

Madagascar: A History of Arrivals, What Happened, and Will Happen Next*

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Abstract

Most of the ancestors of today's human and animal populations reached Madagascar over the last 65 million years, by a variety of routes at a variety of times. Settlers encountered a big, isolated island with an unpredictable climate and a wide array of landscapes. Although patterns of diversification were driven by different mechanisms in humans and animals, the complex interplay between historical contingency and responsiveness to local conditions is evident in both.

Global climate change will affect Madagascar, although exactly how remains unclear, and the immediate impact of human activity on the island is overtaking that of gradual global change. Three themes in this review bear on the future: the continuing impact of recent, cataclysmic events on modern communities of people, plants, and animals; Madagascar's long and dynamic environmental history; and the complicated history of how people settled and interacted with the island's landscapes. A deeper understanding of all three can contribute to wise decision making in the coming years.

INTRODUCTION

This review explores the arrival and subsequent history of animals and people in Madagascar. Too often, these histories are considered in isolation from one another, intersecting only in contentious debates about the causes of recent faunal extinctions and environmental change (Pollini 2010). By framing this review broadly and bringing these histories together, our goal is to amplify understanding of the processes whereby settlers colonized Madagascar's landscapes over the last 65 million years, the particular challenges encountered by those arriving, and the complex interplay between historical contingency and responsiveness to local conditions evident in their responses. We identify three themes from Madagascar's past that can help shape successful responses to present and future change.

Madagascar has been called an "alternate world" (Jolly 1980, p. 10): It is a big, isolated landmass, with an unpredictable climate, many unique plants and animals, and a human population of recent arrival (Goodman & Benstead 2003¹). This distinctiveness has long fascinated scholars and scientists. Questions about the fauna have centered on the timing and dispersal routes of the ancestors of modern populations, the drivers of their subsequent diversification and unusual suite of biological and behavioral features, and the causes of recent extinctions. Rigorous study of the role of historical events in evolution is essential, but difficult (Gould 1986). The challenge is compounded in Madagascar, where the search for Cenozoic outcrops containing deposits with terrestrial plants and mammals has yielded little earlier than 18,000 years ago. With almost no direct record for the critical period during which the modern fauna was forged, understanding is largely based on proxy indicators and inference.

The temporal overlap between recent faunal extinctions and human settlement of the island has led some to cast people simply

as destructive parvenus, agents of extinction (e.g., Gade 1996). Although their role in the extinctions is indeed a matter of current and historical importance, the history of people in Madagascar is complicated and interesting in its own right, and stewardship of the landscape plays a part in that history (Elmqvist et al. 2007).

Today, the Malagasy people are largely unified in speaking an Austronesian language, but they are of diverse ancestry, with an array of contrasting subsistence economies. The modern cultural matrix of Madagascar appears to be equally a response to opportunities the island offered and a product of the particular linguistic, economic, and cultural qualities of settlers arriving from the western Indian Ocean. Research has focused on the origins and timing of arrival of the human population, how Madagascar's landscapes shaped their livelihoods, and how people, in turn, altered and transformed those landscapes.

This review begins with a brief summary of the geological history, climate, and vegetation that shaped the evolution and history of settlers in Madagascar. Then we examine the pathways of settlement and diversification followed by the terrestrial mammalian fauna, and in recent times by people. The island's fauna and flora have become a focus of conservation efforts (Goodman & Patterson 1997, Brooks et al. 2006, Goodman 2008), and climate change is likely to increase the challenges of survival for people as well as for forests and wildlife. We conclude by considering how knowledge about the past can contribute to future strategy and action.

AN ALTERNATE WORLD

Madagascar sits approximately 400 km east of the African coastline, 4,000 km from India, 5,000 km from Antarctica, and 6,000 km from Australia. The tropic of Capricorn (23° 26'16" S) crosses its southern third. Madagascar has a surface area of 587,000 km², which is larger than France or the state of California. But things were not always as they

¹Some articles in this volume can be found in French in Goodman (2008).

are today. The environment awaiting new arrivals was continually reshaped by geological events and changing climatic conditions (Krause et al. 1997, de Wit 2003, Wells 2003, Yoder & Nowak 2006), and by the arrivals themselves.

When the supercontinent of Pangaea broke up approximately 175 million years ago (Ma), the landmasses of eastern Gondwanaland—Africa, Indo-Madagascar, and Antarctica—drifted south together, and Indo-Madagascar subsequently broke loose from Africa and moved away to the southeast. Madagascar reached its present position *relative to Africa* about 130 Ma but probably lay wholly south of a high-pressure subtropical belt, centered about 30°S. This belt encircled the globe then as it does today; it is commonly called the Arid Belt, because of the desert-like conditions that prevail within it.

Approximately 65 Ma, Africa and Madagascar began moving northward again in tandem. By about 30 Ma, Madagascar had cleared the Arid Belt and reached its approximate modern position *relative to latitude*. Paleooceanographic models indicate that during this long passage, strong surface currents flowed eastward from Africa. Thereafter, and certainly by the early Miocene (23 Ma), they reversed and began flowing toward Africa as they do today (Ali & Huber 2010).

Madagascar separated later from India than from Africa, with estimated dates ranging from 100–88 Ma. The timing of the split from Australia and Antarctica is less certain still, with estimates ranging from 130–125 Ma to 80 Ma (de Wit 2003). From at least 80 Ma, however, it is certain that Madagascar was completely surrounded by water and isolated from other landmasses (Ali & Krause 2011).

The modern topography of the island is a geological smorgasbord reaching far into the past (de Wit 2003). The most obvious outcome is the continent-like diversity of landscapes, from the sharp, north-south edge running down the island's eastern side, to the long, gentle slopes of its western flanks. Less obvious is the diversity of substrates into which the island's plants

sink their roots, and on which many Malagasy depend for their living.

The configuration of Madagascar's climate is strongly influenced by the westerly directed convergence of the northern and southern trade winds in the seasonally oscillating Inter-tropical Convergence Zone. Interacting with complex topography, this creates a strong asymmetry between the east and the west, a north-south climatic gradient, and markedly seasonal rainfall in some regions (Donque 1972, July 2003).

