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Patterns of origin and extinction in the mammal fauna of Madagascar

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Madagascar's huge size and long history of isolation have assured ongoing debate about both the origin of its oddly constituted fauna and the nature of the major extinction event that occurred following the first incursion of humans onto the island some two thousand years ago. In this paper I briefly review the geological and biological evidence for the origin of the modern Malagasy fauna, and examine the potential roles of direct human intervention and climatic change in the extinction of Madagascar's large-bodied mammals. Despite the remarkable dearth of evidence for direct interaction between humans and the island's 'subfossil' fauna, available evidence of climatic conditions in Madagascar since the end of the Pleistocene does not indicate that its fauna was under unprecedented environmental stress in this period. It is thus impossible to avoid the conclusion that human activity played a critical role in the elimination of several dozen species of mammals and birds of larger body size than their surviving relatives. In turn, this observation underscores the fact that the documented extinctions do not constitute a static and completed historical phenomenon, but rather form part of an ongoing process that continues today to menace Madagascar's unique fauna and flora.

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INTRODUCTION

A great landmass some 1600 km long and lying about 400 km off the southeastern African coast, Madagascar is routinely referred to as 'the world's fourth largest island', and 'the world's largest oceanic island'. Statements such as these place as much emphasis on Madagascar's sheer size as on its insular nature, and point to the fact that this is a very special kind of island: one that is not only impervious to many of the assumptions of island biogeography, but that in many ways shows the biotic characteristics of a continent. It is possible, of course, to find instances in Madagascar of many phenomena that are generally considered to be characteristic of islands; but in most cases these must be hedged with caveats. Thus, for example, Madagascar shows high rates of endemism, both faunal and floral; but then, so also do continents, in proportion to their own histories of isolation. Similarly, apparent cases of giantism (e.g. in the elephant bird, *Aepyornis maximus*, and in the huge indriid primate *Archaeoindris fontoynonti*), and of dwarfism (e.g. in the smallest primate, *Microcebus myoxinus*, or in the up to three pygmy hippotamus species) can indeed be found in Madagascar; but such examples are better viewed simply as extremes of the local size spectra of the major taxa involved, or explained (in the case of the pygmy hippos) by quite recent immigration.

Nonetheless, one may fairly point to two major aspects of Madagascar's biological history that have been critically influenced by its insular nature. The first of these is the origin of the Malagasy biota, or at least of its post-Gondwanan elements. Here a strong initial filtering effect is discernible, together with dramatic post-filter diversification. Thus, for example, while Madagascar's endemic terrestrial mammals consist today only of strepsirhine primates, nesomyine rodents, tenrecid insectivores, and viverrid carnivores, each of these groups is present in impressive variety. No scenario aimed at explaining this remarkable faunal makeup can ignore the question of Madagascar's geological origin; and although the details of this origin remain an arena for debate, it is by now generally agreed that from a middle Jurassic location adjacent to the modern Tanzania/Kenya/ Somali coast well to the north of its present emplacement (Reeves *et al.* 1987), Madagascar had assumed more or less its current position relative to Africa at some time prior to the late Cretaceous (Cochran 1988), over 120 My. Direct continuity between the African and Malagasy biotas was thus ruptured by around 160 My, although certain paleogeographic reconstructions suggest that indirect interchange via South America, Antarctica and India might have been available until about 130 My (see discussion by Krause *et al.* 1997), or even much more recently, in the 100-80 My range (Sampson *et al.* 1998).

These observations effectively eliminate the older notion that Madagascar's mammal fauna, depauperate in major taxa but rich in endemic species, is a direct insular relic of Africa's early Tertiary biota. For while there can be little doubt that Madagascar's mammals are of African parentage, the island was clearly separated from the mainland by a substantial oceanic barrier by the early Tertiary date at which we can reasonably suppose that the parent stocks of the surviving Malagasy mammal families had evolved in Africa. The almost complete absence of pre-late Eocene mammal fossil records in Africa, Madagascar and India makes precise paleobiogeographical reconstruction speculative at best; but relationships among the living African and Malagasy primates may suggest that at least two successful primate invasions of Madagascar had been achieved before the end of the Eocene (Schwartz & Tattersall 1985), and probably well before. Alternatively, the close relationship between the Malagasy cheirogaleid lemurs and the African lorisoid primates might imply an initial colonization of Madagascar by ancestral African strepsirhines, followed by the evolution in Madagascar of the ancestral lorisoid with a subsequent back-migration to Africa.

