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MADAGASCAR CONSERVATION & DEVELOPMENT

INVESTING FOR A SUSTAINABLE NATURAL ENVIRONMENT FOR FUTURE GENERATIONS OF HUMANS, ANIMALS AND PLANTS OF MADAGASCAR

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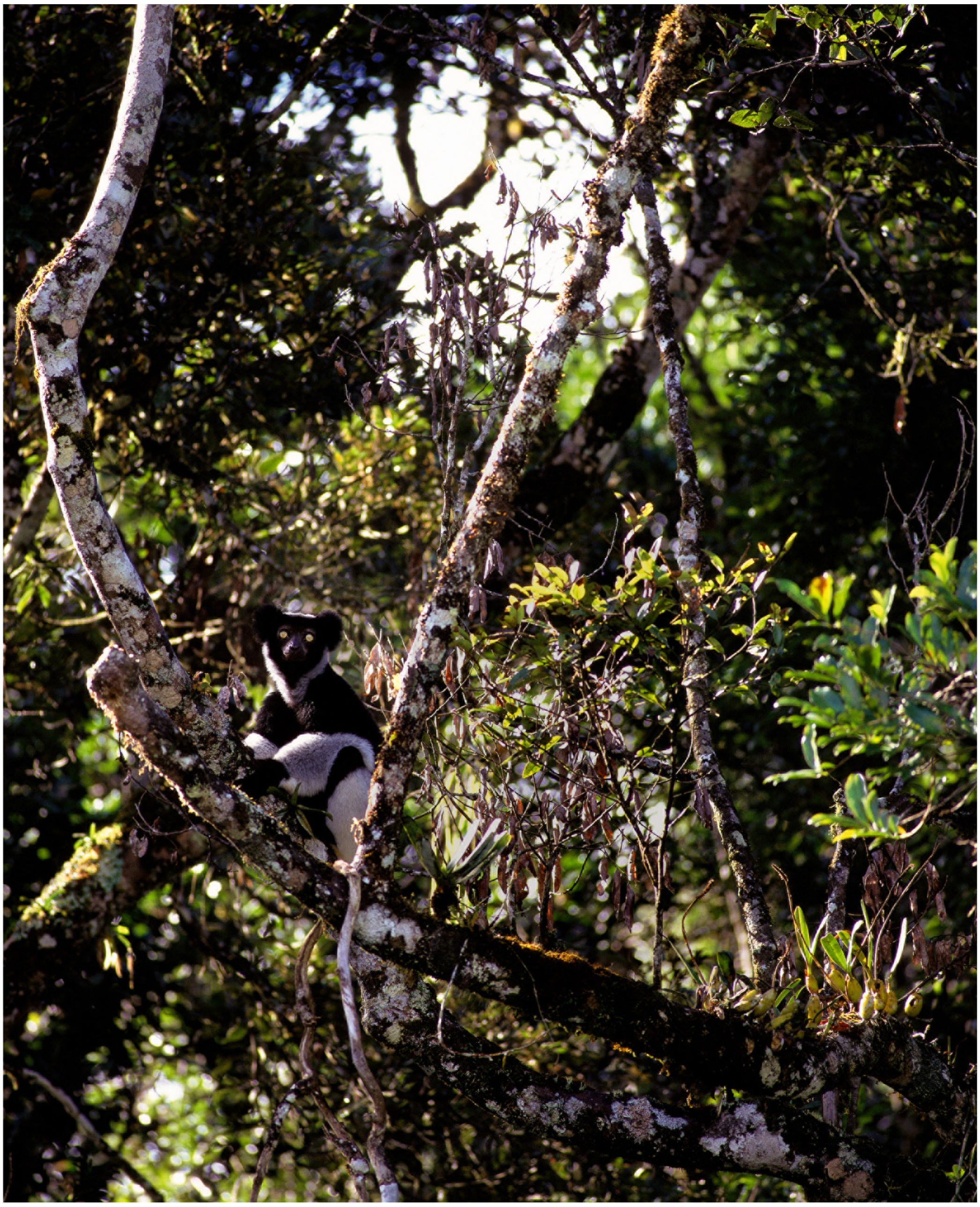

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NÉCROLOGIE. ROBERT EARL DEWAR

Le 7 avril 2013, Robert E. Dewar disparaissait subitement en laissant un grand vide derrière lui. Les membres du journal MCD perdent un ami cher et regrettent un rédacteur important du comité de rédaction qui, sans compter et sans la moindre hésitation, a soutenu le journal dans ses tâches et obligations, en intervenant à plusieurs reprises pour dénouer des situations sensibles.

À Madagascar, Bob était reconnu comme un archéologue pluridisciplinaire. Ses connaissances étendues sur le terrain et dans des domaines variés lui ont permis d'appréhender les grands mystères irrésolus de Madagascar avec une précision et une justesse bien à lui. Bob aimait nous rappeler qu'une trace de lame sur un os fossilisé de lémurien ne signifiait rien d'autre que ce que nous pouvions en déduire, à savoir qu'un Homme a marqué un os de lémurien avec une lame ! Rien ne prouve que cet Homme a tué le lémurien. Habitué aux interprétations des artefacts et écofacts, l'archéologue aguerri que Bob était, nous mettait en garde d'emprunter le raccourci trop facile consistant à considérer un acte de chasse et jamais n'a-t-il concédé que ces indices isolés suggéraient des charniers qui expliqueraient la disparition de la mégafaune endémique. La rigueur, la justesse, une analyse avertie et une approche pluridisciplinaire sont quelques uns des ingrédients dont l'archéologie a profité grâce à Bob ; continuons à nous rappeler ses mises en garde, évitons les spéculations et l'élaboration de scénarios attractifs, interprétons au mieux et justement les faits et rien que les faits. À présent, l'histoire des premiers migrants de Madagascar devra s'écrire sans Bob mais ses écrits et ses pensées continueront à nous influencer durablement.

Nous présentons à son épouse, ses filles, sa petite-fille et ses gendres nos plus sincères condoléances ; la passion et la complicité qui unissaient Bob et Alison nous manqueront, mais nous nous rappelons les yeux de Bob posés tendrement sur son épouse et qui signifiaient : c'est tout à fait ce que je pense mais Alison le dira toujours mieux que moi.

OBITUARY. ROBERT EARL DEWAR

On 7 April 2013, Robert Earl Dewar's sudden death left a gaping hole in Madagascar. The editors of the journal MCD have lost a beloved friend and will miss an important member of the editorial committee who, without the slightest hesitation, supported the journal in all its various endeavors, helping on many occasions to solve sensitive issues.

In Madagascar, Bob was renowned as a multidisciplinary archaeologist. His extensive field experience and deep knowledge in a range of fields placed him in a privileged position to tackle some of the island's greatest unsolved mysteries, using a level of precision and accuracy that was his trademark. Bob often reminded his friends and collaborators that the mark of blade on a fossilized lemur bone meant nothing more than what we can deduce – that a person has scored a lemur bone with a blade! – and he cautioned against anything more, such as interpreting it as evidence that this person actually killed the lemur. As a seasoned archaeologist, Bob was accustomed to the interpretation of artifacts and biofacts, and he warned us to avoid taking the easy shortcut of reading too much into isolated observations: he never believed that they could be invoked to explain mass extinctions as the cause of the disappearance of Madagascar's endemic megafauna. Thoroughness, accuracy, informed analysis, and a multidisciplinary approach are some of the most notable features that Bob brought to archeology, and we would do well to continue to heed his warnings: avoid speculation and the temptation to propose attractive scenarios, and instead develop the best possible interpretation, based on facts and facts only. As his chosen discipline moves forward, the history of Madagascar's early migrants will now have to be written without Bob, but his contributions and thoughts will continue to influence us for years to come.

We express our deepest condolences to Bob's wife, his daughters, his granddaughter and his sons-in-law; the passion and complicity that united Bob and Alison will be missed, but we will forever remember Bob's eyes, looking tenderly at his wife and 'saying", without uttering a single word: 'this is what I think, but Alison would always express it in a much better way'.

Lucienne Wilmé
Editor-in-Chief

EDITORIAL

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Shining a light on Madagascar's mangroves

Madagascar's terrestrial forests contain as much as 5 % of the world's floral and faunal diversity and exhibit >80 % endemism (Giri and Muhlhausen 2008). From the verdant rainforests of the northeast to the dry spiny forests of the southwest, generations of researchers and visitors have been captivated by the country's extraordinarily diverse and unique biodiversity. It is these forested ecosystems which continue to receive the lion's share of attention in many of the documentaries, books, scientific articles and natural history media profiling the island. Far less prominent in western media are the millions of Malagasy people living within and dependent on nearly all of Madagascar's ecosystems. Research and conservation tend to focus on areas of high biodiversity to the detriment of comparatively less biodiverse ecosystems and the crucial services provided to their residents. Mangroves exemplify this – as compared with other Malagasy ecosystems, they're not as biodiverse yet support thousands of people and have received less conservation attention than many of their terrestrial peers. These salt-tolerant halophytic trees and shrubs are found exclusively in tidal and inter-tidal areas within more than 120 countries between 30° N and S latitude (Tomlinson 1986, Kuezner et al. 2011). As of 2005, Madagascar's mangroves represented 2 % of the global distribution (Africa's third largest extent behind Nigeria and Mozambique), covering nearly 2,800 km^2 primarily along the west coast (FAO 2007, Giri and Muhlhausen 2008, Giri et al. 2011).

The tremendous importance of mangrove ecosystems is in their 'provisioning' (food (e.g., fisheries and aquaculture), fuel (e.g., wood) and alternative energies (e.g., wind and wave), natural products (e.g., construction materials, sand and pearls), genetic and pharmaceutical products, ports and shipping), 'regulating' (carbon sequestration, shore-line stabilization, storm and flood protection, waste filtration), 'supporting' (soil and sediment formation, nutrient cycling) and 'cultural' (tourism, recreation, education) services (cf. Lau 2012). Of these services, the carbon captured by these 'blue' (i.e., marine) forests has received considerable attention (cf. Pendleton et al. 2012). Mangroves are amongst the most carbon-dense forests in the tropics, with equal to or greater above- and greater below-ground stocks than terrestrial forests (Donato et al. 2011, Kauffman and Donato 2012, Adame et al. 2013).

Despite their importance and in agreement with global trends (cf. Polidoro 2010, Spalding et al. 2010), Madagascar's mangroves are being rapidly degraded and in some areas clear-cut for wood products (e.g., timber and charcoal) and converted for small- and industrial-scale agriculture and aquaculture. Erosion, sedimentation and siltation from intensive upstream farming, burning and terrestrial deforestation also contribute to loss. Our analysis of mangrove dynamics, assessed using USGS-produced national-level maps (as described in Giri and Muhlhausen 2008) indicates a country-wide net loss of approximately 21 % (57,000 ha) from 1990–2010. While natural processes (e.g., forest succession linked with sedimentological processes and impacts from cyclones) are important factors affecting changes in mangrove cover, there is little doubt that Madagascar's mangroves are subject to significant and increasing anthropogenic impact. While rates of terrestrial deforestation continue to receive lots of attention, our comparison of mangrove dynamics with terrestrial forest-loss data (cf. Harper et al. 2007) indicates that several of Madagascar's largest mangrove ecosystems exhibited higher rates of loss than surrounding terrestrial forests. The long-term ramifications and potential for natural or assisted regeneration remain unclear, but with such widespread modification and conversion, many of the important services associated with relatively intact mangrove ecosystems may be at best compromised and at worst disappear. Of particular global significance, once disturbed, mangrove ecosystems can become significant sources of carbon dioxide emissions (Grimsditch et al. 2012). There is also an equally uncertain and potentially far-reaching ripple effect poised to influence surrounding and closely linked marine and terrestrial ecosystems.

One strategy for combating mangrove loss is through carbon financing mechanisms (e.g., REDD+ – reducing emissions from deforestation and forest degradation) and other payments for ecosystem services (PES). Carbon financing mechanisms such as REDD+ do not lack critics (e.g., Beymer-Farris and Bassett 2012, Corbera 2012), and the concept of "selling nature to save it" (McAfee 1999) generally faces many challenges, including securing land-tenure rights for traditional forest users, equitable cost and benefit sharing, leakage, additionality, the risk of non-permanence and liability. While there are a growing number of international studies demonstrating the potential for mangrove carbon projects (e.g., Donato et al. 2011, Kauffman and Donato 2012, Adame et al. 2013), there are added challenges in actually realizing incomes from 'blue carbon'. In simply measuring emission removals, all current, approved methodologies were designed for terrestrial forests. In addition, vast stretches of mangrove ecosystems fall short of current minimum height and canopy-cover requirements for forest – so they are considered non-forest – and the exact nature of succession dynamics, carbon fluxes and the impacts of climate change (e.g., sea-level rise, cyclone frequency and magnitude) are uncertain and remain areas of active research (Alongi 2011, Beymer-Farris and Basset 2012, Grimsditch et al. 2012, Ullman et al. 2012). In short, while very promising and requiring continued investigation, the long-term appropriateness, success and viability of mangrove carbon projects remain to be seen.

Recently, the multi-faceted value of mangroves has received more attention (Alongi 2011, Grimsditch et al. 2012, Lau 2012, Pendleton et al. 2012). If successfully applied to mangroves, carbon finance generated through REDD+ projects could be part of a consensual, community centred approach that explores "bundling" (single payments for packaged services) or "stacking" (separate payments for each service) (as described in Lau 2012) as many ecosystem services as possible. But as with carbon financing mechanisms, the challenges and costs associated with developing and implementing non-carbon PES are diverse, and the potential outcomes not without legitimate concern (e.g., perverse incentives/preference towards certain services at the expense of others; erosion of traditionally and ethically motivated conservation; involuntary participation of coastal communities; stakeholder coordination) (Corbera 2012, Lau 2012). While the business-as-usual scenario in mangroves would likely be problematic for coastal communities, monetizing ecosystem services is an extremely complex and delicate proposition. PES must look beyond carbon to acknowledge and incorporate the inherent interconnectedness and open nature of ecosystems and their services while also recognizing the holistic values provided for people.

Organizations such as NGOs can play a meaningful role in helping to raise funds for and invest and participate in the research and development of PES schemes and in creating needed inter-sectoral links. Since 2008, Blue Ventures' Blue Forests programme has been working to evaluate and establish community-based conservation in Madagascar's mangroves through scientific research and partnerships on the ground. The Blue Forests programme aims to make tangible contributions to poverty alleviation, climate-change preparedness and biodiversity protection in vulnerable coastal communities by assessing the feasibility of mangrove REDD+ and other PES opportunities for Madagascar's mangroves. By growing partnerships with other conservation organisations and private stakeholders, collaborations with Malagasy institutions and authorities, and participatory planning sessions with local communities, the project has gathered and analysed important information on long-term dynamics and relationships between local people and mangroves in several of Madagascar's mangrove ecosystems. These data have helped guide engagement with communities and other NGOs in numerous locales, including Ambondrolava, where the local management association in partnership with Honko (NGO focussed on mangrove conservation and education) has undertaken mangrove reforestation since 2008; the Baie des Assassins, where communities have had permanent mangrove reserves since 2006 and conducted community-based monitoring since 2008; and Belo sur Mer, where villages have forged partnerships with neighbouring villages and implemented temporary mangrove fishing closures since 2011. In areas which have exhibited substantial mangrove deforestation according to our national analysis (i.e., mangrove loss "hot-spots"), such as Ambanja and Ambaro bays, detailed measurements of carbon stocks have been conducted alongside community consultations to elucidate the drivers of loss and establish the feasibility of mangrove REDD+. Through a joint-effort with Aqualma (aquaculture operations, part of the UNIMA group), we have assessed mangrove carbon stocks and deforestation in Mahajamba Bay. Similarly, our programme has partnered with WWF Western Indian Ocean to study REDD+ feasibility in another mangrove loss "hot-spot", the Tsiribihina Delta. Throughout these study sites, work by multiple conservation organisations and local authorities has led to an increased awareness of the diverse values of mangrove forests to local livelihoods.

When communities acknowledge the full extent of values they are afforded from the services provided by healthy, intact mangrove ecosystems, they can come up with their own workable, practicable conservation strategies. In several locations, our team has witnessed communities initiating conservation without financial compensation. In the Tsiribihina Delta, local women replant areas of deforested mangrove using propagules harvested nearby. In several of Madagascar's largest mangrove ecosystems, such as the Tsiribihina and Mangoky Deltas and the bays of Ambanja and Ambaro, communities have formed forest policing groups and organise voluntary, rotating patrols to prevent illegal logging and charcoal production. In Ambanja, charcoal makers replant mangroves in exchange for using nearby woodlots in the surrounding hills. In Belo sur Mer, increasing numbers of villages implement short term bans on use of mangrove forests to augment the productivity of local fisheries. These inspiring community initiatives could be described as a land ethic, incited by locals and applied to the blue forests of the west coast. The introduction of finance through PES could strengthen and further disseminate this ethic through education and awareness and help ensure long-term support for the continued development and expansion of community-based management. This could spread existing initiatives across Madagascar's mangroves, potentially providing a catalyst for widespread attention towards improving and safeguarding ecosystem functioning.

Given the current status of Madagascar's mangroves, it seems essential that they take a more prominent role in the island's conservation narrative. By shining light on Madagascar's mangroves and sharing the experiences of efforts such as Blue Ventures' Blue Forests programme, we aim to bring the status of the mangroves to the attention of MCD's readers and help empower coastal communities through conservation, restoration, reduced-impact use and the exploration of alternative livelihoods.

For more information on the Blue Ventures Blue Forests project, please contact enquiries@blueventures.org

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SPOTLIGHTS

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Understanding species-level primate diversity in Madagascar

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ABSTRACT

Over the past couple of decades Madagascar has witnessed an explosion in the number of primate species generally recognized. Much of this proliferation can be traced less to increasing knowledge of the lemur fauna than to the complete replacement of biological notions of the species by the Phylogenetic Species Concept (PSC), which views species as irreducible diagnosable units. The consequent focus on autapomorphy (unique possession of morphological and molecular derived features) as 'the' criterion for species recognition has led to the almost complete disappearance of lemur subspecies from Madagascar faunal lists; yet subspecies are an expected result of the evolutionary forces that gave rise to the island's current pattern of biodiversity. Thanks in part to the perspective introduced by the PSC, it has become clear both that there is much more species-level diversity among Madagascar's lemurs than was evident only a couple of decades ago, and that this diversity is much more complexly structured than we had thought. But it does not appear to be aptly reflected in the hard-line procedural adoption of the PSC across the board, a move that typically results in fifty-percent inflation in species numbers relative to those yielded by biological concepts. I argue here that the reflexive wholesale application of the PSC to Madagascar's lemurs is inappropriate from both systematic and conservation standpoints, and that a return to biological species concepts, and to the corresponding criteria for species recognition, will allow us to attain a much fuller and more nuanced appreciation of lemur diversity at low taxonomic levels.

RÉSUMÉ

Depuis la fin du siècle dernier, nous avons été les témoins d'une explosion du nombre d'espèces de primates à Madagascar. Cette profusion découle cependant bien moins de l'évolution de nos connaissances sur les lémuriens que de la substitution des concepts biologiques de l'espèce par le Concept Phylogénétique de l'Espèce (CPE ou Phylogenetic Species Concept – PSC), ce dernier considérant l'espèce comme le plus petit groupe irréductible d'organismes qui puisse être différencié d'un autre groupe. L'autapomorphie (c'est-à-dire la possession de caractères dérivés uniques, morphologiques et moléculaires) est ainsi devenue 'le' critère pour distinguer les espèces, de sorte que la quasi-totalité des sous-espèces de lémuriens ont disparu des listes fauniques de Madagascar ; sachant cependant que les sous-espèces sont un résultat escompté des forces de l'évolution qui ont forgé la biodiversité que nous observons aujourd'hui sur l'île. Élever toutes les sous-espèces au rang d'espèces pour la simple raison qu'elles peuvent être diagnostiquées revient à amputer la faune malgache du mécanisme que nous connaissons et qui est justement à l'origine de la fameuse diversité malgache à des niveaux taxinomiques inférieurs. C'est en partie grâce à la perspective offerte par le CPE qu'il est devenu clair que la diversité des espèces de lémuriens de Madagascar était bien plus importante qu'on ne le pensait il y a encore quelques dizaines d'années, mais aussi que cette diversité avait une structure bien plus complexe que nous ne l'avions imaginée. Il semble cependant que dans l'ensemble, le CPE n'ait pas été adopté correctement dans sa procédure pure et dure, de sorte que nous assistons à une inflation de cinquante pourcent du nombre des espèces par rapport à celles qui sont révélées par les concepts biologiques. Je soutiens ici que l'application globale et réflexive du CPE aux lémuriens de Madagascar est inappropriée aussi bien du point de vue de la systématique que de la protection de la nature, et qu'un retour vers des concepts biologiques des espèces, et leurs critères inhérents à la reconnaissance des espèces, nous permettra de mieux appréhender la diversité des lémuriens avec les nuances nécessaires pour considérer les niveaux taxinomiques inférieurs. Accepter que les espèces sont dynamiques mais aussi des entités historiquement individualisées plutôt que des unités typologiques définies par la seule présence de caractères dérivés uniques nous permettra d'y voir plus clair et de nous poser les bonnes questions afin d'appréhender la diversité et la complexité biologiques de Madagascar.

INTRODUCTION

Madagascar's biodiversity is legendary, although especially in the case of the island's endemic mammals it bears a distinctly insular aspect, with rather few major taxa represented by an undeniable profusion of species. But just how great is that profusion? The question is a deceptively simple one, for it involves not only notions of what species are in the abstract, but of how they may be operationally recognized. This is important; for, while everyone can agree that species are the basic "kinds" of organisms in the living world, opinions may legitimately differ on just how they are bounded, and even on how we can know those boundaries exist, and where they lie.

By the mid-twentieth century most zoologists had moved beyond earlier typologies, and had come to embrace the Biological Species Concept (BSC), in which the species was regarded as the largest effective reproducing population. Individuals resembled each other because they belonged to the same species, rather than vice versa (cf. Mayr 1982). Accordingly, this was largely an age of taxonomic inclusivity. The two major systematic overviews of Madagascar's primates published in the 1970s and 1980s (Petter et al. 1977, Tattersall 1982) both hewed quite closely to Ernst Schwarz's (1931) pioneering genus- and species-level revision of several decades earlier. Based entirely on the scrutiny of museum specimens, Schwarz had reduced the total number of lemur species to 20. Nine of these were polytypic, with a total of 26 subspecies among them. By the time I completed my own synthesis more than half a century later (Tattersall 1982), students of the lemur fauna enjoyed the considerable benefit of a growing corpus of field observations in addition to the museum collections. But, even so, I was still able to recognize only 22 species. Seven of these were polytypic, to a total of 29 subspecies.

So much for minimalism. Over the last two decades, the number of species-level lemur taxa has exploded. When Mittermeier et al. (1994) published the first edition of their field guide to the lemurs, which has by now achieved canonical status, they listed 31 lemur species. By the time the second edition (Mittermeier et al. 2006) was published a dozen years later, there were 68 species, plus some cryptic allusions to species as yet unnamed. And in the third edition (Mittermeier et al. 2010), issued after an interval of only four years, the number of lemur species had soared to 97. Now the total stands at well over 100 (see Tattersall 2013). Significantly, the number of polytypic lemur species simultaneously underwent a marked decline: there were seven in 1994, but only two in 2006 and 2010.

SPECIES CONCEPTS, EVOLUTIONARY PROCESSES, AND LEMURS. Hardly coincidentally, just as lemur species were burgeoning in Madagascar, the total number of different species concepts on offer in the literature was similarly mushrooming. At last count (Coyne and Orr 2004, Hausdorf 2011) there were almost 30 such concepts. Most, however, fall into one of three classes. One large category consists of variants on the Biological Species Concept (BSC). A second contains Hugh Paterson's (1985) Recognition Concept of Species (RCS), a significant contribution that emphasizes the importance of shared common fertilization systems. But the idea of the species that is most closely identified with the recent proliferation of lemur species in Madagascar falls into the third. This most importantly includes Joel Cracraft's (1983) Phylogenetic Species Concept (PSC), a derivative of G. G. Simpson's (1961) "evolutionary" notion of the species.

In what was probably his most influential single articulation of the PSC, Cracraft (1983: 170) defined the species as "an irreducible cluster of organisms that is diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent." For operational as well as theoretical reasons, most subsequent practical applications of the PSC have tended to overlook the last part of this definition, and to focus instead solely upon the criterion of diagnosability (Tattersall 2007). Where it has been applied in vertebrate systematics, the PSC has by one estimate led to a multiplication of species compared to the BSC of around 50 percent (Agapow et al. 2004).

The simplified focus on diagnosability is quite understandable, appealing as it does to the innately reductionist proclivities of the human mind. What's more, on the operational level, narrowing the emphasis to this single criterion hugely simplifies the complex task of identifying species. Whether you are in the field, or in a museum, or in your laboratory, if you can recognize it, it's a species. All it takes is one nice distinguishing feature to do the trick. Both in the forest and in the storage cabinet, favored species-group features of this kind have traditionally consisted of what we used to call 'external' characters, visible to the naked eye: pelage coloration, ear size, and so forth. Particularly in the case of cryptically-colored and mostly small-bodied nocturnal primates, field workers have long also leaned upon vocal characteristics as species recognition criteria. And most recently, of course, the ultimate reductive weapon of DNA distance has been extensively deployed, albeit often via crude base-substitution counts at various marker positions, principally in the mitochondrial genome.