The multiple drivers of Madagascar's climate regime create not only geographic heterogeneity but also an unusual level of temporal unpredictability (Dewar & Richard 2007). The eastern region experiences this as high intra-annual variability in the patterning of rainfall. In other parts of the island, it takes the form of high interannual variability in total precipitation. Compounding the uncertainty, the island's location exposes it to tropical cyclones, which slam ashore erratically, often with devastating results. Forty-eight cyclones made landfall between 1980 and 2007, 19 of them in the northeast (Mavume et al. 2009).

The history of Madagascar's vegetation reflects the dynamic interplay of climate and geological history (e.g., Wickens & Lowe 2008). Today, the island's flora is characterized by high endemism and idiosyncratic diversity (Schatz 2001, Gautier & Goodman 2003). Plant communities most likely developed their current aspect when broadly modern conditions became established about 8 Ma, with subsequent boundary shifts driven by oscillations in climate (Wells 2003). Botanists commonly group these communities into phyto-geographic biomes (Moat & Smith 2007), which provide a useful, broad-brush characterization of the island's climatic and vegetative landscapes (**Figure 1**). In the South, arid spiny bush is dominated by the near endemic family Didiereaceae; in the dry deciduous forests of the West, sclerophyllous trees and shrubs predominate, interspersed with a mosaic of grassland; a small but distinctive area in the far Northwest is known as the Sambirano rainforest; evergreen rainforest runs almost

the entire length of the island in the East, with moist montane forest at higher elevations; montane ericoid thickets occur on the highest mountains; and grassland, woodland/bushland mosaic is found on the western slopes of the Central Plateau.

All biomes are anthropogenically disturbed to varying degrees, and geographic information systems and remote sensing technology have helped map the dynamics of actual vegetative cover (e.g., Faramalala 1988, Green & Sussman 1990, Du Puy & Moat 1996, Harper et al. 2007). Of the primary forest types (18% of total land cover), humid forest covers the largest area (8.1%), followed by western dry forest (5.4%), and arid spiny forest and thickets (3.1%) (Moat & Smith 2007). Approximately 65% of the island is covered by a variety of grasslands.

Two episodes in the island's vegetation history are of particular interest to this review because of events that occurred in their course. The first is the change in vegetative cover that likely happened during the island's northward passage through the Arid Belt, between 65 and 30 Ma. The second is the cyclical shift in vegetation boundaries that took place over the last 150,000 years.

Small enough to fit inside the Arid Belt, Madagascar would have been completely enveloped by harsh conditions for some part of its passage through the Belt. Only drought-adapted plants could have survived, Wells (2003) has argued, and the far south of the island today may be the last refuge of that ancient flora, displaced south by vegetation forms of more recent origin that gradually took hold when the island re-entered moister, warmer climes about 30 Ma. The botanical evidence for this scenario is mixed. Structural features of many southern plants suggest that they coevolved with the ancient radiation of ratites (Bond & Silander 2007, Midgley & Illing 2009), and the southern flora has been judged "extremely ancient" (Koechlin 1972, p. 157) based on particularly high reported levels of endemism. But those reports are contested (Schatz 2000, 2001), and more research is needed to establish Wells' proposition securely.

Over the last 2 Ma, global fluctuations in temperature gave rise to major glaciations at high latitudes and elevations. In Madagascar, paleoecological records reveal an alternation of warm and cold phases over the past 40,000 years at Tritrivakely, at an elevation of 1,778 m in the central highlands (Burney 1987a, Gasse & Van Campo 2001). Cold phases may have seen an annual mean temperature 5°C lower than today, with a complete replacement of tree species by ericaceous heath, a vegetation found today only in mountains at elevations greater than 2,000 m. These conditions likely limited forest to lower elevations and moist riverine habitats (Wilmé et al. 2006).

Paleoecological data also indicate marked climatic shifts, especially apparent droughts, over just the past 6,000 years (Virah-Sawmy et al. 2010; see also Mahé & Sourdat 1972, Goodman & Rakotozafy 1997). Most of the radiocarbon dating of sediment cores from Madagascar has been done on bulk sediment samples (the principal exceptions are Gasse & Van Campo 2001 and Virah-Sawmy et al. 2009), which yield dates of poor resolution that are unsuitable for precise chronologies (Grim et al. 2009). This is especially true for cores taken near calcareous or volcanic landscapes, as are many of the cores from Madagascar. Although the cores reveal important late Holocene vegetation shifts, chronological correlations between cores or with the archaeological record are rarely possible (but see Virah-Sawmy et al. 2009), and the roles played by climatic and anthropogenic drivers remain unclear.

Grasslands are a common feature of the western and central Malagasy landscape. For most of the twentieth century, the prevailing view of naturalists was that these and other grasslands formed as people cut or burned the original forest cover. That view is still upheld by some (see Bond et al. 2008 for overview). The recent, anthropogenic origin of some grasslands is not in doubt, particularly in the East where deforestation has been widespread (Green & Sussman 1990, Dufils 2008), but the antiquity and genesis of the vast

grasslands in central and western Madagascar are hotly debated.

Poverty of grassland species, low levels of endemism compared to forested biomes, and widespread erosional gullies have all been cited as evidence for the recent establishment of Madagascar's grasslands as a result of anthropogenic deforestation (e.g., Koechlin 1972, Lowry et al. 1997). Grass pollen and charcoal have been found in sediments in the central highlands, however, which predate by many thousands of years the estimated arrival time of people (Burney 1987a,b; Gasse & Van Campo 2001), and erosional gullies in fact have a very long history (Wells & Andriamihaja 1993). Bond et al. (2008) searched for endemic species or genera of plants and animals restricted to grasslands in Madagascar and compared numbers of ^{14}C grass genera in Madagascar and southern Africa. Fewer endemic or ^{14}C species and genera in Madagascar would signal a recent origin associated with human activity. Their findings, to the contrary, suggest that grasslands invaded Madagascar after the late Miocene as part of a worldwide expansion of ^{14}C grassy biomes.