Under conventional paleogeographic reconstructions such invasions must have been via a 'sweepstakes' mechanism; and among mechanisms of this kind rafting is the only remotely plausible alternative, despite various factors that point to its inherent improbability, particularly in an eastward direction. Lawlor (1986), for instance, has demonstrated the extreme rarity with which terrestrial mammals have successfully colonized isolated islands anywhere. In a situation of this kind one can only follow Sherlock Holmes and conclude that, once the impossible has been eliminated, what remains, however implausible, must be what happened. Yet if rafting of primates across a Mozambique Channel of roughly modern dimensions was possible during the Eocene or earlier, why not subsequently? After all, among various other forms, the progenitors of the endemic viverrids of Madagascar must have entered the island by the same means subsequent to the Oligocene, when the oceanic barrier was apparently no more formidable than earlier in the Tertiary. As long as we adhere to a scenario of unchanging biogeography, satisfactory potential explanations for the cessation of primate penetration of Madagascar subsequent to some point early in the Tertiary are few, and none is compelling. Perhaps, for reasons of chance in a situation already close to the outer limits of probability, no later crossings were made. Alternatively, in contradiction to the hallowed notion that strepsirhines were able to diversify in Madagascar only due to the absence of competition from competitively superior 'higher' primates, is it possible that Madagascar's strepsirhines were actually successful in outcompeting later arrivals?

The reality may, however, have been totally different. For recently the possibility has been raised again that paleogeography across the Mozambique Channel between Madagascar and Africa has not in fact remained stable throughout the Tertiary. The Channel is today a 400-600 km-wide swath of water of oceanic depth, with a handful of small and relatively recent volcanic islands and atolls. However, the Davie Fracture Zone (DFZ), apparently the remains of the transform fault along which Madagascar moved southwards on its migration from Africa, forms a longitudinal raised structure down the center of the Channel that in places comes to within some 500 m of the surface. Recently, McCall (1997) has interpreted cores taken from the DFZ, and reported by Leclaire *et al.* (1989) and Bassias (1992), as providing evidence of erosional surfaces on the DFZ in the period between about 45 and 26 My, continental basement metamorphics being unconformably overlain by much younger marine strata. McCall believes that uplift along the DFZ was initiated by the collision of India with Asia (c. 42 My), an event that converted tensional conditions in the region of Madagascar to compressive ones for some 20 million years until the development of the East African rifting system in the Miocene again created a tensional setting and crustal subsidence along the DFZ.

At present these speculations are directly supported only by the negative evidence of a handful of cores. However, if ultimately borne out, such evidence would indicate that parts of the DFZ were subaerial from the late Eocene to the early Miocene. At the very minimum this would facilitate an island-hopping scenario for the occupation of Madagascar by the ancestors of today's endemic Malagasy terrestrial mammals, and at its limit it would even introduce the possibility of a more or less continuous land bridge from the continent to the island at least periodically in the 45-26 Ma time window. However, it should be noted that the existence of a land bridge of this kind would raise as many problems as it solves. For, almost regardless of the ecological conditions that reigned along it, a continuous bridge would be expected to have had a substantially less dramatic filtering effect than Madagascar's modern fauna implies. Such a bridge, if it existed, was certainly of an appropriate age to explain the presence in Madagascar of the island's endemic terrestrial mammals; but, particularly in the later part of its time span, it would be expected to have given passage to a much larger variety of mammalian groups than we find endemically in Madagascar, including various higher primates. Once again, then, the highly selective nature of Madagascar's endemic mammal fauna inclines one towards an island-hopping version of the 'sweepstakes' mechanism, although the lack of a Tertiary fossil record in Madagascar makes it impossible to rule out stringent pre-Quaternary extinction effects. Clearly, we are facing a very complex history here: one which we will only begin to unravel with more detailed drilling studies in the Mozambique Channel and the discovery of substantial terrestrial Tertiary fossil records onshore.

QUATERNARY EXTINCTIONS

Given that the origins of today's Malagasy fauna are so fraught with mystery, it is particularly fortunate that recent research has expanded the information base that bears on the second notable aspect of Malagasy biological history that I would suggest has been critically influenced by Madagascar's insular nature. This is the question of the major extinction event that has taken place in the island over the past couple of millennia, roughly the period in which Madagascar has been inhabited by humans. As I have already noted, Madagascar's mammalian fauna today displays low diversity at high taxonomic levels, in concert with an impressive species-level variety within those major taxa that are represented. Yet this latter diversity pales in contrast to that which existed only a thousand years ago. For in this remarkably short space of time, Madagascar has lost an entire megafauna.