Hence the massive loss of lemur subspecies between 1982 and 2010, as the PSC began to bite in strepsirhine systematics. Via the stringent application of the diagnosability criterion, virtually every subspecies out there was promoted to the species level. And while the investigators involved in this wholesale splitting may not always have been aware of it, this stratagem involved abandoning some very basic notions of evolutionary process. Under the BSC, successful and widely-distributed species had been actively expected to spawn subspecies: readily recognizable local variants that were nonetheless reproductively compatible with their conspecifics living elsewhere. Indeed the BSC, and the corpus of evolutionary theory from which it was derived (basically, the New Synthesis of the 1930s and 1940s: see Mayr 1982), saw subspecies as the engines of biodiversity, giving new species a place to start. Without subspecies, or at least differentiated populations, there could be no new species. And my contention here is that this simple proposition remains as valid now as it was twenty years ago, irrespective of whether (or not) you accept the well-substantiated proposition that speciation and morphological divergence are not simply different sides of the same coin (Tattersall 1994).

Saying this is not to deny the utility of the PSC perspective. Indeed, sophisticated applications of the approach in the systematics of a wide range of major taxa have permitted biologists (using both phenotypic and DNA criteria) to identify many cases in which unrelated but phenotypically similar populations had been incorrectly lumped under the same bio-species. As a result, most investigators nowadays would demand data of several different kinds to confirm claims of population status, whether specific or infraspecific. What is more, to acknowledge that subspecies exist as real entities, albeit elusive ones, also involves accepting that the living world is a messy place. Nature is not neatly packaged. At the lowest levels of the taxonomic hierarchy, where divergence is minimal, and where even taxa destined ultimately to be highly distinctive may be hard to differentiate from their sisters, demarcations are often blurry. Subspecies are, of course, diagnosable by definition. But even if future systematists will be able to look back and determine that diagnosably differentiated populations had in fact embarked on separate historical trajectories, prior to the critical (and probably usually fairly short-term) event of speciation the only barriers to genetic interchange among conspecific populations will be geographical ones. What is more, speciation itself is neither a simple process, nor even a unitary one. Indeed, there is a good argument to be made that it is not usefully referred to as a process at all. After all, to do so would be to imply the action of a specific mechanism (Tattersall 1986), whereas many different mechanisms may in fact be involved, acting at anywhere from the molecular to the population levels (Tattersall 1994).

As useful as it may be to think of speciation as an event that 'happens' at a point in time, the reality is that this fundamental generator of biodiversity is something that we invariably infer in retrospect, and that we recognize only via its consequences. Such consequences most fundamentally involve the historical individualization of lineages (Ghiselin 1974), and the establishment of the substantially impermeable reproductive barriers that such individualization suggests. What is more, it is not easily predictable just how those consequences will be expressed, nor even evident that they will be expressed in ways visible to the systematist. Closely related species may show considerable morphological divergence from one another, or they may show hardly any at all. This failure of newly-separated species to conform to an easily quantifiable pattern of morphological divergence not only argues strongly for the notion that speciation is 'not' an 'event' of an inherently specifiable kind, but also for the parallel fact of life that a comprehensive definition of species – like the identification of a unitary 'mechanism' of speciation itself – will always remain out of reach.

Still, nobody would dispute that species-level taxa do exist in some meaningful way. Nature really is packaged, however untidily; and those boundaries actually are there, no matter how blurry or elusive they may be. It is, of course, because they accept this unavoidable reality that the advocates of the PSC so fervently desire some simple and effective operational way of recognizing species. Yet the simple fact is that nature does not always organize itself for the taxonomist's convenience.

It is at this point that Paterson's RCS enters the picture, with its focus upon how conspecifics mutually recognize that they belong to the same exclusive breeding pool. From Paterson's perspective, the significant thing is that the subjects of our studies know perfectly well who they are, irrespective of how difficult it may be for us to 'read their minds' on the matter. Accordingly, he emphasized the importance in species recognition of inter-individual signaling systems, whether vocal, or chemical, or behavioral, or visual (Paterson 1985). Sometimes candidate signaling systems may mislead human observers, as in Madagascar they evidently have done in the case of the several easily recognizable varieties assigned to the *Eulemur fulvus* group. By Mittermeier et al.'s (2010) last count, there are seven species in this group. All are differentiated by marked chromatic differences in the pelage, and some of them are additionally sexually dichromatic. They are certainly diagnosable, at least in terms of mean chromatic tendencies. But since almost all of these purported species readily and successfully interbreed when given the opportunity, and almost anyone who has wandered extensively in the forests of Madagascar has observed *fulvus*-group variants that defied ready classification, the distinguishing features that are so evident to us clearly have little to do with these lemurs' own senses of identity. Similar observations also apply, if less dramatically, to certain other largish-bodied diurnal lemurs, such as some variants of the *Propithecus verreauxi*-group (e.g., King et al. 2012).

Different problems apply to the categorization of the typically smaller-bodied and more cryptically colored nocturnal forms. Between them, the two genera *Microcebus* and *Lepilemur* account for a large proportion of the recent increase in the number of lemur species: in 1982 there were two species of *Microcebus* and only one of *Lepilemur* (albeit with six subspecies); while in 2010 the respective counts were 18 and 26, respectively. Most of these purported species have been diagnosed principally or purely on the basis of mtDNA distances, a procedure recently criticized on multiple grounds by Frankham et al. (2012). Even leaving aside these authors' cogent technical objections, whether the mtDNA distances reported for *Microcebus* and *Lepilemur* samples actually correlate with other valid criteria for species recognition is in many cases unknown. This having been said, however, there is no doubt that there are many more species of both *Microcebus* and *Lepilemur* out there than I was able to recognize in 1982; and indeed, the existence and identities of some of those additional *Microcebus* species have already been quite convincingly demonstrated via the deployment of multiple criteria (e.g., Zimmermann et al. 1998, Rasoloarison et al. 2000, Yoder et al. 2002).

I have reviewed much of the evidence for taxonomic proliferation among the lemurs elsewhere (Tattersall 2007, 2013). It does not seem particularly helpful to repeat this exercise here, except to note that in both contributions I concluded that fully individuated status cannot at present be considered conclusively substantiated for many more than half of the 100-odd lemur species listed in the latest Field Guide (Mittermeier et al. 2010). Still, I would also emphasize that, in pointing to a paucity of decisive evidence for some of the more extravagant estimates of lemur species numbers, I am not in the least disputing that there is far more lemur biodiversity in the forests of Madagascar than we had thought there was only four decades ago. Clearly, there are many species and distinctive populations of lemurs in those forests, some of them with highly limited distributions. Equally evidently, the remarkable diversity of Malagasy primates is systematically, geographically, genetically, morphologically and ecologically structured in a much more complex fashion than we had ever dreamed, even as recently as at the beginning of this millennium.

However, I do urge the exercise of caution in using the criterion of diagnosability as the sole arbiter of species status, whether the diagnostic evidence at hand is molecular, or morphological, or vocal, or whatever. Diagnosability is certainly a major factor to be taken into account in any alpha-taxonomic decision; but using this criterion alone, as the PSC in its currently fashionable form advocates, simply takes us back to the phenetic cacophony of species from which Ernst Schwarz (1930) rescued us the best part of a century ago. In order to determine with any confidence whether or not our subject populations 'behave' as individuated entities – which should surely be our goal – we require evidence from multiple sources, including morphology (in its broadest sense, embracing superficial characters and olfactory signaling systems as well as internal anatomy), DNA markers, social behaviors, vocal and visual communication, geographical and ecological distributions, environmental preferences, and interactions with sympatric populations including putative gene flow.

We are obliged, in other words, to proceed in the manner of many judicial systems, also operating in a complex and murky world, in which decisions are reached on a preponderance of the evidence. Still, we have to be careful with our metaphors; and the familiar criterion of 'beyond reasonable doubt' used in criminal cases may be a little too stringent for some real-world biological data sets. We might more appropriately look to civil law, in which more general probabilities apply. Much as tidy-minded systematists might wish they were not, very closely related species are often genetically leaky vessels, which means that reasonable doubt as to individuation can in some cases be very difficult to banish. As a systematist, I would instinctively prefer in those cases to apply the presumption of innocence, and to regard sister populations as conspecific unless there are compelling reasons to conclude otherwise. But it is also apparent that from a conservation standpoint the evidence might be interpreted differently, particularly where distinctive and highly localized populations are imperfectly known; and clearly, in an arena as complex and nuanced as this, a 'one size fits all' solution is never going to apply. As in the law, a judicious case-by-case approach is indicated.

Still, the reasons for adopting a restrained general attitude toward species recognition are compelling; and they relate not simply to the multifaceted nature of species as reflected in the plethora of definitions available, but to the nature of the evolutionary process that produced the diversity we see in Madagascar today. For there is every reason to believe that, far from being some kind of passive relict that in isolation long ago established an equilibrium with its environment, the Malagasy biota is, instead, in a dynamic state of evolutionary flux (cf. contributions in Goodman and Benstead 2003). This is perhaps more than ever the case since the recent elimination of the island's megafauna.

Above the level of the genome, the fixation of heritable novelties in local populations belonging to existing species is the most fundamental process involved in generating biodiversity. This process is synonymous with the formation of those diagnosable variants we call subspecies. And it is an essential part of the evolutionary dynamic. To promote all subspecies to species simply on the grounds that they are diagnosable is to rob the Malagasy fauna of the very mechanism that we know must have operated to produce the island's famous diversity at low taxonomic levels.

CONSERVATION AND SPECIES. So, what does all this imply for conservation? People concerned with protecting the whole environment at particular places on the planet's surface – which, captive propagation of individual species aside, is all that can be effectively done in this arena – often get rather impatient at what they see as the quibbling of taxonomists, who peddle an inherently unstable product. Their attitude is often a pragmatic "let's just have a set of names that everyone can agree on, so we can get on with protecting what we know is there anyway." Even taxonomists can sympathize with such sentiments; and it is unfortunate indeed that their subjects, as the products of complex and untidy evolutionary processes, do not always compress easily within neat species boundaries. But regrettable as it may be, this messy reality is also unavoidable – even though, because of their understandable frustration, those involved in conservation seem at times to have felt impelled to import their own imperatives into taxonomy.

If a species occurs uniquely at a particular site, that site might rise in the priority list for protection; and certainly in purely pragmatic terms it might be easier to raise funds for a particular locality possessing its own 'flagship' species. A conservationist might well be tempted to believe that, if this perceived advantage has to be gained by promoting what had previously been a subspecies to full species status, then so be it. But then again, if that advantage were to come at the expense of other sites depending on the same funding pool, local conservation gain of this kind might actually lead to a misallocation of resources on a wider scale. What is more, viewing species as irreducible units might in fact produce defined species populations that are simply too small to be viable in the long term: something that for many reasons is, at the very least, unfortunate from a conservation perspective. From the taxonomist's point of view, of course, this approach might also lead to pressure for a biologically unsubstantiated proliferation of names, as one suspects may to some extent have happened in Madagascar.

Fortunately, there is an alternative conservationist view of taxonomy, one strongly advocated recently by Richard Frankham and colleagues (Frankham et al. 2012). These authors argue that, for conservation purposes, the "substantial reproductive isolation" required by the Differential Fitness Species Concept (DFSC: Hausdorf 2011) is greatly preferable to the diagnosability of the Phylogenetic Species Concept. Operationally the DFSC, which is effectively an extension of the Biological Species Concept (BSC), is more demanding than pure diagnosability, since at least in the form advocated by Frankham et al. (2012) it requires quite extensive genetic sampling (looking widely for a dearth of shared alleles at one or more autosomal loci as indicators of a lack of gene flow). But it produces species groupings that are more practical to conserve because they will have larger effective population sizes, and presumably wider distributions. What is more, recognizing species according to the admittedly rather imprecise criterion of substantial genetic isolation will, the authors claim, facilitate "genetic rescue efforts … and [when populations are crossed] the risk of outbreeding depression [will be] minimized" (Frankham et al. 2012: 30). And from a systematist's point of view, this approach also has the advantage of taking into account Nature's blurry lines.

It is true that the information necessary for applying the DFSC will not always be available. But Frankham et al. (2012) also make a persuasive more general case for applying the principles of the BSC, rather than those of the PSC, for conservation purposes. And they very wisely insist that any species listing or classification be accompanied by an explicit statement of the species concept from which it was derived. Crucially, their conservation-oriented recommendations have the additional advantage that they should also be entirely acceptable to any taxonomist who is aware of the complexities of the multi-level evolutionary process(es). If there is one thing we can certainly all agree upon, it is that descent with modification is the only hypothesis we have that predicts the observed organization of biological diversity we find in Madagascar and elsewhere, both at lower and higher levels of the taxonomic hierarchy. And if we deny that species may be polytypic, we shall starve evolution of its most basic component, namely population differentiation.

The bottom line here is that we do not need to gild the lily of Madagascar's altogether remarkable biodiversity by maximizing the possible number of its species. After all, even on the most conservative estimates of species numbers, this unique diversity is already impressive enough to place the island at the forefront of conservationist awareness. To put the matter another way, more is not necessarily better. In fact, in the long run an unnecessary multiplicity of species will almost certainly complicate the conservation enterprise.

Yes, there is without doubt an enormous amount of biological diversity and ecological complexity out there in the forests of Madagascar: a diversity that requires not only to be recognized, but to be appropriately categorized. There can be no doubt that those who have applied the criterion of diagnosability to the recognition of species in the Malagasy primate fauna have performed a salutary service, in drawing attention to the amazing extent of this diversity and complexity. But the effort to understand the multi-level population dynamics involved will not be well served by simply imprisoning the actors in Madagascar's evolutionary play within an irreducible number of pigeonholes. There is clearly a lot more going on in the Malagasy biosphere than this static view would suggest. Accepting that species are dynamic but historically individuated entities, rather than typological units defined by their possession of uniquely derived characters, will free our minds to clarify this complexity. It will help us to ask the right questions.

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ARTICLE

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Partnership in practice: making conservation work at Bezà Mahafaly, southwest Madagascar

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ABSTRACT
Bezà Mahafaly has been the site of a partnership for conservation since 1975, long before the idea of community-based conservation became widely accepted in Madagascar or elsewhere in the world. Today, the Bezà Mahafaly Special Reserve protects 4,600 ha of riverine, transitional and spiny forest with a rich endemic fauna. This paper provides a summary of the thirty-seven year history of the initiative, focusing on three issues: our evolving interpretation of the term 'community', the integral role of politics and economics in developing the partnership, and the linkage between local, regional and national influences that were experienced in some contexts as constraints and in others as opportunities. We draw five conclusions that we hope will be of interest to those engaged in similar activities in Madagascar and elsewhere: (i) the importance of relationships and trust, and the length of time it takes to build both; (ii) the inherent fragility of community-based collaborations, which depend heavily on particular individuals and the pressures on people's lives; (iii) the importance of sustained financial inputs and challenge of diversifying these inputs; (iv) the need for mechanisms to distribute costs and benefits that are accepted as fair, and for methods to track that distribution; and (v) the central roles of improvisation and opportunism in the face of high levels of uncertainty, and the unanticipated key role played by a village-based environmental monitoring team.

RÉSUMÉ
Bezà Mahafaly a été le site sur lequel un partenariat pour la conservation de la nature a œuvré depuis 1975, à savoir bien avant que n'émerge l'idée de la conservation basée sur la participation de la communauté locale qui est maintenant acceptée à Madagascar et ailleurs dans le monde. Aujourd'hui, la Réserve Spéciale de Bezà Mahafaly protège 4600 ha de forêts galeries, de forêts de transition et de forêts épineuses qui abritent une faune endémique d'une grande richesse. Le partenariat engage la Commune d'Ankazombalala, l'Université d'Antananarivo et ses collaborateurs internationaux, et Madagascar National Parks. Dans cet article, nous présentons un aperçu sur l'historique de cette initiative, après lequel nous considérons trois questions. La première question porte sur l'évolution de notre interprétation du terme 'communauté'. Pendant les premières décennies, nous englobions surtout sous ce terme les autorités locales, les chefs traditionnels ou les chefs des associations villageoises. Notre compréhension est plus globale aujourd'hui, mais nous pouvons admettre que nous aussi, les universitaires et les agents de Madagascar National Parks, représentons une 'confusion communautaire' aux yeux des gens de la Commune. La seconde question aborde le rôle intégral de la politique locale et de l'économie dans le développement du partenariat. Le récit historique comprend quatre phases qui correspondent largement aux changements d'approches caractérisant l'initiative depuis son début : conclure un marché, chercher la réciprocité, forger la collaboration et lancer un vrai partenariat équilibré pour la conservation de la nature. L'engagement politique au niveau local était fondamental pour nos efforts à partir de 1975 et rendait des services économiques qui ne portaient pas directement sur la conservation de la nature. Loin de représenter une défaite, ces activités étaient essentielles pour former le partenariat. Enfin, la troisième question concerne les relations entre les influences locales, régionales et nationales, que nous avons parfois ressenties comme des contraintes, mais également comme des opportunités à saisir. En 1975, une grande tension existait entre les buts poursuivis par le partenariat et le contexte législatif national car ce dernier imposait des aires protégées vues 'd'en haut'. L'isolement de Bezà Mahafaly et l'intervention des universités ont pu atténuer en partie le poids de cette hiérarchie. La politique nationale de décentralisation des années 1990, par contre, a renforcé les activités sur le terrain. Pour conclure, nous détaillons cinq considérations qui pourraient servir à de futurs efforts : (i) l'importance de la confiance mutuelle qui dépend des relations humaines et se met en place avec le temps ; (ii) la fragilité des collaborations communautaires qui dépendent de certaines personnes bien particulières et des contraintes de la vie quotidienne de la population ; (iii) l'importance des appuis financiers à long terme ainsi que l'obligation inhérente de les diversifier ; (iv) la nécessité de mettre en place des mécanismes pour partager les avantages ainsi que les coûts des efforts qui soient acceptables aux yeux

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de la communauté ; (v) l'importance capitale de l'improvisation et de l'adaptation face aux incertitudes, et le rôle clé mais inattendu dans la formation du partenariat à Bezà Mahafaly qui a été joué par une équipe villageoise dans le suivi de l'environnement.

INTRODUCTION

The 4,600 hectares Bezà Mahafaly Special Reserve in southwest Madagascar is among those in Madagascar's Protected Area System recognized by a temporary inter-ministerial order issued in 2008 and renewed in 2010. The initial 600 hectares of the Reserve was established by government decree in 1986. The Reserve is sustained by a partnership between the community of Ankazombalala, the School of Agronomy of the University of Antananarivo and its international collaborators, and Madagascar National Parks. A Steering Committee composed of local, regional and national representatives brings the partners to a single table to make strategic decisions and provide general oversight. Within the community, the Reserve is protected through a customary agreement, or *dina*. The *dina* has provided crucial protection for the Bezà forests and wildlife since the national political crisis erupted in 2009.

Efforts to build the Bezà Mahafaly partnership began in 1975 and have continued without interruption. Drawing on this unusually long history against a backdrop of changing national policy and legislation, our paper assesses the relevance and influence of those changes on the partnership's evolution, and contributes to recent discussions about the effectiveness of community-based collaborations with conservation goals in Madagascar (e.g., Raik and Decker 2007, Pollini and Lassoie 2011).

The importance of involving communities in the management of natural resources and conservation of biodiversity gained serious attention in much of the world, including Madagascar, only about 20 years ago (Western and Wright 1994). State-imposed programs had proven ineffective in earlier decades, despite substantial investments and support for high recurrent costs; weak central government made the failure bigger, but it turned out that even strong central governments had limited capacity to coerce their citizens into compliance with unpopular programs: top-down conservation did not work (Wells and Brandon 1992, Agrawal and Gibson 1999, Durbin et al. 2003, Randriamalala and Liu 2010, Pollini 2011). Political and moral arguments were also brought to bear: people living on the land should certainly have a voice and, perhaps, ultimate control in its disposition (Peters 1998). Reflections on the nature of symbolic relationships between people and nature wove their way into the case for community-based conservation, too (Western and Wright 1994, see also review by West et al. 2006).

The shift from 'top-down' to 'bottom-up' approaches cannot ignore the inevitable and necessary linkages between community-based conservation and national policy and legislation (Gezon 1997, Horning 2008). Despite significant effort and some progress, making those linkages work well remains a challenge in Madagascar (Blanc-Pamard 2009, Andriamalala and Gardner 2010, Pollini 2011, Hanson 2012). Accumulating legislation has created a thicket of rules that are sometimes in conflict with one another, and tensions between sectors over national policy priorities create further confusion on the ground, as in many countries.

Several authors have also pointed out that a 'one size fits all' approach to community-based conservation is untenable. Although patches of forest and certain animal species are protected by *fady* (taboos) in some rural communities (e.g., Lingard et al. 2003, Tengö et al. 2007), communities have their own distinctive histories and internal dynamics, with divergent consequences for their capacity to manage natural resources and achieve conservation goals (e.g., Horning 2003, 2008, Ormsby and Kaplin 2005, Gezon 2006, Elmqvist et al. 2007, Toillier et al. 2011). We note too that most community-based conservation initiatives are in fact collaborations, as at Bezà Mahafaly, with the nature of the collaborator(s) and relationships formed adding further diversity.

The late Professor Gilbert Ravelojaona, then President of the School of Agronomy (École Supérieure des Sciences Agronomiques – ESSA) at the University of Antananarivo, made many of the arguments for community involvement in conservation long before they became widespread, and his vision helped inspire the Bezà Mahafaly initiative in 1974. That year, Guy Ramanantsoa (University of Antananarivo), Robert Sussman (Washington University) and AR (Yale University) decided to search for a rural community interested in a collaboration that would have three goals: (i) protecting the community's forests and wildlife, (ii) improving the livelihoods of community members, and (iii) developing a site for training and research. The Ankazombalala community, eventual home of the Bezà Mahafaly Special Reserve, became the universities' collaborator and partner.

The partnership made for considerable 'learning by doing' in the absence of comparable efforts for much of its long history. This paper documents some of the lessons learned, particularly with respect to the first two goals. While agreeing with other authors that no single model will work everywhere, we believe that community-based conservation activities in Madagascar have much in common and that it is useful to share experiences and identify commonalities. After introducing the Commune of Ankazombalala and presenting a brief history of the partnership, we discuss three issues: (i) The meaning of 'community': Decisions about partnership goals were always approved by the Commune, the formal administrative unit recognized by the government; over time, however, decisions came to be reached through informal discussion and negotiation with a wide array of people – the 'community'. We use the word loosely and interchangeably with *fokonolo* (in Mahafaly dialect). Struggling to understand with whom and how we should be collaborating, our experiences taught us the diverse meanings of these words and exposed tensions between the formal processes of the Commune and the informal processes of the *fokonolo*. As our grasp of these complexities increased, it certainly shaped and changed the way we worked. We attempt to capture this dynamic here. (ii) Phases in the development of the partnership: We identify four phases in the partnership's history; during the first, a bargain was struck, grounded in expectations of reciprocity; during the second, the universities attempted to establish reciprocity in practice as well as principle, with mixed results; out of these efforts grew real collaboration in the third phase; and from collaboration came a partnership for conservation in the fourth. Political and economic considerations were more important to the Commune than conservation at the outset, and they weighed heavily in developing the partnership. Based on the Bezà Mahafaly case study, solid political and economic foundations are crucial underpinnings of community-based collaborations for conservation. (iii) Local partnership and national law: Many levels and spheres of authority and influence interacted and were reconfigured at Bezà Mahafaly during its 37-year history. Local leadership was rooted in local history and custom or conferred by the formal structures of government, and sometimes both. The authority accorded each by the community shifted, depending on many factors including the character of incumbents. Meanwhile, highly centralized legislative controls were progressively devolved to non-government institutions and communities. We explore how this shifting, complicated political and legislative web both encouraged and constrained our partnership with the community.

The materials on which this paper draws include the published work of Malagasy and international students and researchers; systematic information collected by the Bezà Mahafaly Monitoring Team since 1995 (Ratsirarson et al. 2001); previously published historical perspectives (Sussman et al. 1994, Richard and Dewar 2001, Ratsirarson 2003, 2008, Sussman et al. 2012); unpublished external evaluations and reports; and the record of progress, setbacks and reflections contained in annual reports to the Malagasy authorities and the funding agency. We also draw upon our own experiences (AR since 1975, JR since 1985).

ANKAZOMBALALA COMMUNE.

Southwest Madagascar, location of the Ankazombalala Commune, was one of the poorest regions of the island in 1975, and it remains so today (Minten et al. 2003). In the area of the Commune, annual rainfall has averaged 460 mm over the last decade. Most rain falls between November and March, but the pattern and volume are highly unpredictable from year to year and, like the 'deep south', southwest Madagascar experiences intermittent droughts (Dewar and Richard 2007, Rasamimanana et al. 2012). These conditions pose challenges for pastoralism and agriculture, the two main subsistence occupations of Commune residents. The challenges are compounded by limited access to the regional market in Betioky Atsimo (E44°23' S23°43') due to poor roads and transportation, high levels of illiteracy, and lack of primary health care. Although progress has been made since 1975, food security remains a major preoccupation and concern.

The Commune encompasses an area of about 400 square kilometers. Administratively, it is one of 27 under the jurisdiction of the District of Betioky Atsimo, itself one of four Districts in the Region of Atsimo-Andrefana. The Commune comprises 17 villages recognized administratively as *fokontany* (Figure 1); many are widely scattered in hamlets. People mostly describe themselves as Mahafaly, but they make strong distinctions between clans. Census data are difficult to obtain and of uncertain accuracy. The Commune population was estimated at 8,090 in 1993 (Commune records), 8,216 in 2001 (ILO/FOFIFA/INSTAT 2001), and 13,900 in 2006 (Randrianandrasana, unpubl.).