THE HISTORY AND DIVERSITY OF MADAGASCAR'S MAMMALS

Origins and Arrivals

Madagascar's modern terrestrial fauna is overwhelmingly the outcome of dispersal by a few ancestors that subsequently diversified (Yoder & Nowak 2006). To a much lesser degree, it is also a product of ancient vicariance, when Madagascar was still connected to other landmasses.

Research on Madagascar's fossil-bearing Mesozoic deposits (245–65 Ma) opens a window into the deep past but offers few clues to the present. Seventy Ma, the island harbored spectacular forms of wildlife, including dinosaurs, crocodyliforms, and an exotic range of mammals, with affinities to Africa, India, and South America (Cooper et al. 2001, Cracraft 2001, Krause et al. 2006). But almost none of them

left living descendants, and even the youngest Mesozoic deposits contain barely a trace of lineages ancestral to modern vertebrates (Krause et al. 1997, Flynn & Wyss 2003).

After 65 Ma, the terrestrial fossil record goes silent. Many or most Late Cretaceous vertebrates in Madagascar may have gone extinct at the Cretaceous-Tertiary boundary. The cataclysmic impact of the earth's collision with an asteroid has been well documented in the faunal history of northern continents but is less certain for the southern continents (Johnson 1993). The array of competitors, predators, and prey awaiting ancestral lemurs when they came ashore a few million years later remains, thus, a matter of conjecture.

Terrestrial mammals must have arrived "by boat," crossing the Mozambique Channel on vegetation mats carried eastward by favorable currents (Ali & Huber 2010, Samonds et al. 2012; but see Martin 2003). Molecular evidence signals that each of the modern mammalian radiations, including the extinct giant lemurs, traces back to its own single colonizing event from Africa, where the closest phylogenetic relatives are found (Olson & Goodman 2003, Yoder et al. 2003, Yoder & Yang 2004, Karanth et al. 2005, Poux et al. 2005). This pattern is also seen in the majority of other vertebrate and invertebrate lineages ancestral to modern endemic species. Birds are a notable exception, with many families most closely related to forms found today in South and East Asia (Yoder & Nowak 2006, Crottini et al. 2012, Samonds et al. 2012).

Members of just 4 of the 17 extant orders of terrestrial mammals are endemic in Madagascar today: lemurs (Order Primates), tenrecs (Order Afrosorida), nesomyine rodents (Order Rodentia), and euplerid carnivorans (Order Carnivora). The first to arrive were lemurs, between 62 and 50 Ma. Tenrecs came later, between 42 and 25 Ma, carnivorans between 26 and 19 Ma, and rodents between 24 and 20 Ma (Yoder et al. 2003, Yoder & Yang 2004, Poux et al. 2005).

Although these four "dynasties" occupy the research limelight, they are not the only

mammals that found their way to the island. Notably, Madagascar's bats (Order Chiroptera) have a long, largely untold history (Samonds 2007), with high endemism (~60%) and low species numbers. The little-known *Plesioryceteropus* may have been an ancient arrival. Two species have been identified from subfossil remains. Once thought to be Malagasy aardvarks, these enigmatic mammals have now been given their own Order, Bibymalagasia (MacPhee 1994). Three species of dwarf hippopotamus (Order Artiodactyla) are common in subfossil deposits until about 1,000 years ago, their strong resemblance to African relatives suggesting a relatively recent arrival (i.e., after 2.5 Ma) (Stuenes 1989). Bush pigs (*Potamochoerus larvatus*) and wild cats (*Felis silvestris*) are widespread in Madagascar today. The common assumption is that they were brought by people, but the evidence is scant (Andrianjakarivelo 2003, Goodman et al. 2003). An array of domesticated mammals, including cattle, goats, sheep, pigs, dogs, and cats, were certainly introduced by people, along with the Indian civet and, probably inadvertently, black and Norwegian rats, pygmy and Asian house shrews, and the house mouse (Goodman et al. 2003).

This account of what is known, or known in part, leaves many questions unanswered. For example, what impact did the arrival of mammalian carnivores have on earlier arrivals? Lemurs and tenrecs would have been accustomed to predatory attacks by raptors and boa constrictors, but the advent of euplerid carnivores must have come as a rude shock. What about other arrivals, of which there is no trace? It seems possible, or even likely, that other mammals rafted ashore before ocean currents began flowing westward (Samonds et al. 2012). Harsh conditions on the island may have imposed a second "filter" on some colonizers that survived the sea journey (Dewar & Richard 2007).

Diversifying Across the Landscape

The pattern of diversity among vertebrates on the island today is highly idiosyncratic:

Madagascar harbors the most extensive radiation of chameleons in the world, for example, whereas the diversity of rodents is spectacularly low. Recent work suggests a burst of diversification among forms with the adaptability to colonize new rainforest habitats as Madagascar emerged from the Arid Belt (Crottini et al. 2012).

With respect to mammals, a consensus view of their diversity would improve our ability to study the evolutionary pathways of diversification, but this has yet to be achieved (Vences et al. 2009). In recent decades, large increases in species numbers have been claimed for many Malagasy taxa, including primates, for which the proposed number of species has risen from 32 in 1994 (Mittermeier et al. 1994) to 60 in 2005 (Groves 2005) and to 97 in 2010 (Mittermeier et al. 2010). This startling increase is based on a combination of fieldwork and morphological, cytogenetic, and molecular genetic studies (e.g., Andriaholinirina et al. 2006). Much of the newly reported diversity reflects intensified fieldwork or the recognition of cryptic species (Yoder et al. 2005), but it has been argued that taxonomic inflation is also driving up the numbers (Isaac et al. 2004, Tattersall 2007, Groeneveld et al. 2010).

In the absence of a fossil record, molecular clocks provide the only way to estimate dates of divergence within lineages. Using this approach, the common ancestors of all extant lemur lineages except *Daubentonia* have been found to trace back only to around 42 Ma, 20 million years after lemurs arrived (Yoder & Yang 2004). This long "quiescence" was during Madagascar's passage through the Arid Belt. A radiation at that time may have been replaced by the ancestors of extant lemur lineages. Or perhaps the opportunities for diversification were quite limited.

