawford et al., in press).

Dental health can also be affected by anthropogenic factors. At Beza Mahafaly some groups of ring-tailed lemurs exploit human refuse. The dental health of these groups is compromised compared to groups inhabiting a nearby protected reserve. For example, those using human resources show a significantly greater frequency of both tooth loss and tooth damage (e.g., broken, cracked, or chipped) and all cases of maxillary canine abscesses (Figure 5) occur in groups inhabiting areas influenced by humans (Sauther et al., in press).

An unidentified eye disease has been documented at Berenty Reserve in both sifaka and ring-tailed lemurs (Porteus, 1998). First noticed in 1987, a formal study conducted in 1993/1994 revealed 6% (26/412 individuals) of the ring-tailed lemur population exhibited eye pathologies including corneal edema and

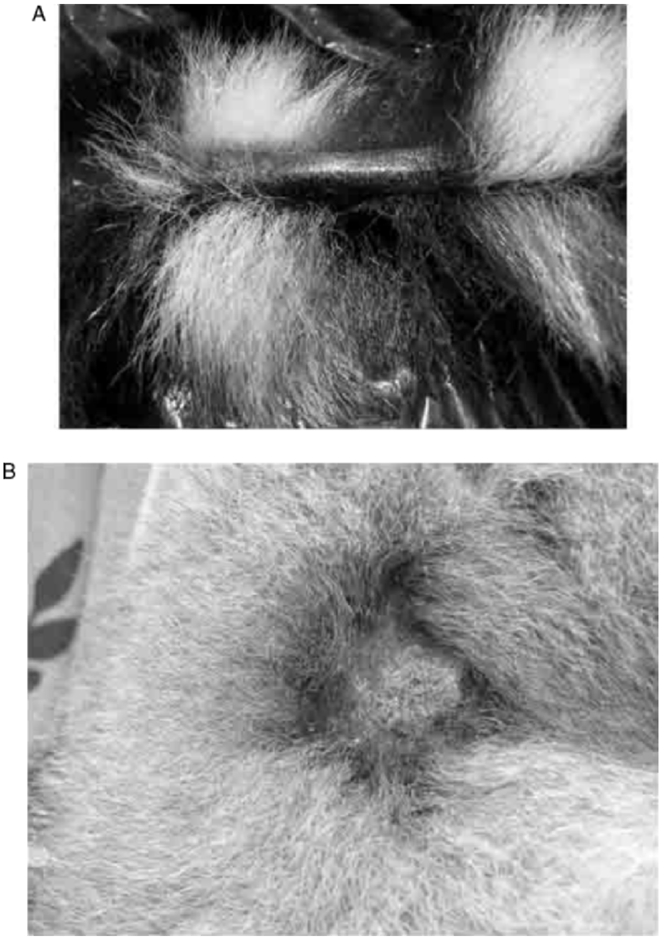

Figure 3. Hair loss on the tail and body of a wild ring-tailed lemur at Beza Mahafaly Special Reserve, Madagascar.

cataracts as well as complete eye loss and blindness. At another site, Beza Mahafaly Special Reserve, a 3-year survey from 2003 to 2005 revealed similar eye pathologies, but in only 1% of the individuals in this population (2/161).

Arboviruses are viruses that are transmitted mainly by arthropods such as mosquitoes and ticks. Of these, members of the Flaviridae family (e.g., West Nile, yellow fever) have been studied in captive lemurs to determine if they may serve as a natural reservoir for human disease (Rodhain et al., 1985). The Rodhain study found that captive lemurs may develop transient viremia with West Nile virus (WNV), without clinical signs, but the study did not evaluate viral infections of

Figure 4. Severe alopecia possibly associated with ingestion of *Leucaena* at Berenty Reserve, Madagascar.

free-ranging lemurs. WNV has been detected serologically in brown lemurs, but no evidence of clinical disease has been reported (Fontenille, et al., 1988). Recently a study was undertaken to evaluate the level of exposure of free-ranging ring-tailed lemurs in the Beza Mahafaly Special Reserve to several viral agents (Sondgeroth et al., in review). Fifty samples were screened for WNV-specific and flavivirus-specific antibodies. Results demonstrated that 47/50 lemurs were positive for WNV antibodies, some with titers over 1280, suggestive of recent infection. These results support that this population of ring-tailed lemurs has been exposed to at least one flavivirus, and requires further investigation. Such information is relevant for management of this endangered species, as a measure

Figure 5. Canine abscess with drainage in a wild ring-tailed lemur at Beza Mahafaly Special Reserve.

of health assessment, and as a method to evaluate the role of this primate in serving as a host species for potential zoonotic pathogens.