Located in the center of the Commune landscape, the Bezà Mahafaly Special Reserve (E44°23', S23°43') is named for a village ten kilometers away. When the Reserve was inaugurated in 1985, it comprised 600 hectares in two non-contiguous patches within a larger forest, their boundaries separated by over 1.5 km. In 2006, the Commune approved the Reserve's extension to encompass the two patches in 4,600 hectares

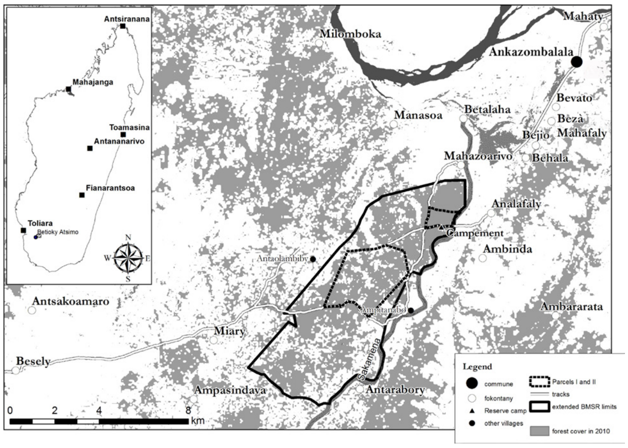

FIGURE 1. Boundaries of Ankazombalala Commune and the Bezà Mahafaly Special Reserve.

(Figure 1). Descriptions of the Reserve's ecology and biodiversity can be found in Ratsirarson et al. (2001), Ratsirarson (2003, 2008), and Sussman et al. (2012).

A BRIEF HISTORY OF THE PARTNERSHIP

The names of some institutions have changed since 1975 (Table 1). We use current names here. Table 2 summarizes relevant changes in national legislation, policies and institutions from 1975–2012, alongside changes in the configuration of responsibilities at Bezà Mahafaly. The following account gives further detail and a glimpse of the human dynamics.

In 1974, the universities' first challenge was to find a community willing to work in partnership. Guy Ramanantsoa, the then Department Head, journeyed far in an oxen cart before meeting the Mayor of Ankazombalala Commune, who found his proposal attractive. Seeking the community's support, the Mayor emphasized economic benefit rather than conservation, though community members regarded the forest and many of its animals as *fady*.

In 1975, all but one of the *fokontany* gave their support to the proposed collaboration. A bargain was struck between the two founding partners, who actually had quite different interests: "we agree to help you protect the forest, but our primary interest is economic development" (the Commune), and "we agree to help you improve your economic circumstances, but our primary interest is conservation" (the universities). The two sides of the bargain were not directly connected, since anticipated economic improvements were not selected to reduce pressures on the forest (Richard and Dewar 2001, see also Pollini

TABLE 1. Changes in names of institutions involved in the partnership since 1975.

Current name	Former name	Year of change
École Supérieure des Sciences Agronomiques	Établissement de l'Enseignement Supérieure des Sciences Agronomiques	1986
University of Antananarivo	University of Madagascar	1988
Ankazombalala	Beavoha	2006
Madagascar National Parks	Association Nationale pour la Gestion des Aires Protégées	2007
Region	Province	2008
District	Fivondronana	2008
Commune	Firaisana	2008

TABLE 2. Changes in relevant national legislation, policies and institutions, and in the configuration of responsibilities at Bezà Mahafaly, 1975–2012. (ESSA-Forêts: Department of Forestry, School of Agronomy; WWF: World Wildlife Fund; MNP: Madagascar National Parks; GELOSE: Secured Local Management; COSAP: Protected Area Oversight and Management Committee; KASTI: Community Conservation Committee).

Year	Management arrangement	Statutory authority
1975	Universities of Antananarivo, Washington, and Yale academics establish inter-university partnership	Land belongs to Government through Ministry in charge of forest domain; forest use regulated by local state agents and customary laws
1986	ESSA-Forêts receives delegated authority to manage Reserve from Ministry in charge of Forest Domain; Government retains ownership, and supervision and enforcement roles	Reserve formally established under the decree # 86-186
1989	ESSA-Forêts enters co-management agreement with WWF	Statutory authority unchanged
1990	ESSA-Forêts/WWF co-management continues after creation of MNP	MNP established to oversee and manage all protected areas, and help implement National Environmental Plan; Ministry in charge of the Forest Domain retains statutory ownership and responsibility for law enforcement
1994	ESSA-Forêts resumes sole management	
1996	Arrangements unchanged	GELOSE legislation enacted
2005	MNP assumes management of Reserve, with ESSA Forêts responsible for research and training	Statutory authority unchanged
2008		Extended Reserve provided temporary protection by Inter-Ministerial Order # 18633/2008/MEFT/MEM
2009	COSAP established for joint oversight of all activities with all partners; KASTI reinforced for patrol and surveillance	
2010		Inter-Ministerial Order providing temporary protection renewed, #52005/2010
2012	Renewal of MNP/ESSA partnership formalized for another 5 years	

and Lassoie 2011). After this first agreement, the universities worked with the Mayor and his advisors toward statutory protection of the forest. In 1984, once again all but one of the *fokontany* supported the proposal. Members of the dissenting *fokontany* used part of the 'protected' forest for grazing, and viewed the reserve as an unacceptable encroachment on their rights. With the support of the majority of municipality committee member, however, the Mayor submitted the proposal through legislative channels, followed by direct petition from the Commune to the central government.

These two key decisions, in 1975 and 1984, were rare moments of almost unanimous accord among the political leaders of the Commune and its constituent *fokontany*. The Commune was fragmented and filled with contention, reflecting diverse views within the *fokontany* as well as differences among the leaders themselves. *Fokontany* distant from the Reserve complained that they benefited little from the arrangement; *fokontany* nearby complained that outlying villages bore few of the opportunity costs of the partnership and benefited too much from its presence, and the naming of the Reserve for a distant village (and home of the Mayor) was a further grievance.

The Bezà Mahafaly Special Reserve was nevertheless established by national decree in 1986 (decree n° 86-168 in June 1986). Under the circumstances, the support of the *fokontany* and Commune seemed ill-deserved: The change made the forest's reserved status permanent, with little evidence that the universities were honoring their side of the bargain. We infer that support was driven by several considerations: local expectations were low, and needs were high; a few things had been 'delivered' by the universities despite the limited capacities, and perhaps more would be coming; the seeds of a relationship had been planted with a few key leaders in the community, and wariness coupled with fearfulness made people reluctant to take on their own leaders or the outsiders with whom those leaders were aligned.

Three developments opened up new opportunities for the universities to make good on their initial commitment to the Commune: (i) international aid to Madagascar increased greatly after 1982; (ii) large-scale, integrated conservation and development projects became a priority for that aid; and (iii) Madagascar was established as a global 'biodiversity hotspot' (Mittermeier 1988, Mittermeier and Bowles 1993).

With USAID funding, the universities were now able to address the Commune leaders' two most urgent priorities: improvements to the road to the weekly market in Betioky, and irrigated water for rice cultivation. The first effort met with modest success.The second did not (Sussman et al. 1994). Good faith with little follow-up had become good faith with counterproductive intervention.

The role of ESSA-Forêts at Bezà Mahafaly underwent two changes during this period. WWF-Madagascar, which provided core funding at the time, pressed for a co-management arrangement. Madagascar National Parks (MNP), established to oversee the national network of protected areas including the Bezà Mahafaly Special Reserve, delegated management of the Reserve to ESSA-Forêts (and WWF) but established new conditions: Reserve entrance fees were to be remitted to MNP headquarters, with half the income put in escrow to fund community projects. In effect, the arrangement established a tense, sometimes confusing truce between MNP and ESSA-Forêts, and maintained the Reserve's anomalous position within the national network.

Dismayed by the outcome of a large-scale canal project in late 1980's, the universities refocused on small-scale activities initiated and implemented by individuals within the *fokonolo*. These activities were still largely separate from conservation in their goals, but differed in two ways from the few undertaken in earlier years: They involved local associations instead of political leaders, and enlisted the collaboration of regional authorities and non-governmental organizations (NGOs) with specific expertise, instead of relying on the universities alone.The new approach made it easier to engage interested and energetic men and women, and circumvented the difficulties and conflicts of the formal political structure. Funds from the first Debt for Nature swap in Madagascar brokered by WWF-Madagascar provided a bigger core budget from 1994–2001.

Newly founded village associations, including three established by and for women, drove a proliferation of small-scale activities, supported by grants from external sources and micro-financing arrangements improvised by the universities. The results were mixed. A few initiatives succeeded, such as a primary care program, new primary schools and wells, and they benefited many in the *fokonolo*. Several associations faded away after an initial burst of enthusiasm, however, and many initiatives failed through bad luck or poor conception: chicks purchased as *poules pondeuses* (laying hens) grew up to crow, for example; technical improvements in crop storage facilities proved less effective against rodents than the presence of a cat, and did not prevent insect damage.

A more fundamental problem was that the approach sidelined the Commune's political leadership. At a stormy meeting in 1998, the Mayor made it clear that there would be no partnership without his active involvement. A shared interest in gaining access to the funds held in escrow by Madagascar National Parks (MNP) provided an apparent way forward: The Mayor and his colleagues, leaders of the *fokontany* and local associations, and the universities would all work together to establish a Local Management Committee (COGES), declared a condition of access to the funds by MNP. In the event, a protracted conflict ensued among *fokontany* over which should be included and represented on the Committee. The COGES was finally established in 2003. Reaching agreement had taken four years and the election of a new Mayor, with the authority and will to resolve the impasse.

Seemingly far removed from such issues, the Bezà Mahafaly Environmental Monitoring Team was launched by the universities in 1995. There was still much to learn about the forest and wildlife, and the nature of threats to their survival. The team in charge of the Monitoring activities (Monitoring Team) would help with that task. With support from LCAOF (Liz Claiborne and Art Ortenberg Foundation), its members were recruited from villages around the Reserve and had little formal schooling, but they knew the forest well and cared deeply about its future. Led by ESSA-Forêts, the Monitoring Team gathered systematic data on climate, biodiversity, and the demography, socio-economy, and perceptions of the *fokonolo*. They became highly expert in these tasks and also de facto ambassadors to and from their villages. When debt-swap funds ran out in January 2001 and national political turmoil brought normal functioning to a halt, the Monitoring Team worked on, supported by LCAOF.

In 2003, MNP provided funds and staff to re-establish a stronger presence at the Reserve, and became a full third partner. This was much needed. Despite the Monitoring Team's efforts, a small group of villagers had made a clearing and planted maize in the southwest corner of the Reserve, and the partnership between the universities and the community seemed to be faltering. In addition, new fields had been opened up illegally in the surrounding forest, making it a high priority to extend the Reserve and connect its two non-contiguous parcels of forest. MNP and ESSA-Forêts launched an intense effort to win the support of the *fokonolo*, through conversation, debate, negotiation, and public service broadcasts by the Monitoring Team from a radio station in Betioky Atsimo. The many collaborative relationships already in place provided a foundation for renewed, urgent discussions about conservation and the value of the forest.

In 2006, agreement on new boundaries for the extended Reserve was reached with the *fokonolo* and subsequently approved by the leaders of *fokontany* and the Commune. The original Reserve forests remained totally protected, and other parts of the extended Reserve were zoned for co-management and controlled use by the *fokontany* to meet their domestic needs, including pasture, and the harvest of forest products for construction, medicine and food.

Several mechanisms were established locally to uphold and implement the agreement. An MNP-mandated committee was set up to monitor management of the Reserve (*Comité d'Orientation et de Suivi des Aires Protégées* – COSAP). The majority of the 24 members were chosen from and by the five *fokontany* closest to the Reserve, with a locally elected Chairman, and the rest of the committee was made up of regional and national representatives including ESSA-Forêts and MNP. In parallel, the *fokonolo* established a *dina*, or customary agreement, subsequently endorsed by the Commune. The *dina* provided a local framework for protection and enforcement, with a village conservation committee (*Komitin'ny Ala Sy ny Tontolo Iainaina* – KASTI) set up to patrol the forest, report infractions, and attempt to identify the culprits. A group of respected elders was designated by the *fokonolo* to hear cases and impose penalties. The idea of the *dina* came from the *fokonolo* and had broad buy-in (cf. Kull 2002). It was a great advance, but also a fragile defense: The *dina* had no power over people passing through the area, and family ties and fear of reprisal limited its effectiveness within the *fokonolo* (cf. Andriamalala and Gardner 2010).

With the extension of the Reserve came assurances from the universities and MNP of continuing investments that would partly offset the impact of new restrictions, but the political crisis in 2009 meant that, for the second time in Bezà Mahafaly's history, it became difficult to honor a commitment made in good faith. Compliance with the rules of the *dina* remained high, nevertheless. This could be because community members saw compliance as a necessary condition for their economic expectations to be met in the long term, or because a real 'partnership for conservation' had been forged. Household survey data suggest that both interpretations are warranted.

DISCUSSION

THE MEANING OF 'COMMUNITY'. The Bezà Mahafaly partnership was a highly political undertaking in the first two decades (Richard and Dewar 2001). For the universities, the question 'who is our partner?' was more about local leadership than inclusiveness, and more about practical outcomes than community. It was a matter of identifying and then working with individuals who were best able to resolve disputes, take decisions, and make things happen. The universities initially looked to Commune leaders to play this role, particularly the Mayor, and subsequently to the founders and members of local associations created for specific purposes. 'Community' was a convenient if misleading way of referring to these individuals.

A broader, more flexible approach has emerged since then, embracing the formal and customary political leadership, local associations, interested individuals, people who have become friends, and – as in all protected areas – two new entities, the COSAP (a committee for the monitoring of the management of the Reserve) and KASTI (a village conservation committee). The benefit is that this has made the partnership more inclusive and effective, but it comes at a cost: maintaining an extensive web of relationships and the structures embedded within them is time-consuming, and makes decision-making a highly iterative process. The arrangement is also fragile, for it depends heavily on the goodwill and leadership of particular individuals over long periods of time, and on sustained external financial support.

Over the years, our reservations about using the word 'community' have grown (cf. West et al. 2006), though we have yet to find an alternative. The Ankazombalala community has developed informal ways of establishing agreement and negotiating compromise more effectively than in the past, and has accorded the universities and MNP a role in those processes. Still, unresolved disagreements and conflicts of interest remain common between households, clans, and *fokontany*. It is easy to get caught in the middle of arguments, and difficult to reach decisions with confidence that they are widely supported. For anyone who has worked with a small community in any context in any part of the world, none of this is news.

The abstraction of real world, complex communities into idealized entities is a frequent feature of community-based conservation collaborations, and a common source of ensuing disappointment and frustration for those involved. It also makes the effectiveness of community engagement difficult to evaluate: Individuals or groups can usually be found who object to actions taken on their behalf, and Bezà Mahafaly is no exception.

Many issues raised in this section also caused puzzlement and disagreement among members of the Ankazombalala community. The *fokonolo* is not a fixed entity for them either (cf. Pollini and Lassoie 2011). The four-year argument about who had the right, through COGES, to participate in and benefit from decisions about funds held in escrow by MNP is an example of that uncertainty. Moreover, from the standpoint of the *fokonolo*, who were and are we, 'the universities', with the eventual addition of MNP? We have no data to trace a history of their answers to this question and would struggle to answer it cogently ourselves. Community members have come to use the name *Antanambazaha* (village of outsiders) for the field station, suggesting that they have found a place for us in their social landscape. It is an ambiguous name, to be sure, and the likely reality is that we are as complicated a *fokonolo* in their eyes as they are in ours.

PHASES IN THE DEVELOPMENT OF THE PARTNERSHIP.

The history of the Bezà Mahafaly partnership can be roughly divided into four phases: striking a bargain (1975–1985), reaching for reciprocity (1985–1993), working at collaboration (1993–2003), and establishing a partnership for conservation (2003 to the present). This framework began to take shape in our thinking about a decade ago (Richard and Dewar 2001). Although our long-term goals were clear (to us, anyway) from the outset, in practice we constantly improvised in our attempts to achieve them. The four phases are not mutually exclusive, but reflect chronological shifts of emphasis made possible by events on the ground and in national and international arenas. Political engagement was central to the initiative's founding and, for most community members, came before they had any direct involvement. It yielded economic objectives that had little to do with biodiversity. We do not view this as evidence of failure, but rather as a necessary and integral part of the process. More complex transactions and the development of shared conservation goals were built upon the rudimentary, bumpy political and economic activities of the first years.

Partnership relationships are very different today from those 37 years ago. We have become neighbors of sorts, within the community's social landscape. Community members stop by to gossip and we return their visits; deaths bring everyone together; we help one another out in simple ways. Increasingly, these informal exchanges touch upon the forest and its protection. We have also become close collaborators on development initiatives. These interactions do not bear directly on our partnership for conservation, but they sustain and reinforce it.

Household surveys carried out by the Monitoring Team in 1999 and again in 2010 substantiate these evolving dynamics. The team held structured conversations with members of 346 (1999) and 200 (2010) households in the *fokontany* closest to the Reserve, during which they asked men and women how the forest was of value to them, and about their perceptions of the partnership (Ratsirarson et al. 2001). The importance of the forest in people's daily lives emerged clearly in both surveys, as a source of firewood, timber, medicinal plants and food, in addition to being a place for hiding cattle from rustlers. In 2011, most (>80 %) of those interviewed also commented that the forest was important as a heritage for their children and grandchildren.

Perceptions of the partnership's importance in conserving the forest changed markedly between the two surveys. In 1999, the most frequent and often only reported benefit of the partnership was occasional access to a car to go to the market or the hospital. In 2010, the great majority (>90 %) talked positively about the partnership's role in protecting the forest, and considered themselves as actively contributing to the effort. Remaining skeptics or opponents came overwhelmingly from the *fokontany* that had opposed the Reserve from the beginning.

The participation of community members in conservation activities is almost always compensated with small payments, but the transaction is more an exchange than a matter of employment in the prevailing non-cash economy: People 'choose to join in', and are thanked in kind. The Young Athletes Association in one *fokontany* is an exception: In recent years, its members have volunteered to help patrol the Reserve and keep trails open without remuneration.

We doubt that a partnership for conservation would have emerged faster if we had started out with the framework described here, but it would have helped us proceed more deliberately on a long-term course of action. Even though largely unarticulated, however, the strategy achieved the first goal set when the partnership was established: Protection of the area's unique forests and rich wildlife. It has also driven progress toward the second goal, improving people's livelihoods, through advances in health and education in particular. The continued existence of the forest is itself viewed as a tangible benefit by many. Defining and mapping the distribution of these benefits, and their costs, within the *fokonolo* remains a task for the future.

LOCAL PARTNERSHIP AND NATIONAL LAW. The Bezà Mahafaly partnership was launched in a legislative context that had changed little since the time of the French colonial administration. Deeply antithetical to the top-down approach of that period, initial work toward the partnership was shielded from national politics and law, because the forest was to be protected as a field station for students and researchers (*terrain d'application*) for ESSA-Forêts, under a simple Memorandum of Understanding between ESSA and the Ministry in charge of Forestry at the time (in the 1980's). The founding spirit of separation and separateness from national environmental strategy endured as a strength and a drawback. At the heart of the ambiguity lay the tension between the universities' aspiration to 'real' partnership, and the reality of management accountability conforming to national statutes. The ambiguity came to the fore in 1986, with statutory recognition of the Special Reserve, after which ESSA-Forêts carried out its responsibilities as the designated primary manager in what it saw as a spirit of partnership with the community – for which there was no legislative basis.

In light of these enduring ambiguities, one could have expected the founding spirit of partnership to fade away. But in fact the opposite happened. ESSA-Forêts and MNP staff have become part of the community's social landscape, many community members are actively involved in the partnership, and the field station has acquired its own informal name. The interests of the three partners are increasingly aligned, and although their roles are nominally distinct, in practice most of the work is shared.

Five factors helped this evolution, three local and two national: (i) The community's remoteness meant that people had little choice but to sort out problems together. (ii) As a result of the unusual organizational arrangements of the partnership, the universities brought a freewheeling culture into the mix that helped downplay the formal, bureaucratic aspects of management accountability. (iii) The Monitoring Team helped blur the contradictory features of the situation. In addition to their formal duties, Monitoring Team members served as knowledgeable intermediaries, the 'glue' that held the partnership together. (iv) A wave of change in national policy took place in the 1990's that would open new opportunities for the Bezà Mahafaly partnership and other grassroots activities. Its spirit was embodied in the GELOSE (*Gestion Locale Sécurisée*: local secured management) legislation (n° 96-025) adopted in 1996, permitting natural resource management transfers outside protected areas. The stipulations of the GELOSE legislation came to be viewed as complicated, burdensome, and administratively challenging, particularly for rural communities where many people had little or no formal education (Pollini and Lassoie 2011). Yet the legislation presented a broad shift toward decentralization, which influenced the management of protected areas as well as less regulated forests. It also highlighted a potentially important role for the *dina,* an institution deeply embedded in Malagasy culture. At Bezà Mahafaly, the effect has been to narrow the gap between the founding aspiration to partnership and the historical reality of centralized management oversight. (v) The commitment to expand Madagascar's protected areas to 10 % of the island's surface made by former President Ravalomanana in his 2003 Durban Vision mobilized political energy, financial resources, and activity. Equally important, for the first time the world heard a President of Madagascar not just strongly assert the inestimable value of Madagascar's natural heritage but couple that assertion with a clear call to action. Even in the remote villages of southwest Madagascar, both messages were heard.

CONCLUSIONS

This article concerns a particular community and a particular period in Madagascar's history. Stepping back from our experiences, however, we draw five conclusions that we hope are relevant to other communities and forests: (i) Community-based collaboration: Building a 'community-based collaboration' is a long and slow process. Collaboration is a political activity based on mutual benefit, shared goals, perceived fairness, and trust. Community-based collaborations involve quite small groups of people working with one another, and trust comes from relationships formed over extended periods of time. This requires individuals willing and able to make long-term commitments; career paths in academic institutions and small NGOs are unusual in making this possible, which may explain their prominence in community-based collaborations in Madagascar. Collaborative conservation initiatives need to be framed and designed with these fundamental considerations and potential constraints in view. (ii) Individual leadership: Community-based collaborations depend heavily on 'individual leaders', are inherently fragile as a result, and should make it a high priority to identify and encourage future leaders. In the case of Bezà Mahafaly, the death of a respected elder, election of a new mayor, or appointment of new university or MNP staff, could mean either a big step forward – or backward. Good governance cannot protect collaborations from the impact of individuals who are uninterested, inept, or corrupt – making it absolutely critical to keep finding people who are passionately concerned, competent, and honest. (iii) Sustained funding: Community-based collaborations need modest but 'sustained financial inputs'. Up to now, these inputs have mostly come from external sources, ranging from large international foundations and aid agencies to small philanthropic organizations. The 'fit' between large organizations and community-based collaborations is often poor, because of widely differing expectations of spatial scale and time frame. Small philanthropies, in contrast, have played a crucial and sustained role in Madagascar, and Bezà Mahafaly has been among the beneficiaries of one of them. Looking to the future, locally generated inputs must become more important, in order to sustain the growing array of community-based, conservation collaborations now underway in Madagascar. Ecotourism and other local income streams offer the prospect of financial self-sufficiency in some contexts (e.g., Rabearivony et al. 2008, Harris 2011), and will surely help in many. Developing these income streams represents a major cultural as well as economic challenge, however. (iv) Shared costs and benefits: Community-based collaborations need 'mechanisms for distributing costs and benefits' that are accepted as fair (cf. Sommerville et al. 2010). We worked to establish such mechanisms through the complex processes of deliberation and feedback described in our study, but lack systematic evidence of the actual distribution of costs, benefits, and inputs. A high priority is to develop and implement workable methods to assess this distribution, not only across the spatial and social scale of the Ankazombalala community but also through time. (v) Accepting the unexpected: 'Improvisation and opportunism' are essential strategic components of community-based collaborations because of the high levels of uncertainty involved (cf. Dewar and Richard 2012). The Monitoring Team provides the best example of this at Bezà Mahafaly. Team members were given the task of inventorying biodiversity and tracking environmental indicators, but they quickly recognized the gap between the aspirations of the partnership and the realities on the ground and set about filling it, with the encouragement of ESSA-Forêts. This was not planned, but it may be the most significant contribution to ideas about making community-based conservation work that Bezà Mahafaly history has to offer.

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ARTICLE

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Verreaux's sifaka (*Propithecus verreauxi*) and ring-tailed lemur (*Lemur catta*) endoparasitism at the Bezà Mahafaly Special Reserve

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ABSTRACT

As hosts, primate behavior is responsible for parasite avoidance and elimination as well as parasite acquisition and transmission among conspecifics. Thus, host behavior is largely responsible for the distribution of parasites in free-ranging populations. We examined the importance of host behavior in acquiring and avoiding parasites that use oral routes by comparing the behavior of sympatric Verreaux's sifaka (*Propithecus verreauxi*) and ring-tailed lemurs (*Lemur catta*) inhabiting the Bezà Mahafaly Special Reserve (BMSR) in Madagascar. For each species, two groups lived in a protected parcel and two groups lived in anthropogenically-disturbed forests. Analysis of 585 fecal samples revealed that the BMSR ring-tailed lemurs harbored six species of nematode worms and three species of protistan parasites. The sifaka harbored only two nematodes. Differences in richness and prevalence appear to be linked to host behavior and the ecological distribution of their parasites. To understand the interplay between behavioral mechanisms to avoid or transmit parasites, we analyzed 683 hours of behavioral observations. BMSR ring-tailed lemurs were observed on the ground significantly more than sifaka and this terrestrial substrate use provides greater opportunities for soil-transmitted parasites to acquire a host. Ring-tailed lemurs using the anthropogenically-disturbed forests harbored parasites not found in the groups inhabiting the protected parcel which they may be acquiring via coprophagy or contact with feces. The arboreality of sifaka allows them to evade most soil-transmitted endoparasites and the patterns of parasitism exhibited by sifaka living in the anthropogenically-disturbed forests did not deviate from the patterns observed among the sifaka living in the protected parcel.