Two mechanisms of species divergence have been posited for Madagascar (Tattersall 1982, Pearson & Raxworthy 2009, Vences et al. 2009): (a) evolutionary adaptation to different habitats, with greatly reduced or no gene flow between populations and (b) accumulation of genetic, but

not necessarily adaptive, differences between populations newly isolated from one another, either by the formation of physical barriers or by climatic gradients. Correlations between vegetation formations and species are taken as evidence of the first, together with little or no positive correlation between biological and geographical distance among related species. Evidence for the second comes from river barriers, watersheds, and refugia and from sharp climatic gradients, associated with a close positive correlation between biological and geographical distance among related species, and high levels of local endemism. Researchers have explored the relative importance of these mechanisms in lemurs (e.g., Martin 1972, Tattersall 1982, Albrecht et al. 1990, Godfrey et al. 1990, Richard & Dewar 1991, Ganzhorn 1998, Godfrey et al. 1999, Muldoon & Simons 2007, Kamilar & Muldoon 2010), bats (Weyeneth et al. 2011), and species assemblages (see below).

Recent studies suggest that evolution occurred along both pathways during Madagascar's long and complicated history of environmental change, with both physical barriers and climate gradients serving as isolating mechanisms (Pearson & Raxworthy 2009). Lemur communities illustrate this point well. Although communities exhibit clear and consistent differences in taxonomic composition and ecological diversity among habitat types (Muldoon & Goodman 2010), they also offer glimpses of the early dispersal history and regionally specific circumstances that shaped them and their constituent members. For example, geographically distant communities resemble one another less than nearby communities do, but the correlation is stronger in the West than the East. The effect of distance is likely an echo of the original geography of speciation (Pearson & Raxworthy 2009), whereas the regional distinction may result from biogeographical differences between the island's eastern and western flanks. Rivers in the East are generally shorter and changes in the surrounding vegetation less abrupt, making it easier for animals to go around their headwaters (Muldoon & Goodman 2010; see

also Goodman & Ganzhorn 2004, Wilmé et al. 2006).

Holocene Extinctions

Mammal, bird, and reptile species disappeared during the Holocene (10,000 years ago to the present), many of them larger than their living relatives. These subfossil species have attracted intense attention (reviewed in Goodman & Benstead 2003), as has the timing of their disappearance (Burney et al. 2004, Crowley 2010). Although some may have survived after AD 1000, the chronology of their disappearances is poorly resolved, as are the causes. Habitats were transformed and fragmented by Holocene climate fluctuations and the activities of people, and large, slow-moving animals would have been easy prey for hunters. The importance of these effects likely differed by species and by region (Dewar 1997, Burney 1999, Crowley 2010, Virah-Sawmy et al. 2010). A full understanding of the extinctions will require better evidence and more precise dating. Except for the eastern rainforest (where subfossil and palynological evidence is lacking), however, it is certain that Madagascar's mid-Holocene animal communities were quite different from those today, and the structure of modern communities is partly a product of these recent changes.

Biology and Behavior of Extant Populations

Madagascar's extant mammalian species are biologically and behaviorally distinctive. Lemurs and tenrecs are the most speciose and extensively studied of the four radiations. Tenrecs exhibit a much higher degree of specialization than lemurs (Eisenberg & Gould 1970, Olson & Goodman 2003), but the two groups have notable features in common (Schmid & Stephenson 2003). This mixed pattern likely reflects ancestral differences in basal biology (Sussman 1978, Martin 1990), overlain by convergent adaptation to environmental conditions encountered after their arrival.

Lemurs exhibit an array of distinctive social, demographic, physiological, and morphological features, some of which are inferred to have been shared by the extinct subfossil species (Godfrey et al. 2007, Catlett et al. 2010). Widespread but not always universal (e.g., Pereira et al. 1990), few of these features can be explained as ancestral retentions (Martin 1990, 2000, 2003). Dubbed the “lemur syndrome” (Kappeler & Schaffler 2008), they include low encephalization compared to other primates, hypometabolism, absence of sexual dimorphism regardless of social system, strict seasonal breeding, cathemerality (an activity pattern largely independent of ambient light levels), a generalist diet with a lack of specializations for frugivory, female social dominance over males, and targeted aggression between females.

The lemur syndrome may be largely explained by the environmental challenges posed by Madagascar. Van Schaik & Kappeler (1996) argued that recent ecological disequilibrium, particularly the extinction of large diurnal raptors, enabled lemurs to become active by day and that their nocturnal past explains some of their unusual features today. However, an examination of the distribution of these features among nocturnal and diurnal primates, including lemurs, provides little support for this hypothesis (Wright 1999, Griffin et al. 2012). Still, it remains hard to conclude that the recent elimination of so many species left no mark on survivors or on the plants that coevolved with them (Ratsirarson 2003, 2005; Kamilar & Guidi 2010).

An alternative hypothesis proposed seasonality as an evolutionary driving force, coupled with unusually high reproductive stress among females (Jolly 1984, Young et al. 1990, Sauter 1993). Seasonality falls short as an explanation, however, because many primates exhibit seasonal adaptations (Ganzhorn et al. 2003, Brockman & van Schaik 2005) without converging on the lemur syndrome, and Madagascar is not in fact unusually seasonal (Richard & Dewar 1991). Moreover, lemur reproduction is associated with low maternal prenatal investment (Tilden 2008), postnatal growth

rates show a wide range of variation and are certainly not uniformly high (Kappeler 1996, Van Schaik & Kappeler 1996, Mumby & Viničius 2008), and the quantity and composition of lemur milk does not suggest unusually high maternal investment (Tilden & Oftedal 1995).