Today Madagascar's largest endemic mammal is the viverrid *Cryptoprocta ferox*, adults of which attain weights of 7-12 kg (Albignac 1973), and its biggest native primate is *Indri indri*, which barely attains the lower end of that range. Subfossil sites in all regions of the island except the east, however, bear witness to the former abundance there of at least 15 reptile, bird and mammal genera, all of which were somewhat to extremely large-bodied in comparison. Such extinct forms included *Aepyornis maximus*, the largest bird on record, with a body weight of perhaps 400 kg (Amadon 1947), and several relatives; the giant tortoise *Geochelone grandidieri*; three pygmy species of *Hippopotamus*; the mysterious *Plesiorycteropus*, recently placed by MacPhee (1994) in its own order; and at least fifteen primate species, ranging from a couple of forms not much bigger than the largest surviving lemur, all the way up to *Archaeoindris fontoynonti*, whose body bulk is estimated to have been around 160-200 kg (L. Godfrey pers. comm.). Many of the classic subfossil assemblages, notably those excavated in the first half of this century and in the waning years of the last, are subject to considerable taphonomic bias; but there is no doubt that the living and subfossil vertebrates formed part of the same fauna, and that the extinct genera are larger in body size, and usually much larger, than their relatives still living today in Madagascar. About the only exception to this latter generalization is the Nile crocodile, probably a relatively recent immigrant and in any event, as Burney & MacPhee (1988) have pointed out, the ultimate survivor.

Radiocarbon determinations on the dozens of sites yielding the remains of recently extinct Malagasy mammals run from under 1,000 y (Dewar, 1997) to as much as 8,000 y (MacPhee *et al.* 1985), and there is one U-series date as old as about 40 Ky (Burney 1997). Nearly all dates, however, cluster in the range of 1-3 Ky, a period that almost certainly straddles the first arrival of humans in Madagascar. The early archaeological record in the island is poor but improving, and so far there is no direct evidence anywhere of permanent human occupation prior to the eighth century A.D. (Wright and Fanony 1992). However, transient camps of fifth to eighth century age have been identified in the north of the island (Dewar 1996), and at the sites of Lamboharana and Ambolisatra in the southwest subfossil lemur bones bearing cutmarks have been tentatively dated to the first to fourth centuries (MacPhee & Burney 1991). It is, then, uncontestable that (with the possible exception of *Archaeoindris*) all of the now-extinct mammal species of Madagascar were still alive when humans first arrived on the island under two thousand years ago. Oddly, though, there is very little direct association between human activity and the bones of giant extinct lemurs at any period, and certainly nothing even remotely resembling the huge middens of moa bones found in New Zealand, the only other major land mass to have been as recently colonised.

In considering the reasons for this it is useful to bear in mind the fact that Madagascar was evidently settled by Iron Age peoples with well-established pastoral and agricultural ways of life. For such people hunting would not, as Dewar (1997) has pointed out, have been a primary focus. Yet it is also true that, in spite of seventeenth-century and subsequent accounts of the existence of mysterious large beasts unmatched in the Malagasy fauna today, there is still no firm evidence that any of the species now known only through subfossils was still extant by the time that the first European explorers made contact with

Madagascar in the sixteenth century. The loss of Madagascar's entire megafauna must thus have taken place extremely rapidly: probably well within the space of a thousand years.

The reasons for this abrupt extinction event have been debated almost since the time of the first discovery of subfossil vertebrates in Madagascar late in the nineteenth century. Two potential culprits, human activity and climatic stress, have most frequently been identified, usually in an either/or context. Until relatively recently, most thought on the matter was heavily influenced by a scenario developed in the first half of this century by the botanists Perrier de la Bathie (e.g. 1921) and Humbert (e.g. 1927). Today what remains of the aboriginal forest of Madagascar and its fauna is distributed around the periphery of the island, in the dry south, the seasonal west, and the humid east. The central plateau, though reasonably well-watered, is covered principally by grassland and bare rock. Subfossil sites are known from all these areas with the exception of the east, but including the center. Humbert, particularly, argued forcefully that, in sharp contrast to this picture, at the time of initial human colonization Madagascar had been more or less totally forested, and that the denudation evident today is the result of intervention by fire-wielding settlers. From this it followed that anthropogenic loss of habitat must have been at least a major factor in the disappearance of the subfossil fauna; and it is certainly undeniable that today this process poses a substantial threat to the forms that still survive. Add to such habitat destruction the fact that the extinction was selective, carrying away those species that on account of their body sizes were individually both most attractive and vulnerable to human hunters, and that as populations must have had the lowest densities and slowest reproductive turnovers, and the circumstantial case for a combination of direct and indirect human activities as the agent of extinction seems compelling.