RÉSUMÉ

En tant qu'hôtes, les lémuriens interviennent dans l'acquisition et la transmission de parasites entre les individus d'une population, mais aussi sur la prévention et l'élimination de ces parasites. Leur comportement est donc largement responsable de la distribution des parasites au sein d'une population non contrôlée. Dans notre étude, nous avons examiné l'importance des facteurs comportementaux lors de l'acquisition et l'évitement des parasites transmis par voie orale en comparant le comportement des Propithèques de Verreaux (*Propithecus verreauxi*) et des Makis (*Lemur catta*) se trouvant dans la Réserve Spéciale du Bezà Mahafaly (RSBM) à Madagascar. Deux groupes de chacune de ces espèces étaient distribués dans une parcelle protégée et deux autres dans des forêts dégradées par l'activité humaine. L'analyse de 585 échantillons fécaux a révélé que les Makis de la RSBM étaient infestés par six espèces de nématodes et trois espèces de parasites protistes tandis que les Propithèques de Verreaux ne l'étaient que par deux espèces de nématodes. Les différences de densité et de fréquence auxquelles étaient trouvés les parasites semblaient être liées au comportement des hôtes et à la distribution écologique de leurs parasites. Pour comprendre la relation entre les mécanismes comportementaux et la transmission des parasites, nous avons analysé le comportement des Propithèques et des Makis lors de 683 heures d'observations. Les Makis de la RSBM ont été observés à terre beaucoup plus souvent que les Propithèques. Cette utilisation du substrat terrestre augmente les possibilités des parasites du sol de trouver un hôte. Les Makis se trouvant dans les forêts perturbées étaient infestés de parasites absents des excréments des lémuriens distribués dans la parcelle protégée. Il est possible que les parasites aient été transmis par coprophagie ou par contact avec des matières fécales. La tendance des Propithèques à vivre dans les arbres leur permet d'éviter la contagion par la plupart des parasites liés au sol et le comportement des Propithèques distribués dans les forêts perturbées ne diffère guère de celui des Propithèques distribués dans la parcelle protégée.

INTRODUCTION

It is well established that parasites influence primate behavior and socioecology (Nunn and Altizer 2006, Huffman and Chapman 2009). Parasites are a polyphyletic group of infectious organisms that rely on their host for energy, shelter, and the dispersal of their offspring (Moore 2002). Microparasites (e.g. viruses, bacteria, fungi, and protozoans) are small in size, short-lived, multiply prolifically in their host, and usually result in lifelong

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host immunity (Combes 2005). Macroparasites (e.g. helminthes and arthropods) are larger and have longer lives, disperse their offspring via their host, and their infections do not result in host immunity. As such, hosts can be reinfected with the same macroparasite species (Moore 2002).

Theoretical models and field studies have demonstrated the impact of parasites on primate dietary patterns, home range size, resource utilization, group size, social organization, and mating system (Nunn and Altizer 2006). Diet is critically important for those parasite species that gain access to their host by way of the consumption of contaminated food or water, feces, or via intermediate hosts. Omnivorous primates may acquire a wider breadth of parasites including those species that use intermediate hosts in comparison to folivorous primates that circumvent these infections by consuming a diet consisting of leaves (Vitone et al. 2004). Thus, the dietary preferences of a primate species should profoundly impact their patterns of parasitism. Another critical variable is daily ranges and habitat utilization. Primates using large home ranges should theoretically be exposed to more microhabitats and a wider breadth of parasite species living in those habitats (Nunn and Altizer 2006, Vitone et al. 2004). Group size, social organization, and degree of sociality result in differences in contact patterns and dyadic behavior among primates, and this may increase the probability of acquiring parasites that use transmission routes dependent on host contact or close proximity between hosts (Altizer et al. 2003). Thus, specific primate behaviors are used by parasites for transmission and aspects of their socioecology may facilitate their spread throughout a group or population. Initial parasite acquisition by a host and its subsequent spread to other hosts is dependent on the life cycle stage of the parasite, as well as its mode of transmission.

Anthropogenic disturbance may alter parasite richness and prevalence. Among the Malagasy primates, changes in parasite dynamics have been found within *Propithecus edwardsi* (Wright et al. 2009), *Eulemur flavifrons* (Schwitzer et al. 2010), and *Indri indri* (Junge et al. 2011) communities inhabiting disturbed forests. Loss of habitat requires primates to use smaller forest plots and may force a primate population to utilize regions of their home range that are soiled with parasites that they would otherwise avoid (Hausfater and Meade 1982). Simulations by Nunn et al. (2011) demonstrated that the intensity of range use by mammals is a primary measure impacting parasite prevalence for fecally transmitted parasites. Overcrowding due to habitat loss can result in higher degrees of overlap, higher probabilities of contact, and closer proximity to conspecifics, theoretically increasing the transmission of communicable parasites (Anderson and May 1992). Furthermore, primate habitats are frequently cleared for crops or used as grazing grounds for livestock, increasing the likelihood for the transmission of generalist parasites (Pedersen et al. 2005).

Here we compare the gastrointestinal parasite richness and prevalence between sympatric Verreaux's sifaka (*Propithecus verreauxi*) and ring-tailed lemurs (*Lemur catta*) inhabiting the Bezà Mahafaly Special Reserve (BMSR) in southwestern Madagascar. We examine the impacts of host behavior and socioecology on the patterns of parasitism for each primate over a nine month period. We collected parasite and behavioral data on groups of ring-tailed lemurs and sifaka which inhabited a protected parcel and anthropogenically-disturbed forests. These different habitats are useful for showing the importance of host behavior regarding parasite acquisition and how habitat disturbance may change primate-parasite dynamics or introduce primates to novel parasites (Chapman et al. 2005). However this study focuses on interspecific comparisons of parasitism between the BMSR ring-tailed lemurs and sifaka and not on intraspecific comparisons between social groups living in the protected parcel against those groups inhabiting the anthropogenically-disturbed forests. The BMSR sifaka and ring-tailed lemurs act as good models for testing how primate behavior and socioecology impact primate parasite patterns. Verreaux's sifaka and ring-tailed lemurs share a common phylogenetic history, with the indriids (i.e. *Propithecus*) and lemurids (i.e. *Lemur*) having diverged approximately 40 million years ago (Roos et al. 2004). This split is quite old, yet indriids and lemurids constitute sister taxa that share a number of morphological and behavioral traits. Sifaka and ring-tailed lemurs both groom orally via a mandibular toothcomb, increasing the likelihood of acquiring parasites that utilize oral transmission routes. Sifaka and ring-tailed lemurs also live in multi-male multi-female groups that are characterized by short, distinct mating seasons that are strongly linked to ecological variables (Richard et al. 2002, Sauther et al. 1999). Stark differences also exist between these species. Ring-tailed lemurs are omnivorous (Sauther et al. 1999) and spend approximately 16-19 % of their time on the ground foraging or traveling (Sauther 1994, Loudon 2009). In contrast, sifaka consume a nearly exclusive folivorous diet precluding the need to descend to the forest floor, although they infrequently do so to consume terrestrial herbs (Loudon 2009). The BMSR ring-tailed lemurs are also more gregarious than the sifaka as they engage in more dyadic behavior including allogrooming, sitting in contact, chasing, displacements, and playing (Loudon unpublished data). Based on these behavioral and socioecological differences, we expect that the BMSR ring-tailed lemurs will harbor a greater richness of parasite communities and a higher prevalence for (a) soil-transmitted parasites and (b) socially-mediated parasites in comparison to the sifaka (Table 1).

METHODS

STUDY SITE. We collected data from November 2005 to July 2006 at the Bezà Mahafaly Special Reserve (BMSR) (E°44°34'20", S23°41'20", 150 m; Figure 1) in southwestern Madagascar. This region is extremely dry, experiencing approximately 550 mm of annual rainfall (Sauther 1998). Throughout this study, BMSR consisted of two noncontiguous parcels of land, approximately 600 ha in size, and a small research camp. In 1986, BMSR was decreed a special reserve by the government of Madagascar (Ratsirarson 2003). The size of each parcel was originally estimated using conventional cartographic methods but has since been measured using a handheld Global Positioning System (GPS) unit (Axel and Maurer 2010). Parcel 1 is an 80 ha riparian forest bordering the Sakamena River. This parcel has been protected against grazing for over twenty years through a local accord with the surrounding Mahafaly villagers. A barbed wire fence surrounds the parcel and facilitates the prevention of livestock grazing. As such, the parcel has remained relatively un-modified and is characterized by a multi-leveled canopy with a rich understory of terrestrial vegetation. The parcel is monitored and managed by the BMSR

TABLE 1. Parasite richness, prevalence, and mode of transmission for each of the gastrointestinal parasites recovered from the Bezà Mahafaly Special Reserve ring-tailed lemurs *(Lemur catta)* and Verreaux's sifaka (*Propithecus verreauxi*) populations. Prevalence refers to the number of individuals infected not the number of samples analyzed.

Parasite species (richness)	Ring-tailed lemur (n = 39)	Verreaux's sifaka (n = 26)	Transmission	Soil-transmitted	Socially-mediated
Balantidium sp.	100.0%	0.0%	direct fecal-oral route	yes	no
Entamoeba sp.	51.3%	0.0%	direct fecal-oral route	yes	no
Coccidia	12.8%	0.0%	direct fecal-oral route	yes	no
Oxyuridae	87.2%	38.5%	direct fecal-oral route	yes	yes
Lemurostrongylus sp.	38.5%	11.5%	unknown	yes	no
Trichostrongyloidea	7.7%	0.0%	direct fecal-oral route	yes	no
Subulura sp.	7.7%	0.0%	intermediate host	no	no
Trichuris sp.	5.1%	0.0%	direct fecal-oral route	yes	no
Unidentified brown nematode	10.3%	0.0%	unknown	unknown	unknown

Ecological Team, which maintains an extensive color-coded trail system that consists of 100 m x 100 m forest plots.

As one travels westward, the vegetation becomes xerophytic and the trees become smaller with a wider distribution (Sussman 1991). The dominant tree species near the river is *Tamarindus indica* (*kily* or tamarind). The vegetation near the Sakamena riverbank is a mosaic of tall trees (~30 meters in height) and thick curtains of vines. Here the forest floor is characterized by a thick leaf litter. The westward, drier region of Parcel 1 is dominated by *sasavy* (*Salvadora angustifolia*) and *famata* (*Euphorbia tirucalli*) trees (Sussman and Rakotozafy 1994). This region of the parcel is more open and less humid. The forest floor in this portion of the reserve is characterized by thick mats of terrestrial herbs (*Metaporana parvifolia*). Surrounding Parcel 1 are landscapes that we refer to as 'anthropogenically-disturbed forests.' The anthropogenically-disturbed forests consist of the same plants species that are found in Parcel 1. However, the structure of the forest differs. The Mahafaly have traditionally used the forests outside of the parcel for fuel and building materials resulting in less tree density and wider spaces between adult trees. The Mahafaly also use these forests as grazing grounds for their livestock which continuously consume many of the bushes, seedlings, and terrestrial herbs (Loudon et al. 2006). As a result, the structure of many of these anthropogenically-disturbed forests is characterized by wide expanses with sparse vegetation or forests with large adult trees lacking an understory. Habitat structural comparisons between the floral communities in Parcel 1 and the surrounding forests also revealed significantly more grazing and fecal contamination by livestock and free-ranging domestic dogs in the anthropogenically-disturbed forests (Whitelaw et al. 2005).

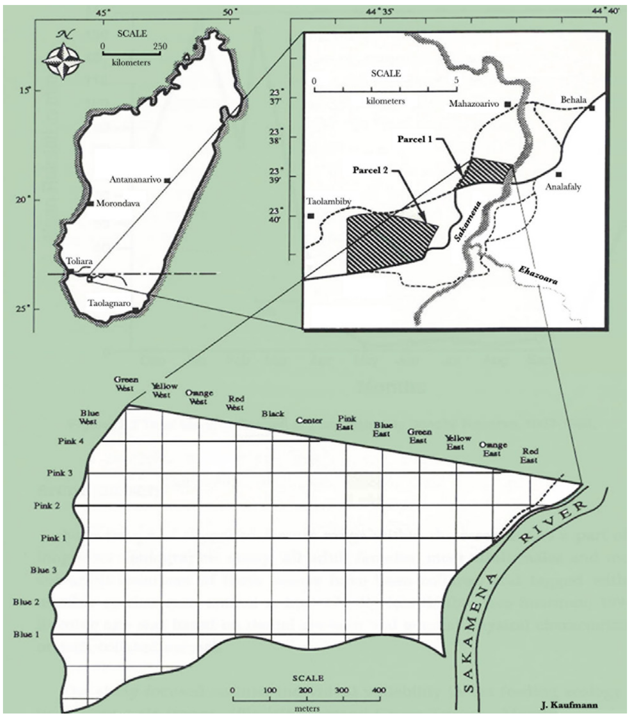

FIGURE 1. Map of Madagascar indicating the location of the Bezà Mahafaly Special Reserve. Map by Jeffrey Kaufmann.

Directly south of Parcel 1 lies the BMSR camp which is surrounded by the anthropogenically-disturbed forests. The camp consists of administrative buildings, a museum, two pit latrines, two shower facilities, a well, an outdoor kitchen, and an area for researchers to set up their tents. The camp is an important component to this study because it is encompassed by the home ranges of two ring-tailed lemur groups, and one sifaka group which we observed during this study. These BMSR ring-tailed lemur groups regularly fed on food scraps within the camp (Loudon et al. 2006) and occasionally ate human fecal matter from traditional open-air latrines used by the Mahafaly that were located just outside the camp during this study (Fish et al. 2007), but which have subsequently been removed.

STUDY GROUPS. We collected behavioral and parasitological data on four groups of sifaka and ring-tailed lemurs. For each species, two groups lived in the protected Parcel 1 and two groups lived in the anthropogenically-disturbed forests. In total, we collected data on 65 animals, of which 39 were ring-tailed lemurs and 26 were sifaka. Each BMSR ring-tailed lemur and sifaka group is fitted with a color-coded collar and an identification tag (Sauther et al. 1999). Collared sifaka also have notched ears to assist identification (Richard et al. 2002).

BEHAVIORAL DATA AND FECAL SAMPLE COLLECTION. We used twenty-minute focal follows with a one-minute interval (Altmann 1974) to record the general behavior of the BMSR Verreaux's sifaka and ring-tailed lemurs. Each focal follow was accompanied with *ad libitum* notes to record behavior that occurred between intervals and follows. We collected behavioral data from 0700h to 1700h. As a consequence of the larger ring-tailed lemur groups, we collected more behavioral data on ring-tailed lemurs (ring-tailed lemurs: 370 hours, sifaka: 313 hours). We analyzed sifaka and ring-tailed lemur behavior that could potentially increase the likelihood of acquiring or avoiding a parasitic infection. These included the frequency of allogrooming, autogrooming, sitting in contact, scent marking, and terrestrial substrate use. Sifaka and ring-tailed lemurs allo- and autogroom orally via mandibular toothcombs and the frequency of this behavior may increase the likelihood of acquiring parasites using fecal-oral transmission routes. Sitting in contact may also facilitate the spread of parasites which rely on host contact or close proximity. Sifaka and ring-tailed lemurs rely heavily on olfactory communication and lay scent via scent glands throughout their environment. Male and female ring-tailed lemurs lay scent via ano-genital glands and scent marking may result in the inadvertent spread of fecally-transmitted parasites throughout their home range. Terrestrial behavior increases the likelihood of acquiring fecal borne parasites harbored by the sifaka and ring-tailed lemurs as well as those carried by the Mahafaly livestock and the Mahafaly themselves who frequently defecate directly on the ground (Muehlenbein et al. 2003). Given the dietary and socioecological differences between each species some behaviors could not be compared. For example, the ring-tailed lemurs that utilized the camp frequently drank well water from discarded basins and buckets and the groups in Parcel 1 and in the anthropogenically-disturbed forests drank water from naturally occurring puddles (Figure 2). Verreaux's sifaka were not observed drinking water from anthropogenic or naturally occurring sources such as arboreal cisterns or puddles. Furthermore, some BMSR ring-tailed lemurs consume human, canine, and livestock feces (Fish et al. 2007) a behavior not observed in the sifaka.

We collected fecal samples from each individual directly after defecation to preclude contamination. Fecal samples were collected in the morning hours (0700h-0900h) at the end of each month. In this study, we analyzed 585 fecal samples (ring-tailed lemurs: 351, sifaka: 234). Fecal matter was placed in 50ml tubes filled with formalin.

PARASITE PROTOCOLS. Parasite abundances were detected using conventional gastrointestinal parasitology protocols. Given our methods, we acknowledge that we are underestimating the parasite diversity and prevalence for each primate species. We used fecal smear, fecal flotation, and fecal sedimentation methods. The fecal smear technique was used to detect the presence of non-buoyant parasites within each animal's feces (Gillespie 2006). For this protocol, fecal matter was placed directly on a slide and homogenized with distilled water. Fecal floatation methods were used to identify buoyant endoparasites and eggs (Gillespie 2006). For each floatation, we placed 2 g of fecal matter in a centrifuge tube containing a solution of sodium nitrate with a specific gravity of 1.2 (Zajac and Conboy 2006). The solution and feces were then homogenized with a wooden applicator and each sample was centrifuged at approximately 1,800 RPM for five minutes. Each test tube was placed in a test tube rack and topped off to a meniscus using more floatation solution. A coverslip was placed on the meniscus for five minutes. Each cover slip was then removed and placed on a microscope slide for viewing. We used the remaining 2 g of fecal matter at the bottom of the centrifuge tube for fecal sedimentation analysis (Gillespie 2006). Fecal matter was placed in a soapy water solution and filtered through a wire strainer. The sediment was left to settle for five minutes. The supernatant was removed, and the fecal sediment was pippetted onto a microscope slide and topped with a cover slip (Gillespie 2006). For each protocol, the fecal sample was scanned and parasites were counted using the 10x objective. The 40x objective was used to identify parasites. Parasites were photographed, measured, and logged into a computer database.

FIGURE 2. Ring-tailed lemurs drinking discarded well water in the camp (a) and rainwater from puddles on the road adjacent to the camp (b).

DATA ANALYSIS. We analyzed the parasite richness and prevalence for each primate host. Parasite richness is the number of parasite species harbored by each host. Prevalence is the number of hosts infected with a specific parasite species divided by the total number of hosts. For this paper, we used interval data to investigate how each primate host used behavior to acquire or eliminate and avoid parasites. We define 'soil-transmitted parasites' as those parasites that are acquired by the host through consumption of contaminated soil, water, or fecal matter that is lying on the ground, and those parasites on the ground which have an active host seeking life cycle stage in which they come in contact with their host while they are terrestrial (Table 1). We define 'socially-mediated parasites' as species whose transmission from one host to the next is facilitated by host social behavior (i.e. allogrooming, huddling, and smelling scent markings). Since parasite infections are generally found in Poisson distributions and do not adhere to the assumptions of parametric tests, we used only nonparametric statistics for all comparisons. Due to unequal sample sizes we also used nonparametric Mann-Whitney *U* tests for all behavioral analysis. Statistical tests were performed on Sigma Plot 11.0.

RESULTS

Table 1 illustrates the parasite richness and prevalence exhibited by each primate host at BMSR. Verreaux's sifaka did not harbor any protistan endoparasites and only two species of nematode worms. In contrast, ring-tailed lemurs harbored three species of protistan parasites and six species of nematodes (Figure 3). Each primate host harbored an oxyurid pinworm. The pinworm harbored by the ring-tailed lemurs was identified as *Lemuricola bauchoti* (del Rosario Robles et al. 2010; Figure 4) and the sifaka harbored *Biguetis trichuroides*. Both primate hosts harbored *Lemurostrongylus* sp. worms. The prevalence for oxyurid pinworms and *Lemurostrongylus* sp. infections was significantly higher in the ring-tailed lemur population (oxyurids: X^2= 22.370; P < 0.0001; *Lemurostrongylus* sp.: X^2 = 4.793; P < 0.05). The BMSR ring-tailed lemurs spent 4241 (19.1 %) intervals on the ground and Verreaux's sifaka were terrestrial for only 1138 (6.1 %) intervals and this difference was significant (*U* =

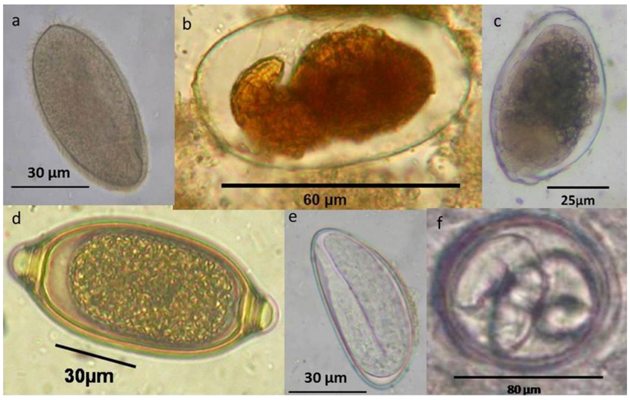

FIGURE 3. Photos of the protistan parasite (a) *Balantidium* sp. and helminth eggs harbored by the Bezà Mahafaly ring-tailed lemurs (b) *Lemurostrongylus* sp. (c) Unidentified trichostrongylid egg (d) unembryonated *Trichuris* sp. (e) *Lemuricola bauchoti* and (f) *Subulura* sp.

1.0; P < 0.001). Ring-tailed lemurs also allogroomed (*U* = 7.5; P < 0.01), autogroomed (*U* = 16.0; P < 0.05), and scent marked (*U* = 12.0; P < 0.05) significantly more frequently than sifaka. No significant differences in the frequency of sitting in contact with conspecifics were found between the BMSR ring-tailed lemur and sifaka populations (U = 32.0; P = 0.48).

DISCUSSION

The BMSR ring-tailed lemurs exhibited a greater endoparasite richness than the sympatric sifaka. The ring-tailed lemur population also exhibited a greater prevalence of infection for those parasites that were soil-transmitted and socially-mediated (Table 1). Furthermore, the BMSR ring-tailed lemurs had a higher prevalence for the two nematodes (oxyurids and *Lemurostrongylus* sp.) that each primate harbored. The BMSR ring-tailed lemurs and sifaka are both group-living, gregarious primates. However, the ring-tailed lemur population was observed on the ground significantly more often. Throughout this study, the sifaka spent 93.9 % of all intervals in the trees. This degree of arboreality decreases the likelihood of acquiring soil-transmitted parasites (Muehlenbein et al. 2003). In contrast, the ring-tailed lemurs were observed on the ground in 19.1 % of all intervals. The extent of their terrestrial behavior may be responsible for the wide diversity of nematode worms harbored by the BMSR ring-tailed lemurs, as *Lemuricola bauchoti*, *Trichuris* sp., and trichostrongylids use direct fecal-oral transmission routes. The prevalence of *Lemurostrongylus* sp. infections were significantly higher among the ring-tailed lemurs and this may be linked to their ground use. The life cycle of *Lemurostrongylus* sp. has yet to be identified and this nematode may use direct fecal-oral route or penetrate the skin of the host via direct contact like some other strongylid nematodes. Both sifaka and ring-tailed lemurs defecate directly onto the ground and are careful not to soil their sleeping trees and core areas (Loudon, per. obs). However, the high degree of terrestriality observed among the ring-tailed lemur population (Sauther 1994, Loudon 2009) increases the probability of acquiring these soil-transmitted parasites that require host ingestion or perhaps physical contact for acquisition and establishment (Anderson 2000).

Differences in the feeding behavior of each primate may also be responsible for the higher parasite richness found among the BMSR ring-tailed lemurs. Ring-tailed lemurs are omnivorous

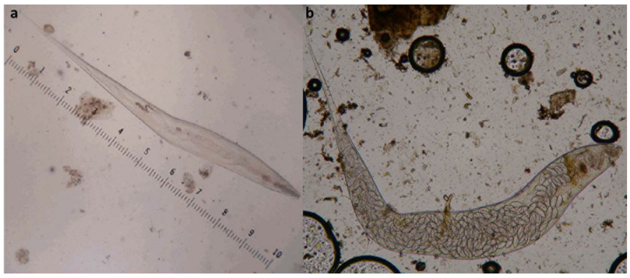

FIGURE 4. Photos of two adult *Lemuricola bauchoti* worms (a) sex unknown (b) gravid female.

and opportunistically feed on leaves, flowers, fruit, and invertebrates (Sauther et al. 1999). Verreaux's sifaka are primarily folivorous but incorporate small amounts of unripe kily fruits (*Tamarindus indica*) and kotipoke fruits (*Grewia grevei*) into their diet (Loudon 2009). The insectivory observed among the BMSR ring-tailed lemurs is most likely responsible for *Subulura* sp. infections. Worms within the genus *Subulura* use invertebrates as intermediate hosts (Anderson 2000), but as of now the identification of this intermediate host eludes us. Potential intermediate hosts include caterpillars or cockroaches. The caterpillars consumed by the BMSR ring-tailed lemurs live in the forest canopy and presumably consume leaves. To date, researchers have not observed this ring-tailed lemur community consuming cockroaches despite over 25 years of field research at BMSR, suggesting that cockroaches are unlikely intermediate hosts for this nematode. *Subulura* infections are rare among Malagasy primates and have only been documented in mouse lemurs (Chabaud et al. 1965, Raharivololona and Ganzhorn 2009). Since the life cycle of *Subulura* is not understood it remains unknown if the ring-tailed lemurs are somehow acquiring these infections from the sympatric mouse lemur (*Microcebus griseorufus*) population at BMSR.