These findings led to a modified proposition: that harsh and unpredictable climate conditions in Madagascar favored the evolution of energy-conserving behavioral and biological traits (Pereira et al. 1999, Wright 1999). The proposition requires a close link between climate variability and food availability. Erratic cycles of leaf, flower, and fruit production have been reported at some sites (Meyers & Wright 1993, Overdorff 1993, Goodman & Ganzhorn 1997, Rasamimanana 2011), with correlated swings in the body mass of lemurs between and within years (e.g., Richard et al. 2000, King et al. 2010). More research is needed on the phenology of Madagascar’s plants, and its critical link with food availability (Terborgh & van Schaik 1987, Ganzhorn et al. 1999).

Many distinguishing features of lemur biology and behavior can reasonably be interpreted as adaptations for energy conservation in the face of unpredictability (Pereira et al. 1999, Wright 1999, Tilden 2008), though by no means all (Kappeler & Schaffler 2008). Adaptation to unpredictability is also evident in the life history patterns of many Malagasy mammals. Some species, including certain lemurs and carnivorans, have an extended reproductive span or reduced litter size compared to closely related taxa in Africa (Dewar & Richard 2007, Lawler et al. 2009). In mouse lemur and tenrec species, selection has favored concentrated reproduction early in life. Indeed, *Tenrec ecaudatus* has the biggest known litters of any mammal, up to 32 neonates, with low adult survivorship and reduced success among females in second-year and subsequent attempts to breed (Eisenberg & Gould 1970, Nicoll 2003).

Confronted by an unpredictable and harsh environment, the evolutionary choice for many animals seems to have been to speed up or slow down their lives and, in either case, conserve energy. Parallels with the evolution of the flora

and fauna of Australia (Flannery 1994, Smith & Ganzhorn 1996) suggest fertile ground for further comparative work.

THE HISTORY AND DIVERSITY OF MADAGASCAR'S PEOPLE

The history of the people of Madagascar poses questions similar to those about the natural history of the island. The answers are mostly quite different, however, starting with the fact that people arrived not as waifs randomly delivered from Africa on vegetal rafts but as active participants in the Indian Ocean network of trade and cultural interchange. Rakotoarisoa (1986, p. 89) noted that Malagasy people present a certain paradox, whose undoubted unity seems to reside in their undoubted diversity, and Ottino (1974, p. 12) explained Malagasy culture as a historical amalgam whereby the cultures of immigrants of different origins, at diverse times, were modified both by their interactions and by necessary adaptation to new ecological circumstances.

Malagasy Origins: Biological and Linguistic Evidence

Scholars today agree that the Malagasy must have had both African and Asian ancestors (Allibert 2008), and indigenous histories from many parts of the island emphasize origins from overseas, often specifically pointing to the Middle East (Beaujard 1991–1992, Rakotoarisoa 1998). All Malagasy groups sampled in recent population genetic studies have both Asian and African ancestors, with a sample from the Comoro Islands indicating links to the Arabian Peninsula, Persian Gulf, and perhaps the Indian subcontinent. Interpretation of the genetic data suggests that Asian and African immigrants to Madagascar included roughly equal numbers of men and women, whereas the western Eurasian contribution to the Comoros seems to have been largely men (Hurles et al. 2005, Forster et al. 2008, Ricaut et al. 2009, Tofanelli et al. 2009, Razafindrazaka et al. 2010, Gourjon et al. 2011, Msaidie et al. 2011).

Today, the people of Madagascar overwhelmingly speak Malagasy, though with significant dialectical differences. Malagasy is an Austronesian language, its closest relationships being with Barito Valley languages of Borneo (Adelaar 2009). In the early seventeenth century, however, people along Madagascar's west coast spoke an African language like that spoken in Mozambique and Malindi, whereas on the rest of the island an Austronesian language was spoken (Grandidier et al. 1903–1920, II:21–22). Today, languages of African origin have essentially disappeared, although there are small west coast communities where Makoa, a language of Mozambique, is still spoken and a village on Nosy-Be where, at least until the 1980s, Swahili was a second language (Gueunier n.d., p. 5).

Lexical borrowings into Malagasy come from many sources. The most obvious are recent, from French and English. Older borrowings are from Arabic, Swahili, Malay, Javanese, and South Sulawesi (Adelaar 1995, Beaujard 2003). Phonological, morphological, and syntactic changes in Malagasy indicate strong interactions with a Swahili language (Dahl 1988, Adelaar 2009). Malagasy was written in Arabic script in the southeast of the island from at least the sixteenth century (Beaujard 1998).

The Malagasy people are commonly assigned to 18 (the official number in colonial times) or more “ethnic groups,” but these groups are neither genetically isolated nor enduringly distinct speech communities (Dewar 1996).

Their historical origins and labeling are varied, and more recent than commonly appreciated (Poirier 1982). Many are products of labeling by Malagasy and European conquerors or originated in recent political contexts (Berg 1985, Larson 2000). In addition, some ethnicities are based not on parentage but on life practices; for example, the Vezo of the southwest coast are emphatic that being Vezo is not a product of ancestry but of learning, enacting, and bearing the physical scars of the Vezo way of life (Astuti 1995). The recentness and volatility of ethnic labels make

their projection into the distant past in search of ancient roots a fruitless endeavor.

Assembling the Malagasy Heritage

When a remote island's human history is discussed, usually the first question asked is "When did people get there?" The question is framed in two ways in Madagascar: "How old are the first human settlements?" and "When does human impact on the island become evident?" At present, there are widely cited dates for human impact substantially older than the date of the oldest known human settlement.

The evidence for human activity before the oldest human settlements derives from paleontological and paleoecological investigations. Two paleontological sites have yielded subfossil bones with postmortem damage attributed to butchery. Widely cited is a date of 402–204 BC² for such a bone from Taolambiby, in the southwest (Perez et al. 2003), and other damaged bones have been dated to 2288–2035 BC at Anjohibe in the Northwest (Gommery et al. 2011). The former has neither stratigraphic context nor a description of the damage; the latter are from an assemblage previously described as the scene of natural mortality (Burney et al. 1997), and in neither case have butchery tools or other evidence of human presence been recovered. The paleoecological evidence for human activity derives from inferences about the causes of changes in pollen, charcoal, and coprophilous spore deposition in stratigraphic column samples. As noted earlier, there are unresolved inconsistencies in chronology of some of these core samples.