CONSERVATION IMPLICATIONS

As already noted, Malagasy lemurs may be especially susceptible to pathogens introduced through recent human occupation. Of importance are several pathogens that could play an important role in lemur disease ecology when associated with increased human presence. The first, *Toxoplasmosis gondii*, is a protozoanl infection that is carried by domestic cats. When the parasite enters an aberrant host, it often causes significant illness and death. *T. gondii* was first documented in captive *L. catta* in 1962 and is believed to have been brought to Madagascar by domesticated cats (Sureau et al., 1962). Of these domesticated cats, many are now feral (locally known as Ampaha), and some reside in lemur habitats. *T. gondii* infection is highly pathogenic in some lemur species (e.g., it is usually fatal for captive ring-tailed lemurs, Dubey et al., 1985), but may be less so for other lemur species (e.g., ruffed lemurs, Junge, 1999). Seropositive titers have been detected for both wild black lemurs (*Eulemur macaco*) in Lokobe reserve and golden-crowned sifaka (*Propithecus tattersalli*) near Daraina (Junge, unpublished data). Screenings of 19 ring-tailed lemurs using antibody titers at the Tsimanampetsotsa reserve (Dutton et al., 2003) and 20 ring-tailed lemurs at Beza Mahafaly using PCR analysis (Miller et al., in press) have been negative. At the first ring-tailed lemur site, which is an isolated reserve with reduced human contact, it is unlikely that domestic or feral cats are common. At the second site, the reserve is intact but the surrounding areas have had considerable human impact. Nearby villages do contain domestic cats in low numbers, and a preliminary screening of several cats found that 50% of the sample (3 of 6) exhibited positive titers to toxoplasmosis (Mills, Conrad, and Lappin, personal communication). A potentially greater threat comes from the more numerous Ampaha (feral cats), which have been seen stalking ring-tailed lemurs in areas outside of the reserve (Sauther, personal observation). It remains to be seen if the Ampaha exhibit positive titers, but if so they could provide an avenue for transmission to the lemurs. Similarly, old and new world primate species are susceptible to herpesviruses, which are generally chronic, and relatively apathogenic for species-adapted strains (King, 2001). However, herpes simplex virus (*Herpesvirus hominis*), which uses humans as its natural reservoir, can be pathogenic to other primates. In captive ring-tailed lemurs the duration of the disease can run from 1 day to 7 months but in all cases it is fatal (Flügger and Pfeiffer, 1992). It has also been associated with encephalitis in captive ruffed lemurs (Kornegay et al., 1993). At Beza Mahafaly a screening of 50 individuals was negative (Sondgeroth et al., in review). This may indicate that the lemurs have not been exposed to *H. hominis*, but it may also indicate that immunity to this introduced pathogen has not been developed.

In both cases it is possible that the apparent high sensitivity of some lemurs to toxoplasmosis and *H. hominis* is a result of geographical isolation. As there are no native felid species in Madagascar, lemurs have not evolved with exposure to toxoplasmosis. Similarly, *H. hominis* presumably arrived with the first humans, only 1500 years ago. With no evolutionary exposure, no resistance has evolved making these types of pathogens particularly problematic as human and lemur habitat converge.

CONCLUSIONS

It is clear from this review that we are only beginning to understand the complexity of lemur disease ecology. What is apparent is that a basic understanding of the natural state of lemur health and disease is essential to identify potential problems in more intact habitats as well as those undergoing rapid anthropogenic change. Such information is also critical for the development of better models of lemur disease ecology. While wild lemurs can sometimes withstand dramatic injuries, as well as other maladies, such existing conditions are likely to affect overall condition and immune systems, making individuals in poor or compromised health less likely to survive additional pressures. It is also critical to understand how age may affect health status as well as disease susceptibility, as younger and older individuals may be at greater risk when habitats are fragmented by human alteration. As humans and their domestic animals come into increasing contact with Madagascar's lemurs, pathogens for which little natural immunity exist will become of increasing importance. Toxoplasmosis, arboviruses such as West Nile virus, as well as herpesvirus, which have been introduced by recent human occupation, are of special concern. Understanding lemur disease ecology at a community level is also important. For example, it is likely that different patterns of socioecology among lemur species may directly affect their natural disease susceptibility, as well as make some species more at risk when human changes occur. What is clear is that a strongly collaborative, multidisciplinary approach will be required to monitor existing health and disease patterns and to facilitate the development of predictive models, all of which will be a critical component of future lemur conservation in lemur populations throughout Madagascar.

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