Host behavior may also be responsible for the oxyurid (*Biguetis trichuroides*) infections we found among the BMSR sifaka. Male sifaka possess scent glands on their neck, which are used to mark the trees in their home ranges (Petter 1962). Male sifaka frequently incorporate fresh female feces into these scent marks. As a female defecates, a male will position himself directly underneath the female and capture the female's fecal pellets between his neck and tree trunk. The feces are smeared onto the trunk, resulting in a mark that includes the male's scent and the female's fecal matter (Loudon 2009). During this process, fecal pellets fall on the male, increasing the likelihood of acquiring a *B. trichuroides* infection. In a similar vein, ring-tailed lemurs may acquire some of their nematode and protistan infections via smelling and licking scent marks left by conspecifics. Ring-tailed lemurs use ano-genital glands to scent mark on substrates within their home ranges. These chemical cues function as a means to maintain home range boundaries and resource ownership, assert group status and intragroup dominance hierarchies, and mediate reproductive behavior (Drea and Scordato 2008). Ring-tailed lemurs that smell, ingest, or lick the scent marks left by a parasitized conspecific may acquire their parasites. Thus, these parasites are potentially utilizing each host's system of olfactory communication to facilitate their transmission to a new host. The BMSR ring-tailed lemurs were observed scent marking significantly more often than sifaka and this may result in the ring-tailed lemur environments that are more saturated with oxyurid eggs leading to the significantly higher oxyurid infections among the ring-tailed lemur population. The specific dynamics between each BMSR primate host and their oxyurids remains unresolved but are perhaps linked to the characteristics of oxyurid eggs which are infective almost immediately after being laid, which can lead to host auto-infection (Roberts and Janovy 2008). Oxyurid eggs are also sticky and adhere to the host's skin and fur (Sengbusch 1970), and bouts of contact by parasitized ring-tailed lemurs and sifaka may facilitate oxyurid transmission among group members. Ring-tailed lemurs and sifaka may acquire oxyurid infections from their oral allo- and autogrooming bouts that focus on the ano-genital region (i.e. genital grooming). Towards this end, the significantly higher prevalence of the socially-mediated oxyurids in the BMSR ring-tailed lemur population may be linked to differences in host behavior, as the ring-tailed lemurs allogroomed and autogroomed more frequently than sifaka.

The ecological challenges provided by the anthropogenically-disturbed forests appear to have little effect on the patterns of parasitism exhibited by the sifaka. Groups of sifaka living in these forests are required to descend to the ground more frequently but do so only to bipedally hop from one forest fragment to the other. The strict vegetarian diet of sifaka appear to circumvent the acquisition of those nematode worms that use invertebrates as intermediate hosts and their arboreal lifestyle evades soil-transmitted parasites that require physical contact or use fecal-oral transmission routes (Muehlenbein et al. 2003). It should be noted that an arboreal existence and a folivorous diet is only effective against evading those parasites that use the aforementioned transmission routes. Opportunistic necropsies of naturally deceased BMSR sifaka demonstrate that this species harbors *Paulianfilaria pauliani*, a filarial worm that uses an insect vector for transmission to new hosts (Chabaud et al. 1961). It is likely that this unidentified insect vector is a biting fly that can obtain a blood meal from animals utilizing arboreal substrates.

The anthropogenically-disturbed forests that surround the protected Parcel 1 present each primate with an entire suite of ecological challenges but it appears to only be influencing the patterns of parasitism among the BMSR ring-tailed lemurs. Our previous work at the site has demonstrated that the anthropogenically-disturbed forests exhibit significantly more tree cutting, grazing and livestock paths, and livestock manure compared to Parcel 1 (Whitelaw et al. 2005).

Furthermore, the ring-tailed lemur groups that utilized the anthropogenically-disturbed forests were observed consuming dog, cattle, and human feces during this study. Coprophagy in this population appears to be a feeding strategy to obtain calories and/or nutrients for those ring-tailed lemurs suffering from tooth loss (Fish et al. 2007). Although coprophagy may confer benefits (Soave and Brand 1991, Graczyk and Cranfield 2003), it also provides an avenue for acquiring new hosts for those parasites that utilize a fecal-oral transmission route. The coprophagic tendencies of these groups may be responsible for whipworm (*Trichuris*) infections, as these nematodes were only recovered among individuals living in the disturbed forests who were observed eating human and cattle feces. During the study, we identified *Trichuris vulpis* infections among the feral dogs living in the forests surrounding Parcel 1 (Loudon 2009). Many nematodes are host species-specific and the whipworm infections found among the BMSR ring-tailed lemurs are probably *T. lemuris*. On rare occasions *T. vulpis* has been known to use other hosts (Kagei et al. 1986, Dunn et al. 2002) and ring-tailed lemurs can act as alternative hosts for species-specific helminths (Shahar et al. 1995). However, further parasitological field research at BMSR is required to determine if the ring-tailed lemurs are in fact parasitized by *T. vulpis* and if these infections are acquired via coprophagy.

Host-parasite evolutionary relationships may also explain differences in the patterns of parasitism exhibited by the BMSR ring-tailed lemurs and sifaka. The ring-tailed lemur and sifaka helminths are likely species-specific and have co-evolved with their hosts (Brooks and Glen 1982, Glen and Brooks 1985). Previous investigations of BMSR sifaka parasitism found no evidence that this population harbored any fecal parasites (Muehlenbein et al. 2003) although we identified two nematode species. The different outcomes between our results and Muehlenbein et al. (2003) are puzzling but may be linked to differences in methodologies and/or ecology. We conducted fecal smear and sedimentation protocol, and for our fecal floatation method we used a sodium nitrate solution while Muehlenbein et al. (2003) report that they conducted fecal floatations with a zinc sulfate solution. Furthermore, Muehlenbein et al. (2003) only sampled sifaka groups inside Parcel 1 while we sampled groups within the parcel (although these may have been different groups) and groups inhabiting the anthropogenically-disturbed forests. Our study was also conducted at least two years later, in a region that is characterized by unpredictable environmental conditions (Dewar and Richard 2007) that may influence parasite abundances and distributions.

Another striking difference between the parasitic burdens of each host is the presence or absence of protistan infections. No sifaka harbored a protistan parasite. In contrast, all the BMSR ring-tailed lemurs harbored *Balantidium* sp. infections and 51.3 % of the population harbored *Entamoeba* sp. infections. These stark differences are arguably rooted in the durable, evolutionary relationships between the BMSR ring-tailed lemurs and their protistan burdens. However, the ubiquitous distribution of these protistan parasites increases the likelihood of accidental infection by hosts, and the BMSR ring-tailed lemurs may be acquiring these parasites by drinking from contaminated arboreal cisterns, puddles or neglected basins of well water within the camp.

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ARTICLE

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Les lémuriens du site Ramsar de Torotorofotsy

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RÉSUMÉ

Les différentes ressources naturelles et potentialités économiques du marais de Torotorofotsy et de ses bassins versants justifient l'appellation de « Ramsar » du site. Ce dernier abrite plusieurs espèces menacées de disparition : des amphibiens (*Mantella aurantiaca* et *M. crocea*), des oiseaux (*Anas melleri, Sarothrura watersi* et *Tyto soumagnei)*, des mammifères carnivores (*Cryptoprocta ferox*) ainsi que des lémuriens. La présente étude stipule qu'il y existe treize espèces de lémuriens ; parmi ces espèces, six sont classées « En danger » (*Prolemur simus, Indri indri, Propithecus diadema, Hapalemur griseus*, *Eulemur rubriventer*, *Daubentonia madagascariensis*), une « Quasi menacée » (*Eulemur fulvus*), une « Non menacée » (*Avahi laniger*) et cinq « Non évaluées » (*Allocebus trichotis, Cheirogaleus major, C. crossleyi*, *Microcebus lehilahytsara* et *Lepilemur mustelinus*). Les potentialités économiques de cette localité (ressources forestières, terrains agricoles et ressources minières) incitent à l'immigration dont on peut déjà voir des conséquences sur une partie de Torotorofotsy et de ses bassins versants : exploitation forestière, transformation de la forêt en *tavy* et altération des marais en zones agricoles. L'implantation du projet d'extraction de nickel-cobalt d'Ambatovy à l'ouest du site a mené à la construction d'un pipeline traversant le marais, ce qui facilite l'accès au site mais amplifie la pression anthropique sur l'environnement et entraine la dégradation de cette biodiversité particulière à la région. Des études environnementales et socio-économiques ont été effectuées pour réajuster le plan de gestion et de conservation du site. Pour ce qui est des lémuriens, les études de pression et de menaces basées sur la méthodologie du 'The Nature Conservancy' et celle de 'la Conservation du site Ramsar', focalise les efforts de conservation, pour ce site, sur six espèces à haut risque de disparition : *Prolemur simus, Propithecus diadema, Indri indri, Eulemur rubriventer, Daubentonia madagascariensis* et *Allocebus trichotis*.

ABSTRACT

The Torotorofotsy wetlands Ramsar site is rich in natural resources and has great economic potential. Several threatened species, including amphibians (*Mantella aurantiaca* and *M. crocea*), birds (*Anas melleri, Sarothrura watersi* and *Tyto soumagnei)*, carnivores (*Cryptoprocta ferox)* and lemurs distinguish the site. This study documents the presence of thirteen species of lemur, of which six are considered threatened (*Prolemur simus, Hapalemur griseus*, *Eulemur rubriventer*, *Propithecus diadema, Indri indri* and *Daubentonia madagascariensis*), one is classed Near Threatened (*Eulemur fulvus*), one Least Concern (*Avahi laniger)* and five Data Deficient (*Allocebus trichotis, Cheirogaleus major, C. crossleyi*, *Microcebus lehilahytsara* and *Lepilemur mustelinus*). The economic potential (forest resources, agricultural land and mineral resources) of the site has stimulated immigration to the area. As a result one part of Torotorofotsy has been subjected to forest exploitation, some areas of forest have been transformed by *tavy* and a large part of the wetlands has come under cultivation. The nickel and cobalt exploitation by the Ambatovy Project is located to the west of Torotorofotsy, thus one part of the pipeline runs through the marshland facilitating access to the site. The attraction and migration of human populations to the site generates pressures on the environment and subsequently accelerates the degradation of its biodiversity. Several studies based on the methodology of the 'The Nature Conservancy' and 'the Conservation of Ramsar site' have been conducted in order to implement and revise the management plan of this site. At Torotorofotsy, lemur conservation efforts should be focused on the six species at higher risk: *Prolemur simus, Propithecus diadema, Indri indri, Eulemur rubriventer, Daubentonia madagascariensis* and *Allocebus trichotis*.

INTRODUCTION

En 2008, le Projet minier d'Ambatovy a apporté son appui à la mise à jour du plan d'aménagement du marais de Torotorofotsy et de ses bassins versants, dans le cadre de sa politique de gestion durable de ce site Ramsar. Cette initiative de conservation à été mise en place dans le cadre de l'engagement au « Projet Ambatovy sur l'environnement à Madagascar » et selon les exigences du texte sur la mise en compatibilité des investissements sur l'environnement (MECIE : décret n° 2004-167 du 03 février 2004). Ce projet est engagé depuis 2006, depuis la signature de l'accord tripartite entre l'État Malgache, représenté

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par le Ministère de l'Environnement des Eaux et Forêts, l'Association Mitsinjo et la Société Ambatovy pour le pilotage du site. Il semble important de rappeler que le marais de Torotorofotsy et ses bassins versants ont été déclarés « site Ramsar », le 2 février 2005 et que l'institution non-gouvernementale « Association Mitsinjo » est, depuis le 22 juillet 2005, l'entité responsable de la mise en œuvre du plan de gestion du site (Attestation n°487-05/MINENVEF/SG/DGEF/DPB/SCBLF du 22.07.2005). Ainsi, la mise en place de la présente étude s'inscrit à la fois dans l'amélioration de ce plan de conservation auquel nous avons ici appliqué le concept du 'The Nature Conservancy' (TNC 2003) et dans les modèles types de conservation de site Ramsar (Ramsar 1999).

À Madagascar, les lémuriens sont parmi les animaux clés du système de conservation de la biodiversité (Ganzhorn et al. 1997). Dans le souci de la conservation de ces animaux, dans le marais de Torotorofotsy et de ses bassins versants, nous avons comme objectifs, dans cette étude, d'identifier les lémuriens existant dans le site, d'analyser les menaces anthropiques qui peuvent influencer le dynamisme de leur population et de formuler des suggestions sur le recadrage de leur conservation en sauvegardant leurs habitats naturels, dans le concept de l'utilisation rationnelle des ressources naturelles actuelles par les populations locales.

TOROTOROFOTSY ET SES BASSINS VERSANTS.

Administrativement, Torotorofotsy est localisé dans la Région d'Alaotra-Mangoro, à une vingtaine de kilomètres au nord-est de Moramanga (Figure 1), à cheval sur trois communes rurales avec Andasibe à l'est, Ambohibary à l'ouest et Ampasipotsy au sud. Torotorofotsy et ses bassins versants ont une superficie de 9 776 ha, dont 1 100 ha sont formés par des marais et le reste est constitué par des collines recouvertes de forêt intacte humide sempervirente (Ministère de l'environnement et des forêts 2009). Les altitudes de ces reliefs varient entre 900 et 1 200 m. La qualité et la structure forestière diffèrent en fonction des facteurs édaphiques et de leurs dégradations ; elles sont parfois fragmentées par des formations secondaires appelées *savoka* et des zones herbeuses arborées (Green et Sussman 1990, Rasoavarimanana 1997). Les études fauniques antérieures ont identifié 334 espèces de vertébrés, présentant un taux d'endémisme de plus de 90 % Les poissons avec les *Rheocles* sp. et *Ratsirakia* sp., les amphibiens avec les *Mantella aurantiaca* et *M. crocea,* les oiseaux avec *Anas melleri*, *Sarothrura watersi* et *Tyto soumagnei*, les mammifères comme *Cryptoprocta ferox* et les lémuriens avec *Daubentonia madagascariensis, Eulemur rubriventer, Indri indri,* et *Propithecus diadema* étaient considérés comme les animaux inventoriés les plus rares (Zimmermann et Andrianarivo 2000).

MÉTHODOLOGIE

Étant donnée l'étendue de l'aire de Torotorofotsy et de ses bassins versants (9 776 ha), trois sites ont été retenus pour nos études, en considérant la densité de la couverture forestière. Le premier site d'étude SE_1 est localisé dans la partie nord et nord-ouest ; le second site SE_2 se trouve dans la zone nord-est et le troisième site SE_3 dans la zone sud-ouest (Figure 1).

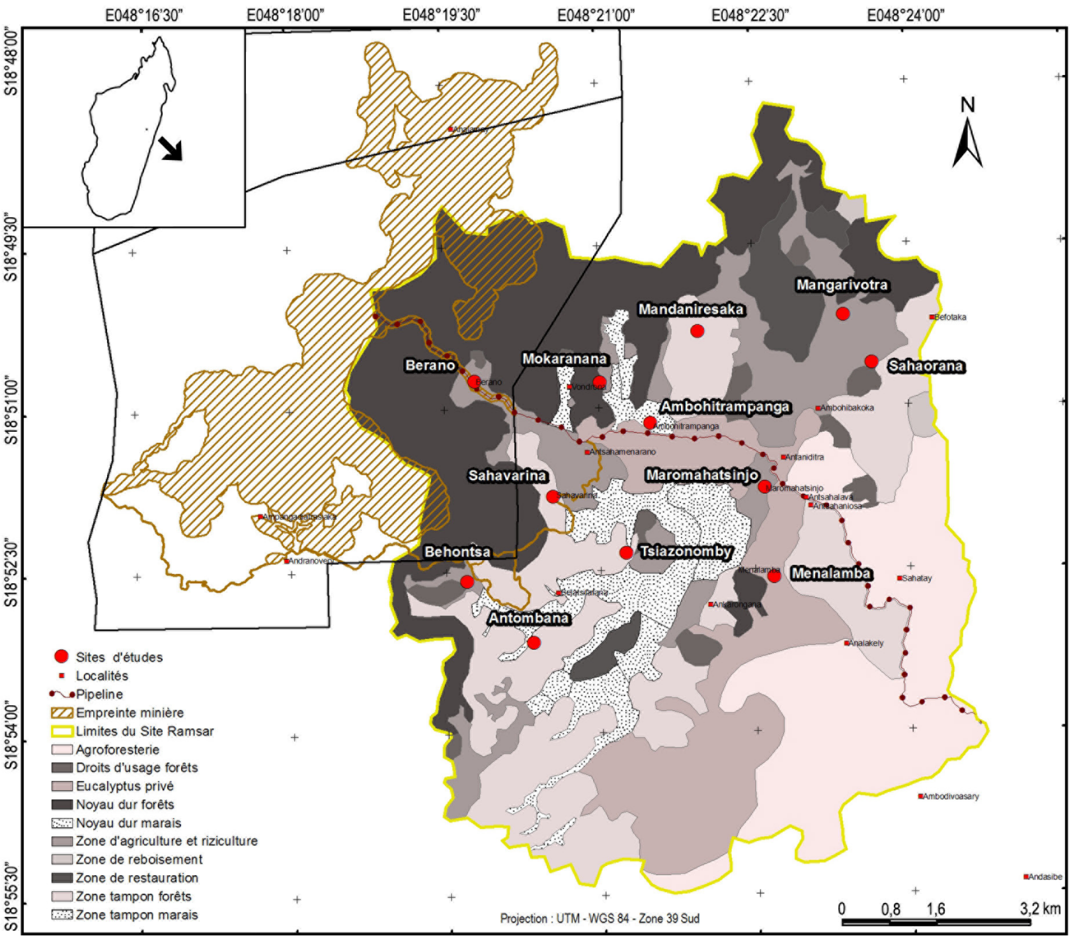

FIGURE 1. Localisation de Torotorofotsy et des sites d'études (Source : Département Environnement Ambatovy ; Site SE_1 : Mandaniresaka, Mokaranana ; site SE_2 : Mangarivotra, Sahaorana ; site SE_3 : Antombana, Behontsa, Sahavarina)

INVENTAIRE DES LÉMURIENS. La méthode de comptage utilisée se base sur l'utilisation d'une ligne « transect » le long de laquelle sont inventoriés les lémuriens. La longueur de chaque transect est d'environ 2000 m. Les observations sont effectuées entre 0700–1000h, 1430–1730h et 1830–2130h. Par soucis d'exactitude, un minimum de trois transects a été installé sur chaque site afin de prendre en compte la variation des observations de l'échantillon. Au total, dix transects ont été placés : trois dans le site SE_1, quatre dans le site SE_2 et trois dans le site SE_3 (Figure 1). Le même protocole d'observation a été adopté pour chaque transect : pendant sept jours et sept nuits d'inventaire, chaque observateur se déplace à une vitesse comprise entre 0,8 et 1 km par heure et à chaque fois qu'il rencontre un groupe d'animaux, il s'arrête et note l'heure de rencontre, la position géographique, le nombre d'individus rencontrés, ainsi que leurs âges relatifs et sexes et la distance perpendiculaire entre le premier animal observé et le transect. Les arrêts ne doivent pas dépasser cinq minutes. Les observateurs utilisent, pendant la nuit, des lumières artificielles atténuées (lampes frontales), qui facilitent le repérage des lémuriens ; une fois un individu repéré, l'utilisation de lumières plus puissantes pendant quelques minutes est indispensable pour identifier l'espèce. Enfin, le sens dans lequel est parcouru chaque transect est inversé tous les jours afin de favoriser le hasard de l'échantillonnage. Les résultats de ces observations permettent d'estimer la densité des lémuriens dans chaque site, à partir du calcul adopté et employé par Ganzhorn (1994) et Schmid (2000), suivant l'équation : D = N/(2 x W x L) avec D : densité estimée de la population (individus/km² ou i/km²) ; N : nombre total de lémuriens rencontrés pendant les observations (individus) ; W : distance perpendiculaire des animaux observés par rapport au transect en km ; L : longueur totale du transect en km. Avec cette méthode de calcul, nous avons exclu les animaux qui se trouvaient à une distance de plus de 15 mètres, afin d'optimiser l'identification des espèces et de limiter les erreurs. Le but de ces inventaires est de constater la présence ou l'absence des espèces de lémuriens et d'apprécier la densité relative des espèces existantes, afin de déterminer l'abondance des espèces cibles à conserver et d'évaluer, par la suite, leur viabilité à partir des études des facteurs écologiques. Des observations éventuelles en dehors de ces transects ont été effectuées pour évaluer la présence ou l'absence des espèces de lémuriens sur la totalité du site de Torotorofotsy.

MÉTHODE D'ENQUÊTE SOCIO-ÉCONOMIQUE EN RELATION AVEC L'ENVIRONNEMENT. Dans l'optique d'analyser la relation entre les pressions anthropiques et la conservation des lémuriens, nous avons adopté la « Méthode Accélérée de Recherche Participative de type exploratoire » ou « MARP exploratoire » (Gueye et Schoonmaker Freudenberger 1991). Cette méthode permet d'évaluer l'importance dans l'étude socio-écologique et sociobiologique de la zone de Torotorofotsy. Huit villages représentatifs de la zone ont été choisis : Ambohitrampanga, Mokaranana et Berano dans le site SE_1, Menalamba, Mangarivotra et Maromatsinjo dans le site SE_2 puis Behontsa et Sahavarina dans le site SE_3. Les thèmes ont été orientés et structurés autour des activités paysannes pour comprendre la signification de la gestion des ressources naturelles pour ces populations. De ce fait, les questionnaires étaient cadrés sur les activités quotidiennes des ménages, sur l'utilisation des ressources forestières (exploitation du bois, des produits végétaux, collecte de miel, chasse et consommation d'animaux sauvages), sur le système d'accaparement des terrains pour l'agriculture (défrichement, champs de culture, utilisation du feu, installation de campements temporaires appelé *lasy* ou de campements permanent appelés *potro*), sur les exploitations minières dans la forêt ainsi que sur les autres utilisations de cette dernière (pacages des bétails, cimetière).

ÉVALUATION DE LA PRESSION ANTHROPIQUE. Nous avons appliqué une approche participative par groupe focal et des interviews semi-structurés dans le cadre de la méthode MARP (Gueye et Schoonmaker Freudenberger 1991), pour évaluer l'ampleur de l'impact des activités quotidiennes des populations sur les ressources naturelles exploitées ; les résultats issus de cette méthode permettent de compléter les informations scientifiques exploitées en vue de la conservation des espèces de lémuriens menacés dans le site et de « valoriser » les pressions anthropiques existantes. Dans notre cas, nous avons estimé la relation entre la densité des lémuriens dans le bloc forestier de Torotorofotsy et les pressions anthropiques qui peuvent affecter ces abondances. C'est à partir de ces densités que l'on déduit l'indice de stabilité de chaque espèce de lémurien en fonction de la moyenne des rangs de ces densités relatives. La relation suivante permet d'effectuer le calcul de cette moyenne $(M){:}\cdot\ M\cdot = \sum_{i=1}^{n} x_i + \sum_{i=1}^{n} y_i / \sum_{i=1}^{n} x_i + y_i$
et les valeurs calculées correspondent à l'indice de stabilité ; où x_i correspond aux différentes espèces étudiées dans le site et y_i correspond aux différentes localités d'études (Martin and Bateson 1993). Dans cette étude, l'indice est dit « plus stable », si la valeur de M ∊ [12 ; 10] ; l'indice est dit « stable », si la valeur de M ∊ [9,99 ; 8] ; cet indice est dit «peu stable» si la valeur de M ∊ [7,99 ; 3] et l'indice est dit « moins stable » si la valeur de M ∊ [2,99 ; 0].

STRATÉGIE ET PRIORISATION DES ACTIONS DE CONSERVATION. Les critères d'identification des zones prioritaires de conservation à Torotorofotsy et ses bassins versants sont établis à partir de la présence de pression et du rang de stabilité de l'espèce ; c'est à dire en fonction de l'aire de distribution, de l'abondance relative des espèces, de la qualité de l'habitat et du niveau de menace qui pèse sur les lémuriens (TNC 2003). En effet, les sites prioritaires en matière de conservation des lémuriens à Torotorofotsy sont ceux qui présentent un taux élevé d'espèces menacées.

RÉSULTATS

LES LÉMURIENS DANS LA ZONE DE TOROTOROFOTSY ET SES BASSINS VERSANTS. Les résultats des inventaires dans les trois sites démontrent que la zone de Torotorofotsy et de ses bassins versants abrite 13 espèces de lémuriens parmi lesquelles six sont menacées, comme *Prolemur simus*, classé « En danger critique d'extinction» (CR) ; *Indri indri, Propithecus diadema* et *Daubentonia madagascariensis* catégorisées « En danger » (EN) (Mittermeier et al. 2010) ; *Hapalemur griseus* et *Eulemur rubriventer* classés « Vulnérable » (VU); une espèce a le statut de « Quasi-menacée » (NT), c'est le cas d'*Eulemur fulvus*; une espèce est classée « Préoccupation mineure » (LC), c'est le cas d'*Avahi laniger*. Enfin *Allocebus trichotis, Cheirogaleus major, C. crossleyi, Microcebus lehilahytsara* et *Lepilemur mustelinus* n'ont pas réellement de statut de conservation et désignées par « Données insuffisantes » (DD) (Tableau 1).

TABLEAU 1 . Densité estimée des lémuriens exprimée en individus/km² ou i/km². (D_1 = densité des lémuriens dans le site SE_1 ; D_2 = densité des lémuriens dans le site SE_2 ; D_3 = densité des lémuriens dans le site SE_3 ; NC = non calculé – statut de conservation des espèces de lémuriens suivant UICN (2009) : CR = En danger critique d'extinction ; EN = En danger ; VU = Vulnérable ; NT = Quasi menacé ; LC = Préoccupation mineure ; DD = Données insuffisantes; NE = Non évalué).