The oldest dated human occupation in Madagascar is from the rock shelter of Lakaton'i Anja, near Antsiranana Bay in the extreme north. The date calibrates to the fourth to sixth century AD and is associated with the debris of coastal and forest foraging, but with few and

nondiagnostic artifacts. The visitors must have had a base elsewhere, but whether it was a ship in the bay or a village on the island is unknown (Dewar & Rakotovololona 1992).

The Indian Ocean has been a zone of long distance commerce for thousands of years (Beaujard 2007). Although Madagascar is peripheral to the most important historical nodes of that network, it is not far from ports active 2,000 years ago. The Egyptian Greek author of the *Periplus of the Erythraean Sea* described the prospects for trade and the routes of navigation in the Indian Ocean in the first century AD (Casson 1989). His knowledge extended down the East African Coast to within 1,200 km of Madagascar. It would not be surprising if trading vessels made landfall in Madagascar 2,000 years ago, and it is possible that smaller watercraft crossed the Mozambique Channel even earlier.

The early expansion of human settlement in Madagascar is best characterized as a progressive colonization of coastal zones with economies assembled from imported domesticates in addition to locally available natural resources, and not simply as a succession of adaptations to the latter. The earliest known residential settlement dates from approximately AD 700 near Mananara and at Nosy Mangabe along the northeast coast (Wright & Fanony 1992). Over the next five-hundred-year period, villages and hamlets are documented in almost every coastal zone that has been archaeologically surveyed to date (Vérin 1986, Dewar & Wright 1993, Rakotoarisoa 1998, Parker Pearson 2010). Dispersal was remarkably unconstrained by the environmental variety of the island's low elevations, and sites have been discovered from the evergreen rainforest biome in the East to the arid spiny bush of the South (Figure 1). Their economies were diverse: Some appear to have been based on hill-slope agriculture, others on herding cattle and goats, and still others on coastal fishing. The crops and animals on which villagers depended were mostly imported from Southeast Asia or East Africa (Blench 2007, Beaujard 2011). Malagasy cattle, usually treated as imports from Africa,

²Radiocarbon dates are calibrated at 2σ , using Calib 6.0 (Stuiver & Reimer 1993) and the Southern Hemisphere calibration curve (McCormac et al. 2004).

actually show strong affinities to Asian cattle (Hanotte et al. 2002).

Human Ecology in Madagascar Today

The diversity of human ecology in Madagascar continues to be a reflection of the island's variety of climate and topography, and a dynamic product of social and cultural history. The Mikea derive much of their food from foraging in the dry forests of the Southwest, evidently a quite recent economic shift rather than a preagricultural survival (Poyer & Kelly 2000). Hunting and collecting wild plants and animals are common outside urban areas. Coastal fishing is important along the west coast, both as a central focus (Marikandia 2001) and a supplement to agriculture. Farmers select from a wide range of species and varieties, including New World foods (notably manioc, sweet potatoes, and maize), and colonial period cash crops (coffee, vanilla, cloves, cacao, ylang-ylang, and pepper). Cattle, chickens, sheep, goats, pigs, ducks, turkeys, and geese are locally common.

Throughout the island, farmers and herders modify their use of domesticated plants and animals according to local conditions (Kistler & Spack 2003). Rice and cattle, culturally as well as economically the two most important domesticates island-wide, provide good examples of this.

Rice is best known as a transplanted crop in irrigated and drained fields of the central highlands, and in swidden fields opened up in forests. But it is cultivated in other ways too: Farmers sow seeds in swamps or along riverbanks after floods and sow or transplant into rain-fed fields. Rice cultivation has expanded into many new areas over the past 500 years (Le Bourdieu 1974, 1977), including some to which it is ill suited and frequently fails (Barbour 2002).

Crop failures and famines are indeed a common feature of life throughout Madagascar, linked to the island's unpredictable rainfall regimes, and the organization of rice production in the central highlands is idiosyncratic, probably in response to uncertainty about

rainfall as well. Two crops of rice are grown, in overlapping seasons, but each field has but one crop a year. The first crop, *vary aloba*, is planted in the dry season and harvested in the wet, whereas the second, *vary sia*, is planted at the beginning of the rains. *Vary aloba* has been called "*une culture contre nature*" (Raison 1972, p. 111), as farmers have to withhold water after transplanting until there is enough rain to ensure its growth, but it is important as a buffer against year-to-year variation in rice yield. Data for Antananarivo (Douessin 1976) show no correlation between first and second crops: Good years for one crop may not be good for the other.

Semi-nomadic cattle pastoralism is a well-known feature of the drier grasslands of the west and south, but in fact cattle are found throughout the island, even in the humid zones of the east (Raison 1969). Almost everywhere, they are ritually important. Like those in East Africa, western pastoralists buffer local rainfall shortfalls by shifting herds to better pasture, although with increasing population density this is becoming more difficult today (Hoerner 1983). Historically, such ecological adaptations to local conditions permitted expansion into the unsettled interior, whereas coastal populations maintained connections with the Indian Ocean world.

Trade, Expansion into the Interior, and Political Evolution

Trade goods from the Indian Ocean network are occasionally found at older sites (e.g., Wright & Fanony 1992), but the twelfth century saw the rise of Mahilaka, a major trading port on the northwest coast (Radimilahy 1998). Substantially larger (with perhaps 3,000–5,000 residents) than any earlier site, or any contemporary site in Swahili East Africa, within its walled 70 ha were mosques, elite residences, workshop areas, access to the anchorage, and abundant evidence of trade. About AD 1400 Mahilaka was partially abandoned, but substantial trading ports replaced it along the northwest and northeast coasts (Vérin 1986, Beaujard 2003). These represent a continuous

tradition of maritime trade for northern Madagascar, often including small groups of resident overseas traders.

