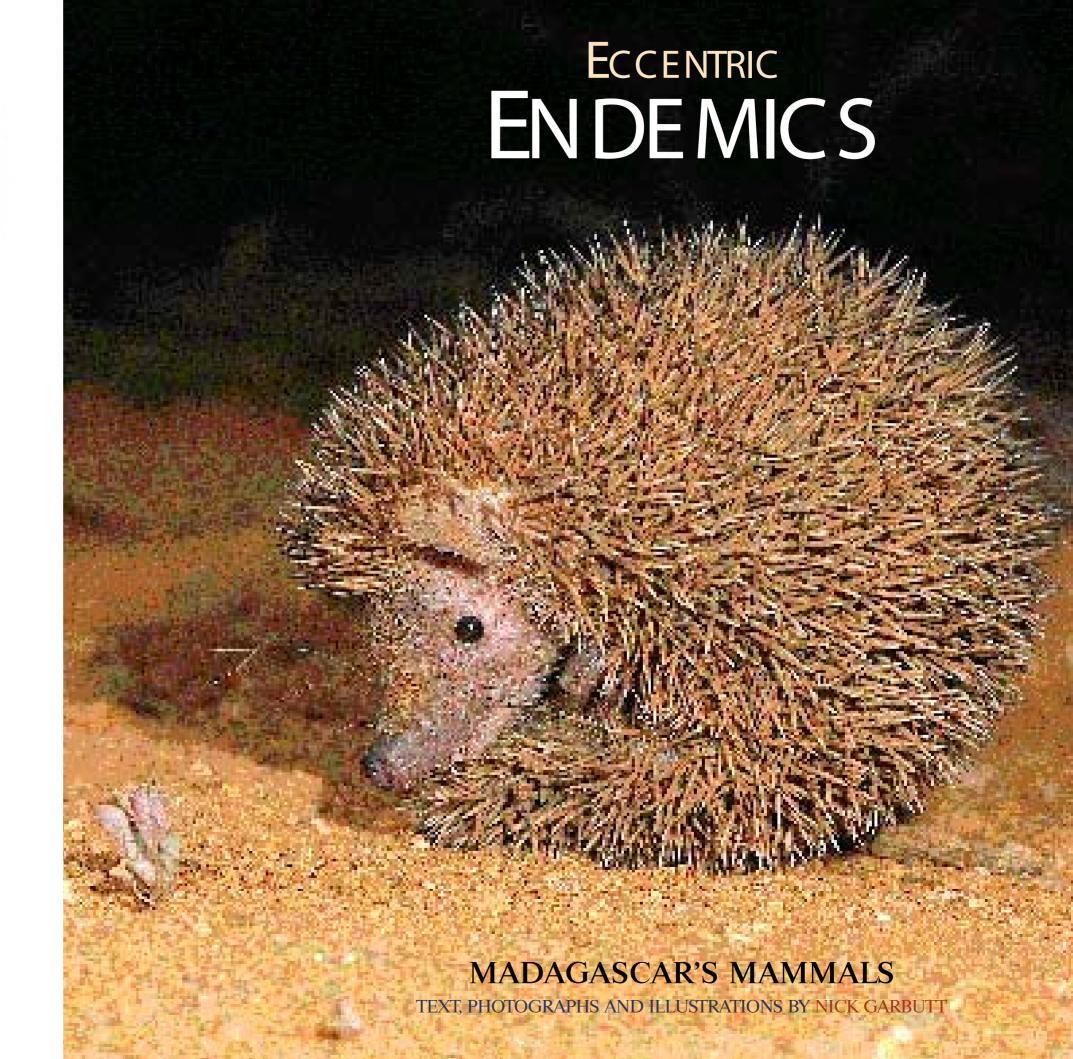
OPPOSITE The lesser hedgehog tenrec is unusual in that it is semiarboreal and capable of climbing along thin branches.