Famille	Noms scientifiques	D1 (i/km²)	D2 (i/km²)	D3 (i/km²)	Statut UICN 2010	Densité (i/km²) dans les autres aires protegées	Localité	Domaine territorial (ha)	Référence
Cheirogaleidae	*Microcebus lehilahytsara*	4,52±1,75	2,31±1,64	2,53±2,12	DD				
Cheirogaleidae	*Cheirogaleus major*	1,64±0,9	0	0	DD	(75–100)	Andasibe	2–4	Pollock 1979
Cheirogaleidae	*Cheirogaleus crossleyi*	0	0,46±0,5	0,44±0,6	DD				
Cheirogaleidae	*Allocebus trichotis*	0,41±0,5	0	0	DD	(7–15)	Makira		Rasolofoson et al. 2007b
Lepilemuridae	*Lepilemur mustelinus*	1,23±0,84	0,92±0,9	0,14±0,75	DD			1–5	Ratsirarson et al. 1988
Lemuridae	*Eulemur fulvus*	32,05±10,45	13,83±8,35	5,22±5,76	NT	(40–60)	Andasibe	7–20	Pereira et al. 1990
Lemuridae	*Eulemur rubriventer*	0	1,84±0,9	0	VU	(20–30)	Ranomafana	10–20	Irwin et al. 2005
Lemuridae	*Prolemur simus*	NC	NC	0	CR				
Lemuridae	*Hapalemur griseus*	6,99±5,44	15,22±6,35	1,64±1,25	VU	(47–62)	Andasibe	6–15	Pollock 1979
Indriidae	*Avahi laniger*	5,75±2,75	13,37±2,55	8,5±4,45	LC	(72–100)	Andasibe	2–4	Ganzhorn 1988
Indriidae	*Propithecus diadema*	0	2,31±1,25	0,44±0,75	EN	(9–17)	Mantadia	20–35	Schmid 2000
Indriidae	*Indri indri*	4,11±2,63	1,38±0,84	0,9±0,9	EN	(2–15)	Andasibe	7–10	Pollock 1979, Powzyk et al. 2003
Daubentoniidae	*Daubentonia madagas-cariensis*	0,82±0,77	NC	NC	EN	(0–3)	Makira	30–200	Sterling 2003, Rasolofoson et al. 2007b
	Total (espèces existantes)	10	11	9					

À noter que pendant nos observations en dehors des transects, nous avons recensé un groupe de six individus de *Prolemur simus* près du village de Menalamba (site SE_2), et des traces d'activités de cette espèce ont été également notées sur des tiges de bambou dans la localité de Mokaranana (site SE_1). Ces deux localités sont constituées par une forêt dégradée et une forêt de *savoka* où se développent des bambous (*Bambusa vulgaris* et *Cathariostachys madagascariensis*). Ces types d'habitats sont appréciés par cette espèce (Wright et al. 1987, Ravaloharimanitra et al. 2011, Olson et al. 2013).

En tenant compte des résultats des inventaires dans les transects et des observations aléatoires (*Prolemur simus* et ses traces d'activités ainsi que les traces d'activités de *Daubentonia madagascariensis*), nous avons recensé dix espèces de lémuriens dans le site SE_1, onze espèces dans le site SE_2 et neuf espèces dans le site SE_3 (Tableau 1). Concernant l'abondance, les résultats démontrent que les densités des espèces de lémuriens varient dans les trois sites d'études. Ainsi, la densité est presque nulle pour *Allocebus trichotis* et *Cheirogaleus crossleyi* ; elle varie entre zéro et deux i/km² pour *Lepilemur mustelinus* et *Daubentonia madagascariensis* ; elle varie entre zéro et trois i/km² pour *Cheirogaleus major, Eulemur rubriventer* et *Propithecus diadema*. Pour le cas d'*Indri indri*, elle varie entre un et quatre i/km² et elle est comprise entre deux et sept i/km² pour *Microcebus lehilahytsara*, entre cinq et seize i/km² pour *Avahi laniger*, entre un et vingt i/km² pour *Hapalemur griseus* et entre cinq et quarante-deux i/km² pour *Eulemur fulvus*.

NOTRE ÉTUDE DES LÉMURIENS DANS LA ZONE DE TOROTOROFOTSY PAR RAPPORT AUX TRAVAUX ANTÉRIEURS. En 1999, les études effectuées dans le cadre de la déclaration du marais de Torotorofotsy en « site Ramsar » ont dénombré 11 espèces de lémuriens, à savoir : *Avahi laniger*, *Cheirogaleus major*, *Daubentonia madagascariensis*, *Eulemur fulvus*, *E. rubriventer*, *Hapalemur griseus*, *Indri indri*, *Lepilemur mustelinus*, *Microcebus rufus*, *Propithecus diadema* et *Varecia variegata variegata* (Zimmermann et Andrianarivo 2000). En 2004, les études d'impact environnemental liées à l'implantation du projet d'exploitation de nickel et cobalt d'Ambatovy dans la zone de Torotorofotsy ont inventorié sept espèces : *Avahi laniger, Cheirogaleus major, Eulemur fulvus, E. rubriventer, Hapalemur griseus, Microcebus rufus* et *Propithecus diadema* (Ambatovy Project 2006). Outre ces études, en 2004, l'équipe de l'Association Mitsinjo a recensé pour la première fois la présence de *Prolemur simus* à Torotorofotsy et, en 2008, la présence des indices d'activités d'autres groupes (Dolch et al. 2004, 2008). Dans cette étude, 13 espèces ont été inventoriées, deux espèces nouvellement recensées, donc, en plus des onze espèces déjà connues : *Cheirogaleus crossleyi* et *Allocebus trichotis*. Dans nos inventaires, l'espèce *Varecia v. variegata* n'a été relevée dans aucun des trois sites d'observation et les microcèbes rencontrés appartiendraient à l'espèce *Microcebus lehilahytsara* (Roos et Kappeler 2006) mais pas à *M. rufus* (Mittermeier et al. 2006). Nous avons remarqué dans le site SE_2, la présence de deux morphotypes de *Hapalemur griseus* qui vivent en sympatrie. Le pelage du premier est gris roux sur la zone frontale et sur la partie dorsale tandis que la partie ventrale est grise clair, la queue de couleur gris foncé est touffue, le museau de couleur noir est court. Le second type a une taille plus petite que le premier. Il présente un dimorphisme sexuel distinctif, c'est-à-dire que le mâle a un pelage uniforme gris foncé, alors que la femelle est gris cendré et présente une face ventrale gris-blanchâtre. À noter que ces variations morphotypiques d'*Hapalemur* existent également dans la forêt de Maromizaha qui se trouve à 10 km à l'est de Torotorofotsy (Rakotosamimanana et al. 2004).

CARACTÉRISTIQUES DES LÉMURIENS DANS LE MARAIS DE TOROTOROFOTSY ET DE SES BASSINS VERSANTS PAR RAPPORT AUX AUTRES AIRES PROTÉGÉES. En comparant la richesse de Torotorofotsy en lémuriens avec d'autres aires protégées comme le parc de Zahamena qui abrite 13 espèces de lémuriens (Rakotoarison et al. 1997), Mantadia qui compte 11 espèces (Groves 2000), Analamazaotra-Andasibe qui abritent 12 espèces (Groves 2000), le Parc National d'Andringitra (Goodman et Rasolonandrasana 2001) et celui du Parc National de Ranomafana (Wright et al. 1987, Goodman et Rasolonandrasana 2001) qui en comptent chacun 12 espèces, nous constatons que Torotorofotsy présente une richesse élevée et une diversité spécifique de lémuriens analogues à celles de ces autres aires protégées qui sont localisées dans les forêts denses humides sempervirentes de moyenne altitude du versant oriental de l'île.

LES EFFETS DES ACTIVITÉS HUMAINES SUR LA FORÊT ET AUTRES RESSOURCES NATURELLES À TOROTOROFOTSY. Menalamba est le seul *fokontany* (quartier constitué par un ensemble de hameaux) prédominant dans le site de Torotorofotsy. Ce *fokontany* et ses environs comptent 1290 habitants (d'après enquête et recensement : 305 habitants dans la zone SE_1, 585 habitants dans la zone SE_2 et 400 habitants dans la zone SE_3) (Fokontany Menalamba 2007). L'application de la méthode « MARP de type exploratoire», nous a permis de mener une enquête auprès de 82 ménages dans les trois sites (21 ménages dans le site SE_1, 40 ménages dans le site SE_2 et 21 ménages dans le site SE_3). Les résultats de cette enquête nous ont permis d'apprendre que les activités quotidiennes de la population se concentrent sur l'agriculture, le bûcheronnage, l'artisanat, la pêche et l'élevage. L'étude de ces activités permet de déduire les pressions existantes sur les ressources naturelles, en particulier leurs effets sur les ressources forestières ainsi que sur la forêt en tant qu'habitat des lémuriens (Tableau 2). Dans le site SE_1, la pression exercée sur le milieu forestier est inférieure à celle exercée sur les sites SE_2 et SE_3. De même, celle exercée sur les ressources du site SE_3 est inférieure à celle du site SE_2. Nous pouvons donc dire que le site SE_2 est le plus vulnérable des trois sites.

RELATION ENTRE LES PRESSIONS ANTHROPIQUES ET LES DENSITÉS DE LÉMURIENS. Comme dans toute communauté paysanne, les activités de la vie quotidienne dépendent des ressources naturelles et de la qualité du terrain exploitable de la localité. Dans la zone concernée par notre étude, nous avons pu constater que plus le nombre d'habitants est élevé, plus la surface dégradée de l'habitat forestier s'agrandit (Tableau 3).

D'après ces résultats, nous avons pu dresser une liste des facteurs générant une perturbation de l'écosystème forestier et marécageux du site de Torotorofotsy. Les feux non contrôlés, par exemple, provoquent un dégât irréversible dans les zones forestières des trois sites; ils sont liés à la « tradition de feu » par la pratique du *tavy* (culture sur brûlis pour l'exploitation du riz), et s'ajoutent parfois à la pratique de l'agriculture vivrière et à la construction de campements temporaires (*lasy*) ou de campements permanents (*potro*). En plus de ces activités, il faut compter l'exploitation directe des ressources forestières et la chasse d'animaux sauvages. Les différents facteurs énumérés ci-dessus peuvent influencer les ressources naturelles et la densité des lémuriens qu'on observe dans le site en raison de la fragmentation de leurs habitats qu'ils impliquent (Andriamasimanana et al. 2001, Lehman et al. 2006).

ABONDANCE ET INDICE DE STABILITÉ DES LÉMURIENS DANS LA ZONE DE TOROTOROFOTSY. La présence des espèces de lémuriens pendant nos observations reposait sur le hasard de l'échantillonnage et sur l'effet des facteurs écologiques que les différents types de micro-habitats de Torotorofotsy subissaient au moment de notre étude. Comme les densités relatives calculées sont des nombres fractionnés, en arrangeant par ordre prioritaire les densités relatives de chaque espèce, nous obtenons un classement de densité des lémuriens dans chaque site (Tableau 4). À partir de ce classement de densités, nous pouvons calculer la moyenne de l'indice de stabilité (M).

Le classement de ces indices définit une hiérarchisation de stabilité des espèces de la plus stable vers la moins stable dans l'ensemble de la zone. Le résultat de ce calcul de stabilité démontre que $M \in [12 , 10]$ pour les espèces *Eulemur fulvus* et *Hapalemur griseus*, elle sont donc considérées comme des espèces « plus stables ». Puis $M \in [9.99 , 8]$ pour les *Avahi laniger* et *Microcebus lehilahytsara*, ces espèces sont dites « stables ». $M \in [7.99 , 3]$ pour *Lepilemur mustelinus, Indri indri, Propithecus diadema, Cheirogaleus crossleyi* et *C. major*, elles sont considérées comme des espèces « peu stables ». Enfin, les espèces « moins stables » dont $M \in [2.99 , 0]$ sont *Allocebus trichotis*, *Daubentonia madagascariensis* et *Eulemur rubriventer*. En terme de sensibilité par rapport à l'abondance relative de l'espèce et à la conservation des lémuriens dans la zone de Torotorofotsy et de ses bassins versants, ces constatations permettent de déduire que les deux espèces *Eulemur fulvus* et *Hapalemur griseus* sont les lémuriens les moins sensibles, que *Avahi laniger* et *Microcebus lehilahytsara* sont peu sensibles, que *Cheirogaleus crossleyi*, *C. major*, *Indri indri, Lepilemur mustelinus* et *Propithecus diadema* constituent les espèces sensibles, et que *Allocebus trichotis*, *Daubentonia madagascariensis* et *Eulemur rubriventer* sont les espèces les plus sensibles (Figure 2).

TABLEAU 2 . La répartition des différentes pressions recensées dans les trois sites d'étude de Torotorofotsy et ses bassins versants. Site SE_1 : Mandaniresaka (E048°21'35" / S18°49'51"), Mokaranana (E048°21'03" / S18°50'10") ; site SE_2 : Mangarivotra (E048°23'07" / S18°49'52"), Sahaorana (E048°23'48" / S18°50'02") ; site SE_3 : Antombana (E048°20'10" / S18°53'40"), Behontsa (E048°19'36" / S18°52'39"), Sahavarina (E048°21'15" / S18°52'50").

Catégorisation des activités dans les zones forestières	Types d'activités identifiés entrainant des perturbations dans les zones forestières	SE_1	SE_2	SE_3	Total
Usage de feux non contrôlés	Feux sauvages (ha)	34	92	40	166
Usage de feux pour l'agriculture	Défrichement des zones forestières, *tavy* (ha)	16	30	10	56
Usage de feux pour l'agriculture et habitation près de la forêt	Accaparement de terrain agricole et campement temporaire, *lasy* (ha)	2	4	2	8
	Accaparement de terrain agricole et campement définitif, *potro* (ha)	4	8	6	18
Défrichement dans les zones forestières	Abattage d'arbres forestiers (diamètre hauteur de poitrine > 12 cm; nombre de pieds)	0	22	40	66
	Cheval de sciage pour bois (nombre de pieds)	0	1	5	6
	Collecte de feuilles de Pandanus (nombre de pieds)	15	3	1	19
	Collecte de fibres et écorces végétales (nombre de pieds)	4	3	0	7
	Collecte de miel (nombre de pieds)	6	0	3	9
Chasse	Pièges pour autres animaux (piège)	5	4	2	11
	Piège à lémuriens (piège)	0	5	3	8
	Chasse observéé dans la forêt (nombre de groupes)	0	2	0	2
Élevage	Pacage des bœufs (nombre de troupeaux)	3	1	5	9
Total des activités identifiées	13	9	12	11	

STRATÉGIE ET PRIORISATION DES ACTIONS DE CONSERVATION DES LÉMURIENS ET DE LEURS HABITATS. Dans la zone de Torotorofotsy et de ses bassins versants, les trois sites SE_1, SE_2 et SE_3 devraient être considérés pour la richesse de leur habitat forestier et des espèces qu'ils abritent dans la cadre des priorités en matière de conservation de la nature. En effet, les sites prioritaires sont déterminés en fonction des critères d'identification des zones prioritaires de conservation établis à partir de la présence d'espèces endémiques locales, spécifiques et représentatives du milieu dont la qualité de l'habitat présente un niveau de menace tolérable (TNC 2003) (Tableau 5).

Selon les caractéristiques des trois sites d'étude de Torotorofotsy, le site SE_2 (Mangarivotra –Sahaorana) paraît être le site le plus favorable à la conservation des lémuriens, suivi par le site SE_1 (Mandaniresaka – Mokaranana) et, enfin, par le site SE_3 (Antombana – Behontsa – Sahavarina).

DISCUSSION

Plusieurs thèmes peuvent être des sujets de discussions dans cette étude, mais nous essayerons de nous cantonner à la relation entre les ressources naturelles et les facteurs anthropiques.

NOMBRE POTENTIEL D'ESPÈCES DE LÉMURIENS DANS LA ZONE DE TOROTOROFOTSY ET SES BASSINS VERSANTS. Les différentes études effectuées à Torotorofotsy démontrent que ce site Ramsar peut contenir 14 espèces de lémuriens, à savoir : *Allocebus trichotis*, *Avahi laniger*, *Cheirogaleus crossleyi*, *C. major, Daubentonia madagascariensis*, *Eulemur fulvus*, *E. rubriventer*, *Hapalemur griseus*, *Indri indri*, *Lepilemur mustelinus*, *Microcebus lehilahytsara*, *Prolemur simus*, *Propithecus diadema* et *Varecia variegata*. Mais depuis l'inventaire de 2004 (Ambatovy Project 2006) et pendant la présente étude, nous avons noté l'absence de *Varecia variegata*. Cette absence peut s'expliquer par une intolérance de cette espèce aux différents facteurs anthropiques entrainant la diminution de son micro-habitat car cette espèce a une préférence pour le support : arbre à haute canopée (Ratsimbazafy 2002), alors que ces arbres sont déjà exploités. Il n'est pas impossible non plus que les groupes qui existaient dans la partie nord-est (site SE_2) ont été chassés.

PRÉSENCE DE DEUX MORPHOTYPES DE *HAPALEMUR GRISEUS.* En raison de la potentielle richesse d'espèces de lémuriens, nous avons observé, pendant cette étude, la présence de deux morphotypes de *Hapalemur griseus.* Une question se pose face à cette observation : s'agit-il d'une indication que le site est une zone de croisement de répartition biogéographique ou s'agit-il d'une source d'endémisme de

TABLEAU 3 . Variation des surfaces forestières dégradées en fonction du nombre des habitants dans les sites SE_1, SE_2 et SE_3 (légende conforme au Tableau 2).

Catégorisation des activités humaines dans les zones forestières	SE_1	SE_2	SE_3
Usage de feux non contrôlés (ha)	34	92	40
Usage de feux pour l'agriculture, *tavy* (ha)	16	30	10
Usage de feux dans l'agriculture et habitation près de la forêt, acquisition de terrain (ha)	6	12	8
Totales des surfaces dégradées (ha)	56	134	58
Taux de dégradation par rapport à la surface de Torotorofotsy (%)	57%	137%	59%
Nombre d'habitants	305	585	400

TABLEAU 4 . Rang de la densité des lémuriens dans les sites SE_1, SE_2 et SE_3 (légende conforme au Tableau 2).

Espèces de lémuriens	SE_1	SE_2	SE_3
Allocebus trichotis	3	1	1
Daubentonia madagascariensis	5	1	1
Cheirogaleus major	6	1	1
Eulemur rubriventer	1	6	1
Cheirogaleus crossleyi	1	3	5
Lepilemur mustelinus	4	4	4
Propithecus diadema	1	7	5
Indri indri	7	4	7
Microcebus lehilahytsara	8	8	9
Avahi laniger	9	9	11
Hapalemur griseus	10	11	8
Eulemur fulvus	11	10	10

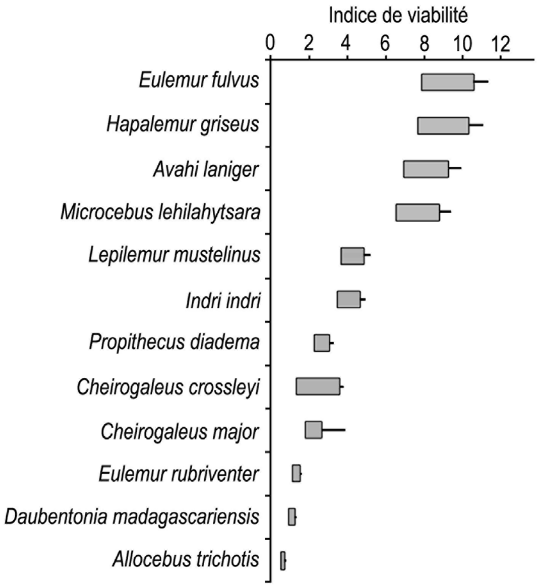

FIGURE 2. Indice de stabilité des espèces de lémuriens dans la zone de Torotorofotsy et ses bassins versants en fonction des facteurs écologiques existants.

cette espèce ? *Hapalemur griseus* est une espèce territoriale et le groupe a un système d'accouplement monogame ou polygyne ; ces comportements sociaux reproductifs sont probablement dus à la défense des ressources et à la défense des femelles (Tan 1999, Mutschler et al. 2000). Par conséquent, l'échange de génotypes entre les deux sous-espèces est limité par ces caractères comportementaux et la naissance d'une population hybride est improbable. L'analyse génétique de ces deux morphotypes de *Hapalemur griseus* pourrait déterminer s'il existe une variation spécifique ou non. Il semble que *Hapalemur griseus*, qui est une espèce peu sensible dans cette zone, s'adapte bien aux facteurs anthropiques dans le milieu où il existe actuellement (Andriamasimanana et al. 2001, Irwin et al. 2005, Lehman et al. 2006).

MODE DE GESTION DES RESSOURCES NATURELLES DANS LA ZONE DE TOROTOROFOTSY. Cette étude démontre que l'Homme dépend de son environnement auquel il a attaché ses valeurs culturelles. Dans le site de Torotorofotsy, l'utilisation des feux et d'autres moyens similaires semble être le principal facteur de pression faisant régresser la superficie des zones forestières existantes et les fragmente. Les autres moyens d'exploitations des ressources peuvent être maîtrisés par des engagements entre les communautés ou bien par l'application des lois imposées par les autorités compétentes. Le présent cas étudié dévoile l'atténuation de la conservation des ressources naturelles dans cette zone. Trois types de gestions de ressources naturelles sont respectés et suivis par les habitants de Torotorofotsy. Deux de ces types de gestions sont axés sur des ressources aquatiques : les poissons et les cypéracées. Ainsi, la pêche et la collecte de ces plantes aquatiques pour la confection de natte est censée s'arrêter pendant la saison des pluies (fermeture de collecte des cypéracées ou *mihidy rambo* en décembre et ouverture de la pêche ou *vaky sihitry* en mai). Le troisième type de gestion consiste en l'interdiction de la chasse des lémuriens, définis comme *fady,* c'est-à-dire tabou, pour tous les habitants qui résident dans le terroir de Torotorofotsy. Ces interdictions sont dictées dans des lois conventionnelles (*Dinam-pokonolona*) établies entre les *fokonolona* (tous les habitants du *fokontany*) depuis l'année 2005 (année de déclaration de Torotorofotsy en site Ramsar). Ces interdictions sont généralement respectées, mais les délinquants existent toujours dans le *fokontany* même ou bien venant d'autres *fokontany* périphériques. Pendant les inventaires, nous avons rencontré des chasseurs dans le site SE_2 et nous avons vu des pièges dans les sites SE_2 et SE_3. Force est de constater que la chasse n'est pas totalement éradiquée dans la zone et les résultats des enquêtes nous révèlent que de nombreuses familles (environ 70 % des ménages interrogés) apprécient et mangent encore les animaux sauvages, appelés *haza* ou

TABLEAU 5 . Priorisation des zones à conserver dans le site de Torotorofotsy et ses bassins versants (légende conforme au Tableau 2).

Sites d'étude	Critères de l'UICN	Activités anthropiques / Pression existante	Diversité spécifique en lémuriens
SE_2	Présence d'espèce menacée : En danger critique (CR): *Prolemur simus* ; En danger (EN) : *Daubentonia madagascariensis, Indri indri, Propithecus diadema*	Défrichement et *tavy*	11
	Présence d'espèces Données insuffisantes (DD) : *Cheirogaleus crossleyi*, *Lepilemur mustelinus, Microcebus lehilahytsara*	Défrichement et campement	
		Défrichement et exploitations forestières	
		Autres pièges - pièges à lémurien	
		Chasse	
SE_1	Présence d'espèce En danger critique (CR) : *Prolemur simus*	Défrichement *tavy*	10
	en danger (EN) : *Daubentonia madagascariensis, Indri indri*	Défrichement et campement	
	Présence des espèces Données insuffisantes (DD) : *Allocebus trichotis*, *Lepilemur mustelinus, Microcebus lehilahytsar*	Défrichement / exploitations forestières	
		Autres pièges	
SE_3	Présence d'espèce En danger (EN) : *Daubentonia madagascariensis, Indri indri, Propithecus diadema*	Défrichement *tavy*	9
	Présence des espèces Données insuffisanets (DD) : *Cheirogaleus crossleyi*, *Lepilemur mustelinus, Microcebus lehilahytsara*	Défrichement et campement	
		Défrichement / exploitations forestières	
		Autres pièges - Pièges à lémurien	

« viande de brousse » (oiseaux, petits mammifères, mammifères carnivores, lémuriens, potamochères, etc.). À Torotorofotsy, la chasse du gibier est destinée à la consommation familiale et sert à satisfaire les apports en protéine des habitants (Jenkins et al. 2011) et les chasseurs ne sélectionnent pas les animaux à chasser, comme dans la zone de Makira, où les chasseurs ont des préférences pour les lémuriens (Rasolofoson 2007b, Golden 2009). Néanmoins, à cause du *fady*, les Betsimisaraka ne chassent jamais des *babakoto* (*Indri indri*).

Ainsi, la sensibilisation doit être axée sur la maîtrise du feu, qui est prisé pour transformer une zone forestière en terrain agricole, car ce facteur est le premier déstabilisateur de l'écosystème forestier (Kiener 1963, Rasoavarimanana 1997, Aubert et al. 2003). Quant au *tavy*, la gestion de la fertilité des terres entraîne écologiquement un dynamisme des formations végétales secondaires qui évoluent vers une formation climacique appelée *savoka* et qui sera à nouveau exploitable après cinq à dix ans de jachère (Kiener 1963, Aubert et al. 2003, Styger et al. 2007). Ce dynamisme de formation végétale entraine un dynamisme d'éparpillement des hameaux en fonction des terrains fertiles.