Concurrent with Mahilaka came settlement of the island's interior, particularly the central highlands around Avaradrano (near modern Antananarivo) (Rakotovololona 1993, H.T. Wright 2007) and the arid bush in the South (Parker Pearson 2010). Highland settlements of the thirteenth century were 1- to 2-ha villages located in small river valleys. Rice phytoliths have been recovered from these sites (D. Pearsall, personal communication), indicating an economy based on wetland farming. The southern economy was founded on cattle and goat pastoralism, evidently an uncertain enterprise then as now. The archaeological record indicates a dramatic decline in human population from the fourteenth to the seventeenth century that ended with the immigration of the ancestors of the Tandroy (Parker Pearson 2010). The decline was likely associated with a perturbation of climate, given the frequent and devastating droughts recorded for this region over the last century.

The Portuguese encountered Madagascar in 1500; other Europeans soon followed. It is easy to understand why: Madagascar sits astride the most common routes from the Cape of Good Hope to India. Europeans quickly turned to slaving, for Malagasy were already being sold to Arab and Swahili merchants in west coast ports. The initial European destination for slaves was the Dutch Cape Colony (Worden 1997). In the eighteenth century, the slave trade shifted to east coast ports for transport to the Mascareignes, along with rice and cattle (Campbell 2005).

European observers of Madagascar in the seventeenth century describe a landscape of small kingdoms, perhaps best characterized as lineage-based polities of limited geographical spread that were frequently unstable and engaged in near-constant competition and conflict (Bloch 1977; and see also Dewar & Wright 1993). The seventeenth and eighteenth centuries also saw the development of much larger polities, especially the Sakalava of the

west coast (Kent 1970, Feeley-Harnick 1991). Although Malagasy polities of the 200 years before colonization were heterogeneous in form (Raison-Jourde 1983), economically driven acquisition of slaves was certainly a central feature of much military and political activity in this period.

The settlement history of the highlands is the best known in Madagascar (H.T. Wright 2007), with an archaeological record strongly reminiscent of sequences leading to state formation in other parts of the world. From the sparse occupations of the thirteenth century, there were progressive population growth, a shift to fortified occupations of hilltops, development of an increasingly elaborate settlement size hierarchy, and by the seventeenth century, a clear shift to rice agriculture in wetlands that required major investments in water control (Bloch 1977, Kottak 1977). By the end of the eighteenth century, the Avaradrano evinces the hallmarks of a hierarchically ordered and administered state (H.T. Wright 2007). The early nineteenth century saw its expansion across most of the island into what came to be known as the Kingdom of Madagascar.

The economic base of this state was rice and slaves (Bloch 1977, Larson 2000, Campbell 2005). The attention given to rice production was intense. Declaring that he had no enemies except famine and flood, King Andriamanpoinimerina (reign: 1785–1810) famously sought to manage irrigation water, requiring under pain of death that dikes be breached if higher lands were flooded (Malzac & Callet 1908, p. 751–52, 804). At the same time, Madagascar was becoming central to the East African slaving network, functioning as a destination, source, and trans-shipper. Campbell (2005) estimates that 400,000 East Africans entered Madagascar as slaves from 1821–1895. In 1830, perhaps 30% of the Imerina population was enslaved (2005, p. 75, 221), including captives from other parts of the island and East Africa as well as Merina themselves. The development of slave-holding societies in the nineteenth century had grave consequences that continue to this day, more

than a century after emancipation (Rakoto 1997, 2001; Larson 2000; Graeber 2007).

In 1895, the French conquered the Kingdom of Madagascar, and it remained a colony until 1960. The period of French domination had profound impacts that still resonate in complicated ways (Althabe 1969, Cole 2001). This history and the postcolonial period require a review to themselves.

WHAT HAPPENS NEXT?

Madagascar's history of environmental change is a prelude to future change, driven by the continuing rise in global temperature predicted over coming decades and the impact of human activity on the island today. These effects threaten the well-being of people as well as the survival of the island's unique fauna and flora.

The rise in global temperature and its impacts are not uniformly or predictably distributed around the world (de Wit & Stankiewicz 2006, Scholze et al. 2006, Willis & Bhagwat 2009), and they remain uncertain for Madagascar, particularly at the local and regional levels (Ingram & Dawson 2005, Tadross et al. 2008, Randriamahefasoa 2011). Tadross et al. (2008, p. 6) explored a "suite of possible futures" for the island over the next half-century. Strong congruence between their model predictions indicates that Madagascar is highly likely to experience a continuing rise in minimum and maximum temperatures. The lowest expected changes will be in the north and along the coastal regions (minimum increase of $>1.1^{\circ}\text{C}$, and maximum of $>1.8^{\circ}\text{C}$) and the highest in the south (minimum $>1.5^{\circ}\text{C}$, and maximum $>2.6^{\circ}\text{C}$). Congruence between rainfall projections is weaker, but much of the island may experience increased rainfall. Only the southern half of the east coast is projected to be drier by 2050. The frequency of cyclones is expected to decline, whereas their intensity may increase.

Possible ecological consequences of these changes include geographical shifts in biome ranges at rates significantly higher than have occurred in the last 150,000 years;

fragmentation or loss of forest habitats where migration corridors are absent; and range contraction in many endemic plant species (Hannah et al. 2008). The economic consequences are likely to vary regionally, with experimental studies of upland rain-fed rice indicating higher productivity (Gerardeaux et al. 2011), whereas the prospect of agricultural breakdown looms in the south.

The impact of human activities on the island today is rapidly overtaking that of longer-term global changes (e.g., Harper et al. 2007, Kelley et al. 2007, Dunham et al. 2008, Wright et al. 2011). These activities include harvesting wood for timber and fuel, clearing forest for small-scale cultivation and commercial agriculture, and exploiting animals for food or sale in the international wildlife trade (Durbin et al. 2003).

On both timescales, the future of Madagascar's surviving plants and animals requires that hunting, trafficking in wildlife, and the further fragmentation and loss of forest cover be slowed and then halted; that existing protected areas be maintained; and that potential retreat and dispersal corridors be protected and restored (P.C. Wright 2007, Hannah et al. 2008, Raxworthy et al. 2008). It is a tall order.

