

CHAPTER TWO

Notes on the History of Ecological Studies of Malagasy Lemurs

Alison Jolly and R.W. Sussman

INTRODUCTION

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

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

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

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

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

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

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

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

(Continued)

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

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

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

(Continued)

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

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

COLONIAL AND PRECOLONIAL TIMES

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

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

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

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

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

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

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

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

1955–1975: INDEPENDENCE AND THE FIRST REPUBLIC

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

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

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

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

Alison Jolly arrived in 1962, funded as a postdoc by NSF in the post-Sputnik phase of the Cold War. Jolly was a student of zoologist G. Evelyn Hutchinson at Yale University. She had completed her thesis work at Yale, working on captive prosimians which had been collected by John Buettner-Janusch, a biochemical geneticist then at Yale. Buettner-Janusch dedicated his life to the study of all aspects of prosimian biology and in the mid-1960s moved his prosimian collection to Duke University establishing the Duke University Primate Center. Buettner-Janusch encouraged Jolly to do research in Madagascar. Jolly was somewhat shocked to arrive in a supposedly independent country only to find a Frenchman behind every government door. However, security was good, roads

passable, and hospitality from both French and Malagasy always forthcoming. She chose a study site at Berenty, a reserve on a sisal plantation founded by the de Heaulme family in 1936. They had created a private paradise, recognizing that the gallery forest of Berenty was too beautiful ever to cut down—ideal for intensive studies of lemur social behavior (Jolly, 1966, 2004).

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

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

Attending this conference were three young primatologists who were just beginning their research on the ecology and behavior of Malagasy lemurs and who have continued to work on lemurs to this day, Robert Martin, Alison Richard, and Robert Sussman. Robert Martin, a professor at University College, London, was assisted by J.-J. Petter and by P. Roederer, then director of ORSTOM. Martin reinforced the Petters’ speculation that nocturnal lemurs have a social life: grey mouse lemurs shared sleeping nests in all combinations of sexes (Charles-Dominique and Martin, 1972). Martin has continued his interest in lemurs and directed the research of many students in Madagascar, first as head of

the Wellcome Laboratories of Comparative Physiology at the Zoological Society of London, then as Professor and Director at the Anthropological Institute and Museum of the University of Zurich, Switzerland, and currently as President of Academic Affairs at the Field Museum in Chicago.

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

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

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

confront the harsh dry winter (Charles-Dominique, 1977; Charles-Dominique et al., 1980).

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

The Duke University Primate Center continued to sponsor research in Madagascar. Peter Klopfer of Duke University visited Berenty and then sent his graduate students. In 1972–1973, Norman Budnitz and Kathryn Dainis (now Blumenfeld-Jones) compared ranging patterns of ring-tailed lemurs in gallery forest and in scrub, noting the importance of succulent plants and the phenomenon of male migration. They censused and mapped a 1 km² study area at Berenty, still in use, both for lemurs and for plant community composition (Blumenfeld-Jones et al., 2006; Budnitz, 1978; Budnitz and Dainis, 1975; Jones, 1983). In 1974, Lee McGeorge (now Durrell) analyzed 24-hour time series of vocalizations of all the Berenty animals. She found vocal niche partitioning not unlike radio stations which broadcast either at different frequencies or at different times (McGeorge, 1978). Also, in 1974, Jay Russell, a student of Buettner-Janusch, was astounded by lepilemurs' (*Lepilemur leucopus*) ability to conserve energy, remaining motionless for long periods and leaping only as absolutely necessary. Charles Dominique and Hladik calculated that at the end of the dry season *Lepilemur* was at the extreme edge of energy balance, but Russell showed that the cold nights of July imposed even more strain on a small-bodied animal. Russell also foreshadowed later interest in ranging patterns by speculating that a lepilemur's brain may only be able to remember a few trees at a time, learning all it needs as a roving adolescent and staying put thereafter. This was not just the bile of a bored graduate student. Leanne Nash summed up in a later decade, "I have studied *Lepilemur* for a year, and the bottom line is that it eats what it sits on and sits on what it eats" (Charles-Dominique and Hladik, 1971; Nash, personal communication and 1998). In 1975, Anne Mertl-Millhollen showed that ringtails and white sifaka scent-mark territorial boundaries, not range boundaries. She noted that core areas of troops, and even some of the frontiers, remained the same from 1963 to 1979—now known to persist even to the present (Mertl-Millhollen, 1979, 1988, 2000; Mertl-Millhollen et al., 1979).

These studies of the early 1970s were the end of an age of innocence—or perhaps, of ignorance. Westerners could imagine themselves as pure scientists following untrammelled intellectual curiosity. They took for granted their privilege as the heirs of Rousseaux—and Commerson—in love with the romance of far-off

wilderness, and boosted like multistage rockets by the funds of the Paris Museum or the NSF.

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

1975–1985: THE SECOND REPUBLIC

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

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

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

Alison Richard and Robert Sussman thought that the best move instead would be local: a new reserve to demonstrate how research meshed with community welfare. Guy Ramanantsoa of the University’s School of Agronomy identified a small

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

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

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

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

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

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

1985–1998: PROGRAMMES D’ACTION ENVIRONNEMENTALES

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

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

A few of the new studies are islandwide in scope. Martin Nicoll and Olivier Langrand surveyed all the protected areas of Madagascar (Nicoll and Langrand, 1989), as has Conservation International’s mapping projects. Peter Raven, who had attended the 1985 conference in Jersey and was the director of the Missouri Botanical Garden (MBG), sent Peter Lowry to Madagascar to develop a countrywide scheme for the classification of vegetation types. The MBG subsequently sponsored a large number of studies of the Madagascar flora, and continues to train Malagasy botanists. Wilson Lourenço and Steven Goodman organized conferences drawing together much current work (Lourenço, 1996; Lourenço and Goodman, 2000). Edward Lewis has toured the country with his blowgun, identifying a wealth of lemurs distinct at the species level. Above all, WWF and the Field Museum of Chicago have sponsored Steven Goodman’s remarkable series

of expeditions and rapid assessment teams to little-known forests, surveying lemurs as well as everything else. Goodman's work has culminated in the 1700-page edited volume, *The Natural History of Madagascar*, which summarizes current knowledge of Madagascar's biodiversity up to the day it went to press (Goodman and Benstead, 2003). Goodman's own fieldwork continues unabated.

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

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

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

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

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

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

PROSPECTS FOR THE FUTURE

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

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

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

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

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

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

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

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