L'exploitation de la mine à Ambatovy et la construction du pipeline le long du marais entrainent également, sur le plan écologique, une fragmentation de différents habitats forestiers et marécageux. Les fragmentations des habitats forestiers entrainent parfois l'isolement de groupes de lémuriens et affaiblissent leurs chances de survie (Lehman et al. 2006). Plusieurs groupes d'animaux vont subir les conséquences de ce changement de territoire et pourront, ou non, tolérer et s'adapter à la modification de leur domaine vital (Andriamasimanana et al. 2001, Irwin et al. 2005). Les travaux de la mise en place du pipeline et des infrastructures du projet Ambatovy ont commencé en décembre 2008, pendant cette étude. En 2013, les infrastructures sont mises en place ; le pipeline facilite l'accès au site de Torotorofotsy en permettant une voie de communication pour tout public. Sur le plan social, l'implantation du projet Ambatovy a accaparé une partie des terrains agricoles. Pour les gens de la région, ce concept reflète la mise en place de nouvelles règles de gestion de l'espace et des ressources naturelles impliquées par la création de ce pôle d'attraction économique (Phillips 2002, UICN 2003). La perception des populations de Torotorofotsy est généralement dominée par une image d'invasion de leur territoire par des personnes venant de l'extérieur qui leur imposent des règles et des interdits.

CONCLUSION

La mise en œuvre du plan de gestion pour la conservation de la forêt des bassins versants de Torotorofotsy appelle à la sauvegarde des habitats naturels des lémuriens existants dans ce site Ramsar. Cette zone abrite actuellement 13 espèces de lémuriens pour lesquelles elle représente une niche écologique importante car ses blocs forestiers sont connectés avec le corridor forestier Ankehiheny-Zahamena (CAZ). Cette connexion forestière offre un écosystème potentiel pour ces espèces et est favorable aux échanges de flux génétiques nécessaires à leur pérennité. Concernant la conservation des lémuriens dans cette zone, leur rang de viabilité montre que les efforts doivent examiner en priorité les espèces menacées de faible densité aux statuts de En danger critique d'extinction, En danger ou Vulnérable ; selon les statuts de menace déterminés par l'UICN et selon les degrés de sensibilité, la conservation des six espèces de lémuriens suivantes sont prioritaires dans cette zone : *Allocebus trichotis, Daubentonia madagascariensis, Eulemur rubriventer, Indri indri, Prolemur simus*, *Propithecus diadema* ; puis les espèces qui ont une densité faible : *Cheirogaleus major*, *C. crossleyi* et *Lepilemur mustelinus* ; enfin les espèces moins menacées comme *Microcebus lehilahytsara, Avahi laniger*, *Hapalemur griseus* et *Eulemur fulvus*.

Les gestionnaires et les différents acteurs du développement dans la zone de Torotorofotsy devront mettre en œuvre une gestion du terroir des bassins versants (ANGAP 2003) pour protéger la biodiversité exceptionnelle. Il est également nécessaire de sensibiliser la population locale et riveraine par l'application effective d'une éducation environnementale, la formation à une meilleure maîtrise du feu, principal facteur de pression sur la biodiversité du site, et à la gestion durable des ressources naturelles. Ces actions sont compatibles avec la politique environnementale que Madagascar a adoptée pour la valorisation de sa biodiversité. L'adoption de cette politique mènerait au développement durable de la zone et de la région tout en permettant la conservation des écosystèmes et le développement économique et socio-culturel.

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MATÉRIEL SUPPLÉMENTAIRE.

DISPONIBLE EN LIGNE UNIQUEMENT.

ANNEXE 1. Méthodes Accélérées de Recherche Participative (MARP) appliquées à l'étude de la conservation des lémuriens du site Ramsar de Torotorofotsy.

SHORT NOTES

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Étude de la sociologie des exploitants de bois de rose malgaches

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RÉSUMÉ

Les exploitants de bois de rose étaient officiellement 13 au début de 2009. Leur nombre est passé à 103 pour la seule région SAVA au début 2012. Mais c'est à Antalaha que leur croissance a été la plus remarquable : les opérateurs historiques ont été rejoints par les membres de leurs familles et leurs anciens collecteurs, puis par des nouveaux venus, pour atteindre le chiffre record de 63 opérateurs dans cette seule ville, malgré l'interdiction d'exploiter le bois de rose depuis mars 2010. Cette communauté a fait d'Antalaha une ville à part à Madagascar car elle y fait jeu égal avec l'État qui n'ose lui appliquer les lois de la République, à moins qu'il n'ait conclu avec elle un mariage d'intérêt. Cette situation s'avère en outre être un invariant historique qui a remarquablement traversé les époques précoloniale, coloniale et postindépendance.

ABSTRACT

At the start of 2009, there were 13 rosewood traders in Madagascar. By early 2012 their number had increased to 103 traders in the SAVA region alone. It has been in Antalaha that the growth of these traders has been the most explosive: the 'original' traders were joined by family members and also by their former wood collectors. These people were followed by newcomers, the result of which is a current total of 63 traders residing in just this urban centre. Notably, this is despite a ban on the exploiting of rosewood having been implemented in March 2010. Because of the rosewood trading community's ongoing and concentrated activities in Antalaha, this small port could be cited as an urban centre where a faction of the community is actively challenging the State. The State dare not apply the laws implemented towards prohibiting trading of rosewood, but of course, there are common interests between the State and the operators. The current situation described here is not unique: it has recurred through various periods: pre-colonial, colonial and post-independence.

INTRODUCTION

Il y a exactement 300 ans, en 1713, Carl von Carlowitz, exploitant forestier allemand, inventait le concept d'exploitation forestière durable, ayant pressenti avant tous les autres que les pratiques en cours à son époque allaient mettre en péril l'existence des forêts dans le long terme. Et ce visionnaire avait de bonnes raisons de penser à l'avenir : l'intérêt économique des hommes pour la forêt était déjà sans limite à son époque. Les principales puissances européennes (Hollande, Angleterre, Portugal, Espagne et France principalement) avaient déjà rasé l'essentiel de leurs forêts de bois d'œuvre dès le XVIII^{e} siècle en particulier pour construire les flottes nécessaires à leur commerce international et à sa protection. Très tôt, ces puissances maritimes s'étaient tournées vers l'Amérique du Sud et l'Afrique pour satisfaire leurs besoins en bois imputrescibles, améliorant ainsi la longévité de leurs navires. Le Gabon, le Congo, la Tanzanie, le Mozambique et Madagascar se sont alors mis à vendre ce que les Européens venaient y acheter : bois d'ébène, bois de rose, okoumé, acajou, pour ne citer que les principales essences. À Madagascar, la forêt de Masoala est à la fois exceptionnellement riche et accessible uniquement par la mer. Son exploitation commerciale a donc commencé avant la colonisation. En effet, selon Petit et Jacob (1964), c'est vers 1850 que Hardwick Wilson, négociant mauricien, monte une première scierie au fond de la baie d'Antongil. Ensuite, à partir de 1887, le Premier ministre Rainilaiarivony accorde des concessions à des étrangers pour une exploitation forestière à grande échelle, en raison de services qu'ils ont rendus pendant la guerre franco-merina de 1883 (Petit et Jacob 1964). Il s'agit de :

- Désiré Maigrot, créole mauricien : 2500 km^2, portés à 7900 en 1891. La concession s'étend d'Antalaha à Cap Masoala et Maroantsetra ;
- Cayeux, Mauricien : 510 km^2 en 1890 autour de Ratsianarana ;
- Kingdom, pasteur anglais : 2600 km^2 en 1887, de Maroantsetra à Rantabe ;
- Thomé, créole mauricien : 2700 km^2 en 1888, de Rantabe à Mananara.

Le pasteur Kingdom était également attributaire en 1889 d'une concession géante d'extraction aurifère, s'étendant de Befandriana à Mandritsara, caché derrière le Gouverneur du Boéni agissant comme prête-nom, moyennant 30 % des revenus extraits de la concession (Decary 1962). À cette époque, les concessions forestières sont soumises par l'État à des clauses financières strictes. L'exploitant doit payer un droit d'exploiter décennal, fournir une part des produits extraits à l'État malgache et verser aux finances publiques un pourcentage de la valeur des produits extraits de la forêt : bois précieux, caoutchouc, gomme copal. Mais déjà, les concessionnaires essaient de se soustraire aux taxes. En 1897, le Résident français de Vohémar estime que Maigrot fraude de 50 % sur ses extractions (soit 10 000 tonneaux de bois et de caoutchouc sortis en fraude sur 10 ans). Ce qui n'empêchera pas Maigrot de faire faillite en 1890, ainsi que son fils en 1896, après avoir repris l'affaire. Le même Résident français de Vohémar rapporte, toujours en 1897, de « véritables faits de brigandage » (Petit et Jacob 1964, p. 42) à l'encontre des autochtones de la part d'un des concessionnaires. L'Administration coloniale ne compte alors que 11 fonctionnaires en 1898 dans cette région d'Antongil, très difficile d'accès. Le commerce du bois est entre les mains de Mauriciens, qui se contentent pour la plupart d'acheter leur production aux villageois, sans organiser eux-mêmes l'exploitation de la forêt. Il faut attendre 1904 pour voir arriver les colons français, conformément aux vœux de l'Administration, puis 1908, pour voir s'installer les Chinois dans la région, libérés de la construction du chemin de fer de Toamasina.

En 1899, alors que 30 000 hectares étaient en concession autour de Maroantsetra, seuls 20 % étaient réellement exploités, principalement sur la frange côtière en raison du coût de transport des billes provenant de l'intérieur. La fraude sur les bois précieux est alors estimée à 50 % du tonnage déclaré, qui varie de 3 000 tonnes en 1910, à 5 000 tonnes en 1914 et 1920, les deux meilleures années (Petit et Jacob 1964). Seul Baron Fraise, avec ses trois employés français et sa centaine d'employés malgaches, a installé en 1920 une scierie hautement mécanisée. Les autres exploitants se contentent d'acheter les billes de bois mal dégrossies que leur amènent les villageois, après que ceux-ci les aient difficilement transportées entre le lieu de coupe et le lieu de vente.

Et Petit et Jacob (1964, p. 54) de conclure ainsi l'analyse de cette première phase : « L'exploitation de la forêt de Masoala fut souvent une dévastation à intérêt économique limité. » Les exploitants de cette époque étaient donc des concessionnaires mauriciens, plus aventuriers économiques que créateurs d'entreprise et ils fraudaient l'État à hauteur de 50 %.

Au début du XX[e] siècle, alors que le pouvoir colonial étend son emprise sur l'ensemble de l'île, de nouveaux prédateurs forestiers apparaissent. Les plus gourmands sont proches du pouvoir. Il s'agit essentiellement de trois sociétés ayant acquis par convention entre 1902 et 1905 un immense domaine forestier (Fremigacci 1998) :

- La société La Grande Île, dont le directeur, M. Sisteron, est un ami personnel du gouverneur général Garbit. Cette société a 28 000 hectares de forêt, qu'elle défriche par le feu à grande échelle.
- La Compagnie Coloniale. Son directeur, M. Bourdariat, siège au Conseil d'administration de la colonie. Elle a obtenu 17 000 hectares de belle forêt grâce à ses appuis politiques à Paris, qu'elle va « exploiter » à blanc.
- La Compagnie Foncière et Minière, M. Glandu, son directeur, est un proche du Gouverneur. Sa société va se distinguer en utilisant du palissandre comme bois de chauffe et charbon de bois.

La forêt offerte en récompense aux proches du pouvoir va faire des émules. De hauts fonctionnaires coloniaux vont demander et obtenir leur part : Maître Lacaille, avocat et président de la chambre de commerce d'Antananarivo (120 hectares de forêt en 1920), le procureur général Reynaud de Lyques, chef du service judiciaire de la colonie, ou les nombreux colons nécessiteux qui estiment avoir mérité de la patrie.

Jean Fremigacci (1998) juge ainsi cette seconde phase de l'exploitation forestière malgache : « Cette société coloniale va mettre en pièces la forêt malgache, ne pouvant pas concevoir que la production soit autre chose qu'une consommation du capital, dans le cadre d'une pratique qui, plus encore que l'appellation d'économie de pillage, mérite celle d'économie de délinquance : dans le contexte des rapports sociaux coloniaux, le droit est fait pour être violé par les privilégiés (et tel est justement leur privilège) tandis qu'il ne peut être qu'ignoré de la grande masse des sujets. C'est là, déjà, une situation qui annonce l'état patrimonial de l'ère postcoloniale. »

Et aujourd'hui : l'exploitation forestière de Masoala est-elle enfin devenue durable ? Qui sont les exploitants de la forêt de Masoala ? Quelles sont leurs techniques d'extraction, leurs perspectives commerciales et environnementales ? Quel rôle l'État malgache joue-t-il dans cette activité économique ? Cette étude a pour objet de faire le point sur ces différents aspects, afin de déterminer ce qui a changé depuis 1850.

MÉTHODE

Pour établir le profil social des exploitants de bois précieux, nous avons analysé divers documents provenant de l'Administration forestière entre 2009 et 2012. L'essentiel de ces documents concerne la SAVA (Sambava, Antalaha, Vohémar, Andapa), principale région d'extraction des bois précieux à Madagascar. La liste nominative des opérateurs connus officiellement en SAVA au 1[er] janvier 2012 est donnée en annexe. Nous avons d'autres documents qui concernent les opérateurs de Toamasina, mais ils ont été exclus du cadre de cette étude, car ils ne sont pas aussi complets que ceux de la SAVA. En outre, ils ne portent pas sur plusieurs années. Le rôle de l'État apparaît à travers l'étude de la presse nationale, des jugements de tribunaux et le décalage entre le volume de bois exporté du pays et celui qui est intercepté par les autorités. Quant aux aspects techniques de l'extraction du bois, ils sont connus par les études précédentes (Randriamalala et al. 2010, Stasse, 2002), actualisées par des témoignages oculaires recueillis sur place entre 2009 et 2012.

RÉSULTATS

Les opérateurs officiels de bois précieux étaient 13 en janvier 2009 (arrêté interministériel n°003/2009, signé sous la présidence Ravalomanana). Leur nombre est passé à 15 en juin 2009, puis à 19 en septembre de cette même année. L'arrêté interministériel n°38244/2009 du 21 septembre 2009 autorise en effet une augmentation du nombre d'opérateurs, moyennant une amende à payer par conteneur et une déclaration des stocks détenus (articles 3 et 5). Le nombre d'opérateurs continue d'augmenter pour atteindre 27 en avril 2010, puis 103 pour la seule région SAVA au début de 2012, selon un recensement officiel du Ministère des Eaux et Forêts. Ces chiffres, ainsi que le chronogramme correspondant, sont résumés dans la figure 1.

Il faut noter que l'exportation du bois de rose s'est féminisée au fil du temps, avec l'arrivée dans la filière des épouses, des sœurs ou des filles d'opérateurs. En janvier 2009, les femmes représentaient 15 % des opérateurs, contre 20 % en 2012 (hommes : 66 %, sociétés : 14 %). Puis au fil des mois, les opérateurs ont ouvert l'activité au reste de leur famille. Si en 2009, quatre des exploitants avaient des relations familiales

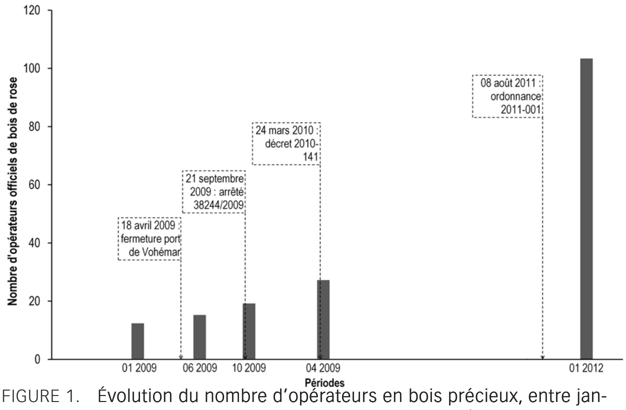

FIGURE 1. Évolution du nombre d'opérateurs en bois précieux, entre janvier 2009 et janvier 2012, inscrits officiellement dans la région SAVA.

(deux fratries), en 2012, ils sont 18 à appartenir à six fratries, trois couples, deux filiations ou à avoir plusieurs de ces liens simultanément.

L'assise géographique de ce commerce s'est également étendue au cours de ces trois années. En 2009, tous les opérateurs étaient originaires d'Antalaha. En 2012, ils proviennent d'Antalaha à 61 %, de Sambava à 17 %, d'Antananarivo à 7 %, de Toamasina et d'Ampanefena (au sud de Vohémar) à 3 % chacune, et de Vohémar à 1 %.

Sur le plan judiciaire, dans la liste de janvier 2009, huit personnes avaient déjà comparu devant un tribunal pour exploitation illicite de la forêt et deux avaient été condamnées. Dans la liste de janvier 2012, ces chiffres passent respectivement à 11 et quatre.

Enfin, deux cas individuels sont dignes de mention :

- Malohely Jean-Michel : opérateur historique (il figure dans l'arrêté de janvier 2009), il est le seul à avoir quitté cette activité puisqu'il n'est plus dans la liste des opérateurs de 2012.
- Befototo Angelin : connu officieusement dans ce commerce dès juin 2009 et officiellement en janvier 2012, il est également le leader du parti TGV (parti présidentiel) pour la Région SAVA.

Dans la monographie du Ministère de l'Agriculture, de l'Élevage et de la Pêche (2003) portant sur la SAVA, le recensement général de la population de 1993 évaluait la répartition socioprofessionnelle des chefs de ménage d'Antalaha conformément au Tableau 2, ce qui permet de replacer l'exploitation du bois de rose dans son contexte social et local. À propos des 27 000 agriculteurs indépendants de la catégorie G que ce document recense, voici ce qui est dit (p. 22) : « À la campagne, les paysans – vieillards, femmes, jeunes – pour subsister, pratiquent la vente illicite des bois précieux – bois de rose – bois d'ébène, au prix de :
- Ø> 20 cm : 1250 à 1000 Fmg la longueur de 2 m.
- Ø < 20 cm : 1000 Fmg.

Cette pratique vient de l'autorisation de ramassage donnée aux paysans par les autorités au lendemain du passage du cyclone Hudah en avril 2000, car en ce temps-là, beaucoup de ces bois ont été arrachés et charriés par les eaux, la pratique est restée jusqu'à maintenant. »

DISCUSSION

L'EXPLOITATION DU BOIS DE ROSE, UNE AFFAIRE DE FAMILLE.

L'étude détaillée des liens entre les individus ayant grossi les rangs des exportateurs ou des détenteurs de stocks de bois de rose entre 2009 et 2012 montre une implication progressive des membres des familles du noyau historique. Si au départ un gros exportateur avait sa sœur dans cette activité et un autre y avait son beau-frère, les exportateurs de 2009, constatant d'une part les bénéfices importants de ce commerce, et d'autre part, la relative impunité des participants, ont décidé de faire profiter leur famille de leur savoir-faire. Frères, sœurs, fils, épouses, belles-sœurs ont alors rejoint leurs rangs. Ce choix s'explique de plusieurs façons :

- le savoir-faire et la réputation : les heureux exportateurs de 2009 ont noué des contacts avec les collecteurs qui leur amènent le bois de rose prêt à embarquer : documents d'exploitation en règle, marquage effectué (alors qu'aucun de ces collecteurs n'a de lot d'exploitation forestière : ils achètent le bois aux villageois qui le coupent dans le Parc de Masoala). Dans bien des cas, les exportateurs ne payent pas les collecteurs au comptant. Manquant souvent de liquidités, ils font des dettes qu'ils ne remboursent que lorsque l'acheteur chinois a payé l'exportation. Pour les collecteurs, c'est donc une affaire de confiance et de réputation. Certains parmi les plus petits d'entre eux n'ont d'ailleurs jamais vu l'argent de leur bois. Ainsi, la réputation d'un exportateur s'étend à sa famille : on peut faire confiance à l'épouse de …, au frère de … car l'intéressé est fiable : il paye avec retard, mais il paye toujours. Ce savoir-faire s'étend également aux contacts noués avec l'Administration : à qui et comment demander les agréments d'exportation, comment et à quelle heure franchir les multiples points de contrôle des forces de sécurité, comment procéder avec les Douanes, à quel transporteur confier cette cargaison spéciale, etc. Ce réseau de contacts ne peut profiter qu'à des proches.
- la quantité de bois qui arrive aux exportateurs plus ou moins spontanément est énorme. Elle excède largement ce que l'Administration semble disposée à tolérer : l'arrêté interministériel n°38244/2009 du 21 septembre 2009 limite à 25 conteneurs la quantité de bois possible à l'export pour chaque opérateur (le conteneur, nouvelle unité administrative ?) La solution adoptée par les exportateurs historiques a donc été de grossir leur nombre. Pour ne pas perdre de l'argent en acceptant une concurrence venue d'ailleurs, ils ont mis la famille sur les rangs. Il apparaît ainsi que le commerce du bois de rose est d'abord une aventure individuelle et non une affaire d'entreprise. Nous sommes clairement dans une logique de prédation plus que dans une perspective d'exploitation durable.
- la réputation commerciale doit être sauvegardée et ne peut s'étendre qu'à des proches. Les acheteurs chinois sont en effet méfiants lorsqu'ils viennent prospecter à Madagascar. Ils savent implicitement que tout ce commerce n'est pas légal, sûrement pas durable et qu'il faut faire vite pour s'emparer du maximum de bois disponible avant que l'inévitable pénurie ne fasse grimper les cours à des sommets vertigineux. Ils sont donc prêts à prendre beaucoup de risques et la concurrence entre eux est rude. Certains opérateurs malgaches malveillants en profitent : dans le Marojejy

en 2009, des collecteurs avaient glissé des pierres dans des billes creuses de bois de rose, alourdissant ainsi le rondin et la facture, mais sans égard pour la scie électrique qui allait le découper en Chine ; plus récemment, en mars 2012, un trafiquant de Toamasina a remplacé le contenu de quatre conteneurs de bois de rose par du pin, après le scellement des conteneurs par la Douane et le paiement de la facture par l'acheteur chinois. En mai 2012, lorsque nous avons été avisés de ces faits, l'acheteur chinois n'a probablement pas encore découvert l'escroquerie. Pour éviter de telles mésaventures dans un commerce par ailleurs assez risqué, la confiance entre acheteur et vendeur est capitale. Cette confiance explique qu'initialement les vendeurs étaient majoritairement des Malgaches d'origine chinoise. Accointances culturelle, linguistique et régionale facilitent cette mise en confiance : beaucoup de vendeurs d'Antalaha et de Toamasina ont leurs racines familiales dans la région de Canton, d'où vient la majorité des acheteurs chinois.

L'EXPLOITATION DU BOIS DE ROSE, UNE AFFAIRE DE VILLAGE.

Si en 2009 les opérateurs étaient tous originaires d'Antalaha, en 2012 cette origine ne représente plus que 61 % du total, soit 63 opérateurs. Cette localisation de la contagion peut s'expliquer de deux façons. La première est bien sûr la proximité de Masoala, lieu de coupe du bois. Le bois est lourd, difficile et dangereux à transporter, il est donc logique de le vendre au port le plus proche, c'est-à-dire Antalaha.

Ensuite, beaucoup d'exploitants historiques sont connus pour leur goût du luxe ostentatoire. Véhicules 4x4 grand luxe du dernier modèle, avion privé pour aller chercher dans la capitale des maîtresses voyantes, grandes fêtes populaires sur le stade d'Antalaha avec force décibels, bière et zébu à profusion quand il s'agit de mobiliser contre une mesure du gouvernement, une population rurale que l'on amène par camions gratuitement depuis la brousse : les exemples sont légion de la réussite affichée sans complexe par ceux qui se sont lancés dans le commerce du bois de rose.

Vis-à-vis de la population environnante, cet affichage est très efficace. La réussite sociale est manifeste et indiscutable. Elle fait donc des envieux et elle suscite l'émulation. Elle impressionne les fonctionnaires chargés de réprimer ou d'encadrer cette activité. Les voisins, les amis et les membres du réseau des exportateurs voudraient en être aussi. Et ils ont été aidés par les exportateurs historiques pour leurs démarches administratives. D'abord, il y avait suffisamment de bois disponible pour faire de la place à de nouveaux exportateurs. Ensuite, plus le nombre d'exportateurs grandit à Antalaha, moins ceux-ci se sentent marginalisés : l'illégalité devient la norme sociale (rappel : couper, transporter et exporter du bois de rose est illégal depuis le 24 mars 2010). C'est ainsi que sur les 63 opérateurs de 2012 à Antalaha, 40 sont totalement nouveaux dans cette activité : ils ne sont pas d'anciens collecteurs de bois pour les exportateurs historiques, ils ne sont pas de leur famille, ils ne sont pas d'origine chinoise. Ils habitent juste dans la même ville, souvent dans les mêmes quartiers.

Si l'on considère que les exportateurs de bois de rose figurent dans la catégorie D du recensement donné par la Monographie de la SAVA de 2003 (profession intermédiaire, entre profession intellectuelle et scientifique et employé de type administratif), leur nombre actuel représente 19 % de cette catégorie. Même si ce chiffre est à prendre avec précaution en raison de l'âge du recensement (20 ans), son ordre de grandeur est significatif : les exportateurs de bois de rose représentent à Antalaha une minorité numériquement importante, socialement visible, enviée et influente. C'est sans doute de ce rapport de forces sociales qu'ils tirent leur sentiment d'impunité et leur audace de défier publiquement l'État. Ils ont en effet à plusieurs reprises exigé le départ de certains fonctionnaires trop zélés ou des représentants de l'État en charge de réguler le trafic de bois de rose, et ce, avec une totale impunité jusqu'à présent.