Nevertheless, it has long been recognised that many Malagasy subfossil sites represent dried-up marshes, and the argument has been developed that, at least locally, natural aridification was responsible for megafaunal extinction in Madagascar (e.g. Mahé & Sourdat 1972). And certainly, it is hard to imagine the dry, xerophytic vegetation of parts of the island's south supporting the giant lemurs that once lived there in apparent abundance (MacPhee 1986). The issue of natural climatic change as a putative agent of extinction has received renewed attention as a result of the elegant work of David Burney, Ross MacPhee and their co-workers (e.g. MacPhee *et al.* 1985; Burney 1987a,b, 1997). These researchers have shown that the denudation of Madagascar's central plateau is not entirely a product of the island's Anthropogene, but that some at least of the region's grasslands are of long standing. Thus, for instance, Burney's (1987a) analysis of a core from Lake Tritrivakely in central Madagascar shows that climate in the lake's vicinity has fluctuated over the Holocene, with open habitats represented in pollen spectra throughout that period, and periodic burning evidenced by charcoal fragments. And while Lake Kavitaha, some distance to the north, produced evidence of a reduction of woody pollens and a rapid increase in grasses in the half-millennium following the presumed incursion of humans into the area, it too showed a mixed vegetation and evidence of natural fire at earlier times (Burney 1987b).

Such observations bring our understanding of climatic events in Madagascar into line with what we know of other parts of the world, where recent decades have seen the abandonment of the idea that the tropics remained relatively stable during the climatic vicissitudes of the Pleistocene. In Africa, for example, Hamilton (1976, 1981) showed some time ago that the six thousand years around the last glacial maximum (c. 21-15 Ky) was a time of considerably greater aridity than the present, and witnessed a dramatic contraction of the area under forest. And it is now known that at around the same time Alaotra, today Madagascar's largest lake, was almost completely dry (Burney 1997). Prior to this, wetter but noticeably cool conditions had prevailed. It seems most likely, then, that at the beginning of the Holocene, roughly when the reasonably detailed pollen record starts, Madagascar's forests were just beginning to recover from a period of maximal contraction. In view of this, it is hardly surprising that the central plateau was not fully forested by the time of human arrival in the late Holocene, although some forest there must of course have been in subfossil times to support the subfossil fauna we know existed. Most likely such forest occurred along watercourses and in the bottoms of drainage basins, with heath or grassland on the higher and better-drained areas of the rugged plateau topography. Modern and subfossil lemur distributions suggest that these forests must have been sufficiently continuous, at least from time to time, to connect the forest expanses of the east and west.

The revelation that the modern grasslands of Madagascar's interior may be at least in part non-anthropogenic, and that fire was a regular feature of Madagascar's pre-human ecology, rather than a novelty sprung by humans on an ill-adapted flora, suggests that the activities of mankind have played a more minor role in the modification of Madagascar's environment than had been envisaged by Humbert and his followers. This certainly makes excellent sense in view of the fact that Madagascar's human population was until recently rather sparse, and of the relatively short time that was available to that population to destroy over 90%, or well over 500,000 km^2, of the posited island-wide aboriginal forest. But does it mean that we must totally reject human activity as a significant factor in the extinction of Madagascar's large mammals?

Although the detailed climatic records of Africa and especially of Madagascar are severely limited in their scope and time depth, there can be no doubt whatever that climate and hence habitat fluctuations have been characteristic of both areas well back into the Pleistocene and earlier. The changes of the end-Pleistocene and the Holocene (perhaps preferably, the Flandrian interglacial) are simply the most recent, and not necessarily the most dramatic, of an almost infinite recession of such events. The lineages that gave rise to the large extinct mammals of Madagascar clearly survived these earlier vicissitudes, including the rather harsh one at the last glacial maximum; and there is no obvious reason why habitat pressures of the late Holocene (which at Tritrivakely showed no severe drying) should have had a fatal effect, especially on a diversity of lineages simultaneously. This is especially the case when we consider that the large extinct Malagasy primates must have been in general rather eurytopic. Almost all of the medium- to large-bodied subfossil Malagasy primate genera had wide geographical and ecological distributions. Subfossil deposits are known from virtually every area of Madagascar except for the heavily vegetated eastern escarpment; and everywhere that sampling is good we find essentially the same extinct primate fauna. Particularly ubiquitous among these forms are *Megaladapis*, *Archaeolemur*, and *Palaeopropithecus*, which, along with other genera, are found in environments that ranged from humid to semi-arid. There can be little doubt that these primates were highly adaptable in habitat choice, and thus theoretically well able to cope with habitat change. Yet they disappeared far more rapidly than did the habitats in which they lived, and in which their smaller surviving relatives still persist. The humid eastern forests of Madagascar represent the only environmental setting in which large lemurs have not been found; and this is probably only because appropriate deposits have yet to be discovered. Vast tracts of such forest still stand, and it is highly probable, if so far unprovable, that they once harbored populations of now-extinct lemurs. If this is indeed the case, something other than simply another cycle of habitat fluctuation must be invoked to explain the absence of giant lemurs from Madagascar's forests today. A novel factor is needed.