f Charles Darwin had travelled to the island of Madagascar rather than to the Galapagos, his journey would probably still have provoked the same thoughts on evolution. He would have noted first the striking absence of many species familiar to mainland Africa: no grazing antelope, giraffe or zebra, no big cats lurking in ambush, no dogs hunting in packs, and no monkeys or apes languishing in the forest canopies. Instead, he would have seen a host of strange and unfamiliar creatures, some showing a basic resemblance to African forms, but nevertheless very different. No large animals browsed the vegetation (although in the past this function was performed by creatures such as giant lemurs, pygmy hippopotami and huge birds, by the mid-19th century these were already extinct). In place of monkeys and apes, he would have seen lemurs – primates living in far more diverse ways than their mainland cousins. Instead of cats and dogs, there were predators such as the fosa - Madagascar's largest carnivore. Darwin may well have been puzzled as to which family the fosa belonged - cat-like, but lowslung and reminiscent of a giant mongoose with a long tail, it is actually a relative of the civets.

Only five major mammal orders are found on Madagascar: bats (order Chiroptera), rodents (order Rodentia), tenrecs (order Insectivora), lemurs (order Primates) and civet-like carnivores and mongooses (order Carnivora). This relative impoverishment at higher taxonomic levels, as much as the adaptations and peculiarities of the species themselves, would have fascinated Darwin, and it is a question that continues to occupy many of the foremost zoological minds of today. Clues to its answer lie in the past.

adagascar was once a small part of Gondwanaland, the giant southern





The nocturnal common tenrec is regularly preyed upon by the fosa.



The patterning and coloration of the lowland streaked tenrec provide a degree of camouflage as it is partially active during daylight hours.



The greater hedgehog tenrec closely resembles the Eurasian hedgehog but is appreciably smaller.

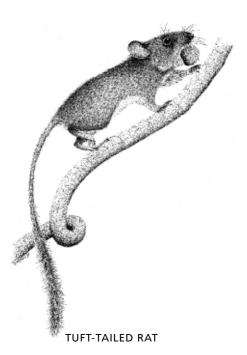
super-continent. Around 160 million years ago, colossal forces wrenched a large chunk away from what is now the coast of Somalia. This fragment drifted south-eastward, eventually coming to rest 120 million years ago about 350 kilometres off present-day Mozambique. Some 40 million years later, the fragment itself split in two. One piece moved northwards to collide with Asia and become the Indian sub-continent, while the second fragment remained stationary and is known as Madagascar.

When the first split occurred, dinosaurs still dominated Madagascar and true mammals had yet to evolve. The ancestors of contemporary mammals must thus have arrived at a later date. Animals such as bats would have flown, perhaps blown off course during bad weather. As would be expected from the geographic position of the island, the majority of bats on Madagascar owe their origins to founder populations from mainland Africa.

But how did terrestrial mammals make it to Madagascar? Improbable as it may seem, they floated, like ancient boat people, on mats of vegetation and debris washed out to sea. After severe storms, the large rivers that disgorged their contents into what is now the Mozambique Channel would have been swollen and full of fallen trees and floating reed beds. Small mammals accidentally caught up in the catastrophe would have clung to these pieces of giant flotsam. A few would have survived until their makeshift raft, by chance, washed up on the distant shores of Madagascar. With the global demise of the dinosaurs around 70 million years ago, these mammalian stowaways would have happened on a pristine island, largely free from the constraints of competition – a world of opportunity, where evolution would subsequently take them down new and uncharted roads of innovation.

Insectivores are amongst the more primitive of present-day mammals. On Madagascar, they are represented by the tenrecs, whose ancestors may well have been the first mammals to arrive on the island, 60- to 65-million years ago. All belong to a single family, Tenrecidae, which also includes the otter-shrews from West and Central Africa. On Madagascar they divide neatly into two subfamilies: the spiny tenrecs and the furred tenrecs. Members of these subfamilies are morphologically quite different, suggesting that they derived from separate lineages that colonised Madagascar independently.