Le respect de la loi, en État de droit, suppose l'adhésion du plus grand nombre de citoyens. Les délinquants doivent être minoritaires, numériquement mais aussi socialement et moralement. Lorsque la loi est bafouée par un nombre de personnes tel que la prison devient trop petite ou que la surface sociale des délinquants devient trop importante, alors le système ne peut plus fonctionner et ceux qui respectent la loi se sentent marginalisés. Cette atmosphère délétère pousse un nombre grandissant de fonctionnaires intègres à vouloir quitter Antalaha, où ils sentent au quotidien la réprobation plus ou moins explicite de la population à leur encontre lorsqu'ils accomplissent le travail que leur a confié l'État.

Faire le procès de la pauvreté n'a pas de sens, mais couper des arbrisseaux de moins de vingt centimètres de diamètre n'en a pas non plus. Et la faiblesse de l'Administration, qui tolère qu'à partir de 2001 (Monographie de la SAVA 2003, Stasse 2002), les villageois continuent de couper de jeunes arbres une fois évacués ceux abattus par le cyclone Hudah, ne peut qu'encourager l'émergence d'une nouvelle classe socioprofessionnelle habituée à changer la loi à son profit et à dicter ses règles à l'Administration. À l'instar de la Nation, l'État de droit existe d'abord dans la tête d'une majorité de citoyens : dans la microsociété d'Antalaha, ce n'est plus le cas. Le sens civique a été remplacé par une cupidité contagieuse.

L'EXPLOITATION DU BOIS DE ROSE, UNE AFFAIRE D'ÉTAT ?

Et cette contagion a fini par atteindre Antananarivo, la capitale, puisque sept opérateurs y sont maintenant officiellement déclarés dans les registres de la SAVA. Un seul y était connu dès la fin 2009, les autres sont récents. Quatre d'entre eux agissent en société commerciale et les trois autres en leur nom propre. Comme il n'y a pas de bois de rose à Antananarivo, la seule raison de l'extension de ce commerce à cette ville est, soit la proximité du pouvoir central qui facilite les procédures administratives, soit la capacité d'investir alliée au sens des affaires de certains opérateurs économiques de cette ville. Le commerce du bois de rose n'est plus lié à la seule proximité de la forêt, mais aussi au capital disponible et au pouvoir d'influence.

Mais le plus étrange est sans doute ailleurs. À Madagascar, aucune activité n'a autant défrayé la chronique (Randriamalala et al. 2012) que le trafic de bois de rose depuis le début de la Transition en 2009. Le sujet est devenu d'une extrême sensibilité, la presse nationale en est friande, la communauté internationale le suit de près. Dans ces conditions, comment expliquer l'extraordinaire essor du nombre d'opérateurs officiels (de 19 à 103, soit 542 % d'augmentation entre fin 2009 et début 2012) alors que nous sommes sous un régime clair d'interdiction de l'activité pendant la période considérée ? Le décret n°2010-141 (24 mars 2010) interdit toutes les phases de cette activité. L'ordonnance 2011-001 du 8 août 2010 alourdit de fortes sanctions pénales le régime d'interdiction en vigueur, mais elle n'empêche pas une augmentation très sensible du nombre d'exploitants officiels. Il n'y a que deux explications possibles :

- L'impuissance de l'État : si cette explication est vraie, alors cela signifie que la stratégie d'intimidation et de défi de l'autorité publique menée par les opérateurs de bois de rose a payé. À de nombreuses reprises, les ministres successivement en charge de ce dossier ont conduit des ateliers de « remise à plat », demandé de procéder à un « inventaire général des stocks » et rencontré les opérateurs en colère. Dans cette négociation, les opérateurs ont montré leur détermination plusieurs fois : grandes manifestations publiques antigouvernementales, intimidation des fonctionnaires locaux et régionaux, saccage des locaux des Eaux et Forêts, pillage de dépôts de bois saisis par l'Administration. Pour un régime dont l'assise populaire venait essentiellement des jeunes de la capitale, le risque politique était grand de laisser se développer un sentiment de rejet dans une région enclavée et difficile d'accès, surtout en période de marasme économique, lié à la chute des cours de la vanille autant qu'à la suspension de l'aide internationale. Si de plus, la plupart des procès n'aboutissent pas à une condamnation ferme, soit par influence sur les magistrats, soit par inapplicabilité d'une législation contradictoire, soit à cause des fautes de procédure de l'Administration forestière, alors le sentiment d'impunité s'installe en même temps que s'affiche la réussite sociale des opérateurs. L'augmentation du nombre d'opérateurs ayant déjà eu affaire à la Justice dans la liste 2012 s'explique par le retour dans cette activité d'anciens exploitants déjà connus de la Justice et elle inclut le départ de l'un d'entre eux (Malohely), qui a subi quatre procès entre 2008 et 2009. La simultanéité de l'intimidation de l'État et du sentiment d'impunité est redoutablement efficace.
- La collusion entre l'État et les trafiquants : depuis la suspension de l'aide internationale suite au coup d'État de mars 2009, l'État malgache se trouve en grande difficulté financière. Dans de nombreuses administrations, dont certaines sont primordiales pour la population (santé, éducation, sécurité et ordre public), les budgets de fonctionnement ont été tellement réduits que l'activité a dû baisser elle aussi. Le moral de la population s'en ressent durement et le même processus que celui qui a amené Andry Rajoelina au pouvoir pourrait bien se retourner contre lui : un mouvement de foule organisé en sous-main par des agitateurs expérimentés, qui s'empare des centres de pouvoir après une brève paralysie du pays. La Transition a donc un besoin urgent et vital pour sa survie de trouver des fonds pour faire tourner *a minima* la machine de l'État. En raison de sa nature même, la Transition est incapable d'avoir une vision politique et économique à moyen terme. L'exploitation des ressources naturelles est donc la meilleure option financière car la plus immédiatement rentable. Il est logique que l'État s'entende avec les opérateurs de bois de rose, quitte à violer les lois et règlements qu'il a lui-même édictés, pour ne pas être balayé par un mouvement populaire plus ou moins spontané. L'État a anobli les trafiquants en les faisant opérateurs (Randriamalala 2012), puis il a conclu avec eux un mariage d'intérêt.

Selon le WWF de Madagascar (2012, p. 8) à propos du changement climatique : « Madagascar a été évalué par un bureau international de consultance comme le 3^{e} pays le plus vulnérable au monde après le Bengladesh et l'Inde. » La déforestation sans contrôle qui a lieu depuis 2009 ne peut qu'aggraver cette vulnérabilité.

CONCLUSION

Les exploitants de bois de rose au début de 2012 sont donc plus nombreux que jamais, sans que l'État ne cherche ou ne parvienne à contenir leur nombre. Ils sont majoritairement originaires d'Antalaha où ils dictent leur loi aux représentants locaux de l'État. Initialement Malgaches d'origine chinoise, ils sont aujourd'hui un peu plus représentatifs de la diversité ethnique nationale. Leur activité a fini par atteindre les milieux d'affaires de la capitale, après s'être étendue aux membres de leurs familles, puis à ceux de leurs réseaux professionnels.

Leur activité est plus cachée des médias qu'elle ne l'est du pouvoir central, avec lequel ils partagent une communauté d'intérêts. L'exploitation de la forêt est conduite dans une perspective exclusivement à court terme, fondée sur l'enrichissement immédiat et la mise à l'abri des capitaux à l'étranger, hors de portée de la Justice malgache.

Par rapport à la période 1850 –1925, évoquée en introduction, certains éléments ont changé :

- Le nombre et la nationalité des opérateurs : de cinq Mauriciens en 1850 à 103 Malgaches en 2012. La localisation des trafiquants est également en train de changer. Avant 2012, ils résidaient tous aux abords de la forêt. Depuis 2012, des opérateurs de la capitale ont rejoint cette activité.
- La quantité de bois extraite annuellement : de 3000 tonnes en 1900 à 52 000 tonnes en 2009 ;
- La destination du bois : l'Europe en 1900, la Chine aujourd'hui ;
- Le statut de la forêt de Masoala : de domaine royal en 1850 ou colonial après 1896, à Parc National en 2012.

En revanche, certains éléments sont invariants :

- Le mode d'exploitation : des investisseurs résidant aux abords de la forêt, qui achètent des billes de bois aux villageois de la forêt, sans se soucier outre mesure de leur origine, de leur diamètre ni de leur nombre. La légalisation a lieu après l'achat. L'exploitation est toujours en mode prédation, avec une préférence marquée pour les zones d'extraction situées à proximité de la côte ou des rivières pour faciliter le transport.
- L'impuissance de l'État au cœur de la forêt : la puissance publique ne peut empêcher la coupe quand elle le décide. Le taux de fraude hors de la forêt (fausses déclarations en Douane) semble à peu près constant, de l'ordre de 50 % pour autant qu'il soit possible d'en juger. Force est de constater que ce qu'écrit Jean Fremigacci (1998) à propos de la première moitié du siècle précédent est toujours vrai : « exploiter la forêt à Madagascar, c'est d'abord exploiter les faiblesses de la réglementation et de l'administration. »

Que peut-on conclure de ces 160 et quelques années d'observations, qui ne représentent après tout que la moitié de la vie d'un bois de rose ? Que la forêt a été harcelée de multiples manières à un rythme incompatible avec sa régénération naturelle et que rien, dans la conjoncture actuelle, ne permet de prédire une amélioration. Carl von Carlowitz (1713) qui prônait l'exploitation durable de la forêt a sans doute été entendu en Allemagne, puis par contagion en Europe, voire en Chine, au gré des déforestations catastrophiques localement constatées. Au fur et à mesure que ces pays prenaient conscience de l'importance de la préservation de leurs forêts, ils se rabattaient sur des pays qui, noyés dans l'impuissance coloniale ou des crises politiques perpétuelles, étaient moins soucieux de leur avenir, et le sont hélas toujours.

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MATÉRIEL SUPPLÉMENTAIRE.

DISPONIBLE EN LIGNE UNIQUEMENT.

TABLEAU S1. Origine socioprofessionnelle des 103 opérateurs de bois précieux connus dans la région SAVA en janvier 2012.

TABLEAU S2. Répartition socioprofessionnelle des chefs de ménage d'Antalaha (extrait du Recensement général de la population de 1993 In Ministère de l'Agriculture, de l'Élevage et de la Pêche 2003)

TABLEAU S3. Liste des opérateurs de bois de rose connus dans la région SAVA en janvier 2012.

SHORT NOTES

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Non-flying mammalian fauna of Ampijoroa, Ankarafantsika National Park

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ABSTRACT
There is no list of the mammalian fauna of Ampijoroa Forest Station, a dry deciduous forest within Ankarafantsika National Park. We set Sherman traps and pitfall traps and carried out transect surveys to survey the non-flying mammalian fauna of Ampijoroa. In total, 19 species of mammals were recorded, comprising 10 families. Records include three species of Tenrecidae, two species of Soricidae, one species of Muridae, three species of Nesomyidae, three species of Cheirogaleidae, one species of Lepilemuridae, two species of Lemuridae, two species of Indriidae, one species of Eupleridae, and one species of Suidae.

RÉSUMÉ
Nous avons procédé à des observations de la faune mammalienne de la station forestière d'Ampijoroa, du Parc National d'Ankarafantsika. Pour compléter les données visuelles, nous avons posé des pièges Sherman, des trous pièges ou *pitfall traps* afin de capturer des animaux vivants qui furent relâchés ultérieurement sur leur lieu de capture. Au total, 19 espèces de mammifères ont été confirmées dans cette forêt, appartenant à 10 familles dont trois espèces de Tenrecidae, deux espèces de Soricidae, une espèce de Muridae, trois espèces de Nesomyidae, trois espèces de Cheirogaleidae, une espèce de Lepilemuridae, deux espèces de Lemuridae, deux espèces d'Indriidae, une espèce d'Eupleridae et une espèce de Suidae.

INTRODUCTION
In Madagascar, there has been a considerable increase in natural history data for a wide variety of land animals in the last 20 years, as well as the description of numerous new species. However, there is still little information about the mammalian fauna of each region and limited ecological data about small mammals in Madagascar. Furthermore, systematic research has been relatively limited in the western dry deciduous forests compared to research in the eastern rainforests (Goodman et al. 2005), despite the fact that more than one-third of Madagascar's surface was formerly covered in dry forests. Given that the remaining dry forests are suffering from severe fragmentation by fires, illegal logging, and deforestation for agriculture (Ganzhorn et al. 2001), ecological surveys of animals within the dry regions of the country are urgently needed to obtain baseline data to develop conservation and management strategies.

The Ampijoroa dry deciduous forest is one of the most important forests for both ecological research and ecotourism in Ankarafantsika National Park, located in the northwestern part of Madagascar. Many biologists have conducted ecological surveys in Ampijoroa forest, which is managed for ecotourism by Madagascar National Parks; therefore complete or updated information on the mammalian fauna of Ampijoroa forest can make a contribution to improve both ecological research and ecotourism activities in the National Park.

Although the avifauna and herpetofauna of Ampijoroa forest have already been reported (Mizuta 2005, Mori et al. 2006), there is no complete mammal inventory focused specifically on the forest. Some information on the mammals of Ampijoroa is available from other sources, including Alonso et al. (2002), which assessed the fauna of Ankarafantsika National Park but excluded Ampijoroa forest, Goodman et al. (2005) on the distribution of bats in the dry regions of Madagascar, and Garbutt (2007), which provides a review of mammals for the whole of Madagascar. Although the mammalian fauna of Ampijoroa can be surmised from these sources, a mammalian inventory of the sites is required to serve as a definitive species list and ensure the availability of information on the mammal fauna. Here, we present the results of a mammal survey of Ampijoroa and provide a list of mammal species at the site.

METHODS
The study was conducted in the forest of Ampijoroa, Ankarafantsika National Park (E46º48', S16º15'). Ampijoroa forest is located in Boeny Region, approximately 110 km from the city of Mahajanga. The vegetation consists of a deciduous canopy 9-12 m high and fairly clear understory (Razafy 1987). Based on meteorological data from 2005 to 2009 at Ampijoroa (Durrell Wildlife Conservation Trust, unpublished data), the annual mean precipitation of the region is 1467.4 mm (range: 1305.1-1528.3 mm). Most rainfall occurs in the rainy season from November to April. Maximum air temperature can reach 34.9 ˚C

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in the hottest month (October), and minimum temperature can decrease to 17.3°C in the coldest month (July). Jardin Botanique A (JBA) is a research plot of approximately 30 ha (500 × 600 m) is located in the western part of Ampijoroa forest. A brief preliminary survey was also conducted in Jardin Botanique B (JBB; a transect along trails of ca. 3 km length) and around Lake Ravelobe (along National Route 4).

Field surveys were carried out from 16 November 2007 to 12 January 2008 and from 1 November 2008 to 10 February 2009. We attempted to capture small terrestrial mammals by setting 37 Sherman live traps and 60 pitfall traps in JBA, around the southern and western sides of an ephemeral pond for 36 days from 16 to 18 November and 22 November to 24 December 2007. The pitfall traps were plastic buckets (275 mm in depth, 290 mm in top internal diameter, 220 mm in bottom internal diameter) that were buried in the ground and arranged in lines. Sherman traps were put on the ground or on branches near pitfalls. Pitfalls were separated by at least 5 m from each other. We made two pitfall-trapping lines with plastic drift fences (700 mm in height, 50 m in length) to increase capture efficiency. We checked the traps every morning.

Collected animals were brought to the station, where we measured their external morphological characters (head-body length (HB), tail length (TL), body mass (Wt), and hind-foot length (HF)). Identification of the species was based on Carleton (2003), Garbutt (2007) and Mittermeier et al. (2010). We identified rodent species and the genus *Microgale* by morphological size and proportional HB and TL. We painted temporary marks on the backs of several species for visual identification. Except for a few individuals of each species, which were preserved in formalin to confirm the species, collected animals were released at the site of capture as soon as possible. We also recorded mammalian species observed in the field.

RESULTS

In total we recorded 19 species of mammal comprising 10 families (Table 1). Ecological features and morphological measurements of small species are summarized in Table 1. Mean values of body measurements of each species were calculated without separating sexes. The following is a brief description of each species.

Afrosoricida, Tenrecidae
Tenrec ecaudatus (Schreber 1778)
We captured three individuals of this species by hand. This strictly terrestrial species was very abundant in Ampijoroa, and was often observed both in the daytime and at night. Juveniles were often observed foraging in a group with their mother during the day.

Setifer setosus (Schreber 1778)
Three individuals were captured, one of which was collected twice in Sherman traps placed on trees. Another individual was collected in a pitfall trap, and the other was captured by hand on the ground. This nocturnal species was common in Ampijoroa.

Microgale brevicaudata (G. Grandidier 1899)
Nine live and three dead individuals were collected in pitfall traps. We collected this species only using this method. We captured one individual every three days on average, suggesting that this species is very abundant in Ampijoroa and is terrestrial.

Soricomorpha, Soricidae
Suncus murinus (Linnaeus 1766)
Although we did not collect this shrew in traps, we observed it on several occasions.

Suncus etruscus (Savi 1822)
We collected only one dead body in a pitfall trap. This shrew is the smallest shrew and the smallest known terrestrial mammal in this forest.

Rodentia, Nesomyidae
Eliurus myoxinus (Milne-Edwards 1885)
Five individuals were collected in Sherman traps. Four of them were captured on trees, and the other on the ground. This species was nocturnal and common in the forest.

Macrotarsomys ingens (Petter 1959)
Only one individual was captured by hand, but this rat is not uncommon based on our observations. This rat was arboreal, terrestrial and nocturnal.

Macrotarsomys bastardi (Milne-Edwards & G. Grandidier 1898)
Only one individual was captured in a pitfall trap, but this rat is probably not uncommon. We observed this rat on several occasions during the night in the survey area.

Rodentia, Muridae
Rattus rattus (Linnaeus 1758)
Although three individuals were captured by Sherman traps on the ground, this rat was observed on both the ground and trees. We tentatively identified these individuals as *Rattus rattus*.

Primata, Cheirogaleidae
Microcebus murinus (Miller 1777) and *M. ravelobensis* (Zimmerman et al. 1998)
During night walks we often found solitary mouse lemurs moving on branches in the shrub layer and canopy, and eating fruits, flowers, gum, nectar, arthropods, and insect secretions in the both around JBA and around the Lake Ravelobe. The two species of mouse lemurs were commonly seen around JBA. In the forest around Lake Ravelobe, however, we observed only *Microcebus ravelobensis* but never saw *M. murinus*.

Cheirogaleus medius (É. Geoffroy 1812)
Cheirogaleus medius was not frequently seen in the Ampijoroa forest. This nocturnal solitary forager moved more slowly on tree branches than the mouse lemurs.

Primata, Lepilemuridae
Lepilemur edwardsi (Forbes 1894)
In Ampijoroa forest, we easily found this nocturnal primate during night walks and also recognized the loud vocalizations. Sleeping individuals were also found during the day in tree holes.

Primata, Lemuridae
Eulemur mongoz (Linnaeus 1766)
This species occurred in small troops composed of a male-female pair with one to four offspring: two or three troops appeared to be habituated around the station area in Ampijoroa, although we never saw them around JBA. *Eulemur*

TABLE 1. List of mammals observed in Ampijoroa with their morphological measurements and ecological features. (Ar: arboreal, C: cathemeral, D: diurnal, HB: head-body length, HF: hind-foot length, N: sample size, Nc: nocturnal, T: terrestrial, TL: tail length and Wt: body weight)

Family	Species	N	HB in mm (range)	TL in mm (range)	Wt in g (range)	HF in mm (range)	Activity	Habit
Tenrecidae	*Tenrec ecaudatus*	3	264.7 (239–290)	Non	549.3 (31.5–40.2)	37.3 (31.5–40.2)	C	T
	Setifer setosus	3	133.5 (120–147)	11.35 (9.65–13.0)	153.0 (88.0–196.0)	26.2 (22.2–30.25)	Nc	Ar, T
	Microgale brevicaudata	12	69.4 (62.9–74.6)	31.9 (29.8–33.7)	9.0 (7.3–10.6)	11.6 (11.4–12.0)	?	T
Soricidae	*Suncus etruscus*	1	39	13.05	-	7.6	Nc	T
	Suncus murinus	2	-	-	-	-	D?	T?
Nesomyidae	*Eliurus myoxinus*	5	117 (115–121)	132.4 (128–133.9)	47.0 (43.3–50.3)	24.4 (23.7–25.2)	Nc	Ar (T)
	Macrotarsomys ingens	1	128	200	53.6	34	Nc	Ar, Tr
	Macrotarsomys bastardi	1	-	-	-	-	Nc	Ar (T)
Muridae	*Rattus rattus*	3	143	191	84.2	30.7	Nc	Ar, T
Cheirogaleidae	*Microcebus murinus*	-	-	-	-	-	Nc	Ar
	Microcebus ravelobensis	-	-	-	-	-	Nc	Ar
	Cheirogaleus medius	-	-	-	-	-	Nc	Ar
Lepilemuridae	*Lepilemur edwardsi*	-	-	-	-	-	Nc	Ar
Lemuridae	*Eulemur mongoz*	-	-	-	-	-	C	Ar
	Eulemur fulvus	-	-	-	-	-	C	Ar
Indriidae	*Avahi occidentalis*	-	-	-	-	-	Nc	Ar
	Propithecus coquereli	-	-	-	-	-	D	Ar
Eupleridae	*Cryptoprocta ferox*	-	-	-	-	-	Nc	Ar, T
Suidae	*Potamochoerus larvatus*	-	-	-	-	-	Nc	T

mongoz exhibited a cathemeral activity pattern, active during both day and night.

Eulemur fulvus (É. Geoffroy 1796)
Eulemur fulvus in Ampijoroa formed multi-male/multi-female troops including five to 12 individuals and was commonly seen around JBA and the station area. We frequently encountered troops ranging around JBA and the station area from the morning to evening.

Primata, Indriidae
Avahi occidentalis (Lorenz von Liburnau 1898)
This nocturnal lemur typically lives in small family groups of up to five individuals composed of monogamous pairs with immature offspring. During day walks, we found several sleeping groups under closed canopies but this species was generally uncommon.

Propithecus coquereli (A. Grandidier 1867)
Propithecus coquereli is the largest lemur species in Ampijoroa forest. This diurnal lemur was commonly seen in the forest in groups of three to ten individuals.

Carnivora, Eupleridae
Cryptoprocta ferox (Bennett 1833)
We observed this species twice, at 1100h on 1 November 2008 and at 1820h on 2 February 2009. In both cases the observed individuals were on the ground and ran away immediately after it noticed our presence.

Artiodactyla, Suidae
Potamochoerus larvatus (F. Cuvier 1822)
The dung, footprints, and foraging signs of this species were often observed in the forest, but we did not directly observe this species.

DISCUSSION

In the present survey we recorded 19 species of mammals in Ampijoroa dry forest. Beyond these, some individuals of *Rattus norvegicus* were collected as stomach contents of snakes (Mori, personal communication), and we also observed at least two species of bats (*Taphozous mauritianus* and *Hipposideros commersoni*). More than 10 bat species are noted in Ankarafantsika National Park (Eger and Mitchell 2003, MacKinnon et al. 2003, Goodman et al. 2005, Garbutt 2007). Other authors have recorded a number of species from the area that we did not observe: Alonso et al. (2002) noted that *Geogale aurita*, *Eliurus minor*, and *Mus musculus* are distributed in Ankarafantsika National Park, Hawkins (1994) noted the presence of *Eupleres goudotii* (it was formerly named as *E. major* see also Garbutt 2007), and Goodman et al. (2003) noted the wide distribution of *Viverricula indica* all over the island. Species accumulation curve suggests that our mammal fauna survey was reasonably complete (Figure 1). These data suggest that more than 20 mammalian species inhabit the dry forest of Ampijoroa.

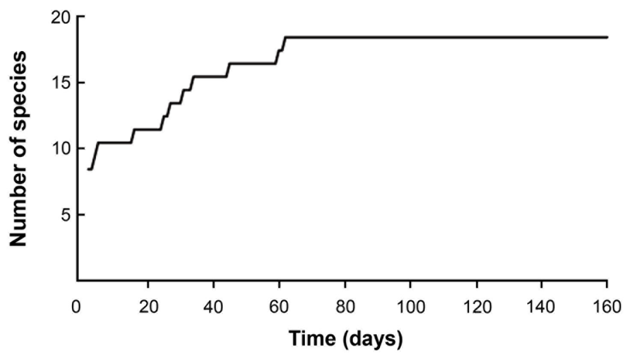

FIGURE 1. Accumulation curve of faunal diversity in mammals in Ampijoroa. The first parts of the curve (58 days) represents the 2007–2008 sampling period, followed by the 2008–2009 period.

We often observed domestic mammals such as cattle, cats and dogs in the forest at Ampijoroa. Although the primary forest in Ampijoroa is managed by Madagascar National Parks, local people leave these domestic animals in the forest. Introduced animals may be a threat to endemic animals. Cattle can be transmitters of common pathogens and are seedling predators, while cats and dogs may be competitors of fosa (*Cryptoprocta ferox*) and predators of small animals: we observed a common tenrec (*Tenrec ecaudatus*) being hunted by a domestic dog in the forest. Therefore, it is necessary for the park managers to consider the management of these domestic animals.

Our results highlight the biological importance of Ampijoroa forest, an important area for ecotourism and biodiversity conservation. However, this forest is suffering from fire-induced fragmentation, illegal logging, and illegal hunting (Ganzhorn et al. 2001). An adequate knowledge of the natural history of species occurring there is essential to ensure appropriate management for both conservation and tourism, such as efficient field guiding. Thus, further research on the biodiversity of Ampijoroa forest should be considered a priority.

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Location map and pictures of the animals observed during our survey.

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Indris: *Indri indri* in the Analamazaotra Special Reserve rainforest, Eastern Madagascar by Gerald Cubitt

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