What that factor is, is suggested not only by the coincidence in time between the appearance in Madagascar of humans and the disappearance of the subfossil fauna, but by the incomplete nature of that fauna. For the sake of convenience we speak of a 'subfossil fauna'; but what we are really referring to is *part* of a fauna, the rest of which still survives, if precariously. That portion of the total Malagasy mammal species complement that has disappeared is readily characterisable neither in terms of phylogeny, nor of habitat; but it is quite efficiently defined by body size. Large body size may indeed make an organism more vulnerable to reductions in food supply; but in this context it appears more germane that large body size makes a prey species both more attractive to human hunters, and an easy target, especially in an arboreal setting. Perhaps even more importantly, animals of great bulk tend to exist in lower individual numbers and to have slower reproductive turnovers than do smaller ones. And historically, these particular large mammals and their precursors were almost certainly subject to relatively low predation pressures, at least as adults, for millions of years. Combine these factors, and the vulnerability to human hunting of the large Malagasy vertebrates compared to the smaller ones is multiplied enormously.

Clearly, environmental factors are capable of producing large-scale extinctions, and have regularly done so over the history of life on Earth. But, equally clearly, there is no such element convincingly identifiable in the late Holocene of Madagascar. There is certainly no evidence of a factor of the requisite magnitude that was operating island-wide in the short window of time under consideration, even though local drying might explain the disappearance of large lemurs from particular areas in the south and west. Indeed, in his core from Tritrivakely Burney (1987a) detected a sedimentary change at around 4.0 Ky that was associated with lessening charcoal – an observation that Clark (1988) has linked closely with humidifying climatic conditions. It is thus plausible that when humans reached Madagascar the local fauna was actually under diminishing environmental stress in the aftermath of the late Pleistocene forest recession. But whatever the case, there is no indication that by themselves climatic factors should at this point have been capable of obliterating the megafauna. A new element has to be sought, and the simple fact that *Homo sapiens* is the obvious candidate should not disguise the fact that it is the only one. Whether humans simply delivered the *coup de grâce* at a moment when the megafauna was especially vulnerable, or whether even in times of more productive or abundant habitat these large forms would have disappeared as rapidly on human contact, will remain a matter for speculation. But despite the remarkable dearth of direct evidence in the archeological record for human predation on the extinct mammals of Madagascar, it is hard to avoid the conclusion that the living Malagasy fauna, like so many others worldwide, would be richer today had humans never colonised the island. And it is a sobering thought that humans are now a permanent factor on the Malagasy landscape, with which their relationship remains essentially unchanged.

CONCLUSION

I tend to the view that each regional extinction event should be examined on its own merits rather than interpreted in terms of a worldwide paradigm. But in view of the debate that still rages between the advocates of human versus natural roles in the notable extinctions of the Quaternary, perhaps

Madagascar does hold a general lesson. The major African megafaunal extinction of the past two to three million years actually took place a little before the beginning of the Pleistocene, roughly coincident with the emergence in that continent of the genus *Homo*. Whether this coincidence implies a causal relationship is, I think, a particularly arguable point. In Eurasia and the Americas, on the other hand, such extinctions were concentrated in the late Pleistocene and early Holocene, admittedly times of environmental change, but in each case around the moment when *Homo sapiens* first appeared in these regions. In Madagascar, whatever the extent of the end-Pleistocene climatic stress, the megafaunal extinction was yet further delayed, once again until the arrival of modern human beings. Even though I can see no way at present of conclusively demonstrating cause and effect in the disappearance of the large vertebrates of Madagascar, the independent and asynchronous repetition of this association in the great island is strongly suggestive.

Which brings us back to Madagascar's insular nature. Faunal 'blitzkrieg' in continental regions has been difficult to substantiate, not simply because of the coarse grain of the archaeological record, but because the evidence that does exist can be interpreted in several ways. In Madagascar, as in many island contexts, we can closely pinpoint the time of extinction of the megafauna, which, as so often in such situations, was extremely rapid. Madagascar, with its large size and extraordinary ecological diversity, has spawned species like a continent; but its extinction pattern is that of an island.

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