The spiny tenrecs (subfamily Tenrecinae), of which there are five species, are all more or less hedgehog-like in appearance. They are principally nocturnal and are found throughout the various native forest environments in Madagascar. The largest (about two kilograms) is the common tenrec Tenrec ecaudatus, whose creamy-brown pelage is sparse and consists of both coarse and spine-like hairs, the latter being more prominent around the crown and nape. However, juveniles appear very different: they are much darker brown, sometimes almost black, with paler cream spines arranged in longitudinal rows, giving an overall streaked appearance. There is a good reason behind this. Common tenrecs produce some of the largest mammalian litters (up to 31, although 12 to 16 is more normal) so the demand for mother's milk is obviously very high. To maximise milk production, females are often forced to extend foraging beyond the hours of darkness, a behaviour that undoubtedly has its risks, especially to their young. However, the coloration and striped pattern of the juveniles increases camouflage on the forest floor and so helps reduce predation. Interestingly, similar patterns and coloration are found in adult streaked tenrecs (genus Hemicentetes) which are also partially active during daylight hours.



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The Malagasy forest mouse is a gerbil-like, diurnal species. Its tail is an impressive 140 per cent of its head/body length.

Two very similar species are the greater hedgehog tenrec *Setifer setosus* and the lesser hedgehog tenrec *Echinops telfairi*, both of which are completely covered in spines and closely resemble true hedgehogs. The lesser hedgehog tenrec, which is found in the drier regions of the south and south-west, is unusual in that it is semi-arboreal. Considering its rotund shape and seemingly ponderous gait, it is surprisingly agile and capable of climbing along thin branches, often using its short tail as a brace.

The furred tenrecs (subfamily Oryzorictinae) consist of four highly diversified genera, some of which have radiated spectacularly - most notably the shrew tenrecs, of which at least 17 species are known. A number of species provide very good examples of convergent evolution, as they have adopted similar morphological and ecological traits to those of other insectivores outside Madagascar. For example, the aquatic tenrec Limnogale mergulus exploits a niche that is occupied elsewhere by the otter-shrews (Potamogalinae) of West and Central Africa or by European desmans (Talpidae), and is one of the most unusual and least known of all Malagasy mammals. The largest of the furred tenrecs, it reaches a total length of 300 millimetres (140 millimetres of which is tail) and a weight of 60-90 grams. The aquatic tenrec lives in the cleaner, faster-flowing streams of the central highlands and is obviously well adapted to an aquatic mode of life, having a flattened head, with small eyes and ears concealed beneath its fur, webbed feet and a powerful tail, flattened towards the tip. It is a voracious nocturnal hunter, actively seeking out and pursuing frogs, small fish, crustaceans and aquatic insect larvae. The catastrophic loss of forest in the highlands and subsequent siltation of the rivers and streams has undoubtedly resulted in a dramatic reduction in the range of this species.

AQUATIC TENREC

The other major group of small mammals to reach Madagascar were the rodents. At present, Madagascar's native rodents are all placed in the endemic subfamily Nesomyinae, and include some 20 species in all. This total is very low for an island the size of Madagascar, for which a figure around 50 would be expected. There are two possible explanations for this apparent paucity: either Madagascar's rodent fauna is unusually impoverished (given the other faunal peculiarities on the island, this is not impossible) or, more probably, the inventory is incomplete.

As with the tenrecs, the morphologies of the different rodent genera have drawn comparison with rodents and similar mammals from other parts of the world. Malagasy forest mice (genus *Macrotarsomys*) have been likened to gerbils (Gerbillinae), vole rats (genus *Brachyuromys*) show obvious parallels with true voles (Microtinae), tree-dwelling tuft-tailed rats (genus *Eliurus*) have behavioural affinities with arboreal dormice (Gliridae), and the giant jumping rat *Hypogeomys antimena* exhibits behavioural and morphological similarities to Old World rabbits (Leporidae).

The endemic rodents are closely associated with indigenous forests or similar primary habitats. Most conspicuous are the red forest rats, *Nesomys rufus* and *N. audeberti*, found in most rainforest areas. Active during the day, they can often be seen foraging around tree trunks for fallen fruits and seeds. Other species, being almost exclusively nocturnal, are much harder to track down.

There are no fewer than eight species of tuft-tailed rat (with four more currently awaiting description). They are all partially arboreal and have a number of adaptations associated with their scansorial way of life,



The red forest rat, a strictly terrestrial and diurnal species, can be encountered in many eastern rainforest parks and reserves.



The giant jumping rat is the largest rodent on Madagascar, and can measure up to 60 centimetres in length. It moves on all fours or in a kangaroo-like hop on its hindlegs.

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The northern ring-tailed mongoose is diurnal and sociable, often being found in family groups of up to five.

The elegant narrow-striped mongoose has a very restricted range in western Madagascar and the deciduous forests of Kirindy, north-east of Morondava, offer visitors the best chance of seeing it.



most notably broad hind feet with long claws for grasping and a very long tail (generally 115–120 per cent of body length). The tail always ends in a brush-like tuft (hence their common name), although its shape and extent varies according to species. As well as foraging amongst vines and lianas in the understorey, tuft-tailed rats are also known to collect seeds from the forest floor. It is here that they excavate their nest burrows, which double as a grain store. The majority of tuft-tailed rat species are restricted to the eastern rainforest belt, with only one species, the western tuft-tailed rat *Eliurus myoxinus*, being found in western deciduous forests.

A small enclave of western dry forest is the last remaining stronghold of Madagascar's largest and most charismatic rodent, the giant jumping rat *Hypogeomys antimena*. Its range is centred around the forests of Kirindy and Andranomena, where the light sandy soils are ideal for the excavation of their large burrow systems. Each burrow lies at the heart of a three- to four-hectare territory and is occupied by a monogamous pair and their dependent offspring. Unusually for rodents, pair bonds last more than one breeding season and normally until one mate dies. Predation is a frequent occurrence, the main culprit being the fosa *Cryptoprocta ferox*.

In the past, Madagascar's remarkable assemblage of endemic rodents was cited as a classic example of adaptive radiation from a single ancestral species. However, more recent and ongoing field research suggests that Madagascar's rodents arrived in several waves of colonisation, such that they do not share an immediate common ancestry.

By contrast, the island's enigmatic carnivores owe their origins to just two founding forms: one of these gave rise to the mongoose lineage, the other to the civet-like carnivores. Old World mongooses constitute the family Herpestidae, but the Malagasy mongooses probably represent a very early offshoot of this lineage and are therefore sufficiently distinct to form their own subfamily, Galidinae. Most common and conspicuous is the diurnal ring-tailed mongoose *Galidia elegans* which is found in both western dry forests and eastern rainforests. Like many of the African mongooses, this is a sociable animal, living in family groups of up to five individuals. Although much of their daily foraging is on the forest floor, ring-tailed mongooses are adept climbers and target birds' nests and fledglings. At Ankarana in the north and Ranomafana in the south-east, these mongooses have become quite tolerant of humans and can regularly be seen along forest paths and scavenging cheekily around camps.

Madagascar is home to just three rather unusual and specialised members of the civet family (Viverridae). The most 'civet-like' is the fanaloka *Fossa fossana*. About the size of a domestic cat, it is the smallest Malagasy viverrid. Its catholic diet includes rodents, small tenrecs, reptiles, frogs and invertebrates.

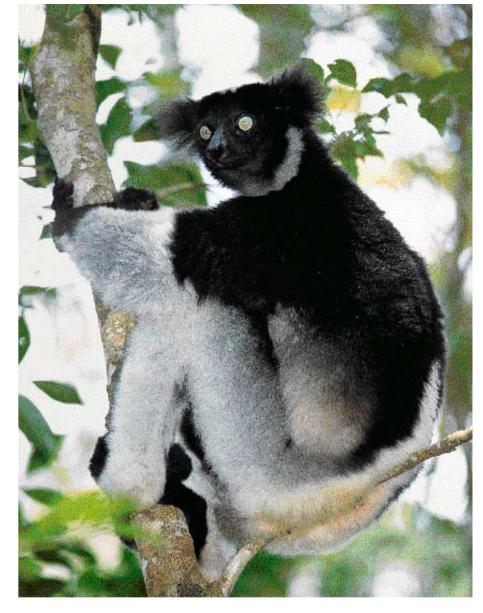
On the other hand, the larger falanouc *Eupleres goudotii* is probably the island's most specialised carnivore. Its elongate snout and tiny conical teeth, resembling those of an insectivore, have evolved to catch the earthworms and other small invertebrates on which it feeds almost



FANALOKA

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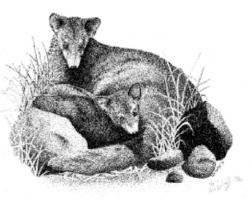
The fosa is most often likened to a dark-coloured, short-legged puma, although it is dramatically smaller and more elongate.

The indri is one of the most familiar lemurs, and is the only virtually tailless lemur.

exclusively, foraging in leaf litter and using its strong forepaws and long claws for digging. The fanaloka and falanouc are the only two members of the endemic subfamily Euplerinae and are unusual amongst carnivores in having very precocious litters. The young are born fully furred with their eyes open and are soon able to walk, following their mothers almost immediately on foraging excursions.

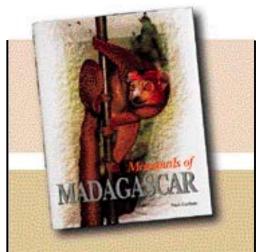
Largest of the Malagasy carnivores (and one of the largest of all viverrids) is the fosa *Cryptoprocta ferox*, which, because of morphological similarities such as retractile claws and facial resemblance, was once thought to be a member of the cat family (see *Africa – Environment & Wildlife*, vol.6 no.2). It is now, however, placed in its own monotypic subfamily, Cryptoprocinae, within the family Viverridae.

The remaining mammalian group found on Madagascar includes the lemurs, which comprise no fewer than 33 extant species, divided between five distinct families. No other group of primates displays such an extraordinary diversity in body shape and size, behaviour and lifestyle. They range from the pygmy mouse lemur *Microcebus myoxinus* (at 25 grams the world's smallest primate), to the seven-kilogram indri *Indri indri*, and the more spectacular, but now extinct *Archaeoindris fontoynontii*, which weighed around 200 kilograms. Genetic studies strongly suggest that these all evolved from a single common ancestor, probably resembling present-day African galagos, which arrived on Madagascar by raft around 50 million years ago.



FEMALE FALANOUC WITH YOUNG

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MAMMALS OF MADAGASCAR

NICK GARBUTT

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Until the publication of Mammals of Madagascar, no single volume has ever covered the entire mammal assemblage of Madagascar. British zoologist/author Nick Garbutt, who has visited Madagascar regularly since 1991, collectively spent two-and-a-half years on the island, photographing his subjects and gathering field data. Researching and writing this remarkable work - which is both an in-depth reference and a field guide - took Garbutt seven years. In terms of its photographic content - 80 per cent of the photographs are the author's - the book features the most complete collection of Malagasy mammal photographs yet published. The informative text is a synopsis of all contemporary knowledge of Madagascar's mammals, and has been likened to a full update of the Red Data Book.

But it's much more than that, because detailed behavioural accounts are included for each taxon. Extensive coverage is given to the 117 indigenous mammals, as well as to introduced species; and an interesting appendix deals with the extinct mammals. Distribution maps accompany each species (or taxon) account. An intriguing biogeographical section suggests reasons for the peculiarity of Madagascar's mammals. Habitats, conservation, protected areas and the top mammal-viewing 'hotspots' are meticulously reviewed.

DEREK SCHUURMAN

So why have so few mammals managed to cross the Mozambique Channel successfully over the past 120 million years? And if the forebears of today's mammals made the crossing, why have others not done so subsequently? To answer this, we need to consider possible reasons that may have made the pioneer mammals better mariners in terms of their ability to survive a long sea crossing than mainland species that came along later in evolutionary history.

It is obvious that a small body size would be an advantage in staying afloat on a makeshift raft. Although relatively large species have existed, and continue to exist on Madagascar, evidence suggests that these evolved later, and that the original colonising stock comprised only small species. But why then are so many small African mammals absent from Madagascar? Moreover, small body size usually correlates to a high metabolism and the need to eat regularly. This trait would appear to place small mammals at a severe disadvantage in the sea-crossing stakes. The results of recent research may provide the missing elements in this riddle.

Investigating the ecology of the nocturnal grey mouse lemur *Microcebus murinus* in the dry forests of Kirindy, Jutta Schmid from the German Primate Centre found that individuals enter a temporary torpor during their day-time rest period by reducing body temperature to ambient temperature. In addition, during the cooler, drier winter months, mouse lemurs choose tree holes closer to the ground, where outside temperatures remain lower and more stable. This allows them to remain torpid for longer and so conserve body resources. In fact, during winter when food abundance is lowest, females may become totally inactive, staying dormant in their tree holes for several months and so maximising the conservation of their body resources. Prior to the cold dry season, both sexes lay down reserves of fat (up to 35 per cent of body weight), which help sustain them through these dormant periods.

These abilities would have been of considerable advantage to the ancestral colonising lemur in terms of surviving a long sea journey with little or no food, and the grey mouse lemur probably closely resembles this ancestor. Other close relatives of mouse lemurs, such as the dwarf lemurs (genus *Cheirogaleus*) also build up fat reserves and become dormant during the dry season.

What of the other mammal groups on the island? It is surely no coincidence that some of the tenrecs, such as the streaked and hedgehog tenrecs that have apparently changed little from their colonising ancestor, also accumulate fat when food is plentiful and aestivate during the dry season. Furthermore, the civet-like carnivores, the fanaloka and falanouc, are also able to lay down fat deposits in their tails (up to 25 per cent of body weight) to help see them through times of food shortage.

It seems highly likely, therefore, that Madagascar was colonised by small mammals from Africa, which either flew there (bats) or rafted on natural debris. Of the latter, the only species to survive were those with the ability to lower their metabolism, become dormant and/or live without food for long periods on previously accumulated reserves. Only five mammalian species were successful: lemurs, civets, mongooses, tenrecs and rodents.

Traveller's advisory



When to visit

For wildlife watching, September to December is the best time to visit Madagascar as many of the lemurs have young and birds are breeding and are thus far more active and vocal. Late December through to April is best avoided because of the rains. April and May are also good, especially for reptiles and frogs, and for lemurs as many trees are in fruit and they tend to congregate in these.

Getting around

There is an extensive domestic flight service in and out of the capital Antananarivo to all regional centres. From here local buses and taxis will take you to the reserves. However, this can be arduous and time-consuming, especially for the first-time visitor. Here an organised wildlife-watching tour is by far the best option. These typically last just over two weeks and visit four or five key areas.

All wildlife watching in the parks is done on foot. In eastern rainforest areas the terrain can be tough: hills are often steep and trails slippery. In the drier western and southern regions the terrain is generally flatter, but it can get very hot.

Accommodation and food

In the cities and larger towns, hotels vary in standard from very good (up to £75 per night) to very cheap and seedy (less than £5 per night). In the rural areas (including around the parks and reserves), allowances have to be made as the hotels and lodges are sometimes more rustic but generally adequate. Expect to pay £8 –15 per night. In the more remote parks, self-sufficient camping is necessary: excursions can often be arranged through local operators.

Food in Madagascar is always very good and cheap. Many places offer traditional Malagasy cuisine, but there is also strong French and even Chinese influence.

Guides

When visiting a park, it is compulsory to employ the services of a local guide. In the more popular reserves, most guides can speak some English and have a very good knowledge of the avifauna.



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