The insights of ecology and paleoecology can be helpful (Dawson et al. 2011) but so too can knowledge of the history of people and their institutions. Three themes emerge from this review with a bearing on the future: the continuing impact of recent, cataclysmic events on modern communities of people, plants, and animals; the dynamism of past environments and ecological communities; and the complicated history of how and why people variously adapted to, transformed, degraded, and protected the landscapes they encountered.

The importance of the Holocene extinctions and human activities for the ecology of Madagascar today is widely recognized. Less widely acknowledged are the continuing reverberations in the human population of the ravages of slavery in the eighteenth and nineteenth centuries, and of colonization and post-colonial political instability in the twentieth and

twenty-first. Although disparate in their causes and consequences, these historic perturbations of nature and society helped shape the nature of present challenges and affect the capacity of society to respond. It is important that they are not only acknowledged but also studied and understood.

The deep history of environmental variability in Madagascar provides a benchmark against which to assess conditions today and design management interventions for the future (Willis et al. 2007). This applies to intermittent phenomena such as wildfires as well as to biogeographic shifts that occur as a consequence of climate change. Paleoecological records can be used to make “backward predictions,” exploring potential errors in bioclimatic modeling of future trends, and to capture the complexity of local patterns often overlooked in coarser spatial-scale models (Virah-Sawmy et al. 2009, Willis & Bhagwat 2009). Historical records pose philosophical as well as biological questions about what is “natural” (Willis & Birks 2006). These questions are particularly acute in a system that has been perturbed as profoundly and recently as Madagascar. They are inherently unanswerable, but that does not alter the importance of considering them in decision making about species management and conservation.

Reconciling conservation and development objectives in national policy has proved difficult in Madagascar. In 1991, the government launched an ambitious National Environmental Action Plan, elaborated by successive governments, to chart and implement sustainable macroeconomic policy with full recognition of the interdependence of conservation and development. In practice, many initiatives at all levels have been thwarted

by political instability, poverty, and their corollaries, and by the highly centralized approach taken in the early years (Durbin et al. 2003, Randriamalala & Liu 2010, Pollini 2011).

In Madagascar, as elsewhere (Western & Wright 1994), this has brought growing recognition of the importance of including and mobilizing local communities in the effort. In many communities, the means and the will to manage have long existed, and the polarized view of inherent conflict between conservation and development is largely absent (Durbin et al. 2003, Andriamalala & Gardner 2010, Harris 2011, Pollini 2011). Historically, local management was often preempted by colonial and national agencies and regulations. Over the last two decades, the recognition by successive governments of the limits of central power and the importance of local control has been an important step toward reestablishment of locally effective management. However, “local communities” glosses a wide range of social, political, and economic conditions (Rabesahala Horning 2003, Elmqvist et al. 2007). Communities vary in their exposure to perturbations of the nineteenth and twentieth centuries, as well as in their recent immigration histories, social cohesiveness, ability to enforce local rules, and ties to the surrounding landscape. In some areas, local management will be embraced and reasserted; in other communities, the absence of the ability to convene, agree, and act in concert will make effective local management unlikely.

The challenges are huge, and knowledge of the past can surely strengthen strategy and action at all levels. To be of greatest value, studies must encompass and bring together the multiple and diverse histories of arrival: “natural” Madagascar today is a landscape with people, not without.

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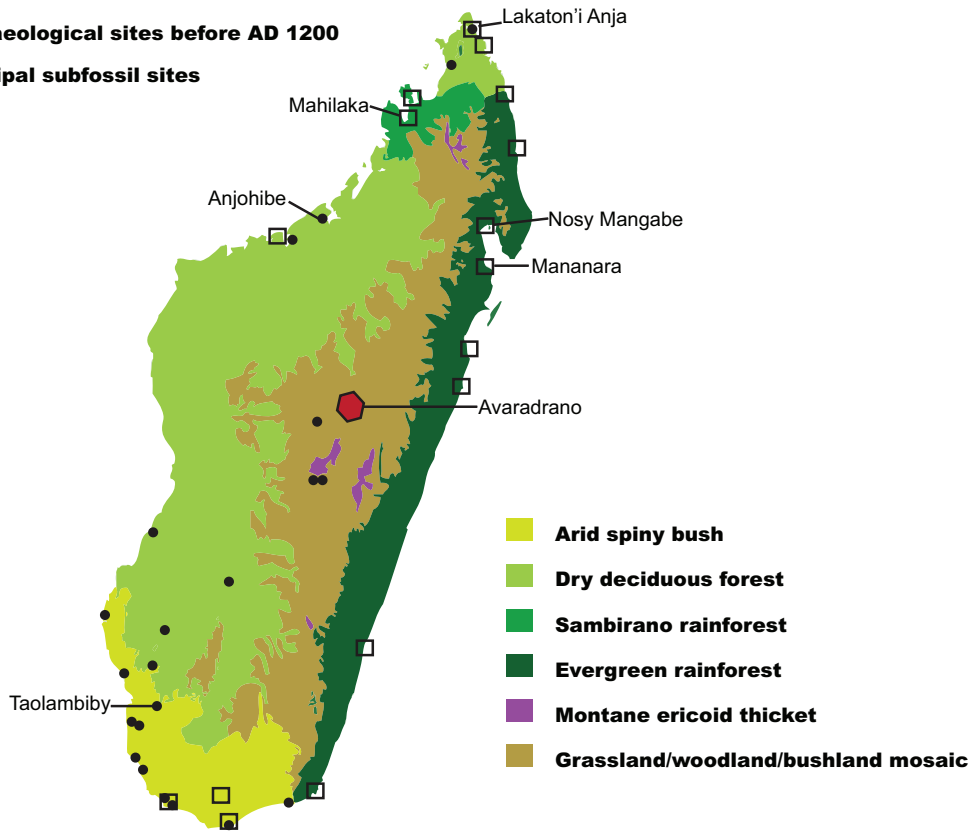


Figure 1

Phyto-geographic biomes of Madagascar with principal subfossil sites and archaeological sites earlier than AD 1200. Localities discussed in the text are labeled. Map redrawn from Yoder & Nowak 2006 based on Faramalala 1988, Du Puy & Moat 1996, and Lowry et al. 